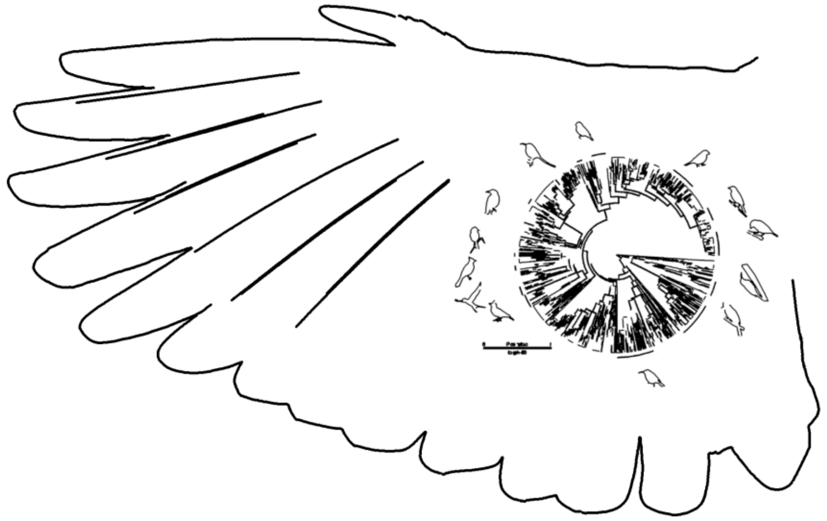
UNIVERSITAT DE BARCELONA

Structure, regulation, and evolution of Passerine molt

Santi Guallar

Santi Guallar STRUCTURE, REGULATION, AND EVOLUTION OF PASSERINE MOLT

STRUCTURE, REGULATION, AND EVOLUTION OF PASSERINE MOLT



Santi Guallar
Doctoral thesis
2020

Layout design, main cover, and chapter illustrations by the author. Back cover Isabelline Wheatear *Oenanthe isabellina*, modified from exhibit #7614 published in featherbase.com.

UNIVERSITAT DE BARCELONA

Facultat de Biologia
Departament de Biologia Animal,
Ecologia i Ciències Ambientals
Programa de Doctorat en Biodiversitat

STRUCTURE, REGULATION, AND EVOLUTION OF PASSERINE MOLT

ESTRUCTURA, REGULACIÓ I EVOLUCIÓ DE LA MUDA EN ELS PASSERIFORMES

Memòria presentada per

SANTI GUALLAR

per optar al grau de Doctor per la Universitat de Barcelona,

Barcelona, 23 de desembre de 2020

Director de tesi	Tutor
Roger J	
Roger Jovani i Tarrida	**Jacob González-Solís Bou**
Department d'Ecologia Evolutiva, Estació Biològica de Doñana, CSIC	Departament Biología Evolutiva, Ecologia i Ciències Ambientals Facultat de Biologia Universitat de Barcelona

A la meva mare, qui sempre ha compartit el meu amor per la natura i els ocells.

Acknowledgements

L'ornitologia ha estat una vocació tardana que m'ha omplert d'il·lusió i m'ha permès mantenir-me en contacte amb la natura. Gràcies a ella he viscut incomptables anècdotes i experiències d'inoblidable bellesa. Aquesta vocació també ha fet que renunciés a una carrera professional més estable i millor retribuïda, però no m'hi vaig poder resistir. Tampoc vaig poder resistir la crida del voler saber més i de voler fer-ho per mi mateix. Així és com la meva feina com a anellador em va dur a fer-me preguntes sobre allò que feia i finalment a estudiar la muda dels ocells.

Aquesta tesi ha estat un pecat de maduresa, fruit dels 25 anys que he dedicat a l'ornitologia. Moltes persones han estat clau abans i durant els cinc anys que he esmerçat en la realització de la tesi. Tots els coautors dels sis articles de la tesi. En primer lloc l'Oliver per la seva generositat i el Kaspar Delhey per convidar-me a col·laborar amb el seu magnífic equip. El Peter i el Rafa pel seu entusiasme a l'hora d'estudiar la muda dels Passeriformes neotropicals. El Roger i el Jacob van accedir a dirigir i impulsar una tesi doctoral que no tenia cap garantia d'arribar a port. Tanmateix, la seva realització hagués estat impossible sense el recolzament, la paciència i la comprensió de l'Olga. I la Nayana, per tant humor i patiment, companyia i afecte.

Sant Fruitós de Bages, 23 de desembre de 2020

ABSTRACT

Molt is the process of plumage renewal by which birds maintain and adjust its functionality throughout their lifecycle. Multiple elements have been tackled in bird molt research (timing, duration, sequence, intensity, extent, feather growth rate, and plumage quality), but major gaps still exist on molt regulation, and especially on molt evolution. This thesis focuses on one molt element extensively recorded since mid-20th century but seldom studied as an individual trait: the set of feathers replaced after a given molt episode by one individual (here referred to as final molt phenotype). This is surprising because feathers differ in their function (e.g. signaling, thermoregulation, contribution to different flight functions, durability), costs of production, and morphology (e.g. exposure, mass, shape), all of which can be targeted by natural selection. Therefore, the final molt phenotype should be under strong selective pressures, suggesting that its regulation has been shaped during evolution to optimize plumage performance throughout the bird's lifecycle. This thesis explores the potential of analyzing final molt phenotypes as is (instead of being analyzed partially or indirectly) to uncover underlying mechanisms of molt regulation and to provide insights on the evolution of molt in passerine birds. Following are the main findings presented in this thesis. Final molt phenotypes differed between the post-juvenile and the pre-breeding molts along the passerine phylogeny. A nested organization of final molt phenotypes suggested a rank of feather molt importance as underlying rule of molt. However, deviations from perfect nestedness were largely associated with the pre-breeding molt. Shared ancestry explained a large portion of final molt phenotype variation, likely due to constraints associated to plumage morphology, which is highly conserved in passerines. Phylogenetic analyses confirmed the phylogenetic independence of the pre-breeding molt and the strong phylogenetic signal of the post-juvenile molt. Further, they showed the overlooked relevance of environmental factors on the evolution of passerine molt, although their effect varied among taxonomic groups and molt episodes, thus highlighting the flexibility and adaptiveness of molt. Findings exposed in this thesis confirm the relevance of the final molt phenotype as a promising element to advance in our understanding of bird molt.

RESUM

La muda és el procés de renovació del plomatge mitjançant el qual els ocells mantenen i ajusten la seva funcionalitat durant tot el seu cicle vital. S'han abordat diversos elements en la investigació de la muda dels ocells (calendari, durada, extensió, intensitat, seqüència, qualitat del plomatge i velocitat de creixement de la ploma), però encara hi ha importants llacunes sobre la regulació de la muda i, sobretot, sobre la seva evolució. Aquesta tesi se centra en un element de la muda àmpliament registrat des de mitjan segle XX, però que encara no ha estat estudiat com a tret individual: el conjunt de plomes substituïdes després d'un determinat episodi de muda per un individu (aquí anomenat fenotip final de muda). Això és sorprenent perquè les plomes difereixen en la seva funció (e.g. senyalització, termoregulació, contribució al vol, durabilitat), costos de producció i morfologia (e.g. exposició, massa, forma), que poden ser objecte de selecció natural. Per tant, el fenotip de muda final hauria d'estar sota fortes pressions selectives, cosa que suggereix que la seva regulació s'ha configurat durant l'evolució per optimitzar el rendiment del plomatge al llarg del cicle de vida de l'ocell. Aquesta tesi explora el potencial d'analitzar el fenotip de muda final tal com és (en lloc d'analitzar-lo parcialment o indirectament) per descobrir els mecanismes subjacents de regulació de la muda i proporcionar informació sobre l'evolució de la muda en els passeriformes. A continuació es mostren les principals conclusions presentades en aquesta tesi. El fenotip de muda final diferia entre la muda post-juvenil i la pre-nupcial al llarg de la filogènia dels passeriformes. Una organització aniuada del fenotip de muda final va suggerir l'existència d'un rang d'importància en la muda de les plomes com a regla subjacent. Tanmateix, les desviacions de l'aniuament perfecte es van associar en gran mesura amb la muda pre-nupcial. L'ascendència compartida explicava una gran part de la variació del fenotip de muda final, probablement a causa de restriccions associades a la morfologia del plomatge, la qual està molt conservada en els passeriformes. Les anàlisis filogenètiques van confirmar la independència filogenètica de la muda pre-nupcial i l'elevat senyal filogenètic de la muda post-juvenil. A més, van mostrar la rellevància que han tingut els factors ambientals en l'evolució de la muda dels passeriformes, tot i que el seu efecte varia entre els grups taxonòmics i també entre els episodis de muda, destacant així la flexibilitat i la naturalesa adaptativa de la muda. Les troballes exposades en aquesta tesi confirmen la rellevància del fenotip de muda final com un element prometedor per avançar en la nostra comprensió de la muda dels ocells.

TABLE OF CONTENTS

ANNEXES: Published articles

GENERAL INTRODUCTION

This PhD thesis fills some gaps on our understanding of bird molt, specifically on molt evolution and on the variation, regulation, and evolution of the final molt phenotype. This introduction has three sections. First, current knowledge on bird plumage and molt relevant for this thesis is reviewed. Second, the major gaps on bird molt research are discussed, introducing poorly appreciated gaps. Third, the goals and approaches of this thesis are outlined.

1. What do we know about molt?

1.1 Plumage

The avian integumentary system is composed by the skin, the appendages (the corneous layer of claws and beak), and the feathers. Although feathers already appeared in dinosaurs (Bock 2000, Long & Schouten 2008, Carney *et al.* 2020), only birds possess them in the extant fauna. Bird plumage appears as a continuous coat covering most of the body of the bird. However, feathers are produced by eight discontinuous clusters of follicles inserted in the skin (the pterylae), separated by extensive areas without follicles (the apteria; Proctor & Lynch 1993). Each cluster (pteryla) produces morphologically diverse feathers, but feathers from different pteryla are perfectly integrated among them to undertake plumage functions. The work developed in this thesis focuses on the dorsal wing pteryla of passerines.

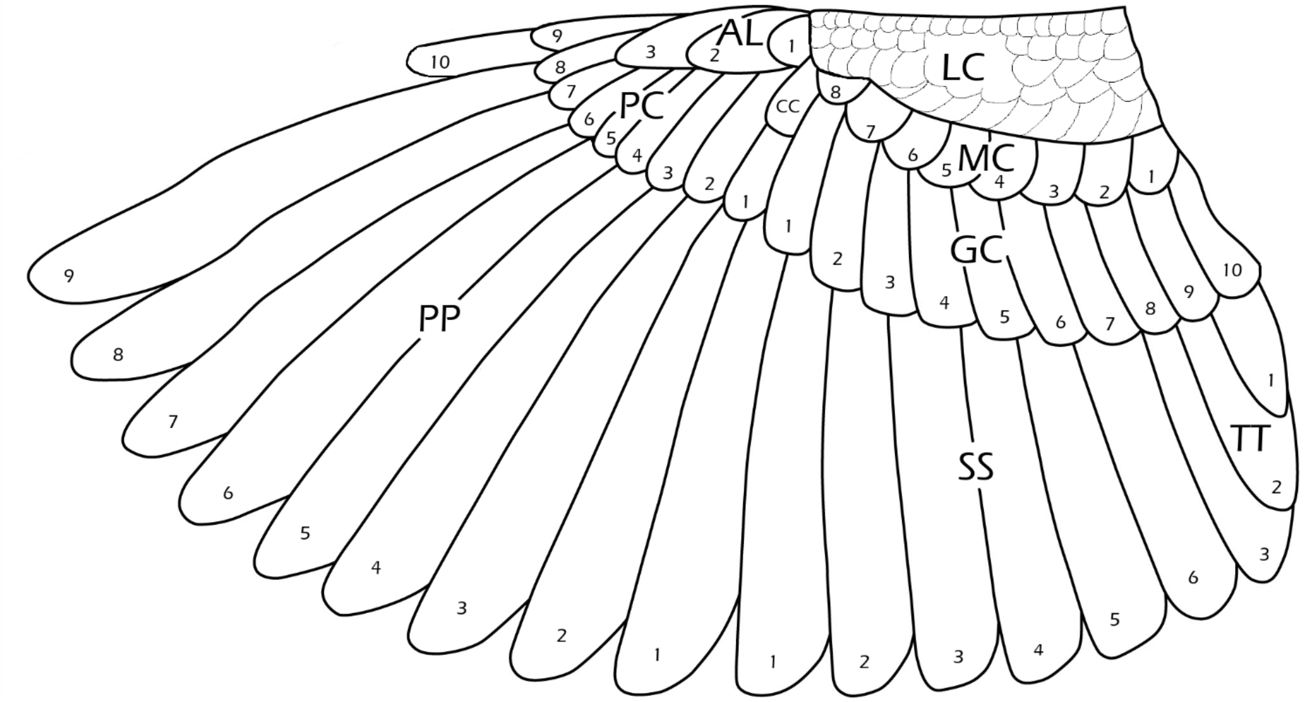
Wing plumage: functions and feather tracts

The wing plumage provides two main functions: flight and insulation; although it may carry out other functions (e.g. sound production), among which visual signaling stands out. For example, it has been shown the association between wing patches and sexual attractiveness (Senar *et al.* 2005, de Heij *et al.* 2011, Hegyi *et al.* 2018), and between the number of post-juvenile greater coverts and social status in immature birds (Senar *et al.* 1998, López *et al.* 2005). The wing plumage comprises three main groups of feathers (also called tracts): remiges, alula, and upper wing coverts (Fig. 1). The principal function of **remiges** is to allow birds to fly. They also provide thermal insulation (Gerken *et al.* 2006), and in some species carry out communication functions, including sound production and nuptial display (Fry 1969, Clark *et al.* 2016, Niese & Tobalske 2016). The **alula** consists of three to four specialized feathers attached at the arm-hand joint that increases lift and enhances maneuverability in flights at high angles of attack (Lee *et al.* 2015). Wing **coverts** insulate the arm and hand, protect the basal portion of remiges, provide aerodynamic camber, and signal status or individual quality (Senar *et al.* 1998, Videler 2005).

The need for plumage renewal

Integument is degraded over time. Skin and appendages are repaired when they are accidentally damaged, but they are also renewed periodically to maintain functionality (Knopf 1974, Pitocchelli *et al.* 2003). Despite birds devote a substantial amount of time to plumage maintenance by preening or bathing (Slessers 1970, Delius 1988, Czirják *et al.* 2013), exogenous agents lead to feather deterioration. Mechanical abrasion, damage by ultraviolet radiation, and action of parasites ultimately impair plumage functionality (Bergman 1982, Willoughby 1991, Gunderson 2008). However, unlike skin and appendages, feathers are inert structures that cannot be repaired; they can only be replaced. This can follow three vias: first, when a feather is accidentally lost (Tonra *et al.* 2014, de la Hera *et al.* 2015, Tomotani *et al.* 2018a); second, some species have been recently discovered to advance the replacement of damaged feathers (Ellis *et al.* 2017); third, and this is the normal process of feather renewal, during the periodical plumage molt. However, feather deterioration is not the only reason behind plumage renewal; plumage can also be replaced to adjust feather function to the upcoming life-history stage.

Figure 1. Wing-feather tracts and feather numeration used in this thesis (notice that underwing coverts are excluded). Passerines have a rather homogeneous wing plumage largely arranged in three concentrical feather rows: i) lesser coverts (composed of several rows), ii) alula and remaining coverts, and iii) remiges. This arrangement is correlated with the size of feathers: small feathers on the leading edge increasing in size toward the large feathers that form the trailing edge of the wing. Median (MC), greater (GC), most lesser coverts (LC), tertials (TT), and secondaries (SS) are inserted in the ulna, whereas primaries (PP), primary coverts (PC), carpal covert (CC), alula feathers (AL), and distal LC (under AL) are inserted in the hand.



1.2 What is molt?

Molt is the physiological process by which birds replace part or all their feathers to restore and adjust plumage functionality (Jenni & Winkler 2020a). Feather replacement comprises two interlocked phases (Humphrey & Parkes 1959, Newton 2011): the shedding of the old feathers and the growth of new ones. New feathers grow in from active cell division within the epidermal collar of the feather papillae. These new cells differentiate into keratinocytes, which begin to form barbs and their barbules (Maderson *et al.* 2009); then, barbs are pushed helicoidally outwards, partially fusing to form the rachis of contour feathers. Keratinocytes synthesize and accumulate β-keratin as they mature and eventually die. The new feather grows within a protective sheath that elongates, forcing the old feather out of the follicle (Lucas & Stettenheim 1972).

Molt episodes, phenotypes, and elements

In most small to medium-size species, molt is organized in nearly discrete **molt episodes** (see Glossary) with a circannual schedule. The number of molt episodes (or the periodicity of molt activation in large species) in addition to their variation within and among annual cycles throughout the bird's lifetime configures its **molt strategy** (see Glossary).

A full description of a molt episode requires two main components: the **active molt phenotype** (i.e. molt process) and the **definitive molt phenotype** (i.e. molt outcome). The active molt phenotype includes feather growth rate, molt intensity, sequence within and among feather tracts, and timing. Other aspects will define the definitive molt phenotype: duration, **extent** (see Glossary), plumage quality, and set of replaced feathers (i.e. the actual feathers eventually molted by a given individual at the end of a given molt episode).

In this thesis, all these observable aspects that affect the molt phenotype are referred to as **molt elements** (see Glossary). **The set of replaced feathers is a major topic of this thesis**, and it will be also referred as (simply) the "**final molt phenotype**".

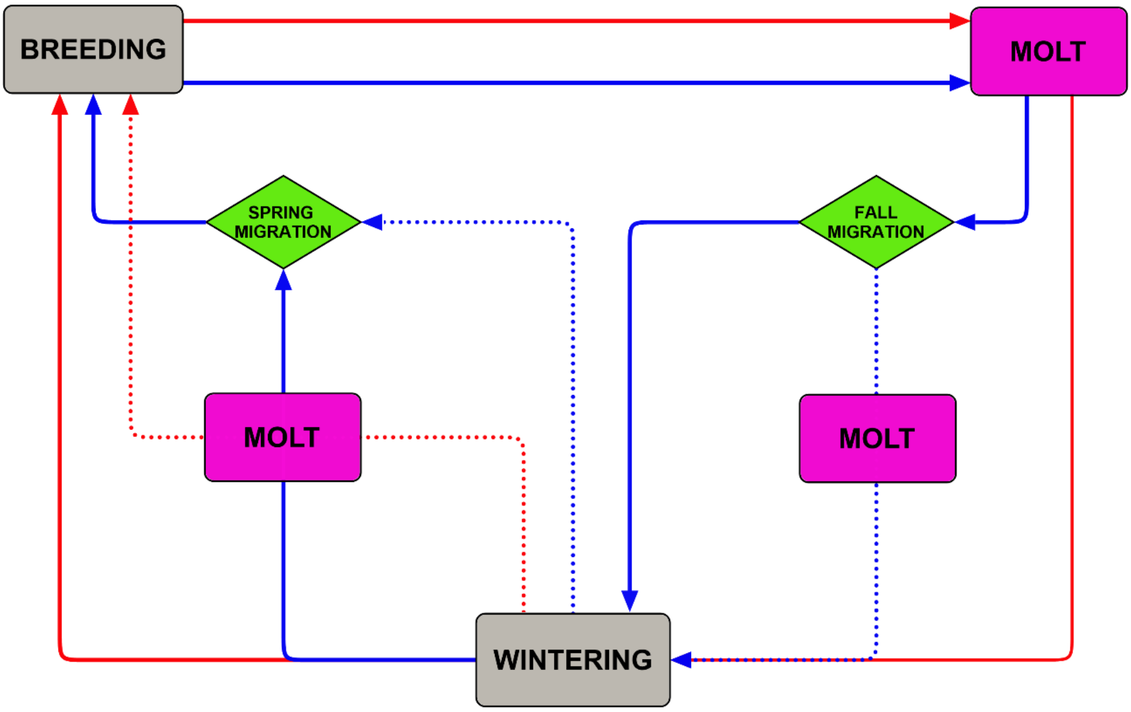
1.3 Molt within the annual cycle

Birds organize their lifetime in annual cycles, presenting at least three life-history stages every year: **breeding**, **molt**, and **wintering** (Fig. 2), although many species, especially long-lived ones, may not reproduce during the first potential breeding seasons (Newton 1989, Cooper *et al.* 2009), and large seabirds may skip one breeding season because of different reasons including the accumulation of molt delays (Langston & Rohwer 1996, Filardi & Rohwer 2001, Edwards 2008). While simple annual molt strategies consist of only one molt episode, the number of molt episodes increases with increasingly complex life histories.

Molt in complex annual cycles

Even though complex annual cycles imply less time to accommodate multiple molt episodes, the fact is that the number of molt episodes increases in most bird families with complex annual cycles. For example, long-distance migrant passerines frequently present three molt episodes: a post-breeding molt restricted to body plumage, a fall complete molt, and a late winter partial molt (Shirihai *et al.* 2001, Alström & Mild 2003, Gualar *et al.* 2009, Kennerley & Pearson 2010). Increasing number of molt episodes allows adaptation to environmental changes, a greater flexibility to accommodate to both current conditions that experience the individual (e.g. parasite load or breeding attempts; Gow & Stutchbury 2013, Marzal *et al.* 2013) and to the other life-history traits (Gromadzka 1989, Wingfield 2008; although see Dietz *et al.* 2013). Also, opportunistic breeders can interrupt molt facultatively (Hahn *et al.* 1992); species living in unpredictable habitats show exceptionally slow molts (Zann 1985, Hoye & Buttemer 2011).

Figure 2. Simplified diagram of life-history stages (boxes) within the annual cycle of most passerine species. Red loops: non-migrant species. Blue loops: migrant species. Dotted lines: alternative strategies. While life-history stages are depicted in different boxes, overlap may occur between molt and the other life-history traits.



1.4 Molt variation

Molt is characterized by a bewildering variation among and within species. This flexibility is likely adaptive and covaries with species' natural histories. For instance, birds living in arid and unpredictable habitats have slow molts (Zann 1985, Oschadleus & Osborne 2005). Large birds molt very slowly, although those large species that do not rely on flight for foraging undergo synchronous remex molt (Bridge 2004, Howell 2010). Hornbills provide one of the most extreme examples of the adaptability of molt: incubating females walled in tree trunks replace their remiges synchronously while males, which feed them during this period, undergo a sequential molt (Kemp 1995).

Variation of molt elements

All molt elements are variable, especially in relation to intrinsic factors, like sex, age, population, and species (Bojarinova *et al.* 1999, Zenatello *et al.* 2002), but they are also affected by environmental factors, including parasites and stress events (Pirrello *et al.* 2015, Jenni-Eiermann *et al.* 2015, Jovani & Rohwer 2017). The latter two tend to correlate negatively with some parameters of the definitive molt phenotype, including number of barbs and feather density (Pap *et al.* 2013). Duration of remex replacement vary from three to four weeks in some synchronous molting species to several annual cycles in some large raptors, although most small to medium-size species of the Holarctic spend 8-12 weeks (Stresemann & Stresemann 1966, Ginn & Melville 1983, Zuberogoitia *et al.* 2016). Duration of molt in Neotropical species is longer probably because of their slower pace of life (Wiersma *et al.* 2007, Guallar *et al.* 2009).

Feather growth-rate scales allometrically with feather size, so that remiges of large birds take longer to grow because of their larger size but also grow at a slower rate than remiges of small birds because they are denser (Rohwer *et al.* 2009, Jenni *et al.* 2020). Feather growth-rate is also higher in migratory populations of a species (de la Hera *et al.* 2009a) and varies among feathers within and among tracts (Newton 1967, Pap *et al.* 2008). Similarly, molt intensity correlates negatively with species size (except in species with simultaneous molt), and is higher in migratory species, such that northernmost populations of boreal passerine species under severe time constraints may become nearly flightless (Haukioja 1971).

Molt sequence varies with feather growth-rate and molt intensity, so that slow molting species and fast molting species adopt different sequence strategies. Fast molters may adopt either a simultaneous remex molt or a sequential molt, depending on its reliance on flight to forage (Kemp 1995, Bridge 2006, Terrill 2020). Slow molters present serial replacement although small-size species stick to the sequential molt (Rohwer & Wang 2010, Zuberogoitia *et al.* 2018). Sequential molt can be descendant, ascendant or divergent (Zeidler 1966, Williamson 1972, Kiat 2017). Serial molt can be very complex, although it usually follows descendant or divergent sequences (Shugart & Rohwer 1996, Rohwer & Rohwer 2018). Finally, molt timing largely varies with species (Earnst 1992, Gwinner 2003, van der Jeugd *et al.* 2009). Remex molt is usually scheduled after breeding in temperate species, but it can be advanced in individuals that fail or skip reproduction (Crossin *et al.* 2012, Strinella *et al.* 2015) or delayed because of a late clutch (Morton & Morton 1990, Stutchbury *et al.* 2011).

Variation of the final molt phenotype

Molt can be **complete** or **partial**. A complete molt leads to a unique final molt phenotype (i.e. all feathers replaced), which is the typical outcome of the post-nuptial molt of most passerines. However, the number of potential final molt phenotypes is huge for partial molts. For example, for partial molts that include 20 out of 50 wing feathers there are 4.7×10^{13} potential final wing-feather molt phenotypes. To deal with variation of final molt phenotypes researchers have historically classified them under certain criteria of similarity, the so-called **molt patterns** (see Glossary), such as the eccentric molt pattern (Pyle 1998) or the general one (Guallar *et al.* 2014). However, while never studied directly, it is apparent that despite final molt phenotypes are very variable, most theoretical molt phenotypes are never observed. Addressing this variation, how it compares to theoretical molt phenotypes, how empirical molt phenotypes relate one another, and what can we learn about underlying rules of bird molt are major topics of this thesis.

Variation among and within molt episodes

Few species are known to undergo two complete molts per annual cycle, and all of them are small sized passerines (Prŷs-Jones 1991, Herremans 2006). Besides these exceptions, small-size species molt their plumage at least once a year, although many of them also present additional annual molt episodes, all of them partial (Svensson 1992, Pyle 1997, Sieburth & Pyle 2018). The final molt phenotype not only varies among species but also intraspecifically among partial molt episodes. On the other hand, most large species cannot renew their whole plumage within a year and molt must be protracted along multiple annual cycles (Zuberogoitia *et al.* 2018, Jenni & Winkler 2020a). Other molt elements also vary among episodes within the individual, including intensity (Zuberogoitia *et al.* 2016) and plumage quality (Weber *et al.* 2010).

1.5 Molt regulation

Regulation of molt comprises a series of **physiological mechanisms** that control the whole process, from gene expression to formation of the definitive molt phenotype. It includes the modulation of molt by environmental factors, and the way environmental signals are transmitted to feather-follicles via hormonal secretions. Molt regulation is a very broad field of study that not only deals with the molecular and tissue levels, but also with the rules that govern all molt elements. The study of molt regulation has largely focused on three areas: nutritional and energetic aspects, endogenous and exogenous cues, and hormonal regulation. Energetic aspects are the ones more related to this thesis (see Chapters 2 and 3), so the rest of this brief account will stick to those energetic aspects.

Molt energetics

Molt is a very inefficient process, with only 5-39% energy conversion to feather synthesis (Dietz *et al.* 1992, Lindström *et al.* 1994, Portugal *et al.* 2007). Part of the explanation of this inefficiency are the costs of development and maintenance of feather follicles that synthesize feathers. Moreover, follicular activity is not a stand-alone system, it requires an expensive machinery to transport and supply resources for their functioning (deGraw & Kern 1985, Taruscio & Murphy 1995, Podlaszczuk *et al.* 2017). Other molt costs are far from being trivial. Molt is synchronized with other processes, that are dependent on or co-occur with molt: organ remodeling, especially leg and pectoral muscles (Young & Boag 1982, Fox & Kahlert 2005, Portugal *et al.* 2009), bone mineralization (Meister 1951, Murphy *et al.* 1992, Portugal *et al.* 2011), detoxification (Braune & Gaskin 1987, Lewis & Furness 1991), and immune response (Moreno *et al.* 2001, Cyr *et al.* 2008, Moreno-Rueda 2010, Ben-Hamo *et al.* 2017).

There are also indirect costs of molt, including increased energy required for flight and reduced aerobic capacity (Rayner & Swaddle 2000, Buttemer *et al.* 2019). The formation of molt gaps by feather loss during molt has especial transcendence because it also affects flight performance, therefore increasing predation risk (Haukioja 1971, Lind 2001, Williams & Swaddle 2003, Navarro & González-Solís 2007). However, there is growing consensus on compensation of heat loss due to both increased metabolism and impaired insulation as the main culprit of the energetic inefficiency of molt (Lustick 1970, Schieltz & Murphy 1997, Buttemer *et al.* 2003, Gerken *et al.* 2006). Further, thermoregulation is likely the reason that explains why passerines wintering in temperate regions do not molt during this stage (Svensson 1992, Pyle 1997).

Molt energetics paradox

Overall, the energetic cost accumulated throughout the molt process is high. However, this cost is distributed over a long period of time, such that the resulting daily energy expenditure is greatly reduced (Murphy & King 1992, Schieltz & Murphy 1997), and in many species (e.g. in many passerines) molt does not overlap with reproduction and migration. This creates a paradox in many bird species: while molt is a costly process within the annual budget, the molting period is, at the same time, the one with minimum daily energy expenditure (Masman & Daan 1987).

1.6 Evolution of molt

Analogously to molt regulation, the study of molt evolution may span from the genotype to the phenotype. It also comprises paleontological research. However, until the publication of the first DNA-based classification of bird species (Sibley & Ahlquist 1990) knowledge on molt evolution was largely speculative. Recent advances have allowed the reconstruction of a robust avian phylogeny (Ericson *et al.* 2002, Barker *et al.* 2004, Klicka *et al.* 2007, Lovette *et al.* 2010, Jetz *et al.* 2012, Prum *et al.* 2015), while the development of ever more powerful statistical techniques and software have allowed the analysis of phylogenetic data (Maddison & Maddison 2001, Pagel *et al.* 2004, Paradis *et al.* 2004, Revell 2012, Ho & Ané 2014). This progress has mostly taken place during the last decade, which explains why the study of molt evolution is still in its infancy.

GLOSSARY BOX

Early life. First stages in the life of a bird. It comprises the embryo, nestling, and juvenile phases. It ends with the replacement of the juvenile (nestling) plumage.

Final molt phenotype. Set (identity) of feathers replaced after a molt episode by an individual bird.

Life-history event. Each realization of a life-history trait that characterizes an organism (e.g. breeding, molt, migration, and wintering). For example, each molt episode is a life-history event.

Life-history stages (also natural-history stages). Each of the main phases in which the life of a bird species can be divided. Each stage consists of several life-history events. The simplest design comprises early life, reproduction, molt, and wintering. More complex life histories include migration periods, and extra molt and reproduction events (Wingfield 2008; Fig. 2).

Molt elements. Observable aspects in a molt episode at individual level: duration, extent, feather growth rate, final molt phenotype, intensity, plumage quality, sequence (within and among feather tracts), and timing.

Molt episode. Each separate molt event in the annual cycle of birds. Many species can interrupt molt and resume it later (e.g. Hirundinidae). Three main episodes are recognized: post-breeding, which produces the post-breeding or basic plumage (equivalent to the prebasic molt); post-juvenile (equivalent to the preformative molt), which produces the post-juvenile or formative plumage; and pre-breeding (equivalent to the prealternate molt), which produces the breeding or alternate plumage. Number of molt episodes are not fixed and can vary among populations of a given species (e.g. sedentary populations of Eurasian Reed Warbler *Acrocephalus scirpaceus* in Morocco undergo one instead of the two typical molt episodes of migratory populations; Amezian *et al.* 2010). Species that cannot replace their plumage in one annual cycle present molt strategies that do not fit an episode-based scheme (Shugart & Rohwer 1996, Zuberogoitia *et al.* 2018).

Molt extent. Amount of plumage replaced during a molt episode. Here, it has been measured as number of feathers, mass, and area.

Molt patterns. Groups of molt phenotypes sharing specific rules of similarity (see Chapter 1).

Molt strategy. Combination of molt elements and molt episodes that each species integrates and distributes throughout its natural-history stages. It allows the adjustment of plumage functions to both changing social and physical environments and to other life-history events. Molt strategies can vary among individuals of the same species (e.g. suspension versus serial replacement in Common Ground-doves *Columbina passerina*; Rohwer & Rohwer 2018).

Thus far, only 26 articles have been published on molt evolution explicitly using phylogenetic analyses (including four contained in this thesis). Some have shown the large influence of time constraints (e.g. associated with migratory behavior and body size) on annual molt strategies, as well as on molt duration, speed, and timing (Svensson & Hedenström 1999, Figuerola & Jovani 2001, Hall & Tullberg 2004, Bridge 2006, Bridge *et al.* 2007, de la Hera *et al.* 2009b, 2010b, 2011, 2012; Kiat *et al.* 2016, Kiat & Izhaki 2021, Pérez-Granados *et al.* 2021). Other studies have investigated the influence of the environment on molt (Guallar *et al.* 2016, Kiat *et al.* 2019b, Pageau *et al.* 2020). Several studies have focused on sequence (Kiat 2017, 2018; Kiat *et al.* 2020, Terrill 2020), while another group of studies have addressed completeness of passerine post-juvenile molt (Tökölyi *et al.* 2008, Kiat & Izhaki 2016). Finally, there is one study that tackles the evolution of new molt episodes (Terrill *et al.* 2020). Much more study is needed on all these topics, as well as on those that have not been addressed yet (e.g. genetic evolution).

2. Gaps in our knowledge of molt

Despite its central role in the life-histories of birds, molt is a relatively neglected field of study, well behind other life-history traits, such as reproduction or migration. This is shown by three facts: the number of molt articles published in high impact journals is reduced, some works of reference in bird biology completely omit molt from their accounts (e.g. del Hoyo *et al.* 1992–2002, 2003–2013), and there are neither conferences nor working groups devoted to molt (Jenni & Winkler 2020a). This section first presents a summary of the three main gaps in our knowledge of avian molt according to Bridge (2011) and finishes with an account of two additional gaps that this thesis attempts to tackle.

2.1 Deficiency of quantitative descriptive data

Geographical bias and low quality of existing data

The first and foremost gap is deficiency of basic descriptive quantitative data of all molt elements. Descriptive data continue to be compiled at a slow pace (e.g. Pyle *et al.* 2017, Johnson & Wolfe 2018, Park *et al.* 2019), with entire biogeographic regions still virtually devoid of information (e.g. Oriental region). Moreover, existing descriptive data often lacks the desirable quality (e.g. 48% molt information used in Chapter 6 was deemed as having low or moderate quality).

Episode bias

This deficiency is exacerbated by the existence of an episode bias. Indeed, most studies have focused on the post-breeding and the post-juvenile molts (Bojarinova *et al.* 1999, MacDougall-Shackleton *et al.* 2009, Ryzhanovsky 2013, Crates *et al.* 2015, Noskov *et al.* 2018). Studies focused on the pre-breeding molt are much scarcer (Noskov *et al.* 1999, Peters *et al.* 2000, Coppack *et al.* 2008, Battley 2006, Barshep *et al.* 2013, Danner *et al.* 2015, Chmura *et al.* 2017), and studies dealing with episodes undergone by long-distance migrants in their winter range (Pinilla 2001, Shirihai *et al.* 2001, Guallar *et al.* 2009) or the "pre-supplemental" molts during the **early life** (see Glossary) of some passerines (Nicolai 1968, Willoughby 1986, Redfern & Alker 1996) are rare and usually purely descriptive. These episodes are important to have a complete overview of molt strategies and a better understanding of the annual cycle.

Efforts carried out in this thesis to alleviate this gap

All this data deficiency severely hampers our efforts to understand bird molt, thus claiming for a collective effort to fill this void in avian biology by gathering information from museum collections and image libraries (Pyle in prep.). A large molt dataset has been created to tackle the objectives of this thesis which contains information on species, sex, age, feather mass, replaced and retained feathers (thus, including final molt phenotype), molt episode, and location. To alleviate the geographic bias, this thesis includes original data from species occurring in the Holarctic and Neotropical regions.

2.2 Neglected aspects in the study of molt physiology

Studies on the nutritional and energetic aspects, endogenous and exogenous cues, and hormonal regulation have provided insights on the regulation of most molt elements (Murphy et al. 1988, Murphy & King 1990, 1991; Fox & Kahlert 1999, Kuenzel 2003, Dawson 2005, 2006, 2008; Pap et al. 2008, Vézina et al. 2009, Remisiewicz et al. 2010, Ellis et al. 2012, Rohwer et al. 2015, Galván & Solano 2016). However, others remain virtually unstudied: physiological mechanisms underlying feather-growth rate, sequence within and among feather tracts, and extent (Miller 1941, Péczely 1992, Herremans et al. 1993, Dawson 2004, Ellis et al. 2006, Hazlerigg & Lincoln 2011). Moreover, the underlying mechanisms controlling variation of the final molt phenotype remain obscure (see 2.5).

2.3 Interaction between molt and flight

This interaction has four relevant aspects. First, it influences the behavior of birds during molt, which become more discrete and reluctant to fly (Vega Rivera *et al.* 1999). Mode of flight also strongly influences molt strategy, especially in relation to intensity and duration (Haukioja 1971, Zuberogoitia *et al.* 2018). Molt gaps theoretically increase energetic costs although birds compensate them by increasing pectoral muscle, reducing body mass, and adapting flight kinematics (Swaddle *et al.* 1999, Lind & Jakobsson 2001, Bridge 2008). Finally, low quality plumage or diminished flight performance during molt rises predation risk (Swaddle & Witter 1997, Hedenström & Sunada 1999, Møller *et al.* 2009).

Difficulties to tackle this interaction

Some topics related to the interaction between molt and flight have drawn quite attention, like the influence of wing gaps on escape flight (Chai 1997, Swaddle *et al.* 1999, Lind 2001, Echeverry-Galvis & Hau 2013), but other topics remain poorly studied. Thus, substantial advances in this area are hindered by the difficulties to both study the dynamic interaction among the multiple variables involved (molt intensity, flight type, wing shape or stage of molt), and measure flight parameters in free-living birds (Tucker 1991, Hedenström & Sunada 1999, Bridge 2004, Dvořák 2016, Achache *et al.* 2018, Tomotani & Muijres 2019). Generation of these data might take decades. However, before they are obtained, advances can be made by simulation studies or models (Bridge 2008); also, the use of proxies of certain feather properties related to flight (e.g. bending stiffness; de la Hera *et al.* 2010a, 2020) can allow to address contribution to flight of individual wing feathers.

2.4 A "new" gap: molt evolution

In addition to the gaps identified by Bridge (2011), there is one gap central to any biological phenomenon that has been barely tackled in relation to molt thus far: evolution. As mentioned in section 1.6, studies on the evolution of molt have not been carried out until the last two decades partly because of a lack of phylogenetic information, but also because of the paucity of basic quantitative data. Phylogenetic comparative studies have mainly focused on the role of time constraints in the evolution of molt (e.g. Pérez-Granados *et al.* 2020, Kiat & Izhaki 2021). However, the social and physical environments are also expected to play a significant part in the evolution of molt, especially in tropical species.

2.5 An overlooked molt element: the final molt phenotype

Phenotypes result from the expression of the genotype under concrete environmental and internal contexts and are the target of selective forces acting upon the individual. Differences in phenotype performance affect reproduction and survival, prompting selection and character evolution. Thus, phenotypes are key to both understand the functional meaning of biological traits and unravel their regulation and evolution.

Molt phenotype

The expression of the molt process can be divided into an **active phenotype** and a **definitive phenotype**, the latter composed of two elements: **plumage quality** and **final molt phenotype** (see 1.2). At least in small to medium-size species, molt is only active during a few months (just weeks in body molts), whereas the definitive phenotype remains until the next molt episode (up to one year in passerine species with only one annual molt episode). While the relevance of feather quality on survival and reproduction has received quite attention (Nilsson & Svensson 1996, Dawson *et al.* 2000, Hall & Fransson 2000, Dawson 2004, Pap *et al.* 2007, Ferns & Hinsley 2010, Serra *et al.* 2010, Vágási *et al.* 2012), the relevance of the identity of the actual set of feathers molted (i.e. the final molt phenotype) has been completely neglected in bird molt research.

A surprisingly overlooked molt element

Final molt phenotypes are implicitly contained in the detailed accounts that have been accrued for many passerine species during the last nine decades (e.g. Sutton 1935, Selander 1958, Newton 1966, 1967, 1968; Ewart & Lanyon 1970, Laesser & van Wijk 2018, Jenni & Winkler 2020b). They have been recorded in countless molt cards and extensively applied to age birds (e.g. Ginn & Melville 1983, Pyle 1997, Demongin 2016). However, final molt phenotypes had neither been explicitly defined nor recognized for its importance from the point of view of the individual. Hence, hypothesis testing explicitly based on the final molt phenotype are completely lacking. This is surprising because: 1) feathers differ in their functionality (e.g. signaling, thermoregulation, contribution to different flight functions, resistance), costs of production, and morphology (e.g. exposure, mass, shape), all of which can be targeted by natural selection; and 2) selective forces may act during a long period of time on the final molt phenotype.

Relevance of studying final molt phenotypes

The consequences of the final molt phenotype for the fitness of the individual may be great, including energetic budget, signaling, and flight performance. Further, variation of the final molt phenotype for a given species and molt episode can be characteristic and reflect how environmental factors and constraints have shaped its evolution. Formation of the final molt phenotype and its variation is expected to deviate from randomness if it has an adaptive value. This implies the existence of mechanisms of control allowing the formation of certain final molt phenotypes while avoiding others. Final molt phenotypes might be especially helpful to understand how energy and nutrients are channeled and distributed through different plumage regions.

3. Approach

This last section proposes how to address the study of the gaps in our knowledge of molt identified in the previous section, focusing on molt evolution and the use of the final molt phenotype (see 2.4 and 2.5).

3.1 Evolution of molt

Sequential molt is already detected in 50 million-old feathered-dinosaurs (Kiat *et al.* 2020). The fact that sequential molt was already present in the Eocene proves that at least some molt elements are highly conserved, which is an expected characteristic of major life-history traits (Pyle 2013). Moreover, broad patterns of similarity have been found for some molt features across the avian phylogeny (e.g. directionality of sequence, photoperiodic response; Gwinner 2003, Kiat *et al.* 2020), with some showing a strong phylogenetic signal (Kiat & Sapir 2017, Terrill 2020). This signal may relate to conserved morphological and physiological traits, such as the arrangement of the wing plumage, the structure of feathers, or the follicle morphology (Prum & Williamson 2001, Rohwer *et al.* 2009, Rohwer & Rohwer 2013, Wang & Clarke 2015, Jenni *et al.* 2020). At the same time, though, molt is an astonishingly variable trait characterized by its evolutionary flexibility (Barta *et al.* 2006, 2008). This flexibility becomes evident examining species size. Size has likely been one of the most important drivers of some elements of molt strategies (e.g. intensity, sequence, extent), since the larger the feather the longer it needs to grow (Rohwer *et al.* 2009, Jenni *et al.* 2020). Eventually, sequential replacement of all remiges cannot fit in a single annual cycle, triggering the evolution of new molt strategies in large birds, including simultaneous remex molt or serial molt across annual cycles (Bridge 2006, Zuberogoitia *et al.* 2018). Molt flexibility is also evident in the interaction with mode of flight. Gliders and aerial foragers replace their primaries very slowly to minimize wing gaps and therefore flight efficiency, whereas flapping flyers tend to replace several remiges at a time (Bensch & Grahn 1993, Edwards & Rohwer 2005, Dittmann & Demcheck 2006, Zuberogoitia *et al.* 2018).

A mechanistic explanation of the evolution of molt

Thus far, most studies on molt evolution have focused on the role of time constraints as evolutionary drivers of molt in Holarctic birds (but see Figuerola & Jovani 2001). A mechanistic explanation for the evolution of some molt strategies links time constraints with the effect of molt on feather quality (Dawson *et al.* 2000). These constraints may be associated with late breeding attempts and/or the evolution of migratory behavior (Nilsson & Svensson 1996, Hall & Tullberg 2004). Thus, birds forced to molt rapidly because of time constraints produce feathers of lower quality (Hall & Fransson 2000, Dawson 2004). Low quality plumage is less efficient and can compromise both winter survival and the next breeding season (Edward & Rohwer 2008, Gienapp & Merilä 2010, Vágási *et al.* 2010, 2012). Large birds can break this vicious circle by skipping breeding some years (Edward & Rohwer 2008). Individuals of migratory passerine species able to suspend or delay their complete molt until after migration might also avoid this constraint. In this way, they can produce higher quality plumages and increase their fitness (Hall & Tullberg 2004, Kiat & Sapir 2017, 2018).

The influence of environmental factors

The flexible and adaptive nature of molt strongly suggests that environmental factors may have also shaped its evolution. These factors have begun to be tackled recently, showing its potential to explain final molt phenotype evolution (Guallar *et al.* 2016). Thus, habitat and climate variables can trigger adaptive changes, including the evolution of new molt episodes (Terill *et al.* 2020). It is known that plumage of birds living in abrasive environments wears off faster, likely prompting a need for more frequent feather replacement, as it has been noticed in passerine species from arid areas (Willoughby 1991, 2007). Moreover, aridity in the breeding range at the end of the reproductive season correlates to molt-migration in western North America (Pageau *et al.* 2020). Similarly, thermoregulatory costs, which are thought to be one of the main causes of the energetic inefficiency of molt (Dolnik & Gavrilov 1979, Dietz *et al.* 1992), may explain why most resident species of temperate regions do not undergo extensive pre-breeding molts (Svensson 1992, Pyle 1997). Along this line, rising planetary temperatures may have driven the evolution of more extensive molts in Palearctic passerines since the industrial revolution (Kiat *et al.* 2019b). On the other hand, warm and humid environments could favor plumage degradation by feather parasites (Azcárate-García *et al.* 2020), therefore increasing the need of more extensive and/or more frequent molt.

The influence of social and sexual factors

While molt episodes associated to plumage maintenance will likely show a high phylogenetic signal, molt episodes associated with seasonal adjustment of plumage functionality are expected to have a low one, suggesting a labile nature. This lability could arise from functions that can be modified in response to features of the social and sexual environment, which can diversify rapidly during speciation (Irestedt *et al.* 2009, Seddon *et al.* 2013). Deep changes in plumage coloration occurring during pre-breeding molts of many long-distance migrants likely allow birds to signal physical condition or dominance to their conspecifics (Watt *et al.* 1984, Danner *et al.* 2015). Sexual dichromatism and gregariousness could have driven the evolution of these changes.

3.2 The final molt phenotype

3.2.1 The study of final molt phenotypes

There is consensus on the relevance of the quality of the new plumage for the individual's performance (e.g. feather size, density, coloration, microstructure, symmetry, immaculateness, and flawlessness (Bustnes *et al.* 2002, Ferns & Hinsley 2004, Griggio *et al.* 2009, Pap *et al.* 2013, Ross *et al.* 2015, Jovani & Rohwer 2017). However, the significance of the final molt phenotype has been completely overlooked. Given the potential relevance of this molt element for the reproduction and survival of the individual (see 2.5), one may wonder about the reasons for this negligence.

State of the art of the final molt phenotype

The final molt phenotype has not been used as is, neither to study questions strictly related to the molt process (e.g. regulation, sequence among tracts, intensity, daily energy cost) nor to investigate aspects of plumage functionality (e.g. signaling, camouflage, flight, resistance to abrasion). Instead, research on these questions either has focused on a single feather tract (usually primaries during complete molts) or has applied simpler approaches usually based on molt extent metrics (e.g. number and mass of feathers; Gargallo 1996, Rymkevich & Bojarinova 1996, Mulvihill & Winstead 1997, Willoughby 2007, Karell *et al.* 2013). However, these approaches may miss the relevant target on which selection forces act because different feathers have different functions and costs. Thus, the objective of a given molt episode for certain species may not be replacing the most exposed feathers but those feathers that convey individual information relevant for mating or competing for territories. In this case, comparison of exposure indexes may lead to different conclusions than comparison of final molt phenotypes. Analogously, two species with very similar feather-mass productions during their pre-breeding molt may allocate it to different wing feathers, one favoring tertials the other greater coverts. Neither the regulatory nor the functional implications of these two strategies would be captured by comparing masses of replaced feathers among individuals.

Complexity of the final molt phenotype

The final molt phenotype is complex and therefore can be approached from multiple angles: topography, feather identity, color patches or folded versus unfolded wing, and many more which will be gradually identified. Properties and functions of feathers, as well as second-order properties that arise from the association among groups of feathers from the same or different tracts (e.g. wing patches) are not well understood, so that quantification of the individual feather contribution to every potential function it may serve remains speculative.

Approaches

Analysis of the final molt phenotype requires methods suited for the object of study. These methods may combine one or more facets of the final molt phenotype with other pieces of information such as area or mass. Thus, the study of the mechanisms of molt regulation may combine information on the set of replaced feathers with information on their anatomical position. Studies focused on signaling functions may require supplementary information on area of color patches, while those focused on the resistance to abrasion may require variation of exposure between folded and unfolded wings or tail. However, phylogenetic analyses may benefit from reducing the high dimensionality of the final molt phenotype, for example, calculating a geometric proxy (Guallar *et al.* 2014) or grouping similar phenotypes into a discrete number of categories (molt patterns). In general, multivariate methods using as many facets as possible of the final molt phenotype may prove helpful to capture the target of selective forces acting on this molt element.

3.2.2 Final molt phenotype variation

Early studies already showed the enormous variation of the final molt phenotype in passerines (Dwight 1900). Final molt phenotype variation pervades all taxonomic levels, from the individual (among molt episodes), to within and among species (Guallar *et al.* 2014, Jenni & Winkler 2020b). This variation is associated with the existence of partial molts, being potentially astronomical, because there might be as many final molt phenotypes as combinations of replaced feathers (number of feathers vary from about 1.000 in hummingbirds up to 25.000 in swans; Wetmore 1936, Amman 1937). Documentation of this variation is usually restricted to the larger wing and tail feathers in large species that undergo serial molts, although is frequently expanded to wing coverts and alula in passerines (Ginn & Melville 1983, Pérez-Granados *et al.* 2021).

Applications

Variation of the final molt phenotype can contribute to a more complete understanding of species molt strategies. In this thesis the final molt phenotype is used to formally test whether molt is a random process. This hypothesis predicts that species do not express final molt phenotypes with an equal probability, instead they are restricted within a limited range: while some are frequent, most are never expressed. The use of the final molt phenotype is extended to address a few gaps concerning molt regulation and evolution. Another basic contribution of this thesis is to show the limitation of molt extent to investigate functional aspects of plumage. Thus, feather number (or mass thereof) do not provide sufficient information about the specific feathers replaced during a molt episode. A given molt extent may be achieved by a large number of final molt phenotypes, which may have different performances and/or efficiencies. Comparison of molt patterns among species will be used to reveal seasonal differences of final molt phenotype expression related to the adjustment of plumage functions. These two aspects related to the expression of the final molt phenotype would indicate that variation of the final molt phenotype is actively and tightly regulated.

3.2.3 Regulation

Proposed mechanism controlling formation of final molt phenotype

Differential investment in feather tracts during the nestling and fledgling periods has been suggested as a control mechanism of the post-juvenile molt in passerines (Pap *et al.* 2007, 2008; de la Hera *et al.* 2010a). This mechanism seems to explain the replacement of the fluffy juvenile body feathers and wing coverts while retaining the sturdier (more adult-like) remiges and rectrices. Differences among individuals of the same species and among species could be simply driven by constraints. This thesis elaborates on this idea and proposes the use of the final phenotype to study the regulation of passerine molt. Specifically, it tests whether the mechanism underlying final molt phenotype is based on a ranking of feather importance. This hypothesis predicts a nested relationship among final molt phenotypes: the more important the feather the more frequently will be replaced. This hypothesis also predicts a perfect nestedness if molt extent depended only on constraints: the least important feathers will be only molted if constraints are completely relaxed.

This mechanism is analogous to the classical island biogeography problem (MacArthur & Wilson 2001): the number of species (feathers) is associated with island size (constraints), although the relation is negative in the case of molt. This approach may bring insights on the structure of the final molt phenotype variation but also may cast light on the ultimate causes of this structure. Accordingly, this thesis evaluates the effect of three feather traits on the ranking of feather importance: exposure, mass, and contribution to flight.

Final molt phenotypes must be flexible to allow individuals responding to their specific requirements and life-history stages. Thus, partial molts could be considered as cheap solutions to reduce the overall cost and duration of molt during certain life-history stages. This thesis uses the final molt phenotype to show how energy invested in molt varies among life-history stages. Specifically, it tests three hypotheses: a) whether energy-saving strategies are applied during molt to tackle constraints and trade-offs with other physiological processes, b) whether plumage exposure is optimized in relation to energy, and c) whether these strategies vary throughout the annual cycle.

However, the final molt phenotype has likely been fine-tuned during evolution to provide an adaptive response to other factors, considering not only constraints but benefits and costs as well. For example, eccentric molt phenotypes (Pyle 1998, Guallar *et al.* 2009) would allow the replacement of the primaries forming the wingtip while retaining the well protected remiges in the middle of the wing, which do not wear off as fast, thus reducing overall molt expenditure and shortening the period of increased predation risk. In this sense, abridged patterns (see Chapter 1) seem to save time during otherwise complete molts (Norman 1991, Kiat & Izhaki 2017) but they might also avoid carry-over effects: by retaining secondaries that accumulate very little wear birds might allocate resources to more important feathers, therefore securing their quality.

3.2.4 Evolution

Incompleteness of molt

The presence of partial molts prompts an obvious question, why molt is not always complete? Answers to this question have been sought in the role of constraints such as time or energy (Danner *et al.* 2015, Kiat *et al.* 2019a). However, partial molts are typical of certain molt episodes and may be highly heritable (de la Hera *et al.* 2013, Jenni & Winkler 2020b), indicating that variation of the final molt phenotype is not only driven by the constraints that individuals face during each molt episode. Partial molts are adaptive solutions largely fixed during the evolution of each species, with constraints likely playing a minor role fine-tuning molt extent.

Adaptive value of the final molt phenotype

Although no specific studies have been aimed at investigating the influence of exogenous and endogenous factors on the final molt phenotype, some studies show that time constraints would play an important role. Plasticity of final molt phenotypes may allow a better adjustment to the new requirements of the upcoming life-history stage while limiting the molt cost to the minimum necessary. European Pied Flycatchers *Ficedula hypoleuca* excel at this purpose: this species enhances the visibility of wing patches that signal sexual attractiveness to potential mates while restricting wing-feather molt to those feathers forming the patch (de Heij *et al.* 2011, de la Hera *et al.* 2013). Final molt phenotype variability could also have important implications for the survival of recently hatched individuals, since retaining remiges in the post-juvenile molt might lower predation risk during the first months of life in inexperienced birds (Naef-Daenzer & Gruebler 2016). Some studies also suggest a correlation both between final molt phenotypes and social relationships among conspecifics (Thompson & Leu 1995, Senar *et al.* 1998, López *et al.* 2005, Vergara *et al.* 2013) and to climate change (Tomotani *et al.* 2018b, Kiat *et al.* 2019b).

This thesis studies the evolution of passerine molt by focusing on the post-juvenile and the pre-breeding at order and family level. Specifically, it analyzes the ontogenetic, sexual, and environmental factors that may have driven the evolution of post-juvenile molt completeness in the order Passeriformes. Then, analyzes which specific factors may have influenced the evolution of primary replacement and molt extent within the American family Cardinalidae. Since life-history stage affects the physical and the social environment of birds (e.g. many Palearctic species become highly gregarious during winter), social pressures may also have played an important role in molt evolution. Thus, this thesis also tests the effect of social factors on the evolution of the pre-breeding molt in Holarctic Motacillidae.

OBJECTIVES AND STRUCTURE OF THE THESIS

This thesis tackles three major gaps in our understanding of bird molt biology. For the realization of this thesis, it has been gathered molt phenotype information from thousands of birds. To establish bridges between the historical European and American molt schools (Howell et al. 2003), these data encompasses four continents and two zoogeographic regions. Further, it has been used an array of analytical tools (ancestral state reconstruction, correlated evolution, network analyses, phylogenetic logistic and random forest regressions) for the first time within the field of molt biology research.

I used passerines as study model because of practical reasons: many passerine species are easy to capture and study in the hand, they are the most abundant taxonomic group in museum collections, comprising more than 60% species of the whole avian class. Passerines have radiated and occupied all terrestrial habitats, making them adequate to investigate the role of environmental factors on the evolution of molt. Passerines show discrete, periodic, and extremely variable molts, three properties that make them especially suited for phenotypic studies designed to unveil rules of physiological control.

I elaborated a full quantitative perspective focusing on an overlooked molt element, the molt phenotype. I used molt phenotype and its variation to make inference on the regulation and evolution of avian molt. Benefits from studying the molt phenotype also go in the opposite direction: insights gained from the study of molt regulation and evolution help understand the biological meaning of molt phenotypes. Thus, I started this thesis describing patterns of molt phenotype variation across phylogeny and between molt episodes. Next, I explored the rules governing formation of the final molt phenotype, applying network theory for the first time in molt studies. Considering the putative role of some morphological characters as phylogenetic constraints (Rohwer et al. 2009) and the disproportionate contribution of shared ancestry on the evolution of post-juvenile completeness (Chapter 6), I explored the role of plumage morphology as a major molt constraint. Physiology provides the mechanistic link between molt phenotype and the evolutionary trajectories engraved in the genotype. Finally, I provided an evolutionary perspective to cover this insufficiently studied aspect of molt. Specifically, I investigated evolutionary drivers for two of the three main molt episodes in passerines, at both family an order level.

The specific objectives presented as chapters of this thesis, were:

1. to quantify wing-feather molt phenotypes between the preformative and the prealternate molt episodes among individuals within species and across the phylogeny,
2. to test for the nested organization of passerine wing-feather molt phenotype variation,
3. to analyze the role of feather mass, exposure, and contribution to flight on wing-feather molt within and across molt episodes,
4. to test whether passerine molt follows an energy-saving strategy optimizing area of renewed plumage in relation to energy investment,
5. to test the influence of environmental and natural-history factors on the evolution of the prealternate molt,
6. to test the influence of environmental and natural-history factors on the evolution of the preformative molt.

This thesis is organized in three parts. The first part describes and analyzes structural factors of passerine molt that had not been explicitly quantified, specifically variation of feather-wing molt phenotype (chapter 1). The second part investigates two factors that may underlie the regulation of molt: rules of molt control (Chapter 2) and constraints imposed by plumage morphology (Chapter 3). The third part explores factors influencing evolution of passerine molt based on the phenotypic approach developed in the first part: extent of the prealternate molt (Chapter 4), extent of the preformative molt (Chapter 5), and completeness of the preformative molt (Chapter 6).

In **Chapter 1**, I built a dataset containing thousands of wing-feather molt phenotypes from Holarctic and Neotropical passerine species. I showed that variation of molt phenotypes was far below that expected by chance, although a portion of these phenotypes were repeated among individuals within and among species, suggesting the existence of shared mechanisms of molt control. I classified molt phenotypes according to nine molt patterns described in the literature and found an uneven distribution between the preformative and the prealternate molt. Molt patterns were phylogenetically conserved for the preformative but not for the prealternate molt suggesting an association between preformative molt and somatic demands, and between prealternate molt and signaling functions. This chapter contributes to objective 1 of the thesis.

In **Chapter 2**, I investigated the variation of passerine wing-feather molt, showing its non-random structure. Differences in feather importance can cause a molt rank, and ultimately create a nested relationship among wing-feather molt phenotypes. I tested whether molt episodes would show nestedness differences, and the adaptive meaning of different molt ranks associated with feather mass, feather exposure, and feather contribution to flight. These findings provide a first model to interpret variation of wing-feather molt phenotypes in passerines, and outline the relevance of season for passerine molt, suggesting a dynamic link between molt expression and plumage requirements. This chapter contributes to objectives 1, 2, and 3 of the thesis.

In **Chapter 3**, I compared mass and exposure of empirical and theoretical passerine wing-feather molt phenotypes to test whether passerine birds present energy-saving strategies, optimize area of renewed plumage in relation to energy investment, and adapt to changes throughout their natural-history stages. Results support these three hypotheses, stressing the importance of morphological constraints in the formation of phenotypes, and specifically its influence on shaping passerine molt strategies. This chapter contributes to objectives 1, 3, and 4 of the thesis.

In **Chapter 4**, I tested the relative influence of ten ecological, ontogenetic, social and sexual factors on the evolution of both autumn molt and prealternate molt among Northern Hemisphere species of the family Motacillidae A high rate of change between related species revealed phylogenetic independence among prealternate molt and examined factors. Natural selection and sociality seem to be the most important evolutionary drivers of prealternate molt in Motacillidae. This chapter contributes to objective 5 of the thesis.

In **Chapter 5**, I explored adaptive factors affecting the preformative molt in the passerine family Cardinalidae and concluded that its ancestor inhabited forest habitats and underwent a partial preformative molt. Later radiations within the family appeared to be characterized by transitions from forests toward more open habitats, and such transitions also correlated positively with increased preformative molt investment, plumage signaling, and flight. I also found that the presence of an auxiliary preformative molt correlated to the extent of the preformative molt, indicating that both episodes form part of the early-life molt strategy in this family. This chapter contributes to objectives 3 and 6 of the thesis.

In **Chapter 6**, It is tested on >1300 passerine species from across the world whether complete post-juvenile molt is more prevalent in species that do not encounter constraints and find favorable environmental conditions. Complete post-juvenile molt has a strong phylogenetic signal, the evolution of which not only depends on whether birds find suitable conditions but also on the strength of selection associated with the need of a complete molt. In particular, the necessity to keep the plumage in good condition in challenging environments, and the benefits associated with producing adult-like plumage colors to attract mates or deter rivals, seem to play an important role. This chapter contributes to objective 6 of the thesis.

SUPERVISOR'S REPORT

Dr. Roger Jovani i Tarrida, as supervisor of the doctoral thesis entitled "Structure, regulation, and evolution of passerine molt" certified that the dissertation presented here has been carried out by Santi Guallar and grant him the right to defend his thesis in front of a scientific panel. The dissertation work comprises one submitted manuscript, two articles published, and three articles accepted in highly ranked peer reviewed journals included in the Science Citation Index.

As supervisor, I have participated in the design, guidance, and correction of the work and earlier drafts of two manuscripts included in this thesis. The contribution of the doctoral candidate to each manuscript and the impact factor (Thomson Institute for the Scientific Information) is detailed below:

CHAPTER 1

Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny

***Guallar S**, Jovani R 2020. Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. Ibis 162: 778–786.*

Impact factor (2019): 2.205

S. Guallar contributed to all aspects of the article.

CHAPTER 2

Nestedness and its imperfections: insights to unravel the nature of passerine wing-feather moult rules

***Guallar S**, Jovani R 2020. Nestedness and its imperfections: insights to unravel the nature of passerine wing-feather moult rules. J. Avian Biol. 51: e02553.*

Impact factor (2019): 2.232

S. Guallar contributed to all aspects of the article.

CHAPTER 3

Plumage morphology channels energy investment during formation of passerine moult phenotypes

***Guallar S**, Planes O. Plumage morphology channels energy investment during formation of bird moult phenotypes. Submitted to J. Avian Biol.*

Impact factor (2019): 2.232

S. Guallar contributed to all aspects of the article.

CHAPTER 4

Factors influencing the evolution of moult in the non-breeding season: insights from the family Motacillidae

***Guallar S**, Figuerola J 2016. Factors influencing the evolution of moult in the non-breeding season: insights from the family Motacillidae. Biol. J. Linn. Soc. 117: 774–785.*

Impact factor (2016): 2.288

S. Guallar contributed to all aspects of the article.

CHAPTER 5

Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats

***Guallar S**, Rafael Rueda-Hernández, Peter Pyle 2021. Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. Ornithology 138.*

Impact factor (2018): 2.659

S. Guallar contributed to all aspects of the article.

CHAPTER 6

Partial or complete? The evolution of post-juvenile moult strategies in passerine birds

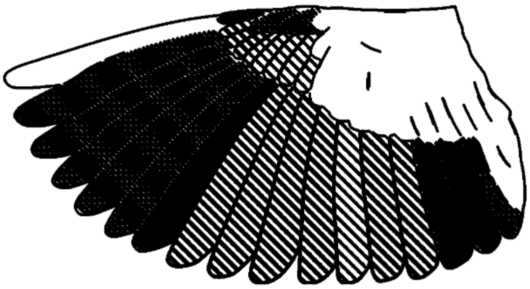
Delhey K, ***Guallar S****, Rueda-Hernández R, Valcu M, Wang D, Kempenaers B 2020. Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. J. Anim. Ecol. 89: 2896-2908.*
Impact factor (2019): 4.55
S. Guallar contributed to article design, data collection and scientific writing.

I also certify that none of the co-authors in the referred papers have used any or part of the work for their own doctoral theses.

Barcelona, 20th December 2020

Roger J

Dr. Roger Jovani i Tarrida
Department of Evolutionary Ecology, Doñana Biological Station, EBD-CSIC



Chapter 1

Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny

Santi Guallar [1*] & Roger Jovani [2]

[1] Department of Animal Biology, University of Barcelona, Av. Diagonal 643, Barcelona 08028

[2] Department of Evolutionary Ecology, Estación Biológica de Doñana, CSIC, Americo Vespucio s/n., 41092 Sevilla, Spain

Published in: Guallar S, Jovani R 2020. Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. *Ibis* 162: 778–786.

ABSTRACT

Passerine wing-feather moult has been historically studied in terms of its intensity, duration, timing, or extent. However, little is known about variation of wing-moult phenotypes (i.e. the identity of moulted wing feathers in a given individual) within species, among moult episodes, and along passerine phylogeny. Here we studied 5373 wing-moult cards from 285 Holarctic and 155 Neotropical passerine species. Variation of moult phenotypes, although high, was far below that expected by chance, and same phenotypes were repeated among individuals within and among species, suggesting the existence of shared mechanisms of moult control. We successfully classified moult phenotypes according to nine moult patterns described in the literature and found an uneven distribution between the preformative and the prealternate moult. Moult patterns were phylogenetically conserved for the preformative but not for the prealternate moult. Our results suggest differential seasonal control of bird moult, preformative moults being associated with (evolutionarily conserved) somatic demands, whereas prealternate moults being likely associated with (rapidly evolving) signalling functions.

INTRODUCTION

Feather evolution eventually led to feathered wings, and these to bird flight, becoming a key innovation in the evolution of tetrapods. The concomitant evolution of feather moult was essential to keep the functionality of these otherwise dead keratin structures that are prone to degradation by biotic (e.g. lice and bacteria; Goldstein *et al.* 2004, Vas *et al.* 2008) as well as abiotic factors (e.g. mechanical abrasion, sunlight; Lennox & Rowlands 1969, Surmacki *et al.* 2011). Within species, the study of bird moult ecology and its evolution has largely focused on: the reasons behind individual variation of moult extent (i.e. quantity of replaced feathers), such as body condition (Gosler 1994) or time available for moulting (Bojarinova *et al.* 1999, Kiat & Izhaki 2017); the overlap with energetically costly activities such as breeding and migration (Hemborg *et al.* 2001, Podlaszczuk *et al.* 2016). Among species, moult research has focused on differences in moult speed, duration, extent, location, and sequence as a result of the interaction of moult with specific traits such as body size (Rohwer *et al.* 2009), sexual dichromatism (Figuerola & Jovani 2001), migratory behaviour (de la Hera *et al.* 2010), and environmental factors (Dawson 2008).

Wing-feather moult phenotypes

Much less attention has been paid to moult phenotypes, i.e. the identity of feathers replaced by an individual bird in a given moult episode. Thus, it is poorly understood the proximate and ultimate reasons explaining which feathers are actually replaced, and why these differ among species, among individuals within species, and among moult episodes. This is surprising for two reasons. First, different wing feathers may play strongly different functions, e.g. status signalling by greater coverts, stall delay by alula feathers, lift by primaries. Second, the identity of retained and replaced feathers has been recorded for decades in moult cards (Ginn & Melville 1983), being summarised in wing diagrams showing the proportion of individuals in a given species replacing each feather (or feather track) as an age determination tool (Jenni & Winkler 1994, Guallar *et al.* 2009). However, moult cards have been largely neglected to study the evolution of bird moult, which precisely requires two characteristic features that the study of moult cards can provide: the individual scale at which natural selection operates, and a feather approach to account for the distribution of functions across the wing.

Here, we focus on the wing-feather moult of passerines, arguably the bird order whose moult has been most thoroughly studied. Passerines moult in a scheduled and periodical fashion, replacing the whole plumage at least once a year (Jenni & Winkler 1994). Full plumage renewal generally occurs right after breeding, during the prebasic moult (Humphrey & Parkes 1959). However, many species undergo extra moult episodes, usually partial (Svensson 1992, Jenni & Winkler 1994, Pyle 1997a). These include the preformative moult of young birds (equivalent to the postjuvenile moult; Jenni & Winkler 1994) replacing their juvenile plumage soon after fledging (Howell *et al.* 2003), and the prealternate moult of older birds (equivalent to the prebreeding moult; Jenni & Winkler 1994) that takes place after the prebasic moult and before the onset of the breeding season (typically in the wintering grounds for migratory species; Humphrey & Parkes 1959).

We accrued a large dataset of individual moult phenotypes gathering finished moult cards (birds in non-active moult) from literature and original data. First, we explored variation of moult phenotypes across individuals, species, and moult episodes. Then, we tested whether moult phenotypes are random sets of replaced feathers for any given moult extent.

Phenotypic variation and moult signatures

The study of moult phenotype variation is challenging and has been largely avoided thus far. Here, we tackled the complexity of moult phenotype variation by using a literature review of the so-called moult patterns, which are labels given to group together similar moult phenotypes. Applying this approach, we aimed to explore three aspects related to the ecology and evolution of moult phenotypes in passerines.

First, we explored whether individuals of a species during a given moult episode showed different moult patterns. Since endogenous (e.g. physical condition) and exogenous (e.g. available time) factors may vary among individuals, we expected that moult phenotypes may reflect these differences and could be classified in different moult patterns.

Second, we examined differences in the frequency of moult patterns between moult episodes across species. Although basic plumage requirements prioritised in each moult episode are poorly understood, they may differ strongly. For instance, the preformative moult has been related to somatic performance (Middleton 1986, Minias & Iciek 2013), while the prealternate moult may also meet signalling functions (Fig. S1), such as social status (Guallar & Figuerola 2016), and sexual attractiveness, at least in species in which this episode takes place close before the onset of the breeding season (Lantz & Karubian 2016).

We also studied the frequency distribution of moult patterns from every species and moult episode (hereafter, moult signatures), then mapped these moult signatures on the bird phylogeny and calculated their phylogenetic signal both in the preformative and the prealternate moult.

MATERIALS AND METHODS

Moult phenotypes

Moult cards of finished moults were retrieved from published sources and mist-netted birds from Holarctic and Neotropical bird species (Table S1). Moult state (1 replaced, 0 retained) was scored for each individual upper wing-feather except for lesser wing coverts, which were collectively scored 1 when more than 70% of the feathers were replaced and 0 otherwise (assessment of the percentage of replaced lesser coverts is rather imprecise; to account for this fact, we defined a value high enough to indicate that nearly the whole tract was moulted). For standardisation purposes, the tenth primary of species with nine visible primaries was given the same moult score as the ninth primary (Hall 2005). We removed 47 moult cards with no wing feathers replaced (or with only less than 70% lesser coverts replaced). Thus, moult extent can range in this study from 1 to 51 (lesser coverts = 1, median coverts = 8, greater coverts = 10, carpal covert = 1, primary coverts = 9, alula = 3, tertials = 3, secondaries = 6, primaries = 10).

While moult is conceived as a non-random process, as far as we know it has been never explicitly tested. The reasons behind non-randomness of moult likely relate to the differential properties (e.g. shape, mass, position) of each feather and its associated function. However, this question is beyond the scope of this article. The total number of potential moult phenotypes (i.e. combinations of replaced feathers) is 2^{51}-1. The number of potential moult phenotypes differs for each moult extent, e.g. there are 51 combinations when moulting one wing feather, but 1275 when moulting two. Thus, for each individual in our dataset we simulated new moult phenotypes of same moult extent but randomizing the identity of replaced feathers. Then, we tested whether feathers are moulted randomly comparing the number of repeated moult phenotypes across individuals between observed and simulated moult phenotypes. If moult is a non-random process, some moult phenotypes would be more repeated than expected by chance.

Phenotypic variation and moult signatures

We reviewed the existing literature for passerine wing-moult patterns. The term moult pattern is rather vague, and it has been applied to refer to features as diverse as duration (Newton & Rothery 2005), sequence of replacement (Edelstam 1984), intensity (Hall & Fransson 2000), timing (Marini & Durães 2001), or interaction of moult with other stages of the annual cycle (Giunchi *et al.* 2008). Here, we restricted the definition of moult pattern to 'classes' of observed wing-moult phenotypes (e.g. Pyle 1997b, Pinilla 2001). Then, we searched the term moult pattern thus defined in the specialised literature and classified the wing-moult cards in our dataset according to the currently proposed moult patterns we found.

Determination of moult homologies is an unsettled issue, with basic questions such as number of annual episodes undergone by a species still under debate (e.g. Howell *et al.* 2003, Piersma 2004, Thompson 2004, Willoughby 2004). We used two working criteria to define our moult episodes: 1) preformative moult as the first moult episode during which the juvenile plumage is replaced (e.g. in the case of non-migratory *Acrocephalus* warblers, the preformative moult is complete, whereas it is partial for migratory species of the genus); 2) prealternate moult as the main moult episode during the non-breeding period (e.g. many species in Laniidae and Phylloscopidae show two non-breeding moult episodes, the prealternate moult is the more extensive of the two episodes).

For each species and moult episode (preformative and prealternate), we calculated the proportion of moult phenotypes classified in each moult pattern (i.e. moult signatures). Then, we used hierarchical clustering with Bray-Curtis distances to group species with similar moult signatures (Fig. S2). We applied the complete linkage method because it tends to maximize dissimilarities between clusters and yield more balanced clusters (James *et al.* 2013). Given the lower abundance of prealternate moult cards in our dataset, we only included species with at least 19 moult cards for the preformative moult and at least 10 moult cards for the prealternate moult. Some species may moult more than once between the prebasic moult and before the onset of the breeding season. In these cases, we only included moult phenotypes from the most extensive of these moults as the prealternate moult (e.g. the late winter moult of Parulidae or the late autumn moult of Acrocephalidae; Salewski *et al.* 2004, Gualllar *et al.* 2009).

To test for the phylogenetic signal of moult signatures, we downloaded 1000 trees for each set of bird species from birdtree.org (Jetz *et al.* 2012). Then, we derived majority rule consensus trees computing mean length branches using phytools (Revell 2012). From these, we estimated phylogenetic signals for moult signatures within each moult episode. Since this variable is categorical, we could not use Pagel's lambda or other methods based on continuous variables. Instead, we adopted the permutation approach proposed by Maddison and Slatkin (1991) (R code available at https://github.com/juliema/publications/tree/master/BrueeliaMS, Bush *et al.* 2016; R Core Team 2017). Specifically, we randomised 999 times the tree tips and compared the scores for each randomisation with the empirical score. Statistical significance indicates both phylogenetic conservation and deviation from randomness. Since p-values slightly vary among permutation tests, we averaged p-values from 10 runs.

RESULTS

Moult phenotypes

We gathered a dataset of 5456 finished moult cards (Guallar & Jovani 2019), discarding 83 moult cards either because of null extent or because they were assigned to an anomalous pattern (i.e. those that could not be assigned to any of the nine moult patterns defined in Table 1; Table S2). The final dataset used in the analyses consisted of 5373 moult cards from 440 passerine species (285 Holarctic and 155 Neotropical), of which 2297 came from unpublished sources (Table S1). 4085 moult cards were preformative, 1141 prealternate, and 147 belonged to other moult episodes.

Moult phenotypes covered the whole moult extent range (i.e. from 1 to 51). 20.5% of the (unique) moult phenotypes occurred at least twice in the dataset, contrasting with only 0.6% of the simulated ones (Chi square test $\chi^2 = 672.1$, $P < 0.0001$; Figs. S3 and S4). In terms of individual moult phenotypes, 73.9% were repeated by at least another individual, but this only occurred in 1.5% of the randomly simulated moult phenotypes (Chi square test $\chi^2 = 4081.0$, $P < 0.0001$; Fig. S3).

Phenotypic variation and moult signatures

We retrieved 14 potential moult patterns from the literature, of which we only retained nine (Fig. 1, Table 1, Table S3). Note that the complete moult pattern includes arrested and suspended moults (i.e. birds that stopped a normal complete moult; Streseman & Streseman 1966, Norman 1991). Thus, under this definition, the complete moult pattern also comprises partial moult phenotypes. Interestingly, 99.1% of the moult phenotypes in our dataset were unequivocally classified using Table 1. Only 48 moult phenotypes (comprising 27 species) could not be classified and might either belong to minority yet undescribed moult patterns or be simply considered as anomalies (Table S2).

Moult signatures strongly differed between moult episodes (G test $G_8 = 1889.7$, $P < 0.001$, Fig. 2). The preformative moult was dominated by the general pattern, whereas the prealternate episode was dominated by the complete pattern, with the rest of patterns more evenly distributed. Species strongly differed in their moult signatures both for the preformative and the prealternate moults (Fig. 3, Fig. S2). Moult signatures were phylogenetically conserved for the preformative moult ($P < 0.001$), and more independent from phylogeny for the prealternate moult ($P = 0.158$, Fig. 3, Fig. S5).

DISCUSSION

Moult phenotypes

We have shown that the identity of replaced feathers is far from random. In fact, more than 70% of moult phenotypes are repeated at least twice in the dataset, compared to the 1.5% expected by chance (Fig. S3b). In other words, individuals often share exactly the same combination of replaced feathers, which is extremely unlikely by chance alone. Moreover, most of these repeated moult phenotypes were shared by individuals of different species and families (Fig. S2b). Therefore, passerine moult is largely a non-random process, strongly suggesting that moult is governed by some underlying rules shared across the whole order (Jenni & Winkler 1994, Kiat *et al.* 2019). These rules could be based on inherent ranks of feather-moult, energy investment or plumage exposure, for example.

Phenotypic variation and moult signatures

The preformative moult of fledglings showed lower moult pattern variation than the prealternate moult of older birds during the non-breeding season (Fig.2).

Table 1. Summary of published passerine wing-feather moult patterns. Traditional nomenclature based on moult extent refers to these patterns as complete and partial moults (from limited to extensive).

Pattern	Description	References
Abridged I	Complete moult aborted within secondaries: 1-6 secondaries retained. Ex: Prebasic moult of Blue Bunting *Cyanocompsa parellina*.	Mead & Watmough (1976), Norman (1991)
Abridged II	Complete moult in which primary coverts are retained. Ex: Preformative moult of Graceful Prinia *Prinia gracilis*.	Pyle (1998), Kiat & Izhaki (2017)
Complete	Full feather replacement following a highly conserved moult sequence in passerines: start at primary 1, replacement of primaries accompanied by respective primary coverts. It can be halted at any point and resumed later on (suspension) or not (arrest). Ex: Preformative moult of House Sparrow *Passer domesticus*.	Zeidler (1966)
Eccentric	Retention of a variable number of (largely inner) primaries and (largely outer) secondaries, and most to all primary coverts. Ex: Preformative moult of *Passerina* buntings.	Winkler & Jenni (1987), Pyle (1998)
General	Replacement of secondary (i.e. lesser, median and greater) coverts. Tertials are replaced only if secondary coverts are moulted. There is a prioritization from leading to trailing edge of wing: filling of an entire feather tract before proceeding with the next. Ex: Preformative moult of *Turdus* thrushes.	Pyle (1997b), Guallar *et al.* (2014)
Proximal	Same as the general pattern but tertials (and adjacent inner secondaries) can be replaced with retention of outer secondary coverts. From leading to trailing edge of the wing: prioritization of feathers closer to the body before finishing replacement of anterior tracts. Ex: Preformative moult of *Henicorhina* wood-wrens.	Pyle (1997b), Guallar *et al.* (2014)
Inverted	Replacement of inner secondaries and secondary coverts. Prioritization of feathers closer to the body from trailing to leading edge of the wing: tertials, secondaries and greater coverts over median and lesser coverts (the latter at low percentages). Ex: Prealternate moult of some trans-Saharan migrants (e.g. European Pied Flycatcher *Ficedula hypoleuca*), and of residents of arid habitats (e.g. *Peucaea* sparrows).	Jenni & Winkler (1994), Guallar *et al.* (2018)
Limited	Replacement of lesser and median coverts; might include the carpal covert. Prioritization of feathers from leading to trailing edge of the wing and from inner to outer feathers. Ex: Preformative moult of dippers, nuthatches, treecreepers or kinglets.	Jenni & Winkler (1994), Pyle (1997a)
Reduced	Replacement of one to a few tertials and/or greater coverts. Strongly asymmetrical moults are considered accidental. Ex: 'winter' moult of some *Myiarchus* flycatchers, presupplemental ('spring') moult of Melodious Warbler *Hippolais polyglotta*.	Pinilla (2001), Guallar *et al.* (2018)

Figure 1. Frequency of feather replacement by moult pattern. Definitions of moult patterns can be found in Table 1.

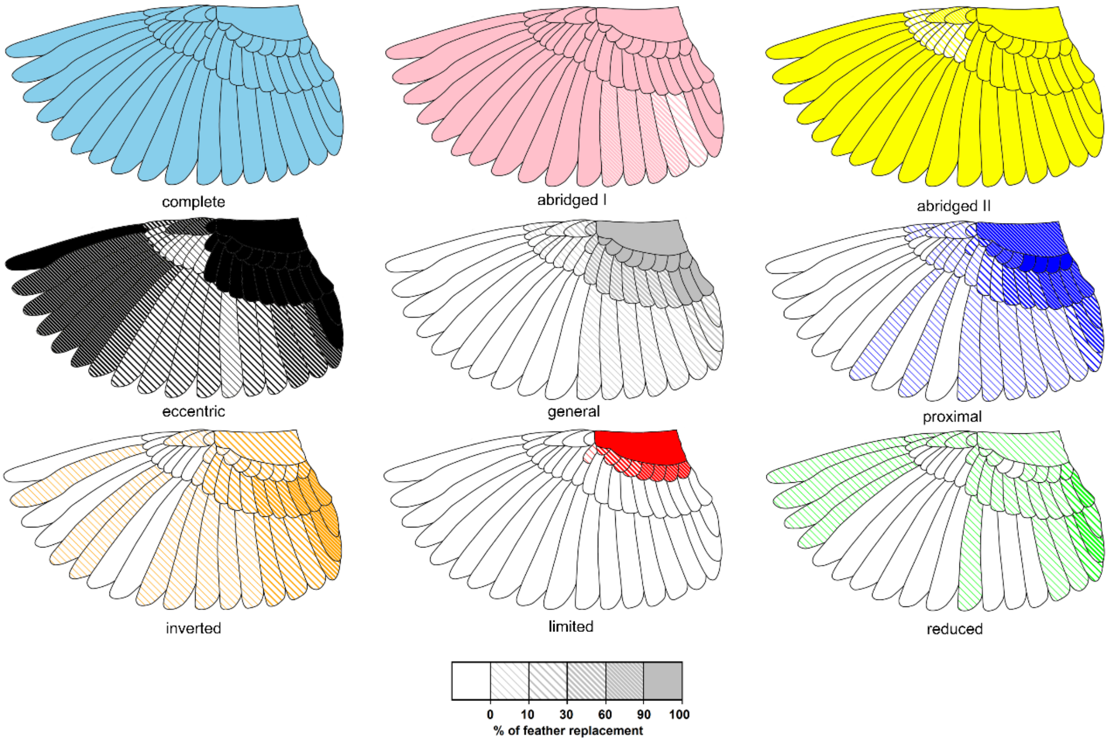


Figure 2. Frequency of moult patterns (Table 1) in the preformative and the prealternate episodes, calculated as the mean percentage of moult cards per species and pattern. Bar colours follow Fig. 1.

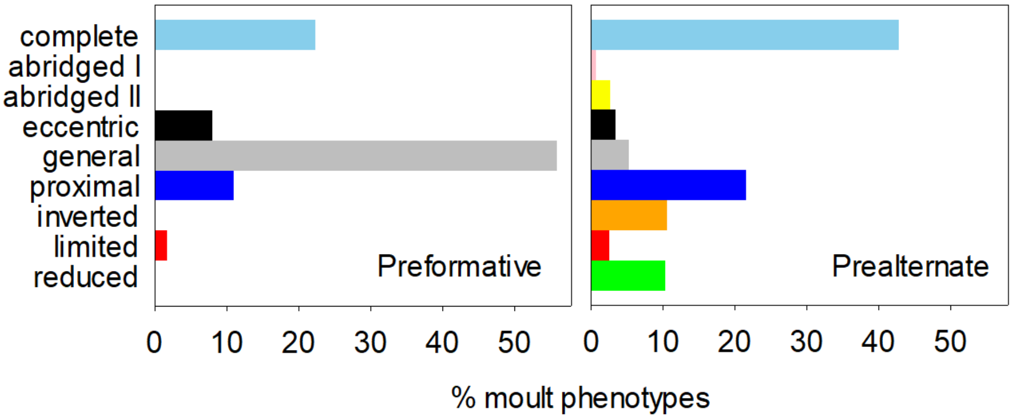
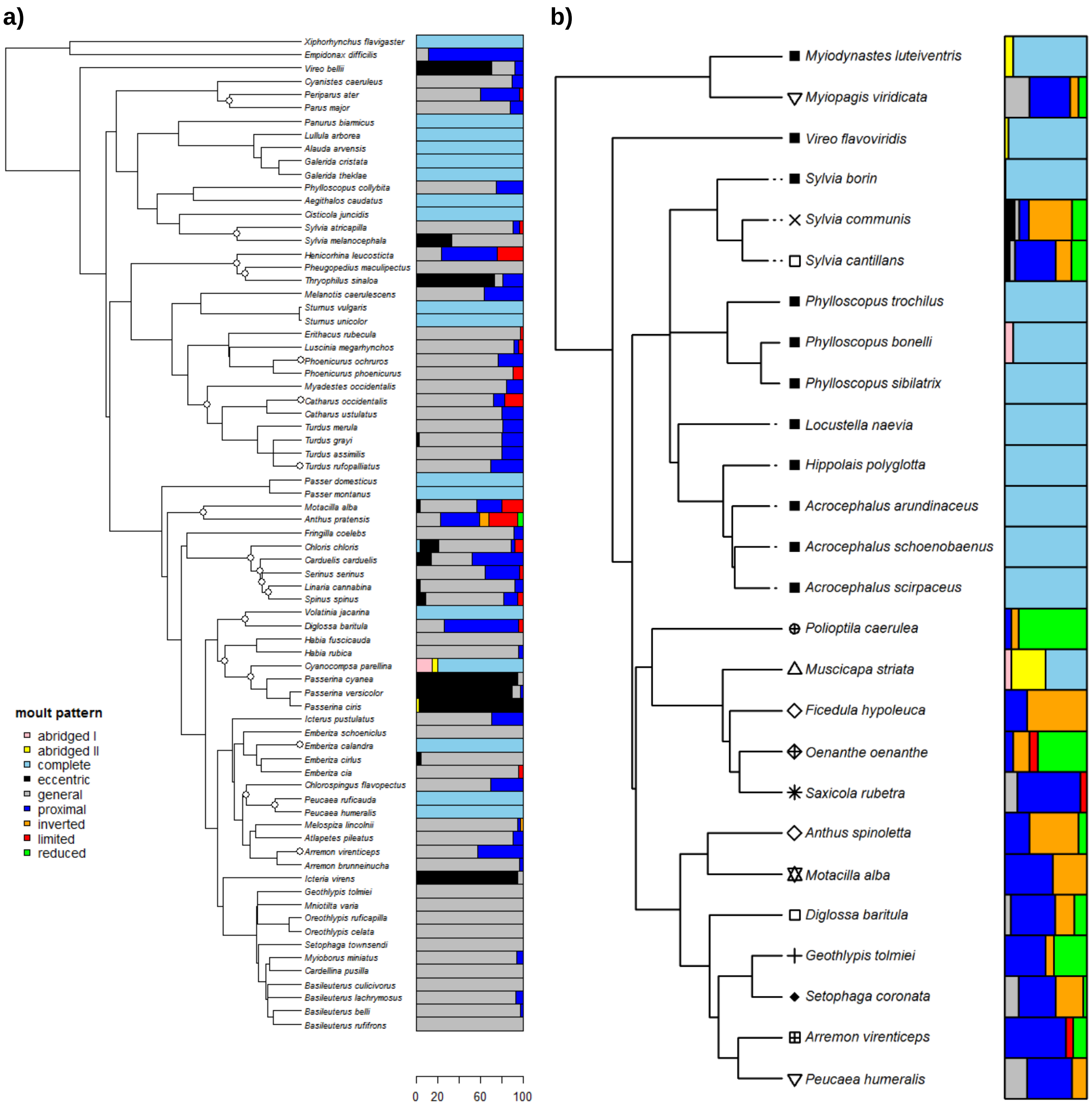


Figure 3. Phylogenetic trees of moult signatures: Barplots show the proportion of moult cards following each moult pattern defined in Table 1. Symbols on the branch tips indicate group membership obtained through cluster analysis of similarity among moult signatures: 15 groups for the preformative moult and 13 for the prealternate moult (Fig. S2). (a) Preformative moult (n = 76 species, 24 families). (b) Prealternate moult (n = 26 species, 12 families). Bray-Curtis distances among species' pattern signatures were 0.57 and 0.67, respectively. Notice the homogenous pattern signatures within Phylloscopidae and Acrocephalidae. Colour of moult patterns follows Fig. 1.



This suggests that plumage requirements of young passerines are less diverse between species than the demands affecting the prealternate moult. The preformative moult of fledglings showed lower moult pattern variation than the prealternate moult of older birds during the non-breeding season (Fig. 2). This suggests that plumage requirements of young passerines are less diverse between species than the demands affecting the prealternate moult. A possible explanation is that the prealternate moult associates with plumage signalling functions in sexual contexts, as evidenced for the higher prevalence of prealternate moults in sexually dimorphic passerines (Omland & Lanyon 2000). More generally, the larger pattern variation in the prealternate moult might arise to tackle with more diverse plumage functions (dominance status or sexual attractiveness) and because these functions are highly species-specific (Andersson 1983). For instance, feather tracts involved in sexual signalling may vary among species, e.g. greater coverts in Eurasian Siskin *Spinus spinus* (Senar *et al.* 2005), greater coverts and tertials in European Pied Flycatcher *Ficedula hypoleuca* (Heij *et al.* 2011; Fig. S1). It is worth noting, the strong homogeneity and low variation in the prealternate moult signatures of Phylloscopidae and Acrocephalidae, suggesting that signalling is not important in these two families (Fig. 3). Interestingly, the 11 species with lowest prealternate moult signature variation are sexually monochromatic (filled squares, Figs. 3 & S2). These results suggest that moult patterns allow passerines to adapt to changing seasonal requirements.

Although moult patterns are shared across species and between moult episodes, species differed strongly in their moult signatures. Nevertheless, closely related species tended to show more similar moult signatures. Our data suggest that this similarity is greater in the preformative than in the prealternate moult (Fig. 3). Accordingly, only the preformative moult showed a statistically significant phylogenetic signal. This is also consistentwith the larger moult pattern variation shown in the prealternate moult, which may be correlatedto the more labile evolution of sexuallydimorphic plumages (Omland & Lanyon 2000).

Phylogenetic conservation of preformative moult signatures phylogenetic signal. This is also consistent with the larger moult pattern variation shown by the prealternate moult, which may be correlated to the more labile evolution of sexually dimorphic plumages (Omland & Lanyon 2000). Phylogenetic conservation of preformative moult signatures further suggests that the underlying mechanisms of moult control have been shaped by natural selection, which have evolved in coordination with other key traits such as flight ability (Swaddle & Witter 1997, Pérez-Tris & Tellería 2001) and camouflage (Berggren *et al.* 2004).

ACKNOWLEDGEMENTS

We thank Javier Quesada of the Museum of Natural Sciences in Barcelona and Begoña Adrados of EBD-CSIC in Sevilla, for assistance and access to specimen collections. We are grateful to László Garamszegi, Alejandro González Voyer and Peter Pyle for their helpful comments. This manuscript has benefitted from the comments of Yosef Kiat and one anonymous reviewer. This is contribution no. 313 from Ottenby Bird Observatory. Javier Blasco Zumeta, British Trust for Ornithology, Carnegie Museum of Natural History's Powdermill Avian Research Center, Marcel Gahbauer of McGill Bird Observatory, Marc Illa, Stephen Menzie, Prof. David Norman of Merseyside Ringing Group, Peter Pyle and Margaret Rhode for permission to use moult data.

REFERENCES

Andersson M 1983. On the functions of conspicuous seasonal plumages in birds. *Anim. Behav.* 31: 1262–1264.

Berggren Å, Armstrong DP, Lewis RM 2004. Delayed plumage maturation increases overwinter survival in North Island robins. *Proc. R. Soc. Lond. B* 271: 2123–2130.

Bojarinova JG, Lehikoinen E, Eeva T 1999. Dependence of postjuvenile molt on hatching date, condition and sex in the Great Tit. *J. Avian Biol.* 30: 437–446.

Bush SE, Weckstein JD, Gustafsson DR, Allen J, DiBlasi E, Shreve SM, Boldt R, Skeen HR, Johnson KP 2016. Unlocking the black box of feather louse diversity: a molecular phylogeny of the hyper-diverse genus *Brueelia*. *Mol. Phyl. Evol.* 94: 737–751.

Buttemer WA, Bauer S, Emmenegger T, Dimitrov D, Hahn S 2019. Moult-related reduction of aerobic scope in passerine birds. *J. Comp. Physiol. B* 189.

Dawson A 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Phil. Trans. R. Soc. B* 363: 1621–1633.

de Heij ME, Gustafsson L, Brommer JE 2011. Experimental manipulation shows that the white wing patch in collared flycatchers is a male sexual ornament. *Ecol. Evol.* 1: 546–555.

de la Hera I, Pérez-Tris J, Tellería JL 2009. Migratory behaviour affects the trade-off between feather growth rate and feather quality. *Biol. J. Linnean Soc.* 97: 98–105.

de la Hera I, Pérez-Tris J, Tellería JL 2010. Relationships among timing of moult, moult duration and feather mass in long-distance migratory passerines. *J. Avian Biol.* 41: 609–614.

Edelstam C 1984. Patterns of moult in large birds of prey. *Ann. Zool. Fennici* 21: 271–276.

Figuerola J, Jovani R 2001. Ecological correlates in the evolution of moult strategies. *Evol. Ecol.* 15: 183–192.

Ginn HB, Melville DS 1983. *Moult in birds* (BTO guide). British Trust for Ornithology, Tring.

Giunchi D, Caccamo C, Pollonara E 2008. Pattern of wing moult and its relationship to breeding in the Eurasian Stone-curlew *Burhinus oedicnemus*. *Ardea* 96: 251–260.

Goldstein G, Flory KR, Browne BA, Majid S, Ichida JM, Burtt Jr EH 2008. Bacterial degradation of black and white feathers. *Auk* 121: 656–659.

Gosler AG 1994. Mass-change during moult in the Great Tit *Parus major*. *Bird Study* 41: 146–154.

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A 2009. *Paseriformes del Occidente de México: morfometría, datación y sexado*. Museu de Ciències Naturals de Barcelona, Barcelona.

Guallar S, Figuerola J 2016. Factors influencing the evolution of moult in the nonbreeding season: insights from the family Motacillidae. *Biol. J. Linn. Soc.* 118: 774–785.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2014. Moult topography and its application to the study of partial wing-moult in two neotropical wrens. *Ibis* 156: 311–320.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2018. Preformative wing molt in 23 Neotropical resident passerine species. *Orn. Neotropical* 29: S3–S10.

Guallar S, Jovani R 2020. Dataset. http://doi.org/[10.6084/m9.figshare.9896516]

Hall KSS 2005. Do nine-primaried passerines have nine or ten primary feathers? The evolution of a concept. *J. Ornithol.* 146: 121–126.

Hall KSS, Fransson T 2000. Lesser Whitethroats under time constraint moult more rapidly and grow shorter wing feathers. *J. Avian Biol.* 31: 583–587.

Hemborg C, Sanz JJ, Lundberg A 2001. Effects of latitude on the trade-off between reproduction and moult: a long-term study with pied flycatcher. *Oecologia* 129: 206–212.

Howell SNG, Corben C, Pyle P, Rogers DI. 2003. The first basic problem: a review of molt and plumage homologies. *Condor* 105: 635–653.

Humphrey PS, Parkes KC 1959. An approach to the study of molt and plumages. *Auk* 76: 1–31.

James G, Witthen D, Hastie T, Tibshirani R 2013. *An Introduction to Statistical Learning with Applications in R*. Springer Science+Business Media, New York.

Jenni L, Winkler R 1994. *Moult and ageing of European passerines*. Academic Press, London.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO 2012. The global diversity of birds in space and time. *Nature* 491: 444–448.

Kiat Y, Izhaki U 2017. Non-moulted primary coverts correlate with rapid primary moulting. *J. Avian Biol.* 48: 380–386.

Kiat Y, Izhaki U, Sapir N 2019. The effects of long-distance migration on the evolution of moult strategies in Western-Palearctic passerines. *Biol. Rev.* 94: 700–720.

Lantz SM, Karubian J 2016. Male Red-backed Fairywrens appear to enhance a plumage-based signal via adventitious molt. *Auk* 133: 338–346.

Lennox FG, Rowlands, RJ 1969. Photochemical degradation of keratins. *Photochem. Photobiol.* 9: 359–367.

Lind J 2001. Escape flight in molting Tree Sparrows (*Passer montanus*). *Func. Ecol.* 15: 29–35.

Lindström A, Visser GH, Daan S 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Phys. Zool.* 66: 490–510.

Maddison,WP, Slatkin M 1991. Null models for the number of evolutionary steps in a character on a phylogenetic tree. *Evolution* 45: 1184–1197.

Marini MÂ, Durães . 2001. Annual patterns of molt and reproductive activity of passerines in South-Central Brazil. *Condor* 103: 767–775.

Mead CJ, Watmough BR 1976. Suspended moult of trans-Saharan migrants in Iberia. *Bird Study* 23: 187–196.

Middleton ALA 1986. Seasonal changes in plumage structure and body composition of the American Goldfinch *Carduelis tristis*. *Can. Field Nat.* 100: 545–549.

Minias P, Iciek T 2013. Extent and symmetry of post-juvenile moult as predictors of future performance in Greenfinch *Carduelis chloris*. *J. Ornith.* 154: 465–468.

Murphy ME 1996. Energetics and nutrition in molt. In Carey, C. (ed) *Avian Energetics and Nutritional Ecology*: 158–198. New York: Chapman and Hall.

Newton I, Rothery P 2005. The timing, duration and pattern of moult and its relationship to breeding in a population of the European Greenfinch *Carduelis chloris*. *Ibis* 147: 667–679.

Norman SC 1991. Suspended split-moult systems – An alternative explanation for some Palearctic migrants. *Ring. Migr.* 12: 135–138.

Omland KE, Lanyon SM 2000. Reconstructing plumage evolution in orioles (*Icterus*): repeated convergence and reversal patterns. *Evolution* 54: 2119–2133.

Pérez-Tris J, Tellería JL 2001. Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. *J. Avian Biol.* 32: 207–213.

Piersma T 2004. Understanding evolution of plumages and other cyclic avian life-history phenomena: role for an improved molt terminology. *Condor* 106: 196–198.

Pinilla J 2001. How does the extent of a partial moult vary? Some data for Melodious Warbler *Hippolais polyglotta* in central Iberia. *Ardeola* 48: 81–84.

Podlaszczuk O, Kamiński M, Włodarczy R, Kaczmarek K, Janiszewski T, Minias P 2016. Plumage quality mediates a life-history trade-off in a migratory bird. *Frontiers Zool.* 13: 47.

Pyle P 1997a. *Identification guide to North American birds. Part I: Columbidae to Ploceidae*. Slate Creek Press, Bolinas, CA.

Pyle P 1997b. Molt limits in North American passerines. *North Amer. Bird Bander* 22: 49–89.

Pyle P 1998. Eccentric first-year molt patterns in certain Tyrannid flycatchers. *Western Birds* 29: 29–35.

Pyle P, Tranquillo K, Kayano K, Arcilla N 2016. Molt patterns, age criteria, and molt-breeding dynamics in American Samoan landbirds. *Wilson J. Orn.* 128: 56–69.

R Core Team 2017. *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing. https://www.R-project.org/

Revell L 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3: 217–223.

Rohwer S, Ricklefs RE, Rohwer VG, Copple MM 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biol.* 7: e1000132.

Senar JC, Domènech J, Camerino M 2005. Female siskins choose mates by the size of the yellow wing stripe. *Behav. Ecol. Sociobiol.* 57: 465–469.

Shirihai H, Helbig A, Gargallo G 2001. Sylvia *warblers*. Christopher Helm, London.

Silveira MB, Marini MÂ 2012. Timing, duration, and intensity of molt in birds of a neotropical savanna in Brazil. *Condor* 114: 435–448.

Stresemann, E. & Stresemann, V. 1966. Die Mauser der Vögel. *J. Ornithol.* 107: 1–337.

Surmacki A, Liu M, Mercadante A, Hill GE 2011. Effect of feather abrasion on structural coloration in male eastern bluebirds *Sialia sialis*. *J. Avian Biol*. 42: 514–521.

Svensson L 1992. *Identification guide to European passerines*, 4th ed. L. Svensson, Stockholm.

Swaddle JP, Witter MS 1997. The effects of molt on the flight performance, body mass, and behaviour of European Starlings (*Sturnus vulgaris*): an experimental approach. *Can. J. Zool.* 75: 1135–1146.

Thompson CW 2004. Determining evolutionary homologies of molts and plumages: a commentary on Howell et al. (2003). *Condor* 106: 199–206.

Vas Z, Csörgő T, Møller AP, Rózsa L 2008. The feather holes on the Barn Swallow *Hirundo rustica* and other small passerines are probably caused by *Brueelia* spp. lice. *J. Parasitol.* 94: 1438–1440.

Williamson K 1972. Reversal of normal moult sequence in the Spotted Flycatcher. *British Birds* 65: 50–51.

Willoughby EJ 2004. Molt and plumage terminology of Howell et al. (2003) still may not reflect homologies. *Condor* 106: 191–196.

Winkler R, Jenni L 1987. Weitere Indizien für 'sektorale' Handschwingenmauser bei jungen Singvögeln. *J. Ornithol.* 128: 243–246.

Zeidler K 1966. Untersuchungen über Flügelbefiederung und Mauser des Haussperling *Passer domesticus*. *J. Ornithol.* 107: 113–15

SUPPLEMENTARY INFORMATION

Table S1. Source of the 5456 moult cards used in this study. Unpublished data were gathered by the first author; among these, field data were gathered in Mexico and Catalonia between 2004 and 2018.

Published data	**n**	**# Species**
Winkler and Jenni (1987)	9	7
Jenni and Winkler (1994)	331	58
Gargallo (1995)	5	4
Froehlich (2003)	18	13
Guallar *et al.* (2009)	1431	75
Pyle & Kayhart (2010)	1	1
Wolfe & Pyle (2011)	1	1
de la Hera *et al.* (2013)	1	1
Guallar *et al.* (2014)	41	2
Kiat & Izhaki (2015)	1	1
Menzie *et al.* (2015)	1	1
Guallar *et al.* (2016)	362	10
Guallar *et al.* (2018)	181	23
Kiat & Napir (2017)	1	1
Johnson & Wolfe (2018)	61	54
Aegithalos	4	4
Pablo Barrena's blog	1	1
AnillaReal	4	2
Birdguides (British Trust for Ornithology)	7	5
Carnegie Museum of Natural History	43	25
Chester River Field Research	1	1
Daniele Occato's blog	2	1
Grupo de Anillamiento Científico EPOPS	9	8
IBRCE	2	2
Identification Atlas of the Birds of Aragon	72	25
Marc Illa's blog	76	35
Margaret Rhode's blog	4	3
McGill Bird Observatory	55	25
Memorias de Overlord	2	1
Mersey Ringing Group	36	12
Petit Manan Point, blog	3	3
Ringers' DigiGuide	182	36
Slater Museum of Natural History	172	99
Stephen Menzie's blog	26	20
Vancouver Avian Research Center	13	12

Table S1 (cont).

Unpublished data	**n**	**# Species**
EBD-CSIC collection, Sevilla (2015)	17	2
Museum of Natural Sciences, Barcelona (2015)	514	60
Authors' unpublished field data (2004-2018)	1766	133

Table S2. Examples of nine moult anomalies. Of the 118 detected cases, 36 showed at least two anomalies simultaneously, and seven showed three anomalies. Atypical eccentric moults are frequent in some species (e.g. 11 of our 35 preformative moult cards of Blue Mockingbirds *Melanotis caerulescens* and Greyish Saltator *Saltator coerulescens*). Anomalies C, D, E, and H were not classified within any of the moult patterns published in the literature and were not included in the analyses.

Anomaly	**Description**
A	Follicular failure in the prebasic moult of a Cinnamon-bellied Flowerpiercer *Diglossa baritula* (Las Joyas Scientific Station, Jalisco, Mexico, January 14 2009). Retention of one central primary covert in an otherwise complete moult. 37 cases.
B	Overinvestment in the preformative moult of a Dunnock *Prunella modularis* (Fig 174 in Jenni & Winkler 1994). The moult signature of the preformative moult of this species consists of the general and limited pattern (69% and 31% in our 13 moult cards, respectively). This bird underwent an exceptionally extensive moult which matches a general pattern with the addition of four primary coverts. Two cases detected.
C	Simultaneous abridged I and abridged II patterns in the preformative moult of an Olive Sparrow *Arremonops rufivirgatus* (Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico, May 11 2005). Only secondaries and primary coverts were retained. 18 cases.
D	Simultaneous eccentric and complete patterns in the prealternate moult of a Yellow Warbler *Dendroica petechia* (Braddock Bay Bird Observatory, New York, USA, May 27 2010). Unlike typical eccentric moults, some birds replace the innermost primaries (and corresponding primary coverts) in an arrested fashion. Five cases.
E	Simultaneous eccentric and proximal patterns in the preformative moult of a Painted Bunting *Passerina ciris* (Lower Ayuquila River, Jalisco, Mexico, May 6 2005). Unlike typical eccentric moults, some birds replace the innermost primaries. 20 cases.
F	Eccentric pattern with random replacement of primaries in the preformative moult of a Tawny Pipit *Anthus campestris* (Fig. 69 in Jenni & Winkler 1994). Unlike typical eccentric moults, some birds replace inner primaries instead of the outermost ones. 32 cases.
G	Eccentric pattern with random replacement of secondaries in the preformative moult of a Yellow-breasted Chat *Icteria virens* (Lower Ayuquila River, Jalisco, Mexico, June 6 2005). Unlike typical eccentric moults, some birds undergo an eccentric moult in which tertials and/or innermost secondaries are retained. 57 cases.
H	Arrested complete pattern with full replacement of secondaries in the preformative moult of an Asian Crimson-winged Finch *Rhodopechys sanguineus* (accompanying photo in Kiat & Sapir 2017, no date provided). Unlike typical arrested moults, this first-cycle male replaced all his secondaries when this tract was expected to show some retained feathers. Three cases.
I	Aberrant prebasic moult in Eurasian Nuthatch *Sitta europaea* (Cheshire, UK, February 24 2003). Eurasian Nuthatches usually undergo a limited preformative moult and a complete prebasic moult. Instead of a complete moult, this definitive female presented an atypical proximal pattern with replacement of outer greater coverts and retention of inner ones, and replacement of inner primary coverts. In subsequent recaptures showed a complete prebasic moult. One case.

Anomaly	**S9**	**S8**	**S7**	**S6**	**S5**	**S4**	**S3**	**S2**	**S1**	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**GC10**	**GC9**	**GC8**	**GC7**	**GC6**	**GC5**	**GC4**	**GC3**	**GC2**	**GC1**	**CC**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**GA**	**MA**	**LA**	**MC1**	**MC2**	**MC3**	**MC4**	**MC5**	**MC6**	**MC7**	**MC8**	**LC**
A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
B	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
C	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
D	1	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
E	1	1	1	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0.8
F	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	1	0.8
G	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
H	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
I	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1

Table S3. Justification of moult pattern rejections. We retrieved 14 potential moult patterns from the literature, of which we only retained nine. We lumped the incomplete, suspended, arrested, and block patterns to other patterns, and discarded the accidental one. n indicates number of cases in our dataset. Incomplete phenotypes are likely caused by physiological errors.

Pattern	**Description**	**Rationale**
Incomplete (n = 37) Cooper & Harrison (1997)	Random retention of usually just one feather mainly detected in the complete prebasic moult of adults	Lumped to the complete pattern because is likely the result of follicular failure
Suspended (n = 6) Newton (2008)	The complete moult sequence is halted and resumed later on, typically after migration	Lumped to the complete pattern because the final phenotype is complete regardless of the sequence being halted at initial or mid stages
Arrested (n = 4) Scheiman & Dunning (2004)	Like the suspended moult but never resumed	Indistinguishable from the first stage of a suspended moult
Block (n = 1401) Pyle (1997a)	Exclusive replacement of all secondary wing coverts	Considered a special case of the general moult pattern
Accidental (n = 0) Cramp & Perrins (1993)	Replacement of feathers lost by either accidental collision or aggression. Highly asymmetrical	Not regarded as true moult since it is not programmed and depends on exogenous events

Figure S1. Male European Pied Flycatcher *Ficedula hypoleuca* shortly after finishing prealternate moult. The forehead patch of this species correlates with individual fighting ability (Järvistö *et al.* 2013, Morales *et al.* 2014), and the white wing patch is a male sexual ornament (de Heij *et al* .2011). Notice that this bird fully renewed his body plumage, but only those wing feathers that form the white wing patch (5-6 inner median coverts, seven inner greater coverts and tertials). Photograph by Pete Walkden (Wales, spring 2012).

Figure S2. Cluster analysis used for estimating phylogenetic signal of moult signatures in two moult episodes. Red dash line: cutoff. (a) preformative moult. 76 species with n > 19, cutoff defines 15 groups. (b) prealternate moult. 26 species with n > 9, cutoff defines 13 groups.

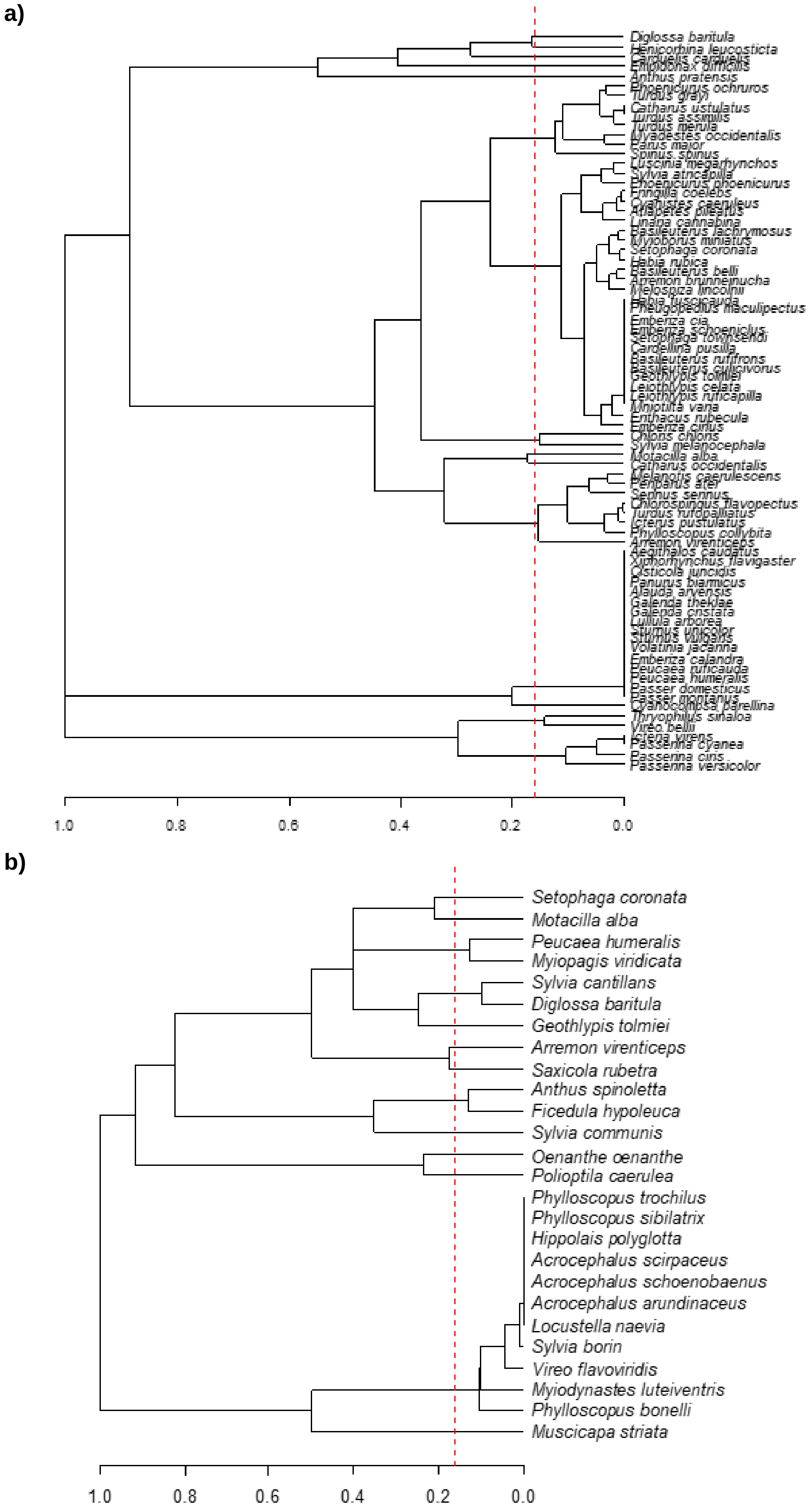


Figure S3. Distribution of repeated moult phenotypes in our empirical dataset and in a simulated dataset. Frequency of repetitions differed for moult phenotypes (upper panels) and individuals (lower panels). The new dataset replicated number of moult cards and extent but randomised identity of replaced feathers.

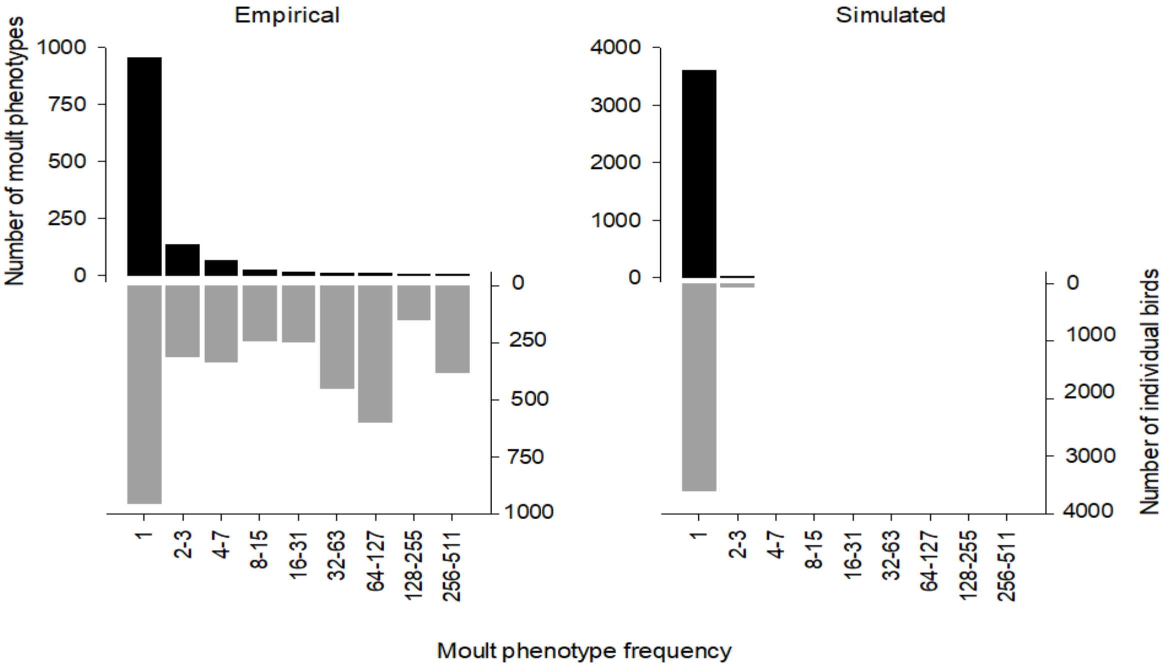


Figure S4. (a) Accumulation curve of unique moult phenotypes in our dataset (new phenotypes accumulate at approximately moult-cards$^{0.75}$). In red, polynomial fit. (b) frequency of repeated moult phenotypes in our dataset (1204). Only 12 % of these phenotypes were repeated more than twice (complete moult was repeated 1461 times in our dataset – indicated by arrow). Inset depicts number of species that share each repeated phenotype. Red point show 24 repeated phenotypes which were found only in one species. In our dataset, we only included moult cards of the prebasic episode when they departed from extent = 51. Certain degree of randomness might explain some of the moult phenotypes studied, as suggested by the fact that about 20% phenotypes are not repeated.

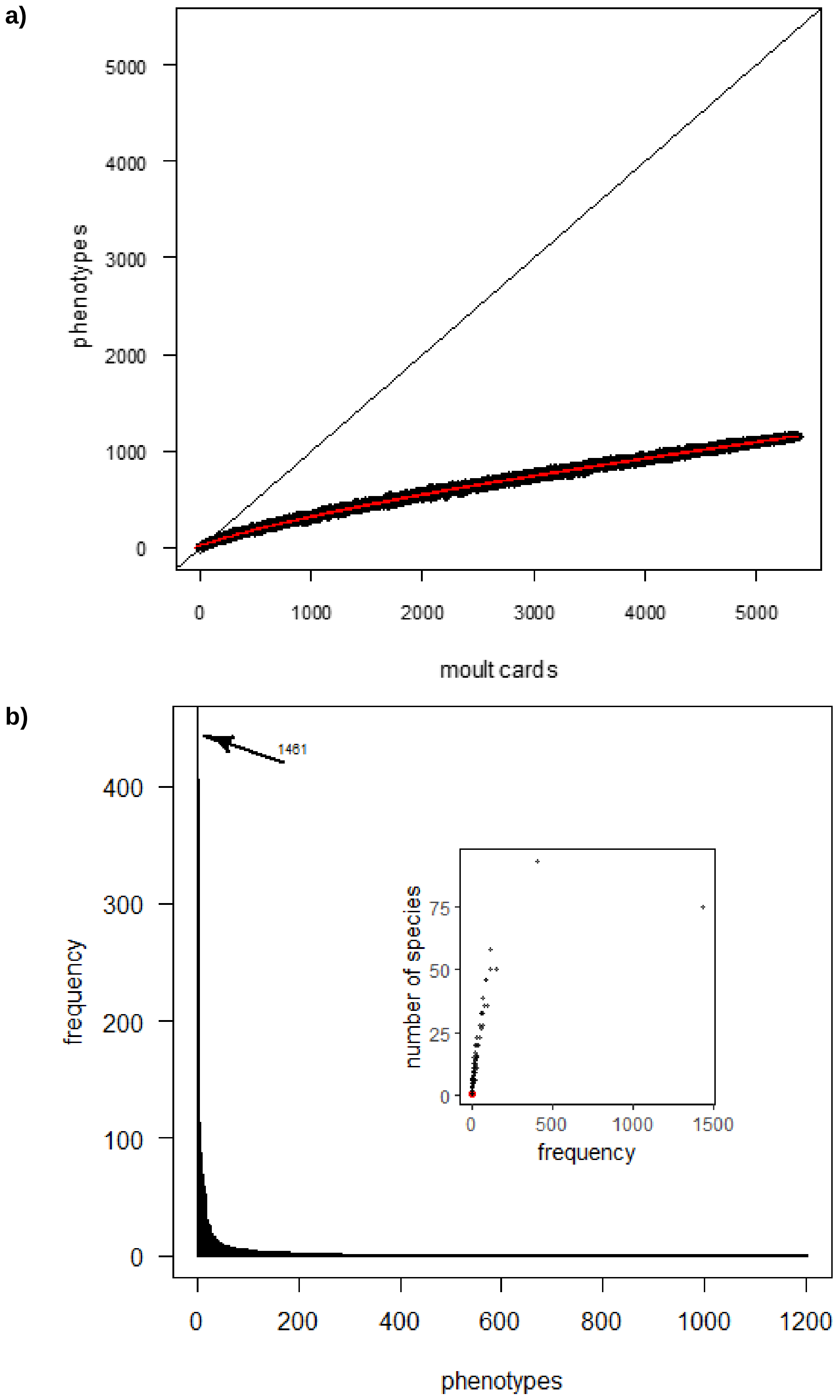
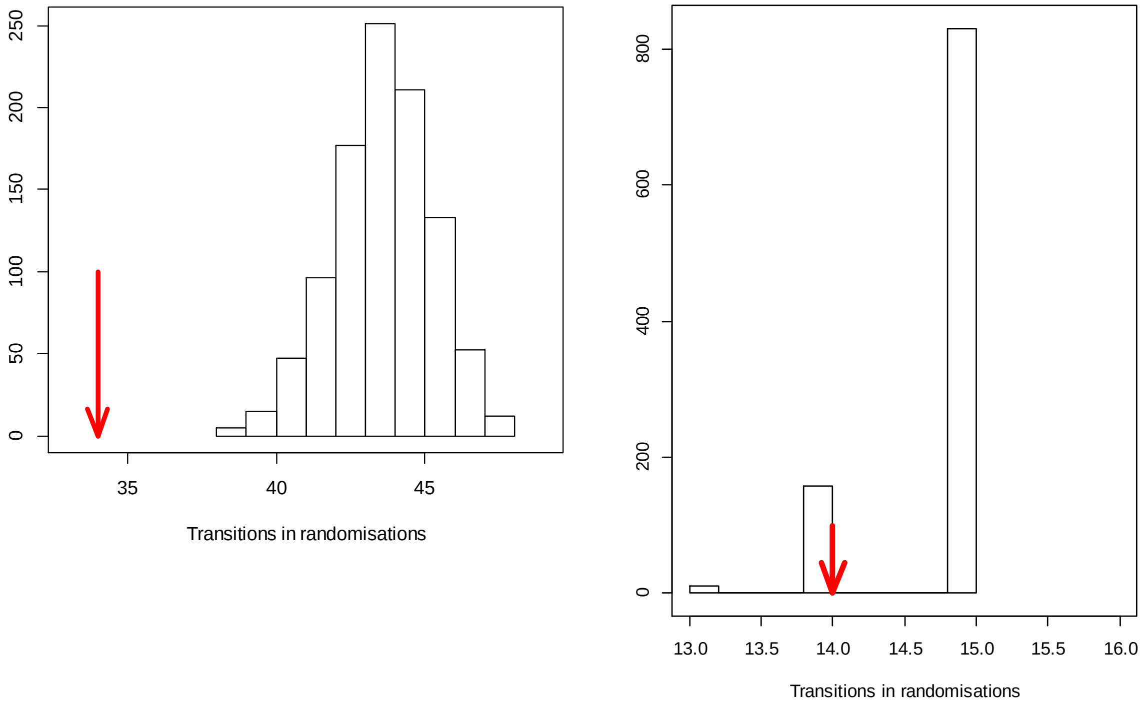


Figure S5. Frequency of evolutionary transitions for the moult signatures in two moult episodes obtained from Maddison & Slatkin tests as implemented in function phylo.signal.disc (available at https://github.com/juliema/ publications/tree/master /BrueeliaMS). Left: preformative moult. Right: prealternate moult. Red arrow indicates observed evolutionary transitions.



REFERENCES

Cooper JE, Harrison GJ 1997. Dermatology. In *Avian Medicine: Principles and Applications* (Ritchie BW, Harrison GJ, Harrison LR eds.). Lake Worth: Wingers Publishing.

Cramp S, Perrins CM eds. 1993. *The Birds of the Western Palearctic.* Volume. VII. Oxford University Press, Oxford.

de la Hera I, Reed TE, Pulido F, Visser ME 2013. Feather mass and winter moult extent are heritable but not associated with fitness-related traits in a long-distance migratory bird. *Evol. Ecol.* 27: 1199–1216.

Froehlich D 2003. *Ageing North American landbirds by molt limits and plumage criteria*. Slate Creek Press, Bolinas, CA.

Gargallo G 1995. Interrupted moult of some passerine birds in southern Europe. *Ring. Migr.* 16: 117–120.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2016. Molt strategies of ten Neotropical forest passerine species. *Wilson J. Orn.* 128: 543–555.

Järvistö PE, Laaksonen T, Calhim S 2013. Forehead patch size predicts the outcome of male-male competition in the Pied Flycatcher. *Ethology* 119: 662–670.

Johnson EI, Wolfe JD 2018. *Molt in Neotropical birds. Life history and aging criteria*. Studies in Avian Biology 51. CRC Press, Boca Raton, FL.

Kiat Y, Izhaki U 2015. Post juvenile moult in Graceful Prinia *Prinia gracilis*. *Ring. Migr.* 30: 7–11.

Kiat Y, Sapir N 2017. Age-dependent modulation of songbird summer feather molt by temporal and functional constraints. *Amer. Nat.* 189: 184–195.

Menzie S, Gil-Velasco M, Illa M 2015. First-year male Whinchat *Saxicola rubetra* with unusually extensive post-juvenile moult. *Rev. Catalana Orn.* 31: 23–27.

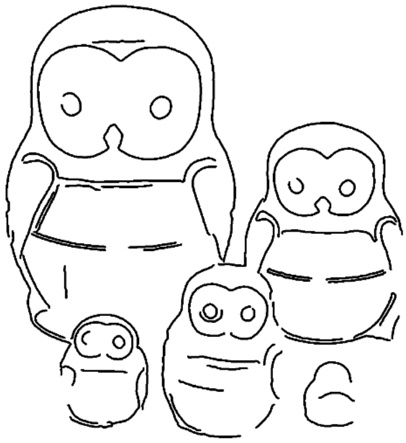
Morales J, Gordo O, Lobato E, Ippi S, Martínez de la Puente J, Tomás G, Merino S, Moreno JE 2014. Female-female competition is influenced by forehead patch expression in pied flycatcher females. *Behav. Ecol. Sociobiol.* 7: 1195–1204.

Newton I 2008. *The migration ecology of birds*. Academic Press, London.

Pyle P, Kayhart R 2010. Replacement of primaries during the prealternate molt of a Yellow Warbler. *North Amer. Bird Bander* 35: 178–181.

Scheiman DM, Dunning JB 2004. A case of arrested molt in the Bobolink. *North Amer. Bird Bander* 29: 105–108.

Wolfe J, Pyle P 2011. First evidence for eccentric prealternate molt in the Indigo Bunting: possible implications for adaptive molt strategies. *Western Birds* 42: 257–262.



Chapter 2

Moult nestedness and its imperfections: insights to unravel the nature of passerine wing-feather moult rules

Santi Guallar[1] & Roger Jovani[2]

1 Department de Vertebrats, Museu de Ciències Naturals de Barcelona, Barcelona

2 Department of Evolutionary Ecology, Estación Biológica de Doñana, CSIC, Spain.

Published in: Guallar S & Jovani R 2021 Moult nestedness and its imperfections: insights to unravel the nature of passerine wing-feather moult rules. *J. Avian Biol.*52: e02553.

ABSTRACT

Passerine moult shows two well-known although intriguing characteristics: i) a varying subset of wing feathers are retained during certain moult episodes, and ii) the identity of the replaced feathers is not random. However, the rules that underlie these moult features are largely unknown. Non-randomness could arise under time and energy constraints if feathers differed in their importance, such that they could be ordered following a hypothetical moult rank. This rule predicts a nested relationship among wing-feather moult phenotypes, where phenotypes of smaller extent would consist of subsets of the wing feathers replaced in phenotypes of larger extent. Here, we analysed a dataset of 3909 preformative and prealternate moult phenotypes from 434 Holarctic and Neotropical passerine species. We found that passerine wing-feather moult was nested (nodf = 84.31). However, systematic imperfections in the nestedness pattern led us to test whether the existence of different feather moult ranks may increase nestedness in homogeneous subsets of moult phenotypes. We tested this hypothesis between moult episodes and found that nestedness increased for the preformative moult (nodf = 90.99) and decreased for the prealternate moult (nodf = 67.28). We further analysed the adaptive meaning of different moult ranks associated with feather mass, feather exposure, and feather contribution to flight. Overall, these three feather traits explained 53.74% of the variation in the priority of wing-feather replacement, with exposure having a stronger explanatory power than the other two traits. Our findings provide a first model to interpret variation of wing-feather moult phenotypes in passerines, and outlines the relevance of season for passerine moult, suggesting a dynamic link between moult expression and plumage requirements.

INTRODUCTION

Bird plumage performs multiple functions thanks to evolutionary feather diversification and specialization. To maintain plumage functionality, feathers have to be moulted, but birds often do not perform a complete moult, leading to individual variation in moult phenotypes (i.e. different sets of moulted feathers in a given bird after a given moult episode). A recent study based on 5373 wing-moult phenotypes from 285 Holarctic and 155 Neotropical passerine species, showed that moult phenotypes were highly variable, but many were repeated much more often than expected by chance (Guallar & Jovani 2020a). This, along with the long known interspecific differences in the priority of wing-feather moult (Jenni & Winkler 1994), shows that birds do not moult feathers at random (formally tested in Guallar & Jovani 2020a). Moult phenotypes differed between the preformative moult of young birds (equivalent to the postjuvenile moult; Jenni & Winkler 1994), which replace their juvenile plumage soon after fledging (Howell *et al.* 2003), and the prealternate moult of older birds (equivalent to the prebreeding moult; Jenni & Winkler 1994), which takes place after the prebasic moult (equivalent to the postbreeding moult; Jenni & Winkler 1994) and before the onset of the breeding season (typically in the wintering grounds for migratory species; Humphrey & Parkes 1959). Moreover, closely related species showed similar frequencies of moult phenotypes within the preformative and the prealternate moult episodes (Guallar & Jovani 2020a), with a large percentage of the variation among species due to shared ancestry (Delhey *et al.* 2020). Altogether, this suggests a complex scenario created by the interplay between seasonal variation, the adaptive value of moult phenotypes, and the constraints imposed by evolutionary history. Despite the enormous variation of moult, moult phenotypes within and among species for each episode are highly predictable, claiming for the existence of both adaptive and evolutionarily constrained mechanisms of moult control. However, our understanding of the nature of both the rules governing the moult process and their physiological mechanisms is in its infancy.

One potential rule of moult control could consist of determining the identity of feathers to be moulted by the extent of moult, that is, some wing feathers would be replaced even in very restricted moults, while others would only be replaced in very extensive moults. This would be analogous to a to-do list in which tasks are carried out in strict descendant order of importance. Feathers to be replaced during a moult episode could be prioritised according to their cost to be produced, their exposure to abrasion and/or their functional contribution to flight. In any case, regardless of the factors that drive this prioritisation, a process based on this feather-moult priority principle would lead to a nested relationship among wing-feather moult phenotypes: phenotypes of smaller extent consisting of subsets of those feathers replaced in phenotypes of larger extent (Fig. 1).

Here, we first tested whether passerines share a unique feather-moult priority list. Nevertheless, current knowledge on wing-feather moult phenotypes suggests the potential existence of different ways of moulting. Thus, it has been proposed that wing-feather moult phenotypes reflect the diversification of plumage moult requirements among species and between preformative and prealternate moult episodes (Guallar & Jovani 2020a). The underlying mechanisms of moult control may vary between moult episodes to allow this diversification, ultimately producing different priority lists. Accordingly, we tested the hypothesis that moult episodes present different wing-feather moult ranks. This hypothesis predicts a decrease in overall nestedness when phenotypes from different moult episodes are pooled.

Given that we found a strong nestedness in our moult dataset, we further studied why some feathers had a higher moult priority than others (i.e. why some feathers are replaced during a given moult episode even when only some few feathers are replaced). Several factors may influence order among wing feathers in a moult priority list. We hypothesise that this order is the result of a trade-off between the costs and benefits associated with moulting each wing feather. To cast some light on the causes that influence the position of each wing feather in the moult priority list defined in our moult dataset, we investigated three feather traits that may potentially influence it:

1) Mass. The energy required to synthesize a feather is proportional to its mass Lindström *et al.* (1993). Therefore, the heavier is a feather the higher the cost to replace it, and hence (all else being equal) its probability of replacement should be lower.

2) Exposure. Wing feathers do not endure a uniform degradation, some are more exposed to mechanical abrasion and solar radiation than others are (e.g. secondaries are nearly hidden in the folded wing; Bergman 1982, Flinks & Salewski 2012). Assuming that more exposed feathers wear off faster, the more exposed the feather the higher the benefit to replace it, and

hence (all else being equal) its probability of replacement should be higher.

3) Contribution to flight. Passerines have wings with low aspect ratios adapted to flapping flight. Thrust and lift are provided by the remiges (particularly by the 10 primaries, which are longer than the six secondaries; Dvořák 2016), with a smaller contribution by three tertials and three alula feathers (Møller 1991, Lee *et al.* 2015). Coverts largely contribute to reduce drag, but also contribute to lift by creating camber (Shyy *et al.* 2013). Replacement of wing feathers imposes an aerodynamic loss along with an increase of predation risk during the period of active moult (Slagsvold & Dale 1996), which might be greater in unexperienced individuals (Martin *et al.* 2018). However, this is an ambivalent factor because fresh feathers would allow greater flight efficiency once moult is finished. Thus, feathers with larger contribution to flight would imply a higher replacement cost during the moulting period, but higher benefits afterwards, making difficult to predict the overall fitness outcome.

In summary, the goals of this study were threefold:

1) to test for the nested nature of passerine wing-feather moult phenotype variation,

2) to test whether passerine wing-feather moult phenotypes are the result of more than one moult rank of wing feathers after grouping by moult episode,

3) to investigate the role of wing-feather mass, exposure, and contribution to flight on moult priority rank across moult episodes.

MATERIALS AND METHODS

More detailed methods can be found in the (Appendix 1).

Data

Moult

We used 3909 moult cards from our recently published dataset (Guallar & Jovani 2020b). Of these, 3455 belonged to the preformative episode and 454 to the prealternate episode from 434 passerine species (279 Holarctic and 155 Neotropical). Moult cards, which are the formal procedure to record moult phenotypes, contained moult state (1 replaced, 0 retained) for each of the larger 50 upper wing feathers (8 median coverts, 10 greater coverts, 1 carpal covert, 9 primary coverts, 3 alula feathers, 3 tertials, 6 secondaries, 10 primaries; Appendix 2 Fig. A1). Lesser wing coverts were collectively scored 1 when more than 70% of these feathers were replaced and 0 otherwise. Thus, moult extent ranged from 1 to 51.

Mass

We weighted the feathers of one wing from 86 birds belonging to 43 Palearctic passerine species (range = 1-13, mean = 2.0 individuals per species). We calculated mean feather mass for each feather of every species, so that each species had the same weight on the final calculation. We averaged feather masses across species, and normalised values dividing by the mass of the heaviest feather.

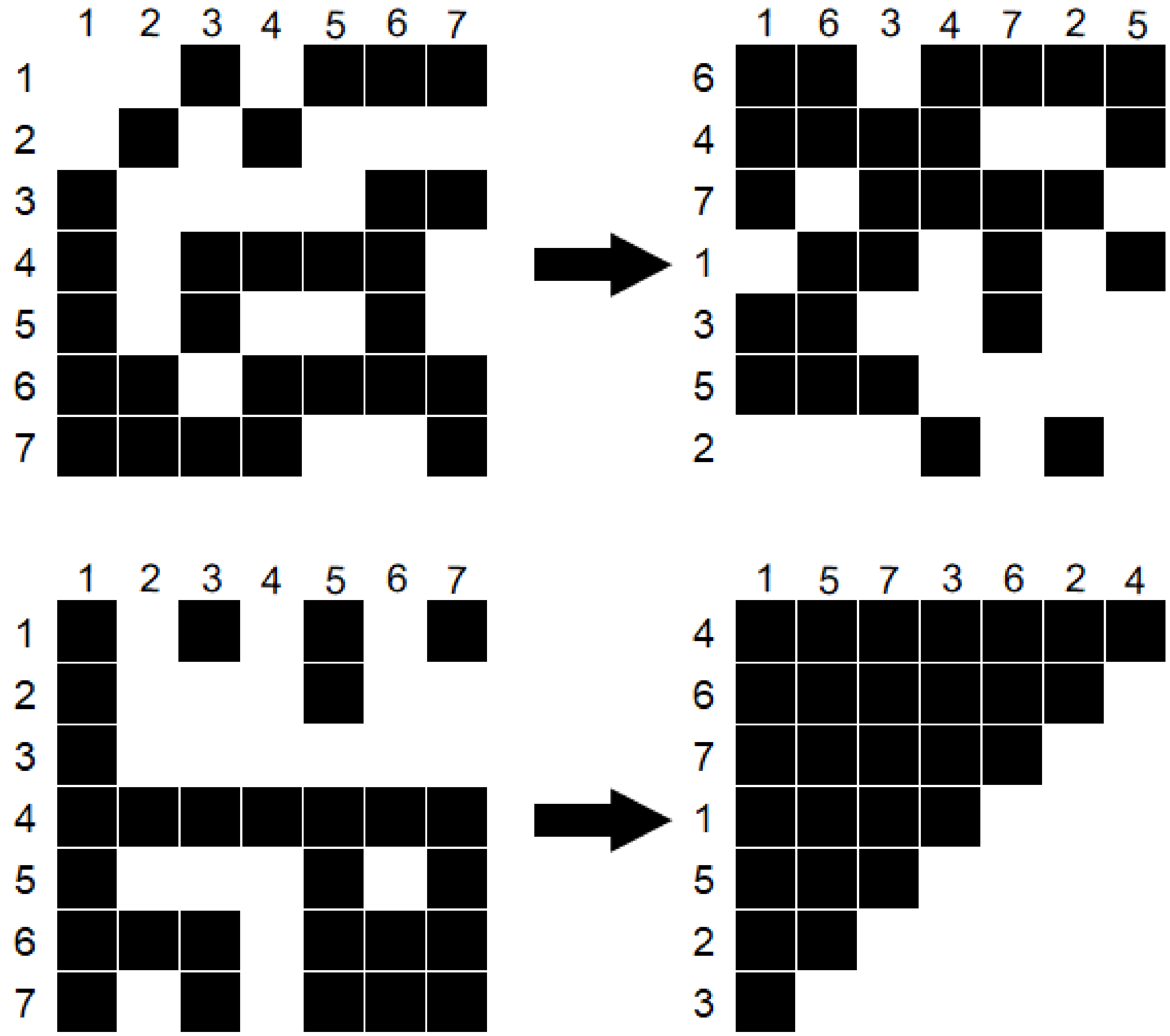
Exposure

Exposure deals with abrasion produced by direct friction with vegetation and by direct insolation. It also deals with signalling, since the most exposed feathers are the most visible ones. We used photographs of 62 live birds from 62 Palearctic species. We obtained the number of pixels visible in the picture for each of the upper-wing feathers using an image-processing program (<www.gimp.org>). Next, we normalised every feather by the most exposed one, and obtained a mean value per feather across species. This approach yields the exposure of each feather in relation to the whole folded wing, regardless of the feather portion that is actually exposed. To address this effect, we corrected the normalised feather-exposure values by their corresponding normalised masses obtained previously.

Contribution to flight

As far as we know, the individual wing-feather contribution to thrust, lift and drag has never been quantified. Here, we tentatively propose a hybrid index based on the correlation between length-corrected mass of primaries and bending stiffness, which is an important mechanical feather property to generate thrust (Dawson 2005, de la Hera *et al.* 2010a, 2020). We expand this approach to secondaries and tertials. Thus, we measured primary length from 196 ringed birds from 29 Palearctic species, and length of secondaries from 29 wings displayed in featherbase.com from the same 29 species. We averaged individual remex lengths per species and divided each of them by the corresponding average remex mass for that species. We normalised remex index by dividing each of them by the remex with the highest index. Then, we averaged feather values across species. We finally assigned constant values to alula feathers and wing coverts. These feathers are not implied in thrust generation, therefore their contribution to flight cannot be measured in the same scale than remiges. For this reason, we gave them arbitrary low values: 0.01 to wing coverts and

Figure 1. Left column: two hypothetical sets of seven moult cards, each of seven feathers. In both sets, 28 feathers were replaced (black squares). Every row corresponds to the moult card of one individual bird. Right column: same data presented in descending order of both replaced feathers (i.e. moult extent) and number of birds replacing each feather (i.e. frequency of replacement). The top set does not show nestedness, whereas the bottom set shows a perfect nestedness. Nestedness implies that birds moulting fewer feathers always replace a subset of the feathers moulted by birds showing larger moult extents. Note that moult cards in the bottom set could result from a shared strategy of moult whereby birds show a decreasing preference of moult for feathers 1, 5, 7, 3, 6, 2, and 4. Thus, feather 1 has the highest priority, being replaced when no other feather is replaced. On the other hand, feather 4 has the lowest priority, being only replaced if and only if all other feathers are also replaced.



lesser alula, 0.03 to medial alula, and 0.06 to greater alula.

Analyses

Nestedness

Frequency of moult phenotypes varied enormously, while some were extremely common throughout species and episodes (e.g. complete phenotype), others were very rare. This natural bias is exacerbated by the fact that some species were much more sampled than others. As a compromise to deal with both over and under-representation biases, we first removed 46 anomalous moult phenotypes that did not match any of the nine currently defined moult patterns (Guallar & Jovani 2020a), and then collapsed our dataset discarding all identical moult cards so that we only retained the unique ones. Thus prepared, the input matrix contained wing feathers in columns and 1082 unique moult cards in rows. We computed the nodf metric to estimate degree of nestedness (Almeida-Neto *et al.* 2008), as implemented in R package vegan (Oksanen *et al.* 2019, < www.r-project.org >). This metric quantifies the overlap of 1's (moulted feathers) from right to left columns and from bottom to top rows of the input matrix, and the marginal totals between all pairs of columns and all pairs of rows. It takes values from 0 to 100, 50 being the value of a pure random pattern, values below 50 indicating anti-nested patterns (e.g. checkerboard patterns; Almeida-Neto *et al.* 2008), and values close to 100 indicating perfect nestedness. We tested whether the nestedness of the input matrix and of each moult pattern deviated from randomness by randomising the identity of the feathers moulted by each individual but maintaining the number of moulted feathers (COL null model implemented in ANINHADO; Guimarães & Guimarães 2006).

Moult nestedness would indicate that birds replacing fewer feathers would moult a subset of the feathers replaced by birds moulting more feathers. From a feather viewpoint, this means that there is one (top priority) feather moulted even if no other feather is replaced, while other (low priority) feathers are only moulted if many other feathers (of higher priority) are also replaced. In other words, the most parsimonious rule behind moult nestedness would be the existence of a feather moult priority.

Feather traits

Using R package randomForest (Liaw & Wiener 2002), we fitted a random-forest model to test the overall and relative contribution of the three feather traits (mass, exposure, and contribution to flight) to explain the frequency of replacement of each wing feather across species, computed as the proportion of moult cards in which each feather was moulted.

In addition, to assess the relevance of feather traits to the wing feather moult priority, we sorted the columns of the input matrix (feathers) for the nestedness analysis in descendant order for each of these variables. As for the frequency of replacement, we ordered moult phenotypes (rows) in descendant order of moult extent. Thus, a feather trait that determined the priority of wing feather moult would show a nestedness value closer to the maximum possible. Note that the maximum nestedness expected when ordering columns according to one feather trait was equal to the nodf obtained sorting the input matrix by frequency of wing-feather replacement (columns) and extent (rows) in descendant order.

We also explored the variation of nestedness among the three influential feather traits between moult episodes to test the consistency of the main results. To carry out these analyses, we selected the 404 unique moult cards assigned to the prealternate moult and 708 assigned to the preformative moult. We discarded other moult episodes due to low sample sizes.

RESULTS

Priority of feather replacement showed a peak on the proximal secondary coverts (i.e. greater, median, and lesser coverts), decreasing towards distal secondary coverts and alula (Fig. 2a). On the other hand, remiges showed a centrifugal pattern: priority of replacement increased from the minimum found in the central remiges toward tertials, and primaries that form the wing tip. Primary coverts and central remiges had the lowest frequencies of feather replacement (Fig. 2a).

We found a high nestedness associated with the whole dataset of unique moult phenotypes (Fig. 3). Nestedness of the complete dataset (nodf = 84.31) deviated significantly from randomness (95% CI expected by random: nodf = 58.63 - 59.68), and was intermediate between the higher nestedness of the preformative moult episode and the lower nestedness of the prealternate (nodf_{PF} = 90.99, nodf_{PA} = 67.28; Fig. 3). Results were nearly identical when nestedness was calculated for the subset of 72 species with both preformative and prealternate moult cards (nodf_{PF} = 91.30, nodf_{PA} = 66.63). Nestedness calculated for each moult episode separately deviated from the expected nestedness according to their sample size, i.e. from random subsets with the same number of moult phenotypes taken from the complete dataset (Fig. 4).

Mass showed a gradual decrease from coverts towards the primaries that form the wing tip (Fig. 2b). Exposure peaked on the tertials and primaries that form the wing tip, with a secondary focus on the medial greater coverts (Fig. 2c). Contribution to flight showed a similar pattern to mass, with a somewhat more abrupt decrease (Fig. 2d). Overall, wing-feather mass, exposure, and contribution to flight explained together 53.74% of the observed variation in the priority of wing-feather replacement across species. Exposure showed a larger predictive strength to explain priority of wing-feather replacement than the other two traits (Table 1).

Nestedness analyses confirmed these results: we found similar nestedness values when we ordered wing feathers according to each of these three traits (nodf$_{mass}$ = 79.05, nodf$_{exposure}$ = 82.35, nodf$_{flight}$ = 73.90; Table 2). Interestingly, these nestedness values based on ranking feathers according to a single feather trait were not far from the maximum nestedness that could be obtained with this dataset, i.e. after ordering feathers according to their frequency of replacement (nodf = 84.31; Fig. 3). Similar results were found when repeating these analyses by moult episode (Table 2), with the preformative moult showing consistently greater nestedness values than the prealternate moult (Fig. 4).

Figure 2. Predicted probabilities of replacement of each wing feather according to four factors. a) Priority of wing feather replacement for 1082 unique passerine moult cards. b) Priority of wing feather replacement based on the normalised mass obtained from 86 birds (43 species). c) Priority of wing feather replacement based on the normalised wing feather exposure obtained from 62 birds (62 species). d) Priority of wing feather replacement based on the normalised wing feather contribution to flight obtained from 196 birds (29 species); here, we considered that priority of replacement was proportional to the cost during the moulting period not to the benefits gained after this period. Percentage shades vary from white (0%) to black (100%). See Materials and methods for details.

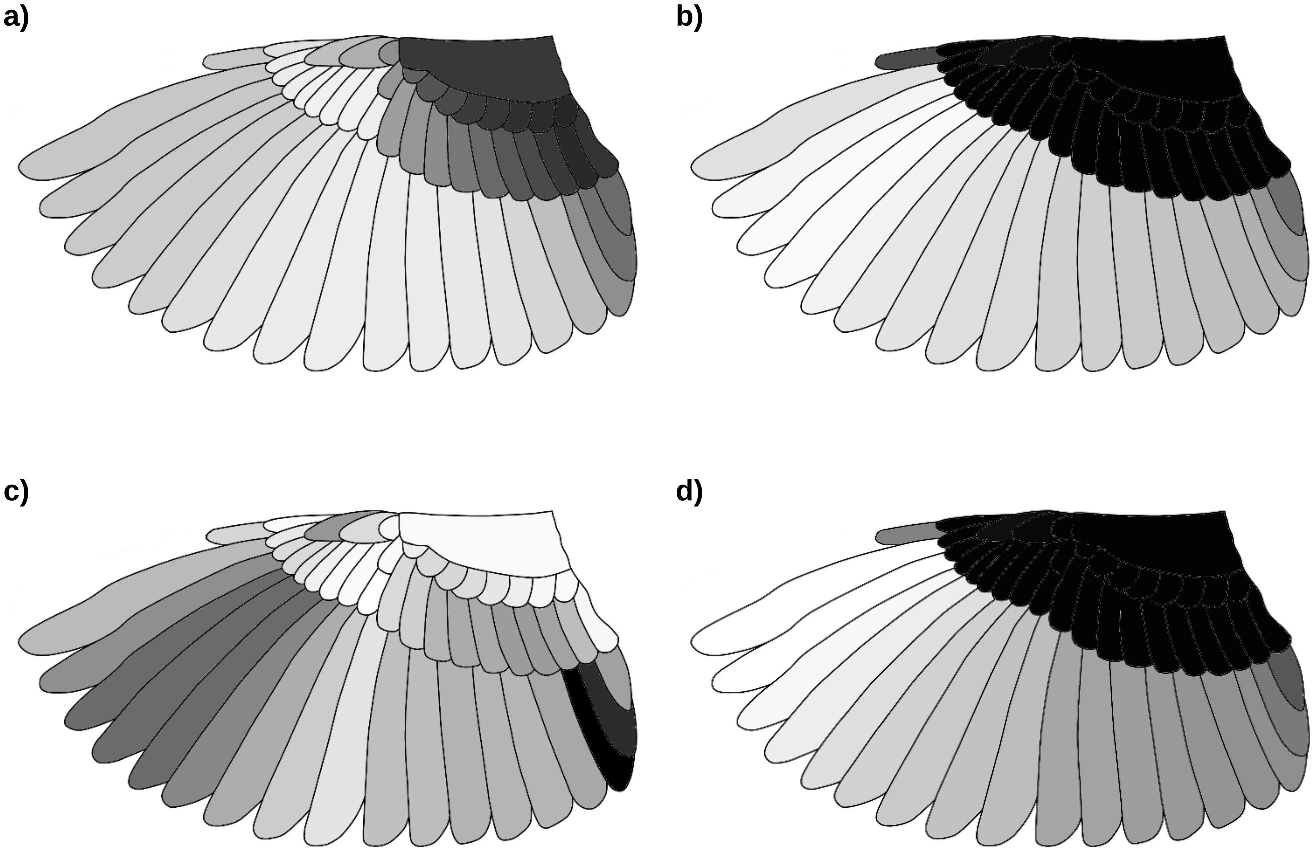


Figure 3. Nestedness plots for the overall dataset and for the two moult episodes separately. Unique wing-moult phenotypes are shown in rows and feathers in columns. Each dash indicates the replacement of a given feather. The matrix is ordered to maximise nestedness: phenotypes are ordered by moult extent and feathers by frequency of replacement across moult phenotypes. For illustrative purposes, feather moult ranks (i.e. feather identity on the x-axis of each panel) are shown on the bottom. Notice that total sample size is smaller than the sum of sample sizes per episode because some unique wing-moult phenotypes are shared by both episodes.

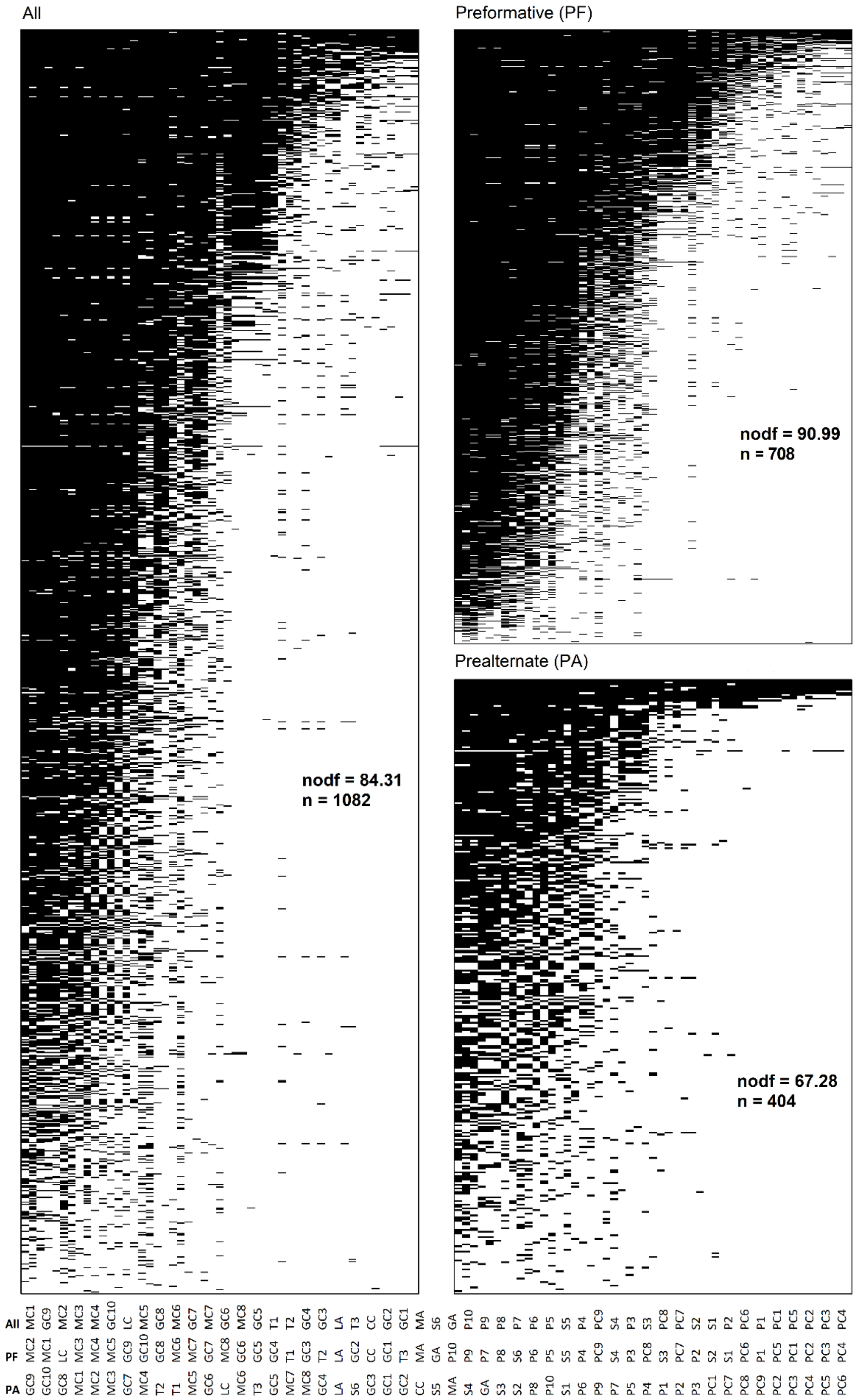


Figure 4. Variation of the expected nestedness for unique moult phenotypes. Blue lines show the bootstrapped mean nestedness obtained from random resamples (i.e. extraction of different number of random rows from Fig. 3); dark grey areas show the 95% bootstrapped interval of the mean; light grey areas show 95% bootstrapped interval of 500 random resamples. Notice that uncertainty on the measure of prealternate nestedness was higher than uncertainty of preformative nestedness. Interestingly, mean nestedness decreased with increasing number of moult phenotypes. This effect is very slight in the preformative moult (peak nodf = 92.10, total nodf = 90.99), but more apparent in the prealternate moult (peak nodf= 77.38, total nodf= 67.28). Mean and bootstrapped intervals estimated using the R library bayesboot (Bååth 2016).

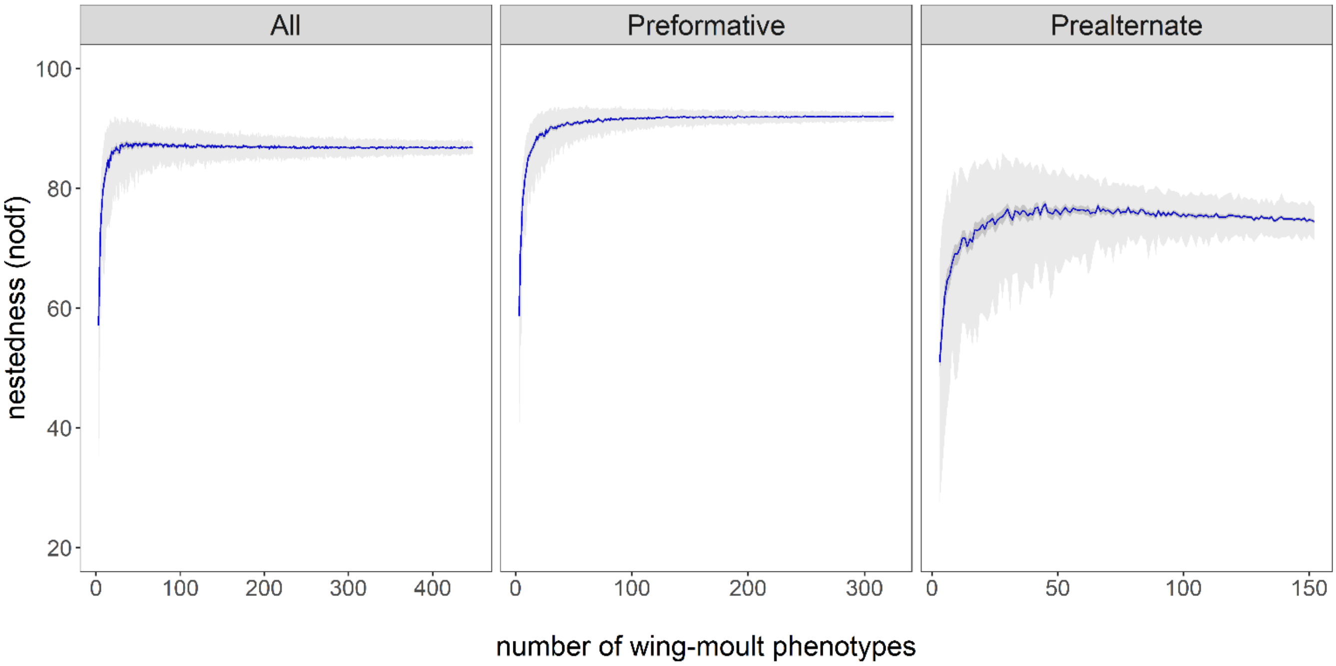


Table 1. Feature importance obtained from a random forest analysis of wing-feather mass, exposure, and contribution to flight on the frequency of wing-feather replacement observed in a dataset of 1082 unique moult phenotypes from preformative and prealternate moults. The method is based on the permutation importance method (Strobl *et al.* 2008, Breiman & Cutler 2019). Importance values do not sum up to one, the essential is the relative predictive strengths of the features.

Feather trait	Importance
Exposure	0.0458
Contribution to flight	0.0277
Mass	0.0256

DISCUSSION

Even before wing-feather replacement diagrams became popular in bird moult research, it was implicitly assumed a strong relationship between moult extent and the increasing probability of replacement of a given wing feather (e.g. Richter 1972, Jenni & Winkler 1994, Guallar *et al.* 2009). However, even studies that mentioned the existence of such moult rule have been always restricted to within-moult episodes and individual species (e.g. Jenni & Winkler 1994, Gargallo 2013). Here, we explicitly tested for the first time the hypothesis that passerines moult their wing feathers following a defined rank, concretely, the existence of a nested arrangement of moulted wing feathers across 3909 moult cards from 434 passerine species.

We did find such a nested relationship among passerine moult phenotypes: birds moulting fewer feathers replaced a subset of the feathers moulted by birds with larger wing-moult extents. The high nestedness we found is remarkable given that we analysed a large and diverse dataset (nodf = 84.31). However, we also found many imperfections graphically detected as black cells below the diagonal and white cells above the diagonal (Figs. 1 and 3, Appendix 2 Fig. A2). Deviations from perfect nestedness (especially in the prealternate moult; nodf = 67.28) further suggested that either a mixture of different lists of moult priorities or a combination of these rank-based lists with other rules of moult control can be at play. The European Pied Flycatcher *Ficedula hypoleuca* may be a good example to illustrate this because it undergoes contrasting partial preformative and prealternate moult episodes. The preformative moult includes all lesser coverts, and usually all median coverts and 1-3 inner greater coverts; on the other hand, the prealternate moult includes few lesser and 4-5 inner median coverts, usually 5-7 inner greater coverts, all tertials, and usually 1-2 inner secondaries (Jenni & Winkler 1994). The nestedness of both episodes are high: nodf_{PF} = 82.34 (n = 12), nodf_{PA} = 84.18 (n = 48). However, the nestedness for both episodes together is lower (nodf = 71.72). This reduction is expected when lumping two moult ranks of wing feathers (Appendix 2 Fig. A2), and strongly suggests a link between seasonal diversification of plumage requirements and priority of feather moult. Insightfully, the prealternate moult of the European Pied Flycatcher includes the wing feathers with white marks (de la Hera *et al.* 2013).

Table 2. Nestedness for the whole dataset and separately for the preformative and prealternate moult episodes after ordering feathers according to three feather traits.

Feather trait	All	Preformative	Prealternate
Exposure	82.35	88.65	62.64
Mass	79.04	86.02	58.32
Contribution to flight	73.89	83.22	54.14

The existence of rank lists controlling wing-feather moult immediately arises the question about their biological meaning, and particularly whether it has an adaptive basis. Moult may be strongly driven by phylogenetic history, since dinosaurian ancestors of birds already showed sequential feather replacement 50 million-year ago (Kiat *et al.* 2020). Analogously, shared phylogenetic history may have played a decisive role on phenotypic diversity. Thus, both the preformative and the prealternate moults show a large phylogenetic signal (Guallar & Jovani 2020a), with many ecological factors explaining a small proportion of the observed variation (Delhey *et al.* 2020), while important evolutionary transitions such as habitat shifts likely explaining adaptive changes in moult (Guallar *et al.* 2020d). This evolutionary balance likely requires the interaction of multiple factors, both adaptive and non-adaptive. Thus, wing-feather mass, exposure, and contribution to flight explained around 54% of the observed variation in the priority of feather moult, suggesting the adaptive value of feather moult priority lists. While the greater prediction power of exposure provides an interesting insight, the fact that 46% of the observed variation remained unexplained indicates that other factors have also driven the evolution of moult priority lists. One such factor cold be the adaptive differential investment in feather tracts during the nestling and fledging periods (Pap *et al.* 2007, de la Hera *et al.* 2010b).

Our study provides a conceptually (and quantitative) solid model of moult control that can be used to contrast empirical moult data. Overall, our results strongly suggest the existence of rank lists underlying the control of passerine wing-feather moult, while deviations from perfect nestedness suggest that other rules of moult control might be in operation and/or the existence of different moult priority lists within moult episodes (Appendix 3). We further suggest that nestedness is the physiological system of moult control evolutionarily conserved in the order Passeriformes given their anatomical constraints and the central role that moult plays in their natural history. Moreover, the imperfections that we found may have arisen as a consequence of the diversification of plumage requirements across passerine species and moult episodes, which might have generated new feather moult priorities and even new mechanisms of moult control along their evolution.

Our approach, borrowed from the study of ecological systems, is adequate to the study of moult phenotypes because it relates moult extent and feather identity (which feathers are actually replaced), thus allowing to establish a relationship among feathers as moult extent increases and providing insight into the underlying rules of moult control. More classical approaches, such as the use of moult patterns allow to categorise the variation of moult phenotypes and also suggest the existence of heterogeneity in the moult process (Appendix 3), although they do not inform about the intrinsic relationships among moult phenotypes. Future studies on this topic should enlarge the number of species sampled (this study comprises around 7% of the approximately 6000 extant passerine species), use new and improved metrics to tackle the influence of plumage functions (including those not treated here, such as thermoregulation or signalling). Future research would also benefit from adding more plumage traits (e.g. feather area, pigmentation), and exploring alternative rules of control not based on lists of priorities.

ACKNOWLEDGEMENTS

We wish to thank for their assistance and access to specimen collections: Maureen Flannery, California Academy of Sciences, San Francisco; Carla Cicero, Museum of Vertebrate Zoology, Berkeley; Dr. Adolfo Navarro and M.C. Fanny Rebón of the Museo de Zoología Alfonso Herrera, Dr. Patricia Escalante and M.C. Marco Gurrola of the Colección Nacional de Aves, Mexico City. Special thanks to the following: Sergi Fernández for access to natural history information; Roger Jovani for helpful discussion; Kaspar Delhey for sharing his code to calculate transition rates.

REFERENCES

Almeida-Neto M, Guimarães P, Guimarães Jr PR, Loyola, R. D. and Ulrich, W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117: 1227–1239.

Bååth, R. 2016. bayesboot: an implementation of Rubin's (1981) Bayesian bootstrap. R package version 0.2.1. <https://CRAN.R-project.org/ package=bayesboot>

Bergman G 1982. Why are the wings of *Larus f. fuscus* so dark? *Ornis Fennica* 59: 77–83.

Breiman L, Cutler A 2019. Random forests – Classification manual. <http://www.math.usu.ed u/~adele/forests/>

Dawson A 2005. The scaling of primary flight feather length and mass in relation to wing shape, function and habitat primary flight feather length and mass. *Ibis* 147: 283–292.

de la Hera I, Hedenström A, Pérez-Tris J, Tellería JL 2010a. Variation and mechanical properties of feathers of blackcap *Sylvia atricapilla* in relation to migration. *J. Avian Biol.* 41: 342−347.

de la Hera I, Pérez-Tris J, Tellería JL 2010b. Migratory behavior and differential resource allocation between wing and tail feathers in a passerine bird. *Auk* 127: 647−652.

de la Hera J, Reed T., Pulido F, Visser ME 2013. Feather mass and winter moult extent are heritable but not associated with fitness-related traits in a long-distance migratory bird. *Evol. Ecol.* 27: 1199–1216.

de la Hera I, Hernández-Téllez I, Pérez-Rigueiro P, Pérez-Tris J, Rojo FJ, Tellería JL 2020. Mechanical and structural adaptations to migration in the flight feathers of a Palaearctic passerine. *J. Evol. Biol.* 33: 979–989.

Delhey K, Guallar S, Rueda-Hernández R, Valcu M, Wang D, Kempenaers B 2020. Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. *J. Anim. Ecol.* 89: 2896–2908.

Dvořák R 2016. Aerodynamics of bird flight. *EPJ Web of Conferences* 114: 01001.

Flinks H, Salewski V 2012. Quantifying the effect of feather abrasion on wing and tail lengths measurements. *J. Ornithol.* 153: 1053–1065.

Gargallo G 2013. Feather selection and replacement patterns demonstrate that Goldfinches *Carduelis carduelis* fix postjuvenile moult extent prior to moult initiation. *J. Ornithol.* 154: 219–230.

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A 2009. *Paseriformes del Occidente de México: morfometría, datación y sexado*. Museu de Ciències Naturals de Barcelona.

Guallar S, Jovani R 2020a. Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. *Ibis* 162: 778–786.

Guallar S, Jovani R 2020b. Data from: Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. Figshare. <http://dx. doi.org/10.6084/m9.figshare.9896516>

Guallar S, Jovani R 2020c. Data from: Moult nestedness and its imperfections: insights to unravel the nature of passerine wing-feather moult rules. Dryad Digital Repository. http://dx. doi.org/10. 5061 /dryad.k6djh9w42

Guallar S, Rueda-Hernández R, Pyle P 2021d. Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. *Ornithology* 138.

Guimarãe PR, Guimarães P 2006. Improving the analyses of nestedness for large sets of matrices. *Environ. Model. Soft.* 21: 1512–1513.

Howell SNG, Corben C, Pyle P, Rogers, DI 2003. The first basic problem: a review of molt and plumage homologies. *Condor* 105: 635–653.

Humphrey PS, Parkes KC 1959. An approach to the study of molt and plumages. *Auk* 76: 1–31.

Jenni L, Winkler R 1994. *Moult and ageing of European passerines.* Academic Press, London.

Kiat Y, Balaban A, Sapir N, O'Connor JK, Wang M, Xu X 2020. Sequential molt in a feathered dinosaur and implications for early paravian ecology and locomotion. *Current Biol.* 30: 1–6.

Lee S-I, Kim J, Park H, Jabłoński PG, Choi H 2015. The function of the alula in avian flight. *Sci. Reports* 5: 9914.

Liaw A, Wiener M 2002. Classification and regression by randomForest. *R News* 2: 18–22.

Lindström Å, Visser GH, Daan S 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Phys. Zool.* 66: 490–510.

Martin TE, Tobalske B, Riordan MM, Case SB, Dial KP 2018. Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. *Science Adv.* 4: eaar1988.

Møller AP 1991. Influence of wing and tail morphology on the duration of song flight in skylarks. *Behav. Ecol. Sociobiol.* 28: 309–314.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL Solymos, P, Stevens MHH, Szoecs E, Wagner H 2019. Vegan: community ecology package. R package version 2.5-6. <http://cran.us.r-project.org>

Pap L, Barta Z, Tökölyi J, Vágási CI 2007. Increase of feather quality during moult: a possible implication of feather deformities in the evolution of partial moult in the great tit *Parus major*. *J. Avian Biol.* 38: 471–478.

Richter A 1972. Zum Umfang der Jugendmauser am Flügel der Amsel *Turdus merula*. *Ornithol. Beob.* 69: 1–16.

Shyy W, Aono H, Kang C-k, Liu H 2013. *An introduction to flapping wing aerodynamics.* Cambridge University Press, Cambridge.

Slagsvold T, Dale S 1996. Disappearance of female Pied Flycatchers in relation to breeding stage and experimentally induced molt. *Ecology* 77: 462–471.

Strobl C, Boulesteix A, Kneib T, Augustin T, Zeileis A 2008. Conditional variable importance for random forests. *BMC Bioinformatics* 9: 307.

SUPPLEMENTARY INFORMATION

APPENDIX 1

Expanded Methods

The 10th primary of species with nine visible primaries was given the same moult score as the ninth primary (Hall 2005). We standardised wing-feather mass, exposure, and length to obtain an average passerine model for these variables. This procedure was necessary since we did not have information on all three variables for each species. This allowed us to work with the entire moult dataset, although at the expense of losing precision.

Mass

We weighted the feathers of one wing from 86 birds belonging to 43 Palearctic passerine species. Birds were collected from traffic collisions in Catalonia, and prey caches in a colony of Eleonora's Falcon *Falco eleonorae* on Alegranza, Canary Islands. We weighted each upper-wing feather at the nearest 0.01 mg. Then, we calculated mean feather mass for each feather of every species and divided each value by the mass of the heaviest feather. We finally averaged these normalised feather masses across species, obtaining a normalised mean mass per feather across species. Because of their small mass, we weighted lesser and median coverts as full tracts. Next, we divided mass of lesser coverts by 50 (the approximate number of these feathers on a passerine wing; Appendix 2 Fig. A1). We estimated the mass of each of the eight median coverts from a sample of known weights (Appendix 2 Table A1).

We imputed values for the 4.8% missing feathers in our dataset using random forest predictions (Stekhoven & Buehlmann 2012).

Table A1. Estimation of relative mass for individual median coverts. We weighted individual median coverts from two individuals of relatively large species: one Eurasian Skylark *Alauda arvensis* and one Eurasian Jay *Garrulus glandarius*, and divided each covert by the total mass of the entire tract. Then, calculated the means and applied them to the remaining individuals of the dataset.

	MC1	MC2	MC3	MC4	MC5	MC6	MC7	MC8
Skylark	0.09913	0.09767	0.11953	0.13703	0.18076	0.14723	0.13120	0.08746
Jay	0.09029	0.10834	0.13325	0.14570	0.14446	0.14197	0.12889	0.10710
Estimates	0.09471	0.10301	0.12639	0.14136	0.16261	0.14460	0.13004	0.09728

Exposure

We used photographs of 62 live birds from 62 Palearctic species (17 from the authors and 45 from the internet). Photographs showed individuals with folded wings in a standardised upright lateral stance, so that the three tertials were visible (notice that tertials lay on approximately the same plane on top of the remaining remiges). We obtained the number of pixels visible in the picture for each of the upper-wing feathers using an image processing program (Appendix 2 Fig. A2; <www.gimp.org>).

The amount of wing exposure varies with individual behaviour and with season. Birds constantly change position, and by fluffing or slicking their plumage modify the wing area exposed. Therefore, intrinsic and extrinsic factors make wing-feather exposure difficult to standardise. We avoided measuring fluffed birds and excluded from our measurements those wing areas covered by scapular and breast feathers.

Figure A1. Lesser coverts (red points) of a House Sparrow *Passer domesticus* ringed in Barcelona on 18 September 2017. Notice that these coverts (around 50 in most passerine species) are arranged in nearly concentric arcs, which gradually increase in size from the tiny feathers forming the leading edge towards the larger feathers adjacent to the median coverts and the scapulars.

We selected photographs from SG and the following online sources:

http://www.worldbirds.co.uk/field_guide.aspx (17)
https://www.featherbase.info/uk/home (4)
https://www.macaulaylibrary.org/the-internet-bird-collection-the-macaulay-library/ (4)
http://www.luontoportti.com/suomi/en/linnut/ (1)
www.arkive.org (1)
https://two-in-a-bush.blogspot.com/ (1)
https://www.pbase.com/dophoto/birds (1)
www.wikipedia.org (1)
https://www.monaconatureencyclopedia.com/category/encyclopedia/animals/birds/passerines/?lang=en (1)
https://www.shutterstock.com/search/bird+photography (1)
https://www.rspb-images.com/ (1)
https://www.worldlifeexpectancy.com/bird-life-expectancy (1)
https://www.flickr.com/photos/tags/bird/ (1)
http://nzbirdsonline.org.nz/species/song-thrush (1)

Figure A2. Outline of some of the wing-feather tracts on one adult male Eurasian Blackbird *Turdus merula*. Risley Moss, Birchwood, Cheshire, 8 March 2008. © Steve Oakes.

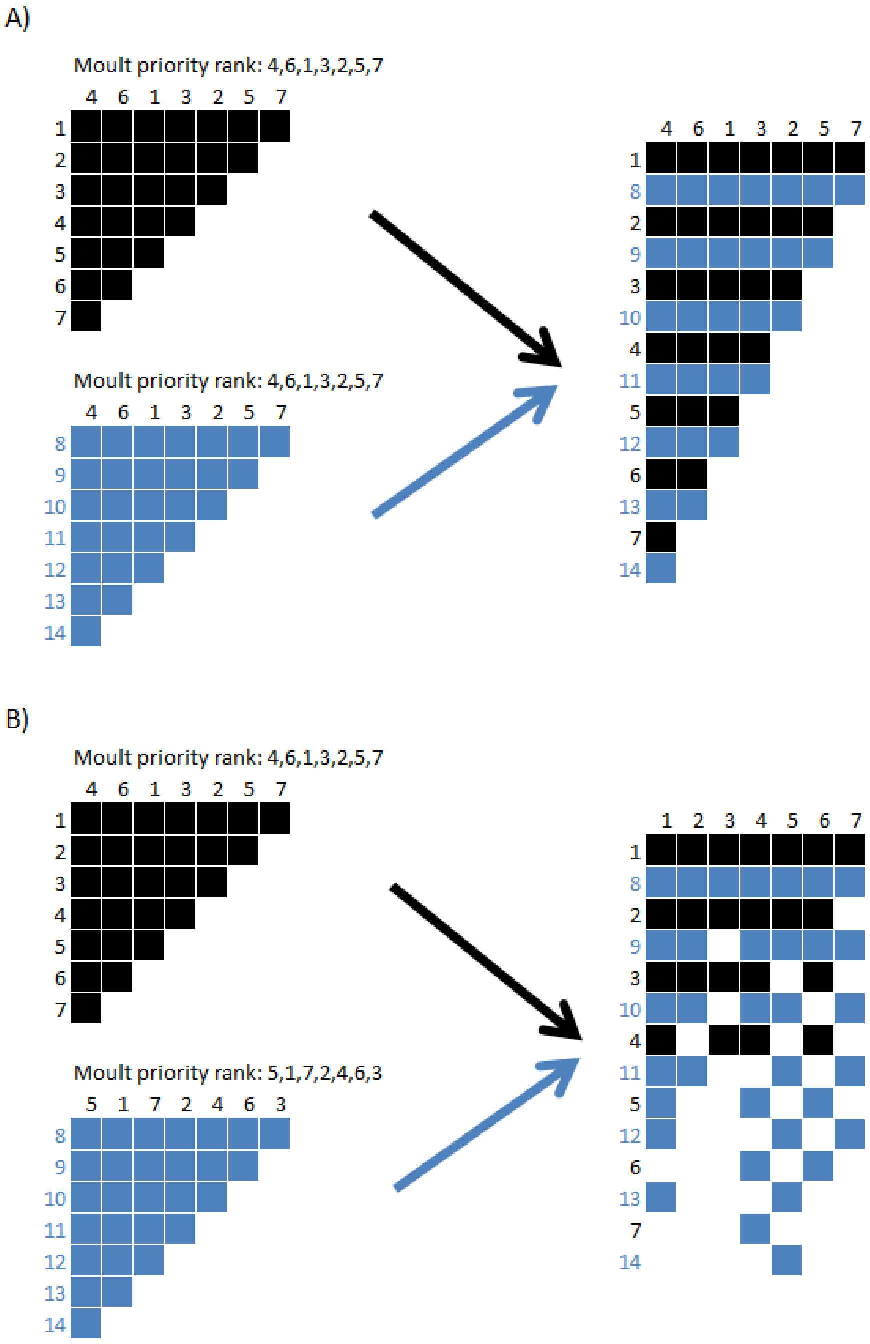
Contribution to flight

Since measurements from primaries and the rest of remiges were not taken from the same individuals, we made calculations separately. To normalise both subsets, we measured the difference between the outermost secondary S1 and the innermost primary P1 from three birds in featherbase.com. We calculated the average difference and applied it to all our individuals.

APPENDIX 2

Figure A1. A) Wings of two male Sardinian warblers *Sylvia melanocephala* after a complete prebasic moult with all feathers replaced, and B) a general preformative moult, with the following feathers replaced (note the greyish colour): LC, MC, GC, c and T1-3. Abbreviations: LA, lesser alula; MA, median alula; GA, greater alula; LC, lesser coverts; MC, median coverts; GC, greater coverts; c, carpal covert; PC, primary coverts; T, tertials; S, secondaries; P, primaries. Birds captured in north eastern Iberian Peninsula in December 26 (top) and October 12 (bottom) of 2017. ©Marc Illa.

Figure A2. Effect of moult priority rank on nestedness. A) Two sets of seven moult phenotypes with same underlying moult priority rank. B) Two sets of seven moult phenotypes with different underlying moult priority rank.



APPENDIX 3

Moult pattern analyses

It has been proposed that wing-feather moult phenotypes can be grouped in the so-called "moult patterns" (Guallar & Jovani 2020a). Moult patterns are classes of observed wing-feather moult phenotypes grouped under certain criteria of similarity (Guallar & Jovani 2020a). However, the rules of similarity used to define the general, proximal and eccentric moult patterns (84% of unique phenotypes in our dataset) are intrinsically nested, which creates a circular argument if moult patterns are used to prove that nestedness among moult phenotypes. Regardless of the circularity between defined moult patterns and nestedness, the high overall nestedness we found indicates that most moult phenotypes show a nested relationship.

In addition to moult episodes, we classified moult cards in our dataset according to nine wing-moult patterns, following (Guallar & Jovani 2020a): complete, abridged I, abridged II, eccentric, general, proximal, inverse, limited, and reduced. Moult patterns likely reflect the diversification of plumage moult requirements among species and individuals within species. Differences among moult pattern nestedness could be used to test whether passerine wing-feather moult phenotypes are the result of more than one moult rank of wing feathers.

For the complete dataset, nestedness of two patterns were higher than expected (Fig. A1): eccentric (4.6% higher), general (5.3%). Nestedness of the remaining patterns were lower than expected: proximal (5.8% lower), inverted (23.7%), complete (25.5%), limited (26.8%), abridged I (34.6%), abridged II (37.7%), and reduced (83.0%). The latter two patterns did not differ from randomness (Table A1). Indeed, the even higher nestedness for the general (nodf = 91.46; Fig. A1) and eccentric moult patterns (nodf = 90.80), which comprise 68% moult cards and 40% unique moult phenotypes, strongly suggests the existence of multiple rank-based lists as a rule of moult control in passerines. Nestedness across feather traits, episodes and patterns was consistent with the remaining analyses (Fig. A2).

Finally, we did not find an increase in nestedness as we generated ever more homogeneous groups of moult phenotypes by moult pattern, episode, and species (Fig. A3).

Table A1. Results of the null model analysis with ANILHADO. Nestedness and bootstrapped 95% confidence intervals (CI) from 1000 iterations. We used COL, one of the program's pre-determined null models to compare moult patterns with theoretical random predictions. This null model generates random phenotypes by randomising columns (i.e. wing feathers) while keeping extent constant. Non-overlapping differences in bold.

Pattern	nodf	95% CI
Complete	59.85	53.43 - 54.96
Abridged I	52.57	**52.05 - 52.96**
Abridged II	52.07	49.86 - 51.86
Eccentric	90.80	77.28 - 80.04
General	91.46	72.31 - 75.71
Proximal	81.51	64.25 - 66.51
Inverted	66.46	49.27 - 53.35
Limited	64.05	48.14 - 58.31
Reduced	14.77	**12.94 - 16.93**
All	84.31	58.63 - 59.68

Figure A1. Variation of the expected nestedness for unique moult phenotypes. Blue lines show the bootstrapped mean nestedness obtained from random resamples (i.e. extraction of different number of random rows from Fig. 3); dark grey areas show the 95% bootstrapped interval of the mean; light grey areas show 95% bootstrapped interval of 500 random resamples. Notice that uncertainty on the measure of prealternate nestedness was higher than uncertainty of preformative nestedness. Interestingly, mean nestedness decreased with increasing number of moult phenotypes. This effect is very slight in the preformative moult (peak nodf = 92.10, total nodf = 90.99), but more apparent in the prealternate moult (peak nodf = 77.38, total nodf = 67.28). Mean and bootstrapped intervals estimated using the R library bayesboot (Bååth 2016).

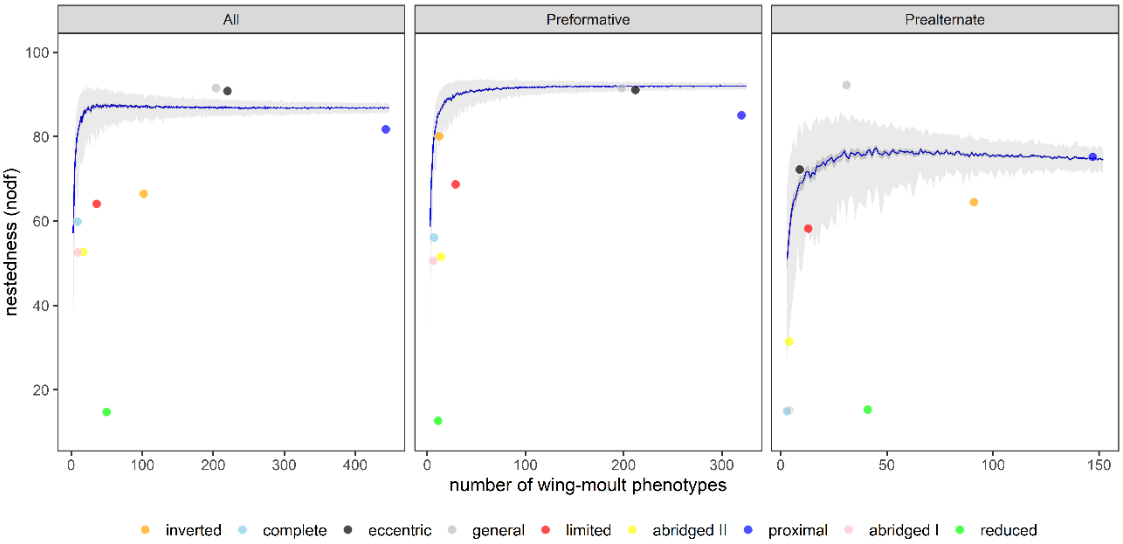


Figure A2. Nestedness for the whole dataset and separately for two moult episodes, and for each moult pattern separately (and all together) when ordering feathers according to three feather traits.

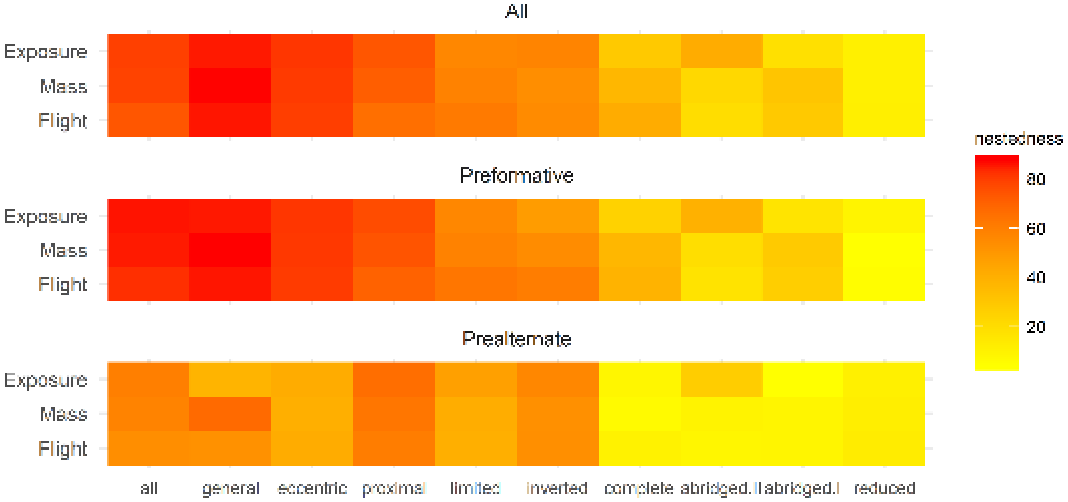
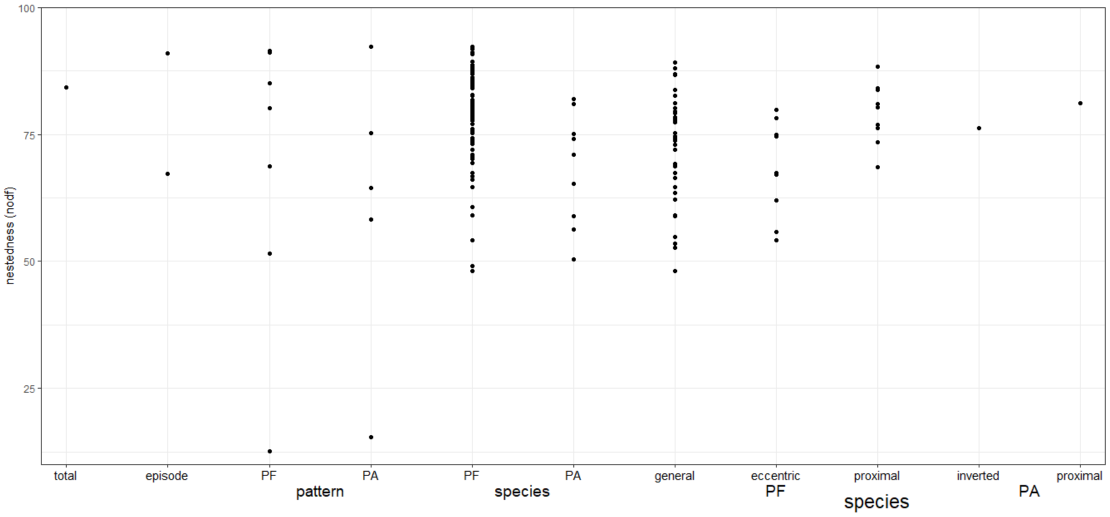


Figure A3. Nestedness variation at episode, pattern, and species levels. Combinations for n < 10 not shown.



REFERENCES

Hall KSS 2005. Do nine-primaried passerines have nine or ten primary feathers? The evolution of a concept. *J. Ornithol.* 146: 121–126.

Lee S-I, Kim J, Park H, Jabłoński PG, Choi H 2015. The function of the alula in avian flight. *Sci. Reports* 5: 9914.

Stekhoven DJ, Buehlmann P 2012. MissForest - non-parametric missing value imputation for mixed-type data. *Bioinformatics* 28: 112–118.

Chapter 3

Plumage morphology channels energy investment during formation of passerine moult phenotypes

Santi Guallar[1] & Oliver Planes[2]

1 Department de Vertebrats, Museu de Ciències Naturals de Barcelona, Barcelona

2 INS Forat del Vent, Cerdanyola del Vallès

Submitted to Journal of Avian Biology: Guallar S & Planes O Plumage morphology channels energy investment during formation of passerine moult phenotypes.

ABSTRACT

Birds modulate genotype expression throughout their annual cycle to adapt to the changing scenarios that they encounter. Regardless of the mechanisms of control, phenotype formation necessarily depends on the morphological traits that channel the resources invested in each process at the end of its regulatory pathway. We studied how the energy invested in moult is channelled via two morphological traits. We compared mass and area of empirical and theoretical passerine wing-feather moult phenotypes to test three hypotheses on passerine birds: a) energy-saving strategies are applied during moult to tackle constraints and possible trade-offs with coincidental physiological processes, b) area of renewed plumage is optimised in relation to energy investment to maintain plumage functionality, and c) these two strategies vary with the upcoming natural-history stage in the bird's lifecycle. We found support for all three hypotheses. Energy saving increases as number of theoretical feather combinations rise across moult extent range. Moult phenotypes with retention of primary feathers show higher energy savings than moult phenotypes with replacement of primaries. Despite empirical area of renewed plumage is lower than theoretical area, passerines manage to optimise this trait as a function of the energy invested in moult. Energy-saving strategies are prevalent throughout the life-history stages of passerines, although diversification of strategies is highest during the wintering stage. Our findings stress the importance of morphological constraints both in the formation of the passerine moult phenotype and shaping moult strategies. Further studies should aim at establishing the link between moult phenotypes and their function throughout birds' life-history stages.

INTRODUCTION

Physiological processes compete among each other for limited resources in the individual, so that increasing the budget of one of them causes a decrease of the available resources for other processes, thus creating trade-offs (Garland 2014). Trade-offs become more evident among resource-costly processes such as egg production in oviparous vertebrates, in which egg size and clutch size are negatively correlated (Garland & Carter 1994). Regardless of the physiological processes involved in a trade-off, resources in conflict must be channelled through concrete anatomical traits, such as the genital tract of oviparous vertebrates in relation to egg production. Therefore, morphological properties of the anatomical traits involved in any given trade-off should play an essential -although frequently overlooked- role.

The distinct and diverse shapes and sizes of birds' wing feathers provide a good example to study how morphology may influence trade-off strategies during formation of the final feather-wing moult phenotype (i.e., the set of wing feathers that a bird replaces during a given moult episode, henceforth moult phenotypes). The wing plumage is laid out in several distinct rows of covert feathers with small within-row differences, and one row of large remiges, which show noticeable differences among them (Fig S1). The wing plumage not only carries out general body-plumage functions (i.e. insulation, signalling; Gerken *et al.* 2006, Senar 2006), it provides all the fine-tune functions that allow an efficient flight (Pennycuick 1989, Hedenström & Sunada 1999). Like the rest of the plumage, the wing plumage needs to be regularly moulted to maintain its functionality (Bridge 2008, Langston & Rohwer 2011, Jenni & Winkler 2020).

Avian moult is an expensive process that substantially increases the cost of metabolic rates (Nagy 1987, Lindström *et al.* 1993). For this reason, we should expect birds to have developed moult strategies to avoid overloading their energy budget (Ben-Hamo *et al.* 2017). One key factor for these strategies to be successful is timing (Hall & Fransson 2000). Thus, failing to adequately scheduling moult among the main stages of the annual cycle may have a severe impact on individual fitness. For example, passerines that overlap breeding and moulting see their time budget affected, and present carry-over effects (Hemborg 1999, Echeverry-Galvis & Hau 2012). Most passerine species replace their whole plumage right after the breeding season (Newton 2008). Duration of this process increases with species size (Rohwer *et al.* 2009), and usually lasts 8-12 weeks in Palearctic species and 11-15 weeks in Neotropical ones of similar size (Ginn & Melville 1983, Guallar *et al.* 2009). However, the interval between the end of the breeding season and the onset of migration may be too tight for long-distance migrants to replace their whole plumage. Many of them have overcome this situation by delaying moult until after leaving the breeding grounds (Pyle 1997, Shirihai & Svensson 2018), when time and energy constraints may be reduced or absent (Barta *et al.* 2008, Kiat *et al.* 2019).

Passerines' needs and constraints vary with seasons and change of environments, so that the same moulting strategy may not be adaptive in different scenarios. Therefore, stage within the annual cycle likely has an important influence on moult strategy. We can observe this, for example, in species with a distinctive breeding plumage, which moult into it right before the onset of the breeding season to enhance sexual signalling during the early stages of reproduction (Wingfield 2008). However, passerines' needs not only vary among stages of the annual cycle, they also vary with age, and particularly between the first months of life and the remaining lifetime. Usually just a few weeks after fledging, passerines start replacing their juvenile plumage. This is a critical phase for the individual's survival because it faces the energy demands and the aerodynamic costs of moult too early to have developed full abilities to forage and evade predators (Heise & Moore 2003, Naef-Daenzer & Gruebler 2016). Not surprisingly, retention of primaries and secondaries during this moult is the most frequent moult strategy among Holarctic passerines (Pyle 1997, Shirihai & Svensson 2018; Fig. S1). These feathers make around 80% of the wing-feather mass and 20% of the whole plumage (Herremans 1988; datasets), therefore its retention also saves a considerable amount of energy.

Thus, a second key factor for the success of passerine moult strategies is moult investment. The most trivial saving strategy is to retain all feathers: not moulting has a zero cost, at least in the short term. In the long term, however, plumage functionality makes it an unfeasible strategy, since feathers lose efficiency as time passes due to both biotic and abiotic degradation (Willoughby 1991, Corning & Biewener 1998, Burtt & Ichida 2004). Decay is even greater for the juvenile body plumage due to its poor quality (Butler *et al.* 2008), which explains the evolution of its rapid replacement (Jenni & Winkler 2020). Plumage deterioration is also thought to have driven the evolution of prebreeding moults, triggering the evolution of other biological traits and plumage functions (Terrill *et al.* 2020), e.g. signalling status during the winter or sexual attractiveness during the breeding season (Senar *et al.* 1998, Badyaev & Hill 2003, López *et al.* 2005). Thus, change of plumage functions throughout both seasons and life-history stages may also affect moult strategies.

Dynamic variation of both functional needs and energy budgets interact to define these moult strategies. Moult investment should be large enough to meet functional needs, but not too large to exceed the energy budget caused by simultaneous occurrence with other costly physiological processes, especially under possible resource limitations (Gosler 1991, Lindström *et al.* 1994, Hoye & Buttemer 2011). This suggests that moult investment might be optimised in certain contexts. It seems plausible that optimisation of moult investment is associated with those factors that have a bigger impact on plumage functionality decay: feather abrasion inflicted by mechanical friction and sunlight (Willoughby 1991, Weber *et al.* 2005). A feasible optimisation strategy would be maximising the plumage surface replaced for a given moult investment.

In this study, we used a large moult dataset to test whether plumage influence passerine moult strategies throughout their natural-history stages. To do this, we (1) compared accumulated mass and area of renewed plumage of 4671 observed wing-feather moult phenotypes from 501 Holarctic and Neotropical passerine species with theoretical moult phenotypes, and (2) associated these values with four moult episodes linked to different natural-history stages throughout the lifetime of passerine species. We hypothesised that passerine moult follows an energy-saving strategy, which predicts that the actual energy invested in moult would be smaller than the energy investment expected by chance. We also hypothesised that passerine moult optimises area of renewed plumage in relation to energy investment. The latter hypothesis has two main predictions: (a) the bivariate values of energy investment and area of renewed plumage would be smaller than expected by chance regardless how many wing feathers are replaced (i.e., wing-feather moult extent), and b) the quotient between energy investment and area of renewed plumage would be smaller than expected by chance. Finally, since passerines may encounter different scenarios with changing demands and constraints throughout their natural-history stages, it can be hypothesised that passerine moult strategies will vary with stage. Under this hypothesis it can be predicted that both energy investment in moult and area of renewed plumage will vary among life-history stages.

MATERIALS AND METHODS

Data

Moult

We used 4671 wing moult cards from 501 passerine species (306 Holarctic and 195 Neotropical). Moult cards, which are the formal procedure to record moult phenotypes, contained moult state (1 replaced, 0 retained) for each of the larger 50 upper wing feathers (8 median coverts, 10 greater coverts, 1 carpal covert, 9 primary coverts, 3 alula feathers, 3 tertials, 6 secondaries, and 10 primaries; Fig. S1). For standardization purposes, the 10th primary of species with nine visible primaries was given the same moult score as the ninth primary (Hall 2005). We scored lesser coverts as an approximate percentage of the feathers forming the tract, and then divided them in 10 equivalent blocks. Thus, replacement of all lesser coverts scored 10, and moult extent ranged from 1 to 60. We also recorded presence/absence of replacement of primaries because these are the heaviest wing feathers and play an essential role in passerine flight.

To assess how moult varies with natural-history stage, we assigned each moult card to a given moult episode inserted in the sequence of stages of the annual cycle. This sequence of stages is tightly coupled to season in Holarctic as well as in most Neotropical passerines (Newton 2008, Johnson *et al.* 2012). We considered four episodes associated with four stages within the life cycle of passerines: postjuvenile (it occurs only once in the bird's lifetime, shortly after fledging), postbreeding, prebreeding, and non-breeding (the latter three occur with circannual periodicity). We defined the postjuvenile moult and the postbreeding moult as the moult episodes that take place on the species' breeding range prior to the onset of autumn migration. The prebreeding moult is defined as the main episode that takes place outside the breeding range during the non-breeding period. The non-breeding moult is a secondary episode shown by many species after the prebreeding moult and prior to the spring migration, which is characterised by a much smaller extent than the prebreeding moult (e.g. Pinilla 2001). To summarise, 3,748 moult cards belonged to the postjuvenile moult, 708 to the prenuptial moult, 102 to the postnuptial moult, and 113 to the non-breeding moult.

Mass and exposure of wing feathers

Wings of Holarctic and Neotropical passerine species have relatively homogenous morphologies. Wing morphology is mainly affected by migratory behaviour and habitat, with migratory and open-habitat species having more pointed wings than non-migratory species and species occurring in cluttered habitats (Mulvihill & Chandler 1991, Keast 1996). Since wing morphology influences both mass and exposure of individual remiges, we gathered data from species representing these four main wing-shape groups. We used accumulated mass of replaced wing feathers as a proxy of energy invested in moult (Dietz *et al.* 1992).

We calculated accumulated mass as the proportion of the total wing-feather mass replaced after a given moult episode (excluding underwing coverts). Since feather mass data is lacking for most species, we built a wing-feather mass model from 67 birds belonging to 32 Palearctic passerine species collected from traffic collisions (see Acknowledgements). We weighed to the nearest 0.01 mg each feather of one wing (remiges, alula feathers, and dorsal coverts). Because of their small size, we weighed lesser and median coverts as full tracts. We subsequently distributed mass of the lesser coverts in 10 equal groups to avoid the paradox that the lightest wing feathers were actually heavier than the heaviest remex. Mass of each of the eight median coverts was estimated from a sample of known weights (Table S1). We imputed values for the 4.9% missing feathers in our dataset using random forest predictions as implemented in the R package missForest (Stekhoven & Buehlmann 2012, R Development Core Team 2020). We calculated mean feather mass for every species (thus giving the same weight to each species), averaged feather masses across species, and normalised values dividing by the mass of the heaviest feather.

We calculated area of renewed plumage as the proportion of wing surface covered by the wing feathers replaced after a given moult episode. As for feather mass, feather exposure data is lacking for most species. We built a wing-feather exposure model using photographs of 32 live birds from the same 31 Palearctic species for which we obtained wing-feather masses (see Guallar *et al.* 2021 for data collection and processing details). We obtained the number of pixels in the photograph for the visible upper-wing feathers using an image-processing program (GIMP 1995-2017). We normalised number of pixels of every wing feather by dividing each by that of the most exposed feather and averaged all normalised values to obtain mean exposure per feather across species. We divided lesser wing coverts in 10 equivalent blocks to match moult extent.

Analyses

To test whether passerines present energy-saving strategies during moult, we compared the empirical values obtained from our moult dataset and theoretical values generated from randomly sampling our wing-feather mass model. Thus, we first obtained empirical values for each one of the 4671 individuals in our dataset by multiplying individual feather scores by their corresponding value in the wing-feather mass model. Then, we calculated for each bird the empirical accumulated mass by summing the values for all moulted feathers. To help interpreting results, we replicated these analyses for area of renewed plumage.

To obtain theoretical values, we generated the mean accumulated mass and area of renewed plumage from random samples across the moult extent range (1-60). We used a number of samples high enough to guarantee the stability of values (up to 10000 for moult extent values with a large number of possible combinations; Fig. S2). Then, we tested whether the accumulated mass and area of renewed plumage were higher than expected using a non-parametric test and checked the effect of primary replacement.

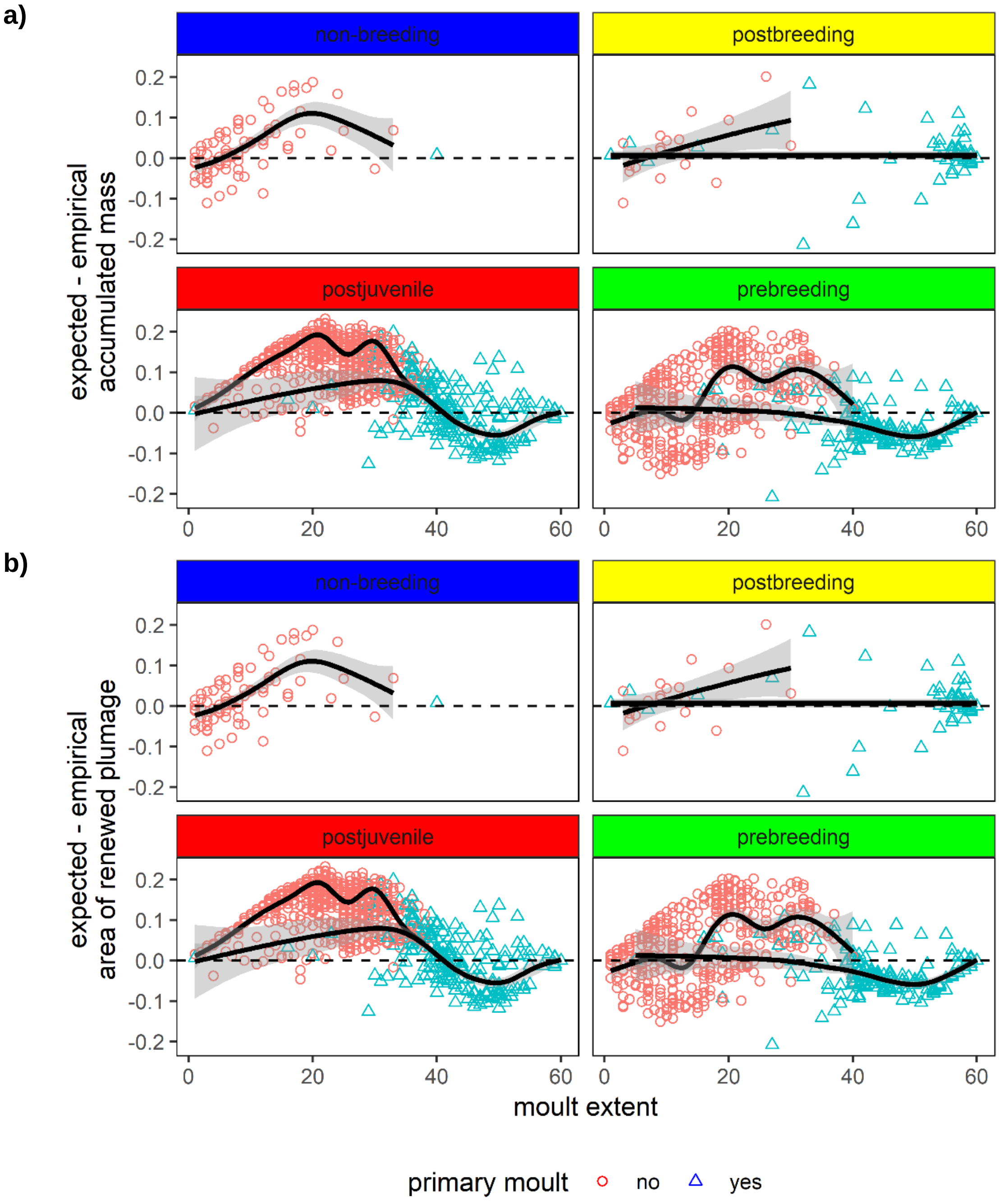
To test whether passerines optimise the relationship between energy investment and area of renewed plumage, we generalised this procedure generating bivariate values of accumulated mass and area of renewed plumage (ϑ_g= (mass,area)). To this effect, we calculated the norm $\eta = \sqrt[2]{mass^2 + area^2}$ for each of the 100000 random samples across the range of moult extent (bivariate values needed a larger number of samples to reach stability). We calculated the minimum, deciles, and maximum to help graphical interpretation. Next, we checked the evolution of the quotient $Q = mass/area$ throughout the moult extent range. Finally, we tested whether the empirical values (ϑ_e= (mass,area)) were larger than theoretical ones for both η and Q.

To test whether passerine moult varies with natural-history stage, we replicated the previous analyses for each moult episode (except for Q). To assess differences among moult episodes, we carried out pairwise comparisons using Dunn tests as implemented in the R package FSA (Ogle *et al.* 2019), and plotted density distributions of accumulated mass and area of renewed plumage for each moult episode using the R package gglogspline (Rudis 2019).

RESULTS

As predicted by the energy saving hypothesis, energy investment during moult was smaller than expected by chance (W = $2.1\text{x}10^7$, P < 0.0001). Only 3.62% empirical values were greater than theoretical ones, most of which occurring near complete moults (Fig. 1a). Overall, moults with primary retention were significantly lighter than those with primary replacement for any given moult extent (W = 83279, P < 0.0001). This was also true across moult episodes (Table 1a-b, Fig. 1a).

Figure 1. Differences between theoretical and empirical values of (a) accumulated mass (a proxy of energy investment) and (b) area of renewed plumage throughout the range of moult extent for four moult episodes. Wing-feather moult data obtained from 4671 birds from 501 Holarctic and Neotropical passerine species. 96.38% empirical mass values are lower than expected by chance, indicating that passerine species present energy-saving strategies during moult. Moult phenotypes that include primaries have significantly higher empirical values. Lines are fitted generalised additive models.



We found similar results regarding area of renewed plumage, although patterns were less clear and differences between empirical and theoretical values were smaller (1b). Area of renewed plumage was smaller than expected by chance ($W = 1.9x10^7$, $P < 0.0001$). Only 12.05% empirical values were higher than theoretical ones, most of which occurring near extreme values of moult extent, except for the postjuvenile moult (Fig. 1b). Overall, moults with primary retention had a significantly lower area of renewed plumage than those with primary replacement for any given moult extent ($W = 210030$, $P < 0.0001$). This pattern was found for the postjuvenile moult, although interestingly the prebreeding and postbreeding moults deviated from it (Table 1c-d, Fig. 1b).

The norm η occupied a relatively small volume of the whole volume through which they could potentially spread (Fig. 2a-c). Results support our optimisation hypothesis: η was smaller than expected by chance ($W = 2x10^7$, $P < 0.0001$). Only 6.40% empirical values were higher than theoretical ones, most of which occurring near complete moults. Overall, η of moults with primary retention had a significantly lower norm than those with primary replacement for any given moult extent ($W = 167442$, $P < 0.0001$). This was also true across moult episodes (Table 1e-f). The quotient Q was significantly smaller than expected by chance ($W = 1.4x10^6$, $P < 0.0001$), supporting the second prediction from the optimisation hypothesis. Only 6.23% empirical values lied on the right side of the bisector, most of which associated with near complete moults (Fig. 2d).

Energy investment showed a bimodal distribution, basically clustering near the minimum and maximum values (Fig. 3a). Non-breeding, prebreeding and postjuvenile moults peaked near the minimum, whereas the postbreeding moult peaked near the maximum. A secondary peak for the postbreeding moult is largely caused by 23 species that undergo partial postbreeding moults with primary retention, all of which long distance tropical migrants that breed in temperate regions (Table S2). Prebreeding and postjuvenile moults also showed secondary peaks near the maximum. Area of renewed plumage showed a multimodal distribution (Fig. 3b), with the non-breeding and postbreeding moults still clearly near opposite extreme values. On the other hand, the postjuvenile moult slid toward mid-range values, and the prebreeding moult broadly spread throughout the entire range.

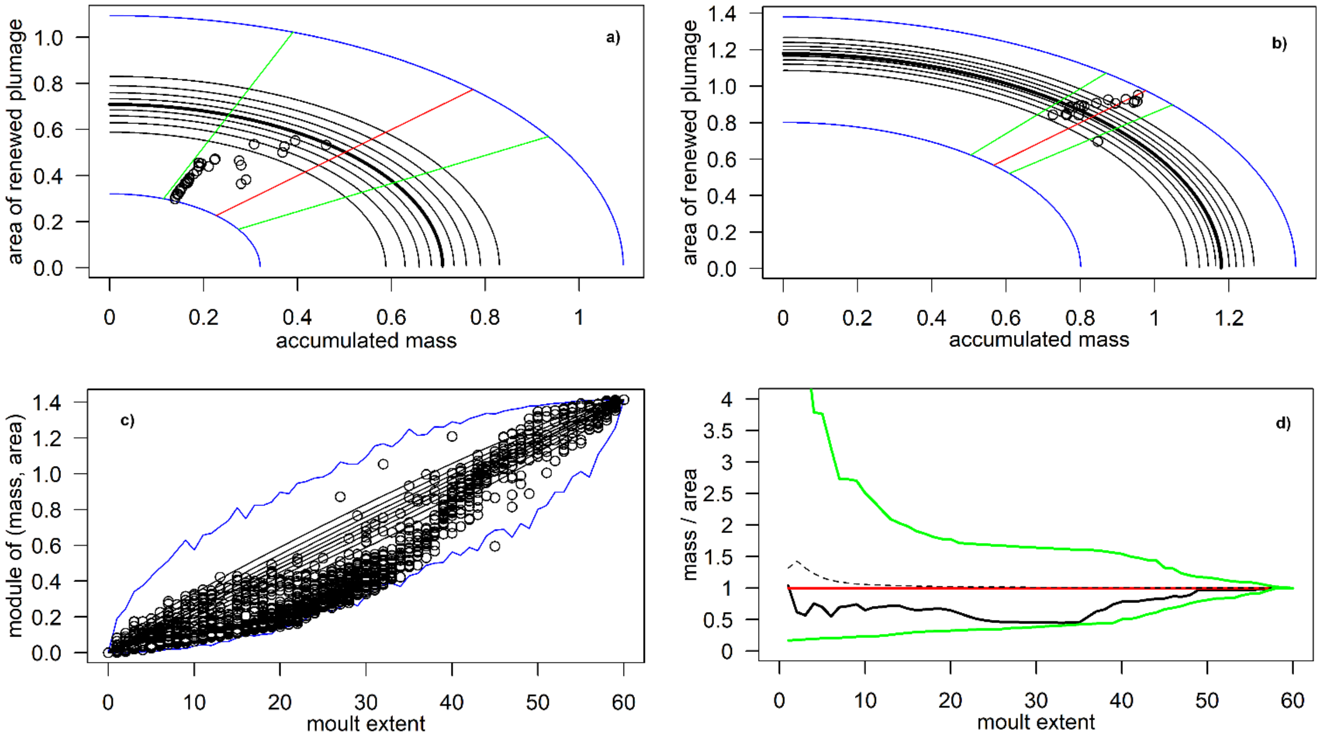
DISCUSSION

Regardless of the evolutionary processes that shaped biological traits and the physiological processes that regulate their expression, the final phenotype is constrained by the morphological properties of anatomical traits. Rohwer *et al.* (2009) proposed that morphological constraints may shape moult strategies, such that the larger the bird species the longer the moult duration, ultimately imposing a limit to the size of flying birds, because flight feathers of larger bird species would degrade too much before being replaced. We studied how morphology can constrain bird moult, specifically how formation of the final moult phenotype is constrained by two morphological properties of the wing plumage in passerines. Our results lend support to the main predictions of three hypotheses about the role that play plumage morphology on the formation of the final moult phenotype: passerines show energy-saving strategies during moult, optimise the energy invested in moult in relation to area of renewed plumage, and vary these moult strategies throughout life-history stages.

Energy-saving strategies

Moult phenotypes of passerines are lighter than expected by chance, which reveals the action of energy-saving strategies that go beyond the mere fact of retaining part of the plumage: passerines favour the replacement of light feathers during partial moults. Peak of energy saving occurs for intermediate values of moult extent, and associates with the retention of primaries. Curve shapes suggest that this saving strategy is constrained by sheer feasibility: the larger the number of possible combinations among replaced feathers the larger the magnitude of energy saving (Figs. 1a, S2). As soon as primaries are moulted, energy investment in moult logically increases because remiges are the heaviest wing feathers (Fig. S3).

Figure 2. Passerine species optimise the relationship between moult investment and area of renewed plumage throughout moult extent. Two slices showing the deciles obtained from resampling (minimum and maximum blue curves, mean green curve, black curves deciles at (a) extent = 30 and (b) extent= 50). Points depict the empirical values obtained for the wing-feather moult of 4671 birds from 501 Holarctic and Neotropical passerine species. Red line is the bisector of the mass / area space (area > mass values lie on its left side) and is defined by the sector comprised within the blue lines (maximum and minimum values of the norm η). The area of feasible mass⁄area values is a circular trapezium delimited by the green lines (maximum and minimum values of the quotient Q). c) Norm $\eta = \sqrt[2]{mass^2 + area^2}$ across moult extent (black curves show first to ninth deciles, mean shown as thicker line). d) Quotient Q = mass⁄area for the empirical and theoretical values across moult extent (thick and thin black lines, respectively). Colour of lines match those defined in panel (b).



Retention of remiges, alula feathers and primary coverts (a common postjuvenile moult phenotype; see Jenni & Winkler 2020) saves on average 85.8% of the wing-feather mass (dataset). Taking the efficiency of feather synthesis as 5% (Klaassen 1995), the energy saved by a 20 g Common Chaffinch Fringilla coelebs that retained the outer two greater coverts, alula, carpal covert, primary coverts and remiges during the postjuvenile moult would have reached 1624-2803 kJ (Dolnik & Gavrilov 1979), which amounts to 19 to 33 times the field metabolic rate for a passerine bird of its weight (Nagy 1987). Additionally, energy-saving strategies may facilitate an adequate allocation of resources among replaced wing feathers (i.e. keeping their quality; de la Hera *et al.* 2010, 2015).

However, there is a small percentage of phenotypes that are heavier than expected. These phenotypes largely correspond to minoritarian and anomalous moult patterns (Guallar & Jovani 2020b; Fig. S4). Among the former, stand out phenotypes that have been associated to a time-saving strategy in nearly complete moults (Kiat & Izhaki 2017), as well as small-extent phenotypes that replace the most exposed feathers at the end of the winter period in species that undergo a complete prebreeding moult at the beginning of the winter season (Pinilla 2001). Therefore, some scenarios may favour moult strategies other than saving energy. For example, to speed up the growth of primary feathers, thus reducing moult duration; or to replace highly exposed feathers, thus increasing signalling (e.g. body condition) and/or maintenance of worn-off areas of the wing plumage (e.g. tertials or innermost greater coverts).

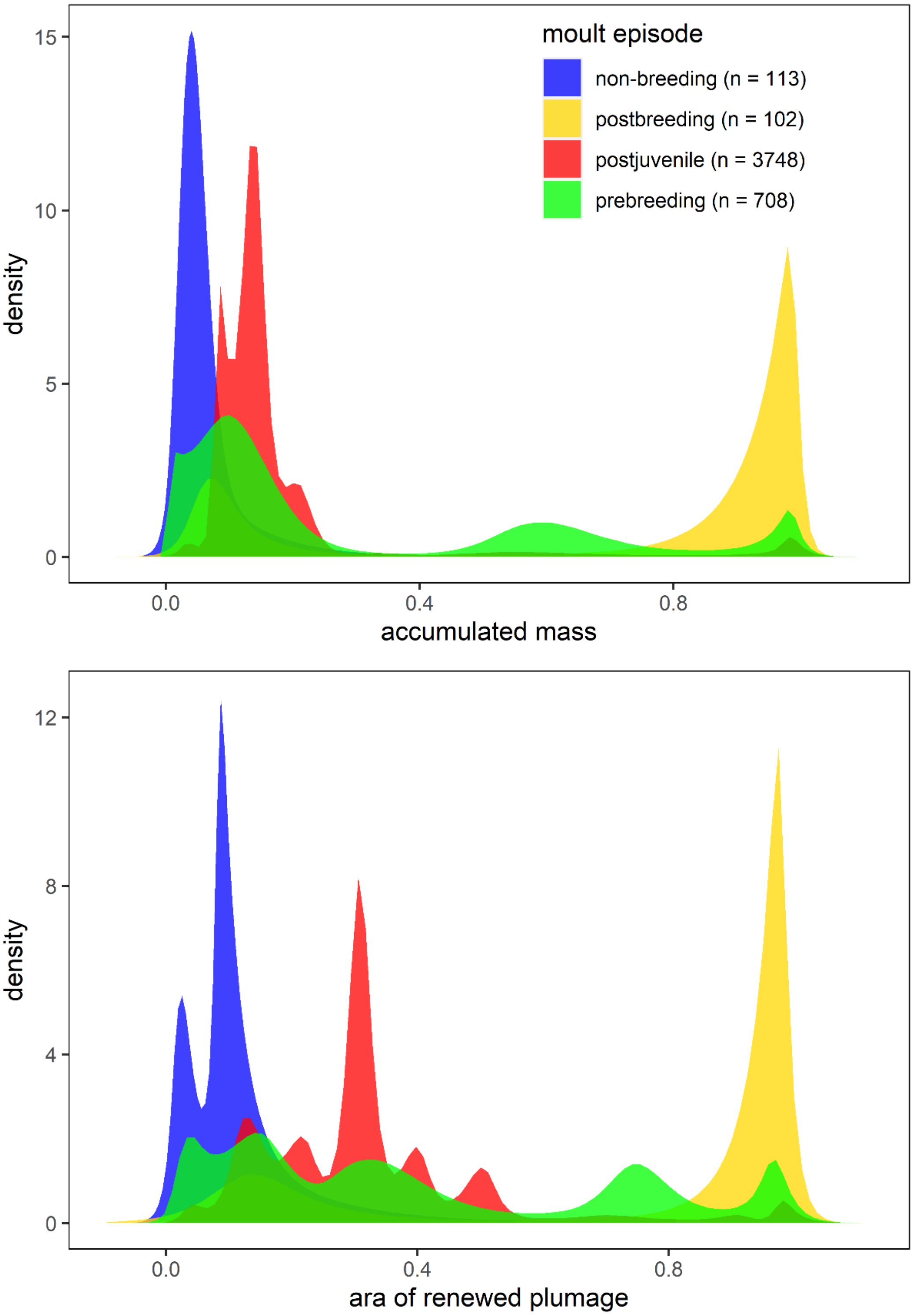
Table 1. Wilcoxon tests comparing empirical and theoretical values for accumulated mass and area of renewed plumage, and the norm $\eta = \sqrt[2]{mass^2 + area^2}$. Wing-feather moult data obtained from 4671 birds from 501 Holarctic and Neotropical passerine species. Infrequent replacement of primaries during the nonbreeding moult (only one case in our dataset) precluded tests for this moult episode.

	W	P
a) **Empirical versus theoretical mass**		
Postjuvenile	$1.4\text{x}10^8$	<0.0001
Postbreeding	8007	<0.0001
Prebreeding	$4.4\text{x}10^5$	<0.0001
Non-breeding	11865	<0.0001
b) **Retained versus replaced primaries for mass**		
Postjuvenile	66742	<0.0001
Postbreeding	262	<0.0001
Prebreeding	30389	<0.0001
Non-breeding	-	-
c) **Empirical versus theoretical area**		
Postjuvenile	$1.3\text{x}10^7$	<0.0001
Postbreeding	7089	<0.0001
Prebreeding	$2\text{x}10^5$	0.4886
Non-breeding	7458	0.0196
d) **Retained versus replaced primaries for area**		
Postjuvenile	34182	<0.0001
Postbreeding	683	0.3659
Prebreeding	26643	<0.0001
Non-breeding	-	-
e) **Empirical versus theoretical norm**		
Postjuvenile	$1.4\text{x}10^7$	<0.0001
Postbreeding	8058	<0.0001
Prebreeding	$3.8\text{x}10^5$	<0.0001
Non-breeding	9153	<0.0001
f) **Retained versus replaced primaries for the norm**		
Postjuvenile	32509	<0.0001
Postbreeding	457	0.0044
Prebreeding	28702	<0.0001
Non-breeding	-	-

Optimisation of area of renewed plumage under moult investment

Passerines also optimise the relationship between moult investment and area of renewed plumage (Fig. 2), which supports the link between moult and plumage deterioration and/or signalling. A closer look at the relation between these variables, however, suggests that replacement of worn-off plumage is not the only moult driver. For example, retention of outer secondaries and inner primaries in eccentric moults coincides with the least exposed remiges (Guallar & Jovani 2020b; Fig. S4), which have the largest detrimental aerodynamic effects during the formation of moult gaps (Hedenström & Sunada 1999). Thus, retention of these remiges not only reduces the cost and duration of feather moult, but it also reduces aerodynamic loss. This is especially important for young birds replacing remiges for the first time, when they have not fully developed yet the ability to obtain resources and to escape from predators (Wunderle 1991, Swaddle *et al.* 1999). Insightfully, eccentric moults are exceptional in adult passerine species of the Holarctic region (e.g. Wolfe & Pyle 2011).

Figure 3. Logspline density plots for accumulated mass and area of renewed plumage throughout moult extent for four moult episodes. Wing-feather moult data obtained from 4671 birds from 501 Holarctic and Neotropical passerine species. Accumulated mass shows a bimodal pattern indicating that moult episodes correlate to different energy-saving strategies. However, area of renewed plumage shows intermediate values for the prebreeding and postjuvenile moult episodes, suggesting that these moults may carry out different functions than the non-breeding and postbreeding moults.



Influence of life-history stage

Energy investment and area of renewed plumage are not uniformly distributed among moult episodes in passerines, suggesting a functional diversification of moult throughout natural-history stages. The non-breeding moult is rather homogenous and might associate to simple maintenance functions (Pinilla 2001). The postbreeding moult shows a clear bimodality, with low energy investments associated with a partial plumage renewal before the autumn migration in long-distance migrants, and maximum investments associated with the complete moult (Figs. 1 and 3). The postjuvenile moult also shows bimodal energy investment, forming two rather narrow peaks (Figs. 1 and 3), although the spread of area of renewed plumage values suggests a more complex functionality. The wide spread of the prebreeding moult also suggests this is a flexible episode, associated with heterogeneous availability of time and resources, and with function diversification (Figs. 1 and 3).

Birds experience variation in resource availability and climate conditions, especially those that live in seasonal environments, so that their ability to allocate resources among competing physiological processes is paramount to reproduce and survive (Nilsson & Svensson 1996, Monaghan & Nager 1997, Barta *et al.* 2006). In accordance, strategies that alleviate conflicts among physiological processes are expected to provide an adaptive advantage, as shown by studies about the impact of time and energy constraints on moult (Partridge & Sibly 1991, Hemborg & Lundberg 1998). These studies have found a detrimental effect on plumage quality (Hall & Fransson 2000, Serra *et al.* 2007, Dietz *et al.* 2013), which may ultimately affect survival and reproductive success (Hinsley *et al.* 2003). Non-optimal strategies may arise because of unavoidable conflicts with other physiological processes or even because of carryover effects (Dietz *et al.* 1992, Langston & Rohwer 2011). Thus, the greater the conflict between moult and other natural-history events the more likely will be the emergence of an energy-saving moult strategy.

After the first annual cycle, passerines replace their entire plumage at least once a year. To deal with this unavoidable task, most Holarctic species moult primaries in the postbreeding period. However, for migratory species, time to complete a postbreeding moult is limited by the start of autumn migration. The fact that duration of the complete moult approximately doubles the one of partial moults (Ginn & Melville 1983) may explain why dozens of long-distance migrant species postpone primary moult after autumn migration (Pyle 1997, Shirihai & Svensson 2018). Thus, for many trans-Saharan migrants, the winter season is the optimal time to moult primaries (Barta *et al.* 2008). This season lasts around six months (Newton 2008), during which no other demanding annual-cycle events might compete with moult, there are no food shortages (Barta *et al.* 2008), and the warmer climates unlikely cause cold stress (Lustick 1970, Beltran *et al.* 2018). Contrastingly, pre-Saharan migrants always schedule moult of primaries before departing the breeding grounds, and do not undergo more than one moult episode in the wintering areas (Barta *et al.* 2006, Shirihai & Svensson 2018), suggesting that the high cost of thermal insulation during the cold season and/or a decrease in food resources may inhibit moult during this period.

The regulatory pathway of moult, from gene expression to final phenotype formation, is largely unknown. However, and regardless of the involved mechanisms of control, phenotype formation necessarily depends on the morphological properties of the feathers that will channel the resources invested in moult at the end of its regulatory pathway (Minias *et al.* 2015). Variation in the investment of resources are linked to the biology of each species, and specifically associates with the life-history stages throughout their lifetime (Guallar & Jovani 2020a, 2020b). As species' natural histories have become more complex, physiological, and ecological constraints may have played ever more important roles in the evolution of their moult strategies (e.g. Kiat & Sapir 2017). Among them, energy-saving strategies may be paramount to an adequate resource allocation among moult and other physiological processes (Perrin & Sibly 1993).

Rohwer et al. (2009) proposed that size of remex-follicles determines moult duration, ultimately affecting large-scale moult strategies in the whole avian class. Here, we have shown that moult strategies within the order Passeriformes may also be constrained by morphological traits of the wing plumage, specifically wing-feather mass and area. Future studies should aim at establishing the relationship between final moult phenotypes and plumage function throughout the annual cycle of passerines and identifying the trade-offs between moult and other physiological processes especially during the early life of passerines.

ACKNOWLEDGEMENTS

Marina and Walo Moreno, and Laura Gangoso provided wings from prey caches. Permits to collect carcasses were granted by the Spanish regional administration Consejería de Medio Ambiente, Caza y Patrimonio, Cabildo de Lanzarote (permit ES-000687/2015), and Departament de Territori i Sostenibilitat. Generalitat de Catalunya (permit SF/0229/2019)

REFERENCES

Badyaev AV, Hill GE 2003. Avian sexual dichromatism in relation to phylogeny and ecology. *Ann. Rev. Ecol. Evol. Syst.* 34: 27–49.

Barta Z, Houston AI, McNamara JC, Welham RK, Hendenström A, Weber TP, Feró O 2006. Annual routines of non-migratory birds, optimal moult strategies. *Oikos* 112: 580–593.

Barta Z, McNamara J, Houston AI, Weber TP, Hedenström A, Feró O 2008. Optimal moult strategies in migratory birds. *Phil. Trans. R. Soc. Lond. B* 363: 211–229.

Beltran RS, Burns JM, Breed GA 2018. Convergence of biannual moulting strategies across birds and mammals. *Proc. R. Soc. Lond. B* 285: 20180318.

Ben Hamo M, Downs CJ, Burns DJ, Pinshow B 2017. House sparrows offset the physiological trade-off between immune response and feather growth by adjusting foraging behavior. *J. Avian Biol.* 48: 837–845.

Bridge ES 2008. How does imping affect wing performance. *J. Wildlife Rehab.* 29: 4–9.

Burtt EH, Ichida JM 2004. Gloger's rule, feather-degrading bacteria, and color variation among song sparrows. *Condor* 106: 681–686.

Butler LK, Rohwer S, Speidel MG 2008. Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. *J. Avian Biol.* 39: 629–639.

Corning WR, Biewener AA 1998. In vivo strains in pigeon flight feather shafts: implications for structural design. *J. Exp. Biol.* 201: 3057–3065.

de la Hera I, Hedenström A, Pérez-Tris J, Tellería JL 2010. Variation in the mechanical properties of flight feathers of the blackcap *Sylvia atricapilla* in relation to migration. *J. Avian Biol.* 41: 342–347.

de la Hera I, Pérez-Tris J, Tellería JL 2015. Adventitious feather replacement favours a more rapid regeneration of primaries over rectrices in two passerine bird species. *Ibis* 157: 883–887.

Dietz MW, Daan S, Masman D 1992. Energy requirements for molt in the Kestrel *Falco tinnunculus*. *Physiol. Zool.* 65: 1217–1235.

Dietz MW, Rogers KG, Piersma T 2013. When the seasons don't fit: speedy molt as a routine carry-over cost of reproduction. *PLoS ONE* 8: e53890.

Dolnik VR, Gavrilov VM 1979. Bioenergetics of molt in the chaffinch (*Fringilla coelebs*). *Auk* 96: 253–264.

Echeverry-Galvis MA, Hau M 2012. Molt–breeding overlap alters molt dynamics and behavior in zebra finches, *Taeniopygia guttata castanotis*. *J. Exp. Biol.* 215: 1957–1964.

Garland T Jr 2014. Quick guide: tradeoffs. *Current Biol.* 24: R60–R61.

Garland T Jr, Carter PA 1994. Evolutionary physiology. *Ann. Rev. Physiol.* 56: 579–621.

Gerken M, Afnan R, Dörl J 2006. Adaptive behaviour in chickens in relation to thermoregulation. *Arch. Geflügelk.* 70: 199–207.

Ginn HG, Melville DS 1983. *Moult in birds*. BTO, Tring.

Gosler AG 1991. On the use of greater covert moult and pectoral muscle as measures of condition in passerines. *Bird Study* 38: 1–9.

Guallar, S. and Jovani, R. 2020a. Moult nestedness and its imperfections: insights to unravel the nature of passerine wing-feather moult rules. – J. Avian Biol. 51: e02553.

Guallar S, Jovani R 2020b. Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. *Ibis* 162: 778–786.

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A 2009. *Paseriformes del Occidente de México: morfometría, datación y sexado*. Museu de Ciències Naturals de Barcelona, Barcelona.

Guallar S, Hernández-Rueda R, Pyle P 2021. Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. *Ornithology* 138.

Hall KSS 2005. Do nine-primaried passerines have nine or ten primary feathers? The evolution of a concept. *J. Ornithol.* 146: 121–126.

Hall KSS, Fransson T 2000. Lesser Whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. *J. Avian Biol.* 31: 583–587.

Hedenström A, Sunada S 1999. On the aerodynamics of moult gaps in birds. *J. Exp. Biol.* 202: 67–76.

Heise CD, Moore FR 2003. Age-related differences in foraging efficiency, molt, and fat deposition of gray catbirds prior to autumn migration. *Condor* 105: 496–504.

Hemborg C 1999. Sexual differences in moult-breeding overlap and female reproductive costs in pied flycatchers, *Ficedula hypoleuca*. *J. Anim. Ecol.* 68: 429–436.

Hemborg C, Lundberg A 1998. Costs of overlapping reproduction and moult in passerine birds: an experiment with the pied flycatcher. *Behav. Ecol. Sociobiol.* 43: 19–23.

Herremans M 1988. Postjuvenile moult, phenology and biometry of Grey Wagtails *Motacilla cinerea* migrating over central Belgium. *Ring. Migr.* 9: 103–116.

Hinsley SA, Rothery P, Ferns PN, Bellamy PE, Dawson A 2003. Wood size and timing of moult in birds, potential consequences for plumage quality and bird survival. *Ibis* 145: 337–340.

Hoye BJ, Buttemer WA 2011. Inexplicable inefficiency of avian molt? Insights from an opportunistically breeding arid-zone species, *Lichenostomus penicillatus*. *PLoS ONE* 6: e16230.

Jenni L, Winkler R 2020. *Moult and ageing of European passerines*, 2nd ed. Academic Press, London.

Johnson EI, Stouffer PC, Bierregard RO 2012. The phenology of molting, breeding and their overlap in central Amazonian birds. *J. Avian Biol.* 43: 141–154

Keast A 1996. Wing shape in insectivorous passerines inhabiting New Guinea and Australian rain forests and eucalypt forest / eucalypt woodlands. *Auk* 113: 94–104.

Kiat Y, Izhaki I 2017. Non-moulted primary coverts correlate with rapid primary moulting. *J. Avian Biol.* 48: 380–386.

Kiat Y, Sapir N 2017. Age-dependent modulation of songbird summer feather molt by temporal and functional constraints. *Amer. Nat.* 189: 184–195.

Kiat Y, Izhaki I, Sapir N 2019. The effects of long-distance migration on the evolution of moult strategies in Western-Palearctic passerines. *Biol. Rev.* 94: 700–720.

Klaassen M 1995. Moult and basal metabolic costs in males of two subspecies of stonechats: the European *Saxicola torquata rubicula* and the East African *S. t. axillaris*. *Oecologia* 104: 424–432.

Langston NE, Rohwer S 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. *Oikos* 76: 498–510.

Lindström Å, Visser GH, Daan S 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiol. Zool.* 66: 490–510.

Lindström Å, Daan S, Visser GH 1994. The conflict between moult and migratory fat deposition: a photoperiodic experiment with bluethroats. *Anim. Behav.* 48: 1173–1181.

Lindström Å, Alerstam T, Hedenström A 2019. Faster fuelling is the key to faster migration. *Nature Climate Change* 9: 288–289.

López G, Figuerola J, Varo N, Soriguer R 2005. White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed. *Ardea* 93: 237–244.

Lustick S 1970. Energy requirements of molt in cowbirds. *Auk* 87: 742–746.

Minias P, Włodarczyk R, Surmacki A, Iciek T 2015. Silver spoon effects on plumage quality in a passerine bird. *R. Soc. Open Sci.* 2: 140459.

Monaghan P, Nager RG 1997. Why don't birds lay more eggs? *Trends Ecol. Evol.* 12: 270–274.

Mulvihill RS, Chandler CR 1991. A comparison of wing shape between migratory and sedentary Dark-eyed Juncos (*Junco hyemalis*). *Condor* 93: 172–175.

Naef-Daenzer B, Gruebler MU 2016. Post-fledging survival of altricial birds: ecological determinants and adaptation. *J. Field Ornithol.* 87: 227–250.

Nagy K 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* 57: 111–128.

Newton I 2008. *The migration ecology of birds*. Academic Press, London.

Nilsson JA, Svensson E 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proc. R. Soc. Lond. B* 263: 711–714.

Partridge L, Sibly R 1991. Constraints in the evolution of life histories. *Phil. Trans. R. Soc. Lond. B* 332: 3–13.

Pennycuick CJ 1989. *Bird flight performance: a practical calculation manual*. Oxford University Press, Oxford.

Perrin N, Sibly RM 1993. Dynamic models of energy allocation and investment. *Ann. Rev. Ecol. Syst.* 24: 379–410.

Pinilla J 2001. How does the extent of a partial moult vary? Some data for Melodious Warbler *Hippolais polyglotta* in central Iberia. *Ardeola* 48: 81–84.

Pyle P 1997. *Identification guide to North American birds. Part I: Columbidae to Ploceidae*. Slate Creek Press, Bolinas, CA.

R Development Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rohwer S, Ricklefs RE, Rohwer VG, Copple MM 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biol.* 7: e1000132.

Rudis B 2019. gglogspline: A 'ggplot2' extension for visualizing density, distribution, hazard, or survival functions using the 'logspline' package. R package version 0.1.0. https://gitlab.com/hrbr mstr /gglogspline

Schmaljohann H 2019. The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: a cross-continental analysis. *Movement Ecol.* 7: 25.

Senar JC 2006. Color displays as intrasexual signals of aggression and dominance. In *Bird coloration: function and evolution* (Hill GE, McGraw KJ, eds.). Harvard University Press, Cambridge.

Senar JC, Copete JL, Martin AJ 1998. Behavioural and morphological correlates of variation in the extent of postjuvenile moult in the Siskin *Carduelis spinus*. *Ibis* 140: 661–669.

Serra L, Griggio M, Licheri D, Pilastro A 2007. Moult speed constrains the expression of a carotenoid-based sexual ornament. *J. Evol. Biol.* 20: 2028–2034.

Shirihai H, Svensson L 2018. *Handbook of western Palearctic birds: passerines.* Helm, London.

Stekhoven DJ, Buehlmann P 2012. MissForest - non-parametric missing value imputation for mixed-type data. *Bioinformatics* 28: 112–118.

Swaddle JP, Williams EV, Rayner JMV 1999. The effect of simulated flight feather moult on escape take-off performance in starlings. *J. Avian Biol.* 30: 351–358.

Terrill, RS, Seeholzer GF, Wolfe JD 2020. Evolution of breeding plumages in birds: a multiple-step pathway to seasonal dichromatism in New World warblers (Aves: Parulidae). *Ecol. Evol.* 10: 9223–9239.

Weber TP, Borgudd J, Hedenström A, Persson K, Sandberg G 2005. Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species. *Biol. Lett.* 1: 27–30.

Willoughby EJ 1991. Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proc. West. Found. Vert. Zool.* 4: 247–286.

Wingfield JC 2008. Organization of vertebrate annual cycles: implications for control mechanisms. *Phil. Trans. R. Soc. B* 363: 425–441.

Wolfe JD, Pyle P 2011. First evidence for eccentric prealternate molt in the Indigo Bunting: possible implications for adaptive molt strategies. *Western Birds* 42: 257–262.

Wunderle JM 1991. Age-specific foraging proficiency in birds. *Current Ornithol.* 8: 273–324.

SUPPLEMENTARY INFORMATION

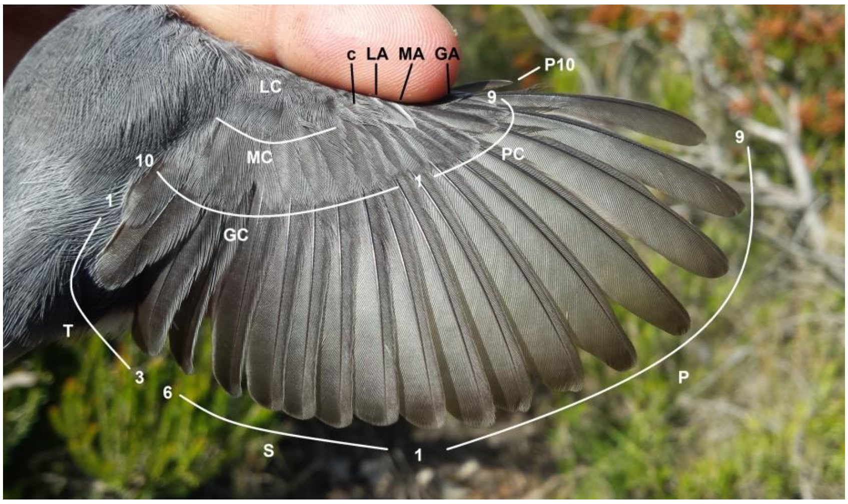
Table S1. Post-hoc Dunn tests (following Kruskal-Wallis test) using Benjamini-Hochberg adjustment as implemented in the R package FSA (Ogle *et al.* 2019). Results from multiple comparisons among moult episodes.

	Z	P
Mass		
non-breeding - postbreeding	0.7080	0.4789
non-breeding - postjuvenile	-16.2793	< 0.0001
postbreeding - postjuvenile	-16.4524	< 0.0001
non-breeding - prebreeding	-3.1604	0.0016
postbreeding - prebreeding	-3.9360	0.0001
postjuvenile - prebreeding	30.1180	< 0.0001
Area		
non-breeding - postbreeding	0.2985	< 0.7653
non-breeding - postjuvenile	-14.4551	< 0.0001
postbreeding - postjuvenile	-14.1594	< 0.0001
non-breeding - prebreeding	-1.0623	0.3457
postbreeding - prebreeding	-1.4011	0.2418
postjuvenile - prebreeding	31.0541	< 0.0001
Norm (mass, area)		
non-breeding - postbreeding	0.3321	0.7398
non-breeding - postjuvenile	-16.0371	< 0.0001
postbreeding - postjuvenile	-15.7102	< 0.0001
non-breeding - prebreeding	-1.9223	0.0655
postbreeding - prebreeding	-2.2669	0.0351
postjuvenile - prebreeding	32.6142	< 0.0001

Table S2. We found 28 species in our dataset that may undergo incomplete postbreeding moults. Of these, 23 undergo true partial postbreeding moults, whereas we detected suspended or anomalous moults in five species (anomalies are likely ubiquitous). Within some genera, species that breed in temperate regions and winter in the tropics may undergo partial postbreeding and complete prebreeding moults, whereas species that breed and winter in temperate regions always undergo complete postbreeding moults (in case they present prebreeding moult, it is always partial).

Species	**Postbreeding moult**
Acrocephalus warblers (seven trans-Saharan migrants)	partial
Anthus campestris	suspended
Arremon aurantiirostris	suspended
Nearctic *Contopus* (two Neotropical migrants)	partial
Dolychonix oryzovorus	partial
Empidonax traillii	partial
Hippolais polyglotta	partial
Hirundo rustica	partial, suspended
Lanius bucephalus	partial
Lanius collurio	partial
Lanius isabellinus	anomalous, partial
Lanius schach	partial
Locustella luscinioides	suspended, eccentric
Locustella naevia	partial, suspended
Motacilla flava	anomalous
Muscicapa striata	partial
Myiodynastes luteiventris	partial
Oriolus oriolus	partial
Phylloscopus warblers (two trans-Saharan migrants)	partial
Riparia riparia	partial, suspended
Saltator coerulescens	suspended
Sitta europaea	anomalous
Sylvia borin	partial, suspended
Sylvia hortensis	suspended

Figure S1. The upper-wing plumage is arranged in several feather rows of three types: alula or bastard wing, coverts, and remiges. Alula: LA, lesser alula; MA, median alula; GA, greater alula. Coverts: LC, lesser coverts; MC, median coverts; GC, greater coverts; c, carpal covert; PC, primary coverts. Remiges: T, tertials; S, secondaries; P, primaries. Sardinian Warbler *Sylvia melanocephala*, Catalonia 26 December 2017.



©Marc Illa

Figure S2. Mean wing-feather mass accumulated during moult for the Spotted Flycatcher *Muscicapa striata*. Each line shows the values obtained by sampling all possible wing-feather combinations for a given moult extent along a range of sample sizes, from 10 up to 50 million. Notice that the values converge very fast and stabilise around 10000.

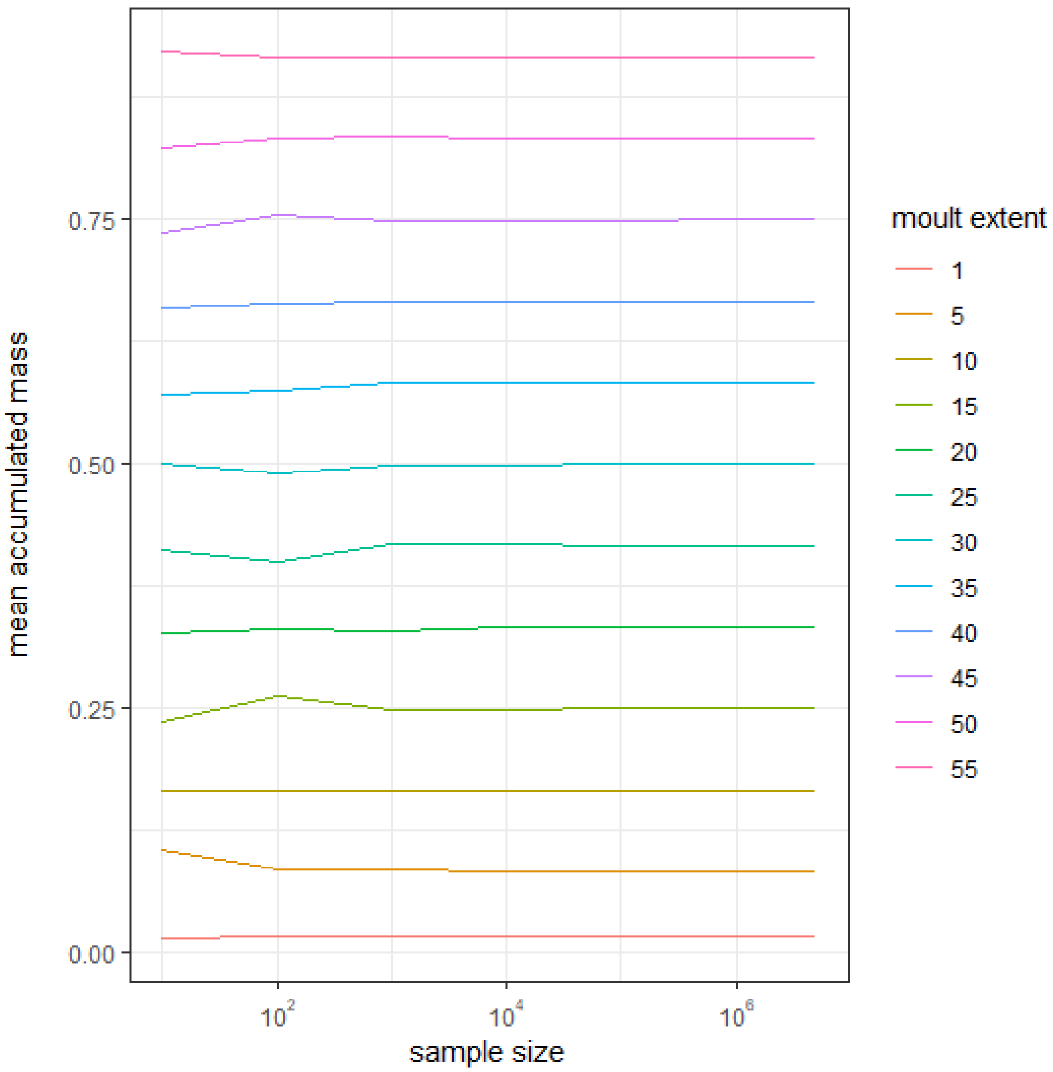


Figure S3. Differences between theoretical and empirical values of wing-feather mass throughout the range of moult extent in four moult episodes. Wing-feather moult data obtained from 4671 birds from 501 Holarctic and Neotropical passerine species. 96.38% empirical mass values are lower than expected by chance, indicating that passerine species follow energy-saving strategies during moult. Lines are fitted generalised additive models.

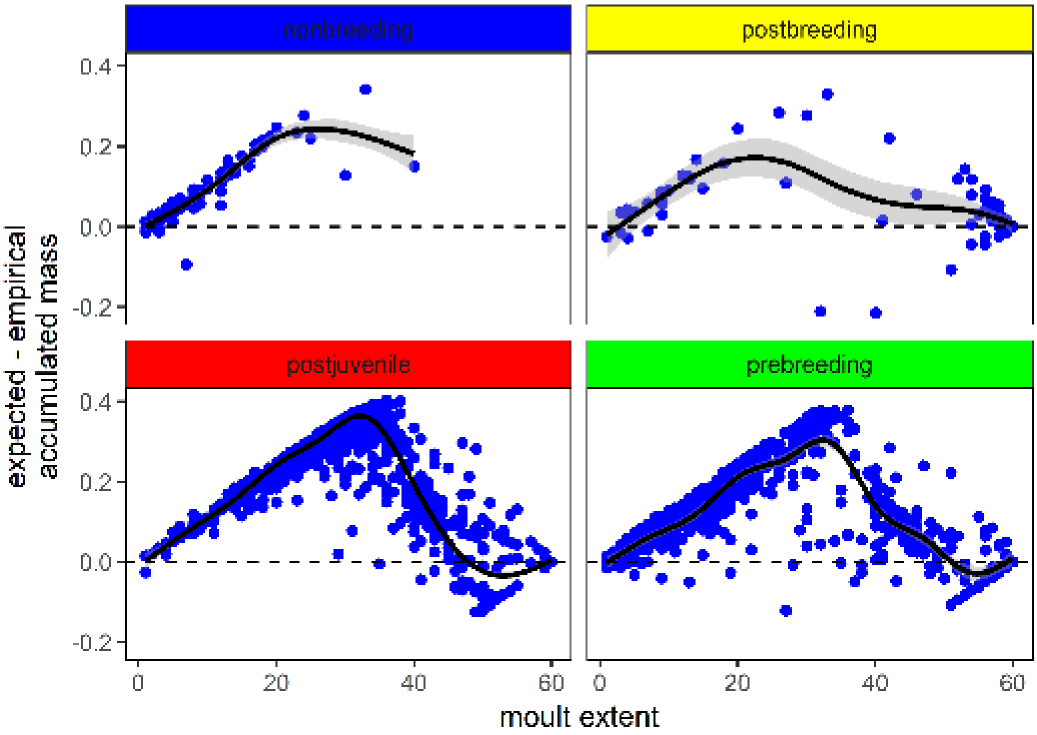


Figure S4. Distribution of relative masses of individual remiges and wing coverts (n = 86 individuals of 43 species). Feather masses for each species normalised by total wing-feather mass. Carpal covert included within the median coverts (MC). Red point and lines indicate mean and standard deviation. Variation of greater, lesser, median, and primary coverts (GC, LC, MC, PC) largely driven by variation among feathers within these tracts. Variation of alula feathers driven by size differences of greater alula among species. Primaries forming the wing tip (P6 to P9) show the largest variation among species.

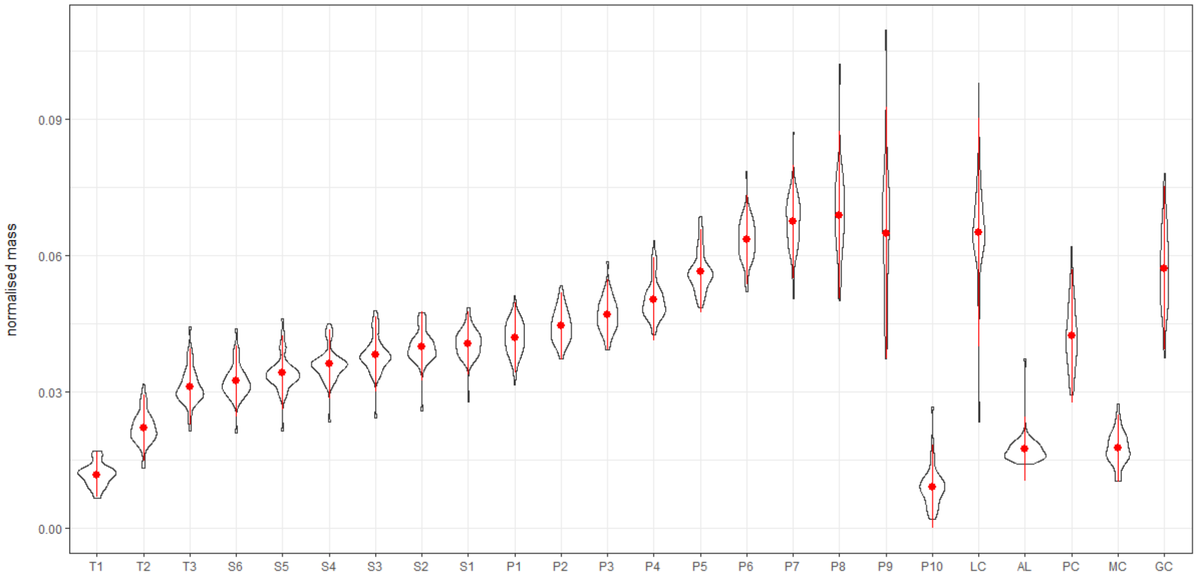
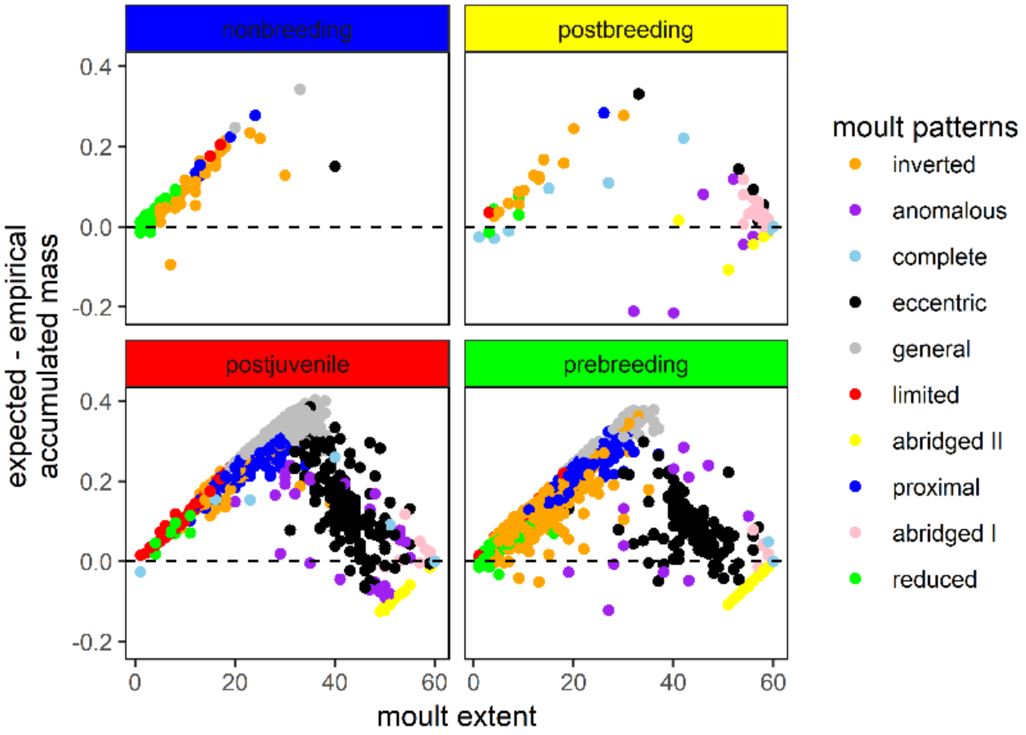
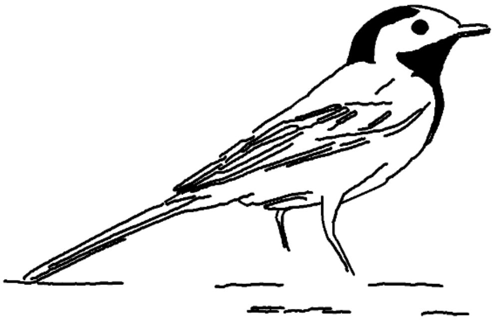


Figure S5. Differences between theoretical and empirical values of wing-feather mass throughout the range of moult extent in four moult episodes. Wing-feather moult data obtained from 4671 birds from 501 Holarctic and Neotropical passerine species. Points show 10 moult patterns (Guallar & Jovani 2020). 98.65% abridged II (replacement of all feathers except primary coverts), 33.93% anomalous (phenotypes that cannot be assigned to the other nine moult patterns), and 24.34% reduced (replacement of one to a few tertials and/or greater coverts) phenotypes are heavier than expected by chance. Remaining moult patterns show fewer than 7% phenotypes heavier than expected.





Chapter 4

Factors influencing the evolution of moult in the nonbreeding season: insights from the family Motacillidae

Santi Guallar [1*] & Jordi Figuerola [2]

[1] Galanthus, Carretera de Juià, 46, Celrà, Girona, 17460

[2] Department of of Wetland Ecology, Estación Biológica de Doñana, CSIC, Americo Vespucio s/n., 41092 Sevilla, Spain

Published in: Guallar S, Figuerola J 2016. Factors influencing the evolution of moult in the nonbreeding season: insights from the family Motacillidae. *Biol. J. Linn. Soc.* 118: 774–785.

ABSTRACT

The number of moults per annual cycle and their final spatial pattern (i.e. topography) show high interspecific variation in the order Passeriformes. Factors behind this variability remain obscure, especially for variability in spatial pattern among species. Here, we explored the relative influence of ten ecological, ontogenetic, social and sexual factors on the evolution of autumn moult (feather replacement largely undertaken by migratory species, which is not necessarily an independent episode within their moult cycle) and prealternate moult among Northern Hemisphere species of the family Motacillidae using phylogenetically controlled analyses, ancestral state reconstruction and analyses of correlated evolution. The results strongly support the presence of prealternate moult and absence of autumn moult as ancestral states in this family. A high rate of change between related species indicates phylogenetic independence among prealternate moult patterns and examined factors. Migration distance and gregariousness are the most important factors influencing prealternate moult evolution and point toward natural selection and sociality as the most important evolutionary drivers of prealternate moult in Motacillidae. Breeding latitude, seasonal plumage change, winter plumage conspicuousness, sexual dichromatism, plumage maturation and extent of preformative moult show a minor influence and suggest that ontogeny and sexual selection may have played a limited role in shaping prealternate moult in Motacillidae.

INTRODUCTION

Moult is the process that allows the maintenance and adjustment of plumage functionality throughout the annual cycle (Jenni & Winkler 1994). A high amount of variability in moult strategy within and among species (Svensson 1992, Pyle 1997) is achieved through many elements that integrate a species' moult strategy (Barta *et al.* 2006): topography (the spatial configuration of the replaced feathers after a moult; Guallar *et al.* 2014), energetic requirements, feather quality, number and timing of moults per cycle, intensity, duration and order of replacement. Moult strategies may affect survival and fitness (Holmgren & Hedenström 1995) and have likely evolved in response to shifts in natural history and environmental parameters (Rohwer *et al.* 2009, Pap *et al.* 2015).

Until now, most studies have emphasised the evolution of the preformative and definitive prebasic moults (equated to the postjuvenile and postnuptial moults, respectively; terminology follows Howell *et al.* 2003), while other moults have received less attention. The presence of a single moult within the annual cycle, the prebasic moult, is the ancestral state in passerines, and the addition of the prealternate moult (equivalent to the prenuptial moult) is considered an autapomorphy with multiple independent evolutionary origins (Figuerola & Jovani 2001, Howell *et al.* 2003). The prealternate moult is largely undertaken by migratory species before departing their wintering grounds. However, the existence of other moult episodes is controversial. In particular, the replacement of feathers upon arrival into the winter grounds - usually in early autumn- is rarely acknowledged as an independent episode (Howell *et al.* 2003, Newton 2008: 305-306). Autumn feather replacement of migratory passerines has been routinely reported in their winter grounds (Shirihai *et al.* 2001; Alström & Mild 2003, Guallar *et al.* 2009), but it usually involves only body feathers, suggesting the end of a previous 'true' moult episode, suspended or not (birds may migrate while still replacing part of their body plumage, even the juvenal one, which may affect aerodynamics; Butler, Donahue & Rohwer 2002). Some migratory species are known to suspend their prebasic/preformative moult by the onset of migration (e.g. Alström & Mild 2003), although some clearly have an autumn moult episode (e.g. *Passerina* buntings and Bell's Vireo *Vireo bellii*; Guallar *et al.* 2009). Anyway, autumn moulting may constitute an individual or species level strategy to cope with tight complex annual cycles (Wingfield 2008). Besides taking place outside the breeding grounds, prealternate and autumn moults neither overlap in time nor interact directly with reproduction. For these reasons, we categorise them as "non-breeding moults". Migration is a strong selective factor that influences the evolution of non-breeding moult strategies (Svensson & Hedenström 1999, Figuerola & Jovani 2001), but other factors may also affect the timing and duration of moult. For example, depletion of food resources and presence of predators may affect schedule of primary moult (Ydenberg *et al.* 2007, Voelker & Rohwer 1998, Rohwer *et al.* 2005), and moult duration is related to wing size (Bridge *et al.* 2007, Rohwer *et al.* 2009)

Evolution of moult may have not only been affected by natural selection, but also by sexual selection (Simpson & Campbell 2013). Birds use different plumage characteristics for mate choice (Zahavi 1997), and the emergence of the prealternate moult in a species annual cycle could have been targeted by sexual selection to produce a brighter plumage during the mating season (Figuerola & Jovani 2001, Peters 2007). The extent of the preformative moult may also serve as an indicator of health status (Senar *et al.* 1998, López *et al.* 2005).

For these reasons, natural and sexual selection appear to be drivers of moult evolution. Here, we use phylogenetically controlled comparative analyses to evaluate the relative influence of different ecological, social and sexual factors on the evolution of non-breeding moult among species of the family Motacillidae, which has a well-documented and highly diverse natural history (Cramp 1988, Alström & Mild 2003). We focused on the 25 of the 31 species of this family breeding in the Northern Hemisphere with published descriptions of non-breeding moult.

We test six hypotheses on the potential factors mentioned above. First, migratory behaviour may have favoured the evolution of non-breeding moults. If this is the case, we can expect more extensive non-breeding moults as migratory distance increases. This hypothesis has already received support from previous studies analysing the number, seasonality and extent of moult in some European passerines (Svensson & Hedenström 1999, Figuerola & Jovani 2001) although it has not been tested for the autumn moult. One mechanism proposed to explain this effect is a reduction in feather quality induced by time constraints (de la Hera *et al.* 2009) arising from ever tighter moult schedules, so that birds which have less time available to grow high quality feathers (Hall & Fransson 2000, Dawson 2004). Species under strong time constraints before departing the breeding grounds tend to present more moult episodes and more extensive ones than those that do not face time constraints (Holmgren & Hedenström 1995). Exposure to increased solar radiation in winter grounds as migration distance increases is also thought to explain this effect (Bergman 1982, Figuerola & Jovani 2001).

Latitude may have influenced the evolution of non-breeding moult episodes as well. This second hypothesis suggests that time for moult is constrained by climatic conditions at northern latitudes (Dawson 2008). According to this hypothesis, species breeding at higher latitudes may experience increasing time constraints and may grow lower quality feathers (Hall & Fransson 2000, Kiat & Izhaki 2016) which they would tend to renew as soon as possible after departing the breeding grounds. Consequently, autumn moult will be more frequent and will tend to be more extensive in these species. Extreme time constraints before migration would tend to cause very reduced prebasic or preformative moults (Barta *et al.* 2006). However, sexual selection would not exert pressure on this moult in Motacillidae, since autumn moult in species of this family do not involve changes in coloration, and autumn plumage is overridden by the prealternate moult before the onset of the breeding season.

The third hypothesis states that the prealternate moult may have evolved to allow plumage coloration changes. Seasonal changes can be achieved through wear (e.g. in Common Reed Bunting *Emberiza schoeniclus*; Cramp & Perrin, 1994), photooxidation (e.g. in Common Linnet *Carduelis cannabina*; Blanco *et al.* 2005), but most species achieve them through moult. The prealternate moult may become more extensive to allow larger plumage changes. The same effect could be found in conspicuous species to allow the acquisition of brighter alternate plumages. Note that seasonal changes in plumage coloration are not necessarily associated with sexual dichromatism (e.g. Water Pipit *Anthus spinoletta*).

The fourth hypothesis posits that the evolution of prealternate moults may have been driven by sexual selection. Moult is an energetically costly process (Murphy 1996), and as such may honestly signal physical condition; therefore, individuals with more extensive prealternate moult may have an advantage as potential breeding mates. Sexual selection also predicts more extensive prealternate moult as sexual dichromatism becomes greater: species with sexual marks restricted to an area of the body - such as the eyebrow of Blue-gray Gnatcatcher *Polioptila caerulea* (Guallar *et al.* 2009)- would tend to replace fewer feathers than species with overall dichromatic plumage such as Summer Tanager *Piranga rubra* (Pyle 1997). Here, we test the second prediction of this hypothesis: the influence of dichromatism on moult evolution.

The fifth hypothesis posits that social selection may have influenced the evolution of non-breeding moults through the acquisition of new functions such as status signalling. Gregarious species display badges of status (Tibbets & Safran 2009, Chaine *et al.* 2013) and their signal phenotype likely express other aspects of their social environment (Dey *et al.* 2014) which can be mediated through non-breeding moults. This hypothesis predicts more extensive non-breeding moults in more gregarious species (likely associated with higher social complexity).

Finally, the sixth hypothesis posits that ontogenetic factors may have contributed to shaping non-breeding moults. Plumage maturation is delayed in first-cycle individuals of many species until the prealternate moult (Rohwer *et al.* 1980, Hill 1996). This delay may have selected for a more extensive first prealternate moult in order to acquire an alternate plumage as similar to the definitive alternate plumage as possible. Partial preformative moults could have influenced non-breeding moult evolution, since plumage gaps should be filled and formative feathers of potentially lower quality (Butler *et al.* 2008, Echeverry-Galvis & Hau 2013) replaced as soon as possible.

MATERIALS AND METHODS

Dataset and phylogenetic relationships

We obtained information on moult strategies, plumage characteristics, gregariousness, habitat occurrence and latitudinal distribution of Motacillidae of the Northern Hemisphere from Alström & Mild (2003; see Table S1 and the online data file). When intraspecific variation in the variable of interest exists, we discarded infrequent values and calculated the arithmetic mean of the remaining ones. We completed gaps on gregariousness using information from Étchecopar & Hüe (1983) and Ali & Ripley (1993).

We visually scored dichromatism, conspicuousness and seasonal plumage change for each species using illustrations in Alström & Mild (2003). To reduce subjectivity, we averaged the scores of three observers for each of these variables.

We included body mass as a surrogate of size (data from Dunning 2007). Since no information on body mass of the recently described Mekong Wagtail *Motacilla samveasnae* is available, we took it as the mean of White Wagtail and African Pied Wagtail *Motacilla aguimp*, due to the similarity to these two species (see Diagnosis in Duckworth *et al.* 2001).

Species range maps were downloaded from BirdLife International and NatureServe (2014). Migration distance was computed as the kilometres between the centroid of the wintering range and the centroid of the breeding range using QGIS (QGIS Development Team 2015). Centroids were weighted by the area of polygons. Latitudinal distances between the breeding and wintering centroids were calculated using Geographic Distance Matrix Generator (Ersts 2015).

We created four categories of mass and breeding latitude from the computation of three quartiles on our dataset (Table S1). Likewise, we created three categories of migration distance by computing two quartiles for migratory species and added a fourth category for non-migrant species. The purpose of using the same scale for all covariates was to allow direct comparisons among the model estimates.

For our working phylogeny we downloaded 10000 trees for our set of species from birdtree.org (Jetz *et al.* 2012), and then derived a consensus tree, assigned all internode branches equal to one and forced tips to be contemporaneous (Page 1992). We used Slate-throated Redstart *Myioborus miniatus* as the outgroup (data from Guallar *et al.* 2009).

To check sensitivity to phylogeny, we replicated all our analyses using published phylogenetic trees for this family (Voelker 1999, Alström & Ödeen 2002). Since results only show minor differences, we included our replicates in the Online Supporting Information (Figs. S4, S5, Table S5).

Influence of natural history factors

To control for the phylogenetic relationship among the sampled species we used phylogenetic generalised least squares regression models (PGLS; Pagel 1997, 1999) as implemented in the R statistical environment (R Foundation for Statistical Computing 2015) and the libraries ape, geiger and nlme. The PGLS approach controls for non-independence among species by incorporating a matrix of the covariances based on their phylogenetic relationships (Martins & Hansen 1997, Pagel 1997, 1999).

We estimated the phylogenetic signal (λ) using the unpublished function pglm3.3.r, (R. Freckleton, University of Sheffield). The phylogenetic signal represents the importance of phylogenetic correlation within the data (Freckleton *et al.* 2002) and varies between 0 and 1. We then tested the statistical significance of λ against theoretical values of 0 and 1 using likelihood ratio tests. Finally, λ was incorporated in the correlation structure of the PGLS models to control for the effect of phylogenetic relationship (Harvey & Pagel 1991, Martins & Hansen 1997).

We first explored the relative importance of nine covariates on the prealternate and the autumn moults in two sets of PGLS models: migratory strategy, mean breeding latitude, seasonal plumage coloration change (only in prealternate models since autumn moult are not associated with changes in plumage coloration), male basic plumage conspicuousness, sexual dichromatism in alternate plumage, gregariousness in the non-breeding season, non-breeding moult pattern (autumn on models with prealternate moult as response and vice-versa), habitat, and body mass (Table S1). Each set of models contains all combinations among the covariates (2048 models for the prealternate moult as response, and 512 models for the autumn moult as response).

We also investigated the possible influence of ontogeny on prealternate and autumn moults by including two age-specific covariates, plumage maturation and preformative moult, in two new sets of models. Again, each of these two sets of PGLS models contains all possible combinations among the covariates.

We ranked the models according to their AICc values and calculated the relative importance of each covariate based on its Akaike weight using the zero-method implemented in package MuMIn. In the zero method (Burnham & Anderson 2002), all covariates absent from models are substituted by zeros, and estimates are obtained by averaging over all models in the top model set (Grueber *et al.* 2011). This method is recommended in studies aiming at determining which factors have the strongest effect on the response variable (Nakagawa & Freckleton 2011). As we standardised our covariates, we assessed their relative magnitude and direction directly. Each estimated coefficient in the average model equates to effect size of its corresponding covariate (Grueber *et al.* 2011). We expressed parameter uncertainty by means of the estimated standard error (Burnham & Anderson 2002), and model uncertainty as the percentage of models used to create the 95% confidence sets of models (McAlpine *et al.* 2008).

We compared migration distance and breeding latitude among species with or without non-breeding moults, using phylogenetic ANOVA (Garland *et al.* 1993) using the phytools package.

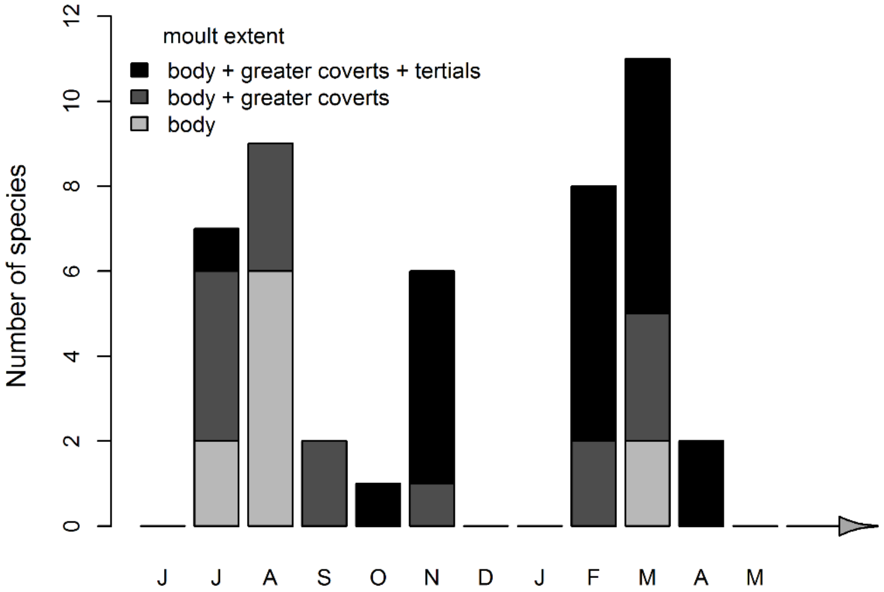
Ancestral state reconstruction and correlated evolution

We first tested for differences in transition rates between states using default settings in BayesTraits (Pagel 1999, Pagel *et al.* 2004). The significant differences between transition rates were incorporated in subsequent analyses. Next, we checked whether the evolution of non-breeding moult was directional. Model selection was based on Bayes factors (Kass & Raftery 1995).

We reconstructed ancestral state of non-breeding moults in our replicate phylogeny (Fig. S1) calculating state likelihoods at each node to determine final maximum likelihood of the ancestral state (Schluter *et al.* 1997). We dealt with the polytomy by averaging the values of the involved species (all absences for the autumn moult, two presences and two absences for the prealternate moult).

Reliable statistical inference could not be drawn for the autumn moult because of the low number of species which present it (n = 7). Nevertheless, we show the output of correlated evolution and relative importance analyses for this moult in the Supplementary Information.

Figure 1. Annual moult cycle of Northern Hemisphere Motacillidae (prebasic moult is not shown). Preformative moult shows the widest range of moult extent values. Autumn moult takes place right after migration from the breeding grounds and prealternate moult before the migration to the breeding grounds. It is important to bear in mind that autumn moulting could actually be the completion of suspended or protracted prebasic/preformative moults in some cases. Moult extent values were rounded to the nearest integer. Each species' moult was assigned to the second month of the period recorded by Alström & Mild (2003) because this likely coincides with moult peak (highest overlap of individuals and highest moult intensity). Prealternate moult phenology of Paddyfield Pipit *Anthus rufulus* and Mekong Wagtail have not been documented yet and are not included here. Legend refers to categories defined in Table S1.



RESULTS

Phenology of non-breeding moults in Motacillidae of the Northern Hemisphere is synthesised in Fig. 1. Only four species (16%) do not show non-breeding moults, all of which are non-migratory except the Japanese Wagtail *Motacilla grandis* (a short-distance migrant). The remaining species undergo either prealternate moult or autumn plus prealternate moults (only seven species show autumn moult, 28%). There were no species which only underwent autumn moult. Alström & Mild (2003) state that in species with two non-breeding moults the same feathers are replaced in both episodes.

Relative importance of natural history factors

Migration distance, gregariousness and seasonal change are the most important factors influencing prealternate moult, with maturation ranking fourth in first-cycle birds (although the latter two factors with much lower relative importance values; Fig. 2). However, only migration reached statistical significance in the averaged model. Breeding latitude, sexual dichromatism, plumage conspicuousness and preformative moult had little influence. Coefficients of the covariates had the expected signs: positive for all of the previously mentioned covariates except preformative moult, conspicuousness, dichromatism and habitat (Table 1). Model and parameter uncertainty are moderately high (Fig. 2, Table 1).

The phylogenetic signal λ < 0.001 for all models was significantly different from 1 (loglik > 8.43, P < 0.004) but not from 0 (loglik < -0.001, P = 1), which implies phylogenetic independence due to a very high rate of change between related species.

Species with autumn moult (mean ± SE migration distance 3158.58 ± 2064.08 km, n = 7) and species without it (2856.23 ± 2463.72 km, n = 18) did not show significant differences ($F_{1,24}$ = 0.08, P = 0.88). We did not find significant differences between the number of migratory and non-migratory species with autumn moult (Chi square test χ^2 = 0.30, P = 0.58). Species with prealternate moult (mean ± SE migration distance = 3426.78 ± 2195.46 km, n = 21) undertook significantly longer migrations than species without it (389.96 ± 799.92 km, n = 4; $F_{1,24}$ = 7.26, P = 0.007).

Species with autumn moult (mean ± SE breeding latitude = 35.55 ± 21.05°, n = 7) bred farther south than species without it (43.63 ± 19.88°, n = 18). Again, differences were not significant ($F_{1,24}$ = 0.81, P = 0.60).

Migration distance did not influence the occurrence of non-breeding moults, and no differences in migratory distance were found between species with prealternate moult 3560.87 ± 2321.85 km, n = 14) and species with both prealternate and autumn moult (3158.58 ± 2064.08 km, n = 7, $F_{1,24}$ = 1.84, P = 0.21).

Table 1. Results of PGLS analyses of 10 natural history covariates on prealternate moult. Coefficients (adjusted standard error) with shrinkage are based on the subset of total averaged models whose accumulated Akaike weights reached 95%. Significance is indicated by bold type. Only migration distance and gregariousness had noticeable effect sizes.

	Autumn	**Conspicousness**	**Dichromatism**	**Gregariousness**	**Habitat**	**Latitude**	**Mass**	**Maturation**	**Migration**	**Preformative**	**Season**
First-cycle	0.01	-0.04	-0.05	0.25	-0.01	0.04	0.03	0.08	**0.59**	-0.05	0.09
	(0.07)	(0.19)	(0.21)	(0.29)	(0.08)	(0.20)	(0.10)	(0.21)	**(0.30)**	(0.15)	(0.20)
Definitive cycles	0.01	-0.02	-0.03	0.28	-0.01	0.05	0.03		**0.61**		0.11
	(0.07)	(0.13)	(0.17)	(0.29)	(0.08)	(0.20)	(0.10)		**(0.30)**		(0.21)

Ancestral state reconstruction and correlated evolution

Evolutionary gains of prealternate moult were more frequent than losses (logBF = 7.88) and transitions towards autumn moult were also more frequent than losses (logBF = 2.54).

We found no support for directionality in the evolution of non-breeding moults (logBF = 0.45 for prealternate moult; logBF = 1.12 for autumn moult).

Our reconstruction of non-breeding moult strongly supports the presence of prealternate moult as an ancestral state (likelihood = 0.96) of Motacillidae breeding in the Northern Hemisphere but not autumn moult (likelihood = 0.82) (Fig. 3).

The four wagtails included in the polytomy, plus the clade encompassing the seven species from Long-billed Pipit *Anthus similis* to Upland Pipit *Anthus sylvanus* contain all non-migratory species that breed in more southern latitudes (Fig. 3). Unexpectedly, the latter clade contains 71% (5) of all species with autumn moult (Fig. 3). We found very strong support for the correlated evolution of the prealternate moult and the two most important covariates that influence it:

migration and gregariousness (Table 2). Species without autumn moult have a plumage throughout the winter that is acquired either in the prebasic or the preformative moult. As the prebasic moult is always complete in this family, variation in the extent of the preformative moult might be influenced by some of these natural history factors. Since 16 of the 18 species which did not present autumn moult showed winter gregariousness, we also checked the correlation between preformative moult and winter gregariousness and found a strong association (logBF = 2.65), which suggests an influence of sociality on the evolution of this moult episode.

Figure 2. Relative importance of covariates used for prealternate moult models based on the subset whose accumulated Akaike weights reached 95% of the total averaged models: 529 and 154 for first and definitive cycles, respectively, which corresponds to 25.8% and 30.1% model uncertainty. The scale indicates sum of Akaike weights.

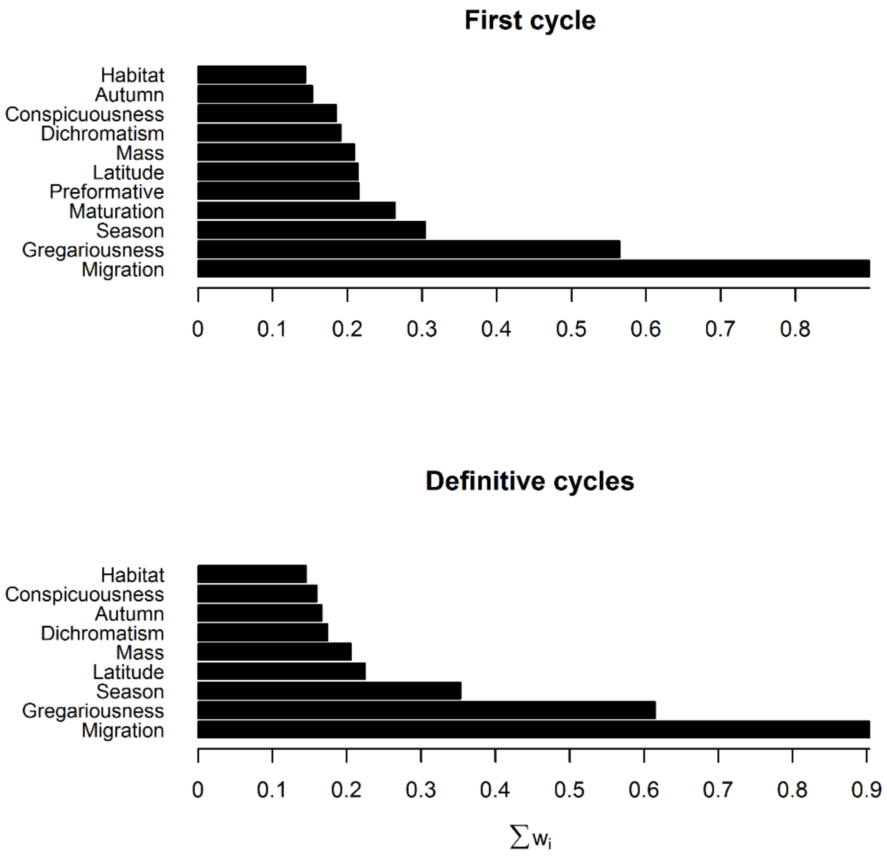


Table 2. Evidence of correlated evolution between prealternate moult and influential covariates.

	logBF	**Evidence**
Conspicuousness	-0.96	weak against
Dichromatism	2.80	positive
Gregariousness	10.29	very strong
Breeding latitude	1.93	weak
Habitat	'1.17	weak
Mass	0.70	weak
Maturation	1.29	weak
Migration distance	10.88	very strong
Preformative moult	1.97	weak
seasonal change	1.08	weak

We found a very strong support for the correlated evolution of the prealternate moult and the two most important covariates that influence it: migration and gregariousness (Table 2). Species without autumn moult have a plumage throughout the winter that is acquired either in the prebasic or the preformative moult. As the prebasic moult is always complete in this family, variation in the extent of the preformative moult might be influenced by some of these natural history factors. Since 16 of the 18 species which did not present autumn moult showed winter gregariousness, we also checked the correlation between preformative moult and winter gregariousness and found a strong association (logBF = 2.65), which suggests an influence of sociality on the evolution of this moult episode.

We found a direct relation between migration distance and breeding latitude in Motacillidae (in accordance with Outlaw & Voelker 2006 but contrasting with the results obtained from a broad taxonomic group by Figuerola & Jovani 2001; Fig. S7). We also found a positive although weak correlation between breeding latitude and extent of prealternate moult (logBF = 1.93). This could be an additive effect which would enhance the effect of migration distance, especially in species without autumn moult.

DISCUSSION

To examine evolutionary pressures that underlie non-breeding moult strategies, we tested multiple hypotheses for the evolution of non-breeding moult using broad scale natural-history information of the Motacillidae breeding in the Northern Hemisphere.

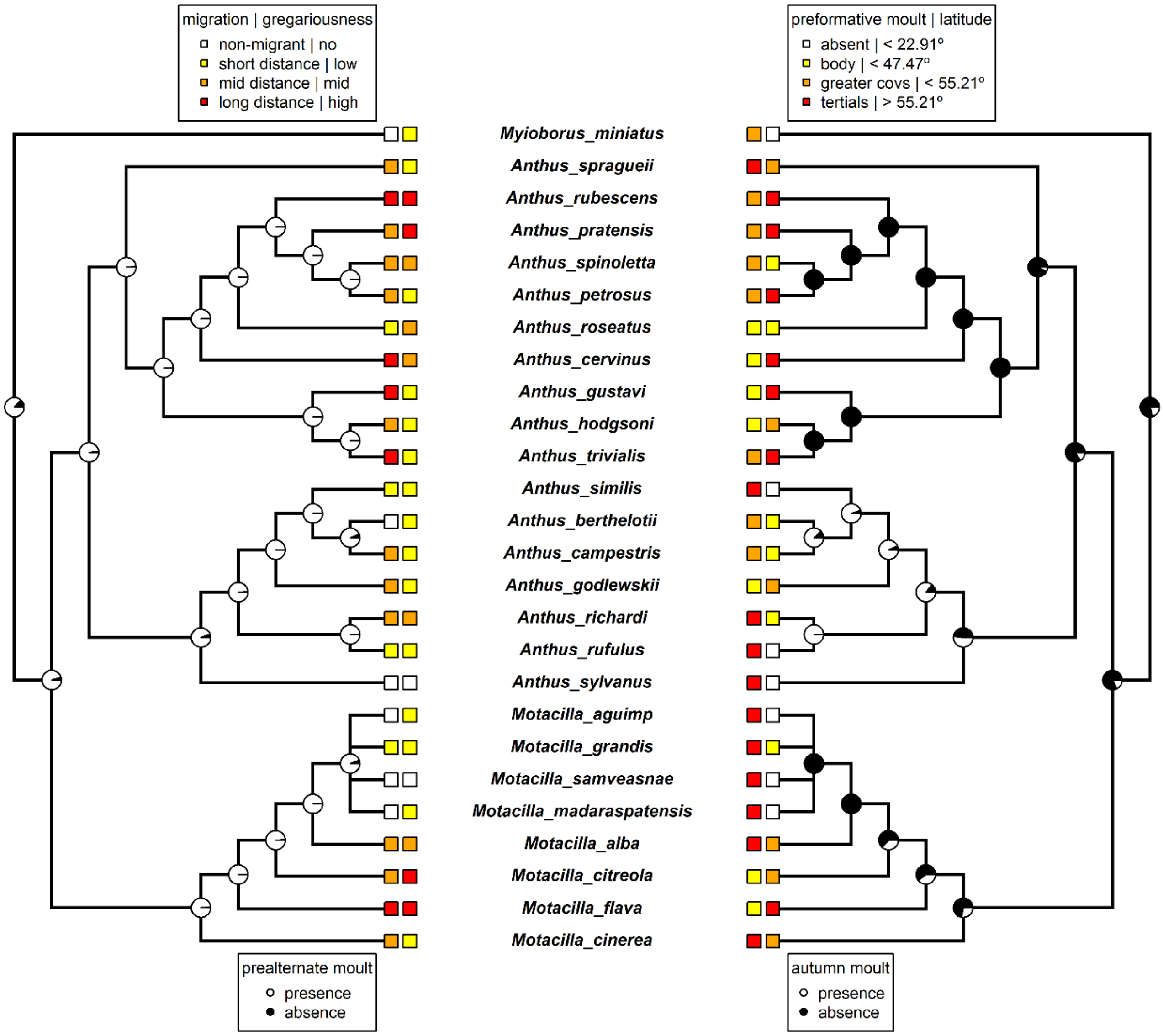
In agreement with previous studies (Svensson & Hedenström 1999, Figuerola & Jovani 2001), we found that migration distance is the most important factor influencing non-breeding moults. Species that undertake longer migrations are also likely to be exposed to more intense solar radiation in the wintering grounds, a factor that may increase plumage deterioration (Lennox & Rowlands 1969, Surmacki *et al.* 2011; but see Willoughby 1991). While the evolution of prealternate moult is highly correlated with migration distance the occurrence of non-breeding moults was not related to migration distance.

Relationship between non-breeding moults and breeding latitude does not support the hypothesis predicting more extensive autumn moult as species breed at higher latitudes, suggesting phylogenetic inertia.

Seasonal plumage change is an important life-history trait in the annual cycle of many bird species, including Motacillidae, since it involves behavioural (Ruff *Philomachus pugnax* and Rock Ptarmigan *Lagopus mutus* are extreme cases; Hogan-Warburg 1966, Montgomerie *et al.* 2001) and physiological changes (Brush 1990) with fitness consequences mediated by variation in predation rates (Montgomerie *et al.* 2001) and mating success (Andersson 1994). Seasonal change was the third most important factor but was weakly correlated to prealternate moult. This low influence on the evolution of prealternate moult is likely due to the limited seasonal plumage changes which undergo the species of this family (only four of 25 species presented changes that were scored as moderate). Seasonal plumage changes may take place to a greater extent in males than in females (e.g. they are very conspicuous in the migratory species of genus *Piranga* in the family Cardinalidae). Since few sex-specific differences in moulting strategies are mentioned in the literature (Pyle 2007), it is thus not surprising that seasonal change was only weakly correlated with prealternate moult extent. It again points to the occurrence and extent of prealternate moults being driven by the need to replace feathers due to loss of functionality, at least partially. Any increase in colour change in males based on sexual selection would then have occurred after the moult had evolved in both sexes due to other factors.

In agreement with Figuerola & Jovani (2001), sexual dichromatism showed a low influence on prealternate moult. Sexual dichromatism is associated with losses of female ornamentation in other passerine families (Friedman *et al.*, 2009, Simpson *et al.* 2015), so that prealternate moult is not necessarily linked to an increase in sexual dichromatism. Thus, sexual selection seems to have played a limited role in the evolution of prealternate moult in Motacillidae.

Figure 3. Phylogenetic reconstruction of non-breeding moults. Pie charts on internal nodes depict likelihood of presence/absence for prealternate moult on the left tree, and for autumn moult on the right tree. The four tip nodes depict from left to right: migration distance, gregariousness, preformative wing-moult extent (categorisation in Table S1) and breeding latitude.



Sociality had a remarkable influence on the evolution of prealternate moult as shown by its very strong correlation with gregariousness and by the fact that this covariate is the second most important one explaining variation of prealternate moult. Gregariousness characterises the winter social behaviour of many species of Motacillidae but, contrary to predictions from our hypothesis, of nine species that showed mid to high gregariousness only Yellow Wagtail *Motacilla flava* and Citrine Wagtail *Motacilla citreola* presented autumn moult. Given this, why might gregariousness exert its influence at the end of the winter period? February to April, the peak of prealternate moult in our study species (Fig. 1), coincides with depletion of food resources in many regions (Lack 1966, Karr 1976, Sherry *et al.* 2005), which can influence prealternate moult (Danner *et al.* 2015). In this context, prealternate moult (and particularly, extent and feather quality) could constitute an honest signal of physical condition. Premigratory roosts (López *et al.* 2005) also take place at the end of this period, in which signal of a higher status could be advantageous for example to claim the safest places in the roost (Beauchamp 1999).

As expected, higher scores of delayed plumage maturation were associated with more extensive prealternate moults, and prealternate moult extent decreased with extent of preformative moult. The prealternate moult was weakly correlated with these two factors, which were the fourth and fifth most influential ones in first-cycle birds. Altogether, these ontogenetic factors do not seem to have played an important role in the evolution of prealternate moult, although preformative moult may have had a stronger influence on autumn moult (see Online Supporting Information).

We have studied the effect of multiple natural history factors on the evolution of non-breeding moults in the family Motacillidae. Lack of information for many species reduces the scope of our conclusions but we can still provide insight on the fact that non-breeding moult may have evolved under different selective forces in different taxonomic groups. We found that migration distance is the most influential force in Motacillidae, although gregariousness has also been an important driver of moult evolution. However, we still lack detailed information on other essential factors that may have played an even more important role on the evolution of non-breeding moult strategies in Motacillidae, such as feather quality and variation of feather coloration throughout the year. Differences in feather quality among species and even within individual feathers (especially in nestlings) are important drivers of the extent of the preformative moult of passerines (Weber *et al.* 2005, Kiat & Izhaki 2015).

There was a remarkable versatility in the evolution of moult strategies as suggested by the lack of phylogenetic inertia. This capacity for rapid change highlights their adaptive character which introduces a great deal of flexibility in the moult strategies of passerines, and also has contributed to diversification of their natural-histories by taking up new functions such as social signalling under selective pressures conditioned by changes in the state of other traits. For example, the gain of a prealternate moult might subsequently be targeted by sexual selection to originate sexual dichromatism. Phylogenetic analyses may help elucidate the selective forces at work, but the genetic basis of moult evolution remain virtually unexplored. Future research should investigate which genes are involved and how differences in gene regulation relate to different moult strategies in birds.

ACKNOWLEDGEMENTS

We are deeply grateful for the comments of Ray Danner, Peter Pyle, Stephen Winter and one anonymous reviewer. Natàlia Pérez and Marcos Pérez assisted with the covariate scoring. José Luis Copete helped with bibliography search. Alejandro González-Voyer advise on the use of BayesTraits. We are indebted to Juan José Soler for sharing with us function pglm3.3.r.

REFERENCES

Ali S, Ripley D 1993. *Handbook of the birds of India and Pakistan. Vol 9.* 2nd ed. Oxford University Press, Oxford.

Alström P, Mild K 2003. *Pipits and wagtails of Europe, Asia and North America*. Identification and systematics. Christopher Helm, London.

Alström P, Ödeen A 2002. Incongruence between mitochondrial DNA, nuclear DNA and molecular data in the avian genus *Motacilla*: implications for estimates of species phylogenies. Unpublished PhD thesis, Uppsala University.

Andersson M 1994. *Sexual selection*. Princeton University Press, Princeton, NJ.

Barta Z, Houston AI, McNamara JM, Welham RK, Hedenström A, Weber TP, Feró O 2006. Annual routines of non-migratory birds: optimal moult strategies. *Oikos* 112: 580–593.

Beauchamp G 1999. The evolution of communal roosting in birds: origin and secondary losses. *Behav. Ecol.* 10: 675–687.

Bergman G 1982. Why are the wings of *Larus f. fuscus* so dark? *Ornis Fenn*. 59: 77–83.

BirdLife International and NatureServe 2014. *Bird species distribution maps of the world*. BirdLife International, Cambridge and NatureServe, Arlington, VA.

Blanco G, Frías O, Garrido-Fernández J, Hornero-Méndez D 2005. Environmental-induced acquisition of nuptial plumage expression: a role of denaturation of feather carotenoproteins? *Proc. R. Soc. Lond. B* 272: 1893–1900.

Bridge ES, Voelker G, Thompson CW, Jones AW, Baker AJ 2007. Effects of size and migratory behavior on the evolution of wing molt in terns (Sternae): a phylogenetic-comparative study. *Auk* 124: 841–856.

Brush AH 1990. Metabolism of carotenoid pigments in birds. *FASEB J.* 4: 2969–2977.

Burnham KP, Anderson DR 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd ed. Springer, New York.

Butler LK, Donahue MG, Rohwer S 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): age effects, aerodynamics, and conservation implications. *Auk* 119: 1010–1023.

Butler LK, Rohwer S, Speidel MG 2008. Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. *J. Avian Biol.* 39: 629–639.

Chaine AS, Roth AM, Shizuka D, Lyon BE 2013. Experimental confirmation that avian plumage traits function as multiple status signals in winter contests. *Anim. Behav.* 86: 409–415.

Cramp S ed. 1988. *The birds of the Western Palearctic, Vol. 5: tyrant flycatchers to thrushes*. Oxford University Press, Oxford.

Cramp S, Perrins CM eds. 1994. *The birds of the Western Palearctic, Vol. 9: buntings and New World warblers*. Oxford University Press, Oxford.

Danner RM, Greenberg RS, Danner JE, Walters JR 2015. Winter food limits timing of pre-alternate moult in a short-distance migratory bird. *Func. Ecol.* 29: 259–267.

Dawson A 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starling Sturnus vulgaris. *Ibis* 146: 493–500.

Dawson A 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Phil. Trans. R. Soc. Lond. B* 363: 1621–1633.

de la Hera I, Pérez-Tris J, Tellería JL 2009. Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. *Biol. J. Linn. Soc.* 97: 98–105.

Dey CJ, Dale J, Quinn JS 2014. Manipulating the appearance of a badge of status causes changes in true badge expression. *Proc. R. Soc. Lond. B* 281: 20132680.

Duckworth JW, Alstrom P, Davidson P, Evans TD, Poole CM, Setha T, Timmins RJ 2001. A new species of wagtail from the lower Mekong basin. *Bull. Brit. Orn. Club* 121: 152–182.

Dunning JB 2007. *CRC handbook of avian body masses*. Second Edition. CRC Press, Bocaraton, FL.

Echeverry-Galvis MA, Hau M 2013. Flight performance and feather quality: paying the price of overlapping moult and breeding in a tropical highland bird. *PLoS One* 8: e61106.

Ersts PJ 2015. Geographic Distance Matrix Generator (v. 1.2.3). American Museum of Natural History, Center for Biodiversity and Conservation. Available at http://biodiversityinfo rmatics.amnh .org/open_source/gdmg.

Étchecopar RD, Hüe F 1983. *Les oiseaux de Chine. Passereaux*. Boubée, Paris.

Figuerola J, Jovani R 2001. Ecological correlates in the evolution of moult strategies in Western Palearctic passerines. *Evol. Ecol.* 15: 183–192.

Freckleton RP, Harvey PH, Pagel M 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Amer. Nat.* 160: 712–726.

Friedman NR, Hofmann CM, Kondo B, Omland KE 2009. Correlated evolution of migration and sexual dichromatism in the New World orioles (*Icterus*). *Evolution* 63: 3269–3274.

Garland T, Dickerman AW, Janis CM, Jones JA 1993. Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* 42: 265–292.

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG 2011. Multimodel inference in ecology and evolution challenges and solutions. J. *Evol. Biol.* 24: 699–711.

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A 2009. *Paseriformes del Occidente de México: morfometría, datación y sexado*. Museu de Ciències Naturals de Barcelona, Barcelona.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2014. Moult topography and its application to the study of partial wing-moult in two Neotropical wrens. *Ibis* 156: 311–320.

Hall KSS, Fransson T 2000. Lesser Whitethroats under time constraint moult more rapidly and grow shorter wing feathers. *J. Avian Biol.* 31: 583–587.

Harvey PH, Pagel MD 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

Hill GE. 1996. Subadult plumage in the house finch and tests of models for the evolution of delayed plumage maturation. *Auk* 113: 858–874.

Hogan-Warburg AJ 1966. Social behavior of the ruff (*Philomachus pugnax*). *Ardea* 54: 108–229.

Holmgren N, Hedenström A 1995. The scheduling of molt in migratory birds. *Evol. Ecol.* 9: 354–368.

Howell SNG, Corben C, Pyle P, Rogers DI 2003. The first basic problem: a review of molt and plumage homologies. *Condor* 105: 635–653.

Howell SNG 2010. *Molt in North American birds*. Houghton Mifflin, New York.

Jenni L, Winkler R 1994. *Molt and ageing of European passerines.* Academic Press, London.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO 2012. The global diversity of birds in space and time. *Nature* 491: 444–448.

Karr JR 1976. Seasonality, resource availability, and community diversity in tropical bird communities. *Amer. Nat.* 110: 973–994.

Kass RE, Raftery AE 1995. Bayes factors. *J. Amer. Stat. Assoc.* 90: 773–795.

Kiat Y, Izhaki I 2016. Why renew fresh feathers? Advantages and conditions for the evolution of completes post-juvenile moult. *J. Avian Biol.* 47: 47–56.

Lack, D 1966. *Population studies of birds*. Oxford University Press, Oxford.

Lennox FG, Rowlands RJ 1969. Photochemical degradation of keratins. *Photochem. Photobiol.* 9: 359–367.

López G, Figuerola J, Varo N, Soriguer R 2005. White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed. *Ardea* 93: 237–244.

Martins EP, Hansen TF 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Amer. Nat.* 149: 646–667.

McAlpine CA, Rhodes JR, Bowen ME, Lunney D, Callaghan JG, Mitchell DL, Possingham HP 2010. Can multiscale models of species' distribution be generalized from region to region? A case study of the koala. *J. Applied Ecol.* 45: 558–567.

Montgomerie R, Lyon B, Holder K 2001. Dirty ptarmigan: behavioral modification of conspicuous male plumage. *Behav. Ecol.* 12: 429–438.

Murphy ME. 1996. Energetics and nutrition of moult. In *Avian energetics and nutritional ecology* (Carey C ed.). New York, NY: Chapman Hall, 158–198.

Nakagawa S, Freckleton RP 2011. Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behav. Ecol. Sociobiol.* 65: 103–116.

Newton I 2008. *The migration ecology of birds*. Academic Press, London.

Outlaw DC, Voelker G 2006. Phylogenetic tests of hypotheses for the evolution of avian migration, a case study using the Motacillidae. *Auk* 123: 55–46.

Pagel M 1992. A method for the analysis of comparative data. *J. Theor. Biol.* 156: 431–442.

Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zool Scripta* 26: 331–348.

Pagel M 1999. Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.

Pagel M, Meade A, Barker D 2004. Bayesian estimation of ancestral character sates on phylogenies. *Syst. Biol.* 53: 673–684.

Pap PL, Osváth G, Sándor K, Vincze O, Bărbos L, Marton A, Nudds RL, Vágási CI 2015. Interspecific variation in the structural properties of flight feathers in birds indicates adaptation to flight requirements and habitat. *Func. Ecol.* 29: 746–757.

Peters A 2007. Testosterone treatment of female Superb Fairy-wrens *Malurus cyaneus* induces a male-like prenuptial moult, but no coloured plumage. *Ibis* 149: 121–127.

Pyle P 1997. Identification guide to North American birds. Part I. Slate Creek Press, Bolinas, CA.

Pyle P 1997. Revision of molt and plumage terminology in ptarmigan (Pashianidae: *Lagopus* spp.) based on evolutionary considerations. *Auk* 124: 508–514.

QGIS Development Team. 2015. QGIS 2.8.2 Wien. Available at http://qgis.org/es/site/

Rohwer S, Fretwell SD, Niles DM 1980. Delayed maturation in Passerine plumages and the deceptive acquisition of resources. *Amer. Nat.* 115: 400–437.

Rohwer S, Butler LK, Froehlich DR, Greenberg R, Marra PP 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. In *Birds of Two Worlds: The Ecology and Evolution of Migration* (Greenberg R, Marra PP eds.). Johns Hopkins University Press, Baltimore.

Rohwer S, Ricklefs RE, Rohwer VG, Copple MM. 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biol.* 7: e1000132.

Schluter D, Price T, Mooers AØ, Ludwig D 1997. Likelihood of ancestor states in adaptive radiation. *Evolution* 51: 1699–1711.

Senar JC, Copete JL, Martin AJ 1998. Behavioural correlates of variation in the extent of postjuvenile molt in the Siskin *Carduelis spinus*. *Ibis* 140: 661–669.

Sherry TW, Johnson MD, Strong AM 2005. Does winter food limit populations of migratory birds? In Greenberg R, Marra PP eds. *Birds of two worlds: the ecology and evolution of temperate-tropical migration*. John Hopkins University Press Baltimore, MD.

Shirihai H, Helbig A, Gargallo G 2001. Sylvia *warblers*. Christopher Helm, London.

Simpson JA, Campbell L 2013. *The Oxford handbook of close relationships*. Oxford University Press, Oxford.

Simpson RK, Johnson MA, Murphy TG 2015. Migration and the evolution of sexual dichromatism: evolutionary loss of female coloration with migration among wood-warblers. *Proc. R. Soc. Lond. B* 282: 20150375.

Surmacki A, Sieffermann L, Yuan Hsiao-We. 2011. Effects of sunlight exposure on carotenoid-based and structural coloration of the Blue-tailed Bee-eater. *Condor* 113: 590–596.

Svensson E, Hedenström A 1999. A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: Sylviidae). *J. Biol. Linn. Soc.* 67: 263–276.

Svensson L 1992. *Identification guide to European passerines.* 4th ed. L. Svensson, Stockholm.

The R Foundation for Statistical Computing 2015. Version 3.2.0 (2015-04-16).

Tibbets EA, Safran RJ 2009. Co-evolution of plumage characteristics and winter sociality in New and Old-World sparrows. *J. Evol. Biol.* 22: 2376–2386.

Voelker G, Rohwer S 1998. Contrasts in the scheduling of molt and migration in eastern and western Warbling-Vireos. *Auk* 115: 142–155.

Voelker G 1999. Molecular evolutionary relationships in the avian genus *Anthus* (pipits: Motacillidae). *Mol. Phyl. Evol.* 11: 84–94.

Weber TP, Borgudd J, Hedenström A, Persson K, Sandberg R 2005. Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species. *Biol Lett.* 1: 27–30.

Ydenberg RC, Butler RW, Lank DB 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. *J. Avian Biol.* 38: 523–529.

Willoughby EJ 1991. Molt of the genus Spizella (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proc. West. Found. Vert. Zool.* 4: 247–286.

Wingfield JC 2008. Organization of vertebrate annual cycles: implications for control mechanisms. *Phil. Trans. R. Soc. B* 363: 425–441.

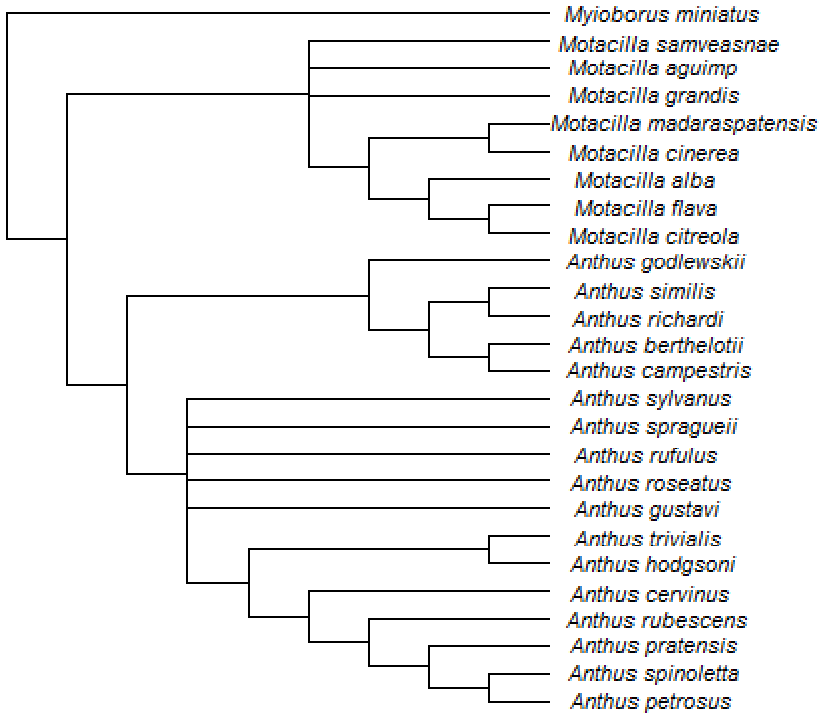
Zahavi A 1997. *The handicap principle: a missing piece of Darwin's puzzle*. Oxford University Press, Oxford.

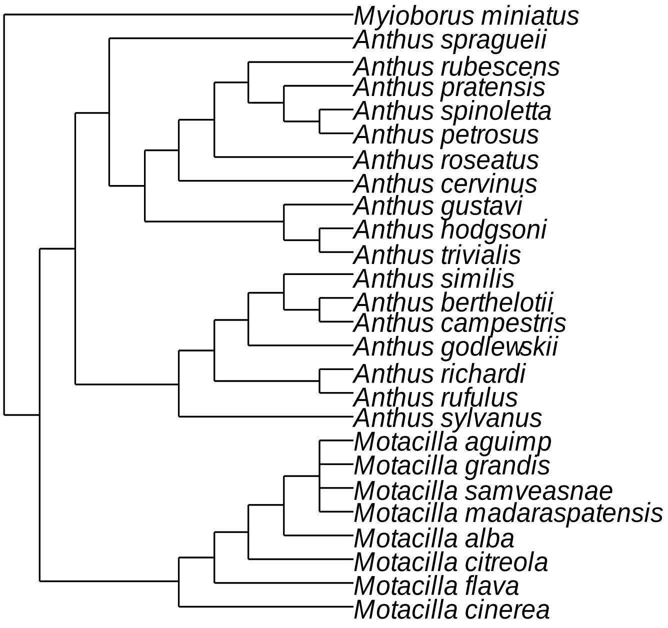
SUPPLEMENTARY INFORMATION

Table S1. Categorisation of natural history information used in analyses. Plumage maturation refers to acquisition of adult-type plumage in first-cycle males (Rohwer 1978). Seasonal plumage change indicates the degree to which basic and alternate plumages differ. The last column (HT) references the hypotheses in which covariates were used matching the order in which hypotheses were enunciated in the text (adj = adjustment covariate; res = response variables, also used as adjustment covariates).

Covariate	**Categories**				**HT**
	1	**2**	**3**	**4**	
Migration (migratory strategy)	non-migrant	short-distance migrant (< 2011 km)	mid-distance migrant (< 4959 km)	long-distance migrant (> 4959 km)	1
Latitude (mean breeding latitude)	< 22.91°	< 47.47°	< 55.21°	> 55.21°	2
Season (seasonal plumage change)	no	slight	moderate	strong	3
Conspicuousness (male basic plumage conspicuousness)	dull (drab and uniform coloration)	moderate (some contrast present)	striking (presence of bright coloration)		3
Dichromatism (sexual dichromatism in alternate plumage)	no	slight (subtle changes in coloration)	strong (obvious changes in coloration)		4
Gregariousness (in the non-breeding season)	solitary	small groups (< 10 individuals)	mid-size groups (< 30 individuals)	large groups (> 30 individuals)	5
Maturation (plumage maturation of first-cycle males)	no	delayed until autumn moult	delayed until prealternate moult	delayed until first prebasic moult	6
Preformative * Autumn and Prealternate † (patterns of feather replacement)	absent	body (may include marginal and median wing-coverts)	2 + greater coverts	3 + tertials (may include alula and s6)	*6, †res adj
Habitat (in the wintering grounds)	open-arid (savannah, steppe, high mountain)	open-dry (scrub, tundra, grassland, rocky shores)	wet (riparian, groves, wetlands)	semi-closed (open woodlands)	adj
Mass (g)	< 20.36	2< 21.15	< 24.98	> 24.98	adj

Figure S1. Consensus trees. Top: tree based on 10000 trees downloaded from birdtree.org (Jetz *et al.* 2012). Bottom: tree based on Voelker (1999) and Alström & Ödeen (2002) used for replicate analyses to check sensitivity to phylogeny.





Output of relative importance and correlated evolution analyses of the autumn moult

Migration distance and breeding latitude are the most important factors influencing autumn moult. Preformative moult, habitat and conspicuousness rank third to fifth in first-cycle birds (Fig. S2). Migration reached significance in first-cycle birds. Relationships between response and covariates were positive except for breeding latitude, gregariousness, habitat, maturation and preformative moult. Model and parameter uncertainty were moderately high (Fig. S2, Table S2).

The phylogenetic signal $\lambda > 0.999$ for all models. λ did not differ significantly from 1 (loglik $< -3x10^{-4}$, $P = 1$) but it did from 0 (loglik > 6.45, $P < 0.014$), indicating covariation with evolutionary history.

The output of this analysis, however, was sensitive to the phylogenetic tree used. Our replicate analysis ranks habitat as third most important factor with a high accumulated Akaike weight. Nevertheless, models using the replicate tree have considerably poorer fit (on average ΔAICc > 6 between same rank models).

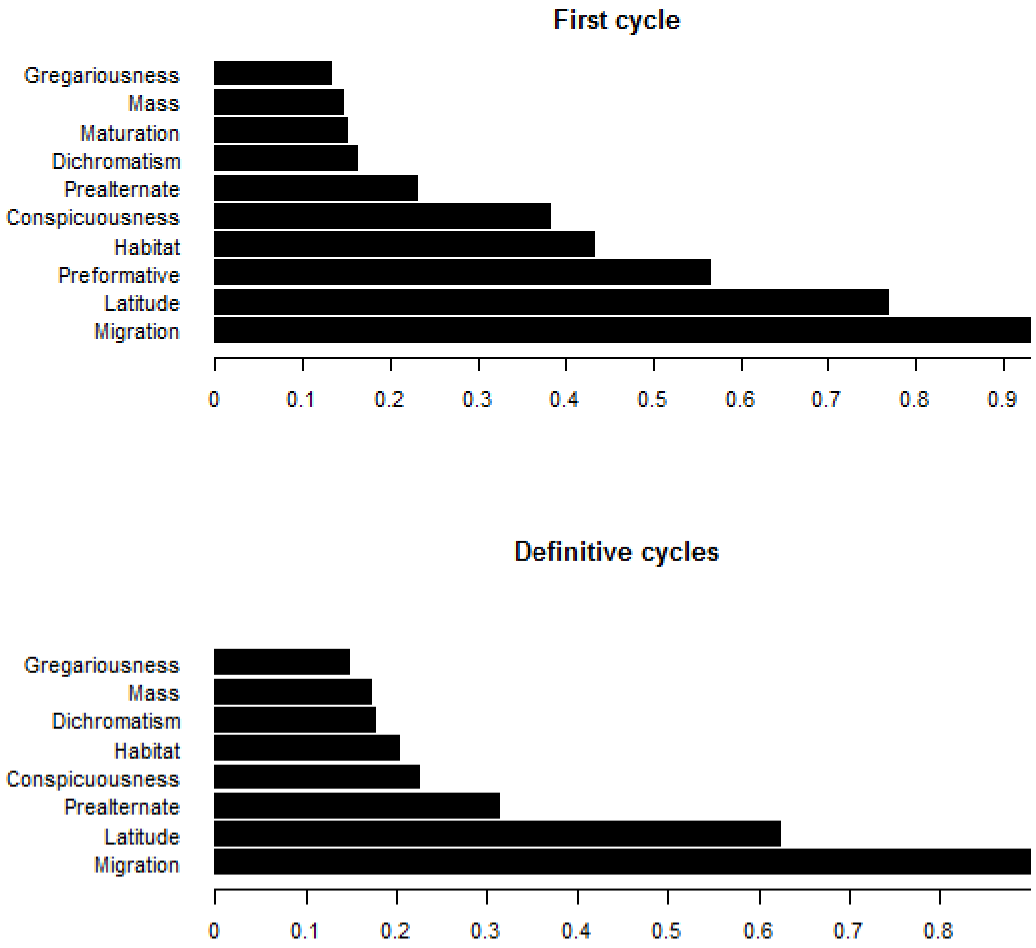
Table S2. Results of the PGLS of 10 natural history covariates on autumn moult. Intercepts and coefficients (adjusted standard error) with shrinkage are based on the subset of the total averaged models whose accumulated Akaike weights reached 95%. Significance is indicated in bold. Only three covariates had effect sizes bigger than 10% (five in first-cycle birds).

	Intercept	**Conspicuousness**	**Dichromatism**	**Gregariousness**	**Habitat**	**Latitude**	**Mass**	**Maturation**	**Migration**	**Prealternate**	**Preformative**
First-cycle	1.81 (2.31)	0.37 (0.63)	-0.01 (0.24)	-0.01 (0.09)	-0.26 (0.39)	-0.46 (0.35)	0.01 (0.07)	-0.02 (0.12)	**0.80** **(0.38)**	0.04 (0.13)	-0.32 (0.37)
Definitive cycles	0.37 (1.45)	0.13 (0.40)	0.04 (0.25)	-0.00 (0.10)	-0.05 (0.19)	-0.30 (0.31)	0.01 (0.07)		0.66 (0.37)	0.06 (0.13)	

Table S3. Evidence of correlated evolution between autumn moult and influential covariates.

	LogBF	**Evidence**
Conspicuousness	1.73	weak
Dichromatism	0.03	weak
Gregariousness	7.57	strong
Breeding latitude	0.26	weak
Habitat	1.55	weak
Mass	0.33	weak
Maturation	0.94	weak
Migration distance	0.81	weak
Preformative moult	4.45	positive
Prealternate moult	6.87	strong

Figure S2. Relative importance of the explanatory variables for the autumn moult based on the subset whose accumulated Akaike weights reached 95% of the total averaged models. The scale indicates sum of the Akaike weights (Σwi). Analysis leaving prealternate moult out: 270 and 97 for first and definitive cycles, respectively, which corresponds to 26.4% and 37.9% model uncertainty.



Output of average model of autumn moult as response variable excluding prealternate moult as covariate

It may be argued that prealternate moult lies ahead in the future and therefore should not influence the autumn moult. When leaving out prealternate moult from analyses, model uncertainty and AICc decreased considerably. Migration distance and breeding latitude are the most important factors.
The phylogenetic signal $\lambda > 0.99$ for all models. λ did not differ significantly from 1 ($P = 1$) but it did from 0 ($P < 0.022$), indicating covariation with the evolutionary history.

Figure S3. Relative importance of the explanatory variables for the autumn moult based on the subset whose accumulated Akaike weights reached 95% of the total averaged models. The scale indicates sum of Akaike weights (Σwi). Model uncertainty: 437 and 182 for first and definitive cycles, respectively, which corresponds to 21.3% and 35.5%.

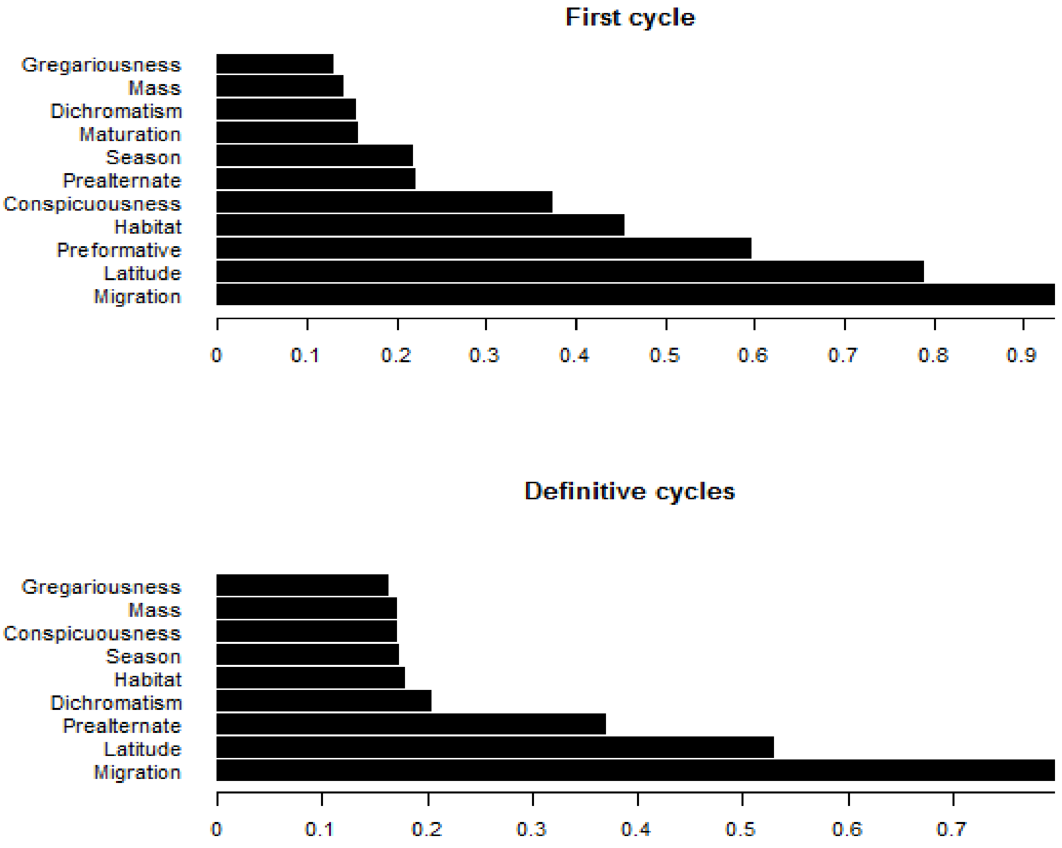


Table S4. Results of the PGLS of 11 natural history covariates on autumn moult. Intercepts and coefficients (adjusted standard error) with shrinkage are based on the subset of the total averaged models whose accumulated Akaike weights reached 95%.

	Intercept	**Conspicuousness**	**Dichromatism**	**Gregariousness**	**Habitat**	**Mass**	**Latitude**	**Maturation**	**Migration**	**Preformative**	**Prealternate**	**Season**
First-cycle	2.08 (2.47)	0.36 (0.63)	-0.01 (0.24)	-0.01 (0.09)	-0.28 (0.40)	0.01 (0.07)	-0.50 (0.37)	-0.01 (0.14)	0.84 (0.39)	-0.35 (0.38)	0.04 (0.13)	-0.05 (0.17)
Definitive cycles	0.44 (1.24)	0.05 (0.29)	0.08 (0.30)	0.01 (0.11)	-0.03 (0.16)	0.01 (0.08)	-0.26 (0.32)		0.58 (0.43)		0.09 (0.17)	-0.02 (0.12)

Results from replicate analyses based on an alternative tree based on Voelker (1999) and Alström & Ödeen (2002)

PGLS

Autumn

$\lambda < 0. 001$ for all models, neither significantly different from 1 ($\chi^2 < 3.30$, P > 0.07) nor from 0 ($\chi^2 < 5x10^{-4}$, P = 1).

Prealternate

$\lambda < 0.001$ for all models, marginally different from 1 ($\chi^2 < 7x10^{-4}$, P > 0.052) but not from 0 ($\chi^2 < 3.76$, P = 1).

Figure S4. Relative importance of the explanatory variables for the autumn moult based on the subset whose accumulated Akaike weights reach 95% of the total averaged models: 231 and 87 for first and definitive cycles, respectively, which corresponds to 22.6% and 34.0% model uncertainty. The scale indicates sum of Akaike weights.

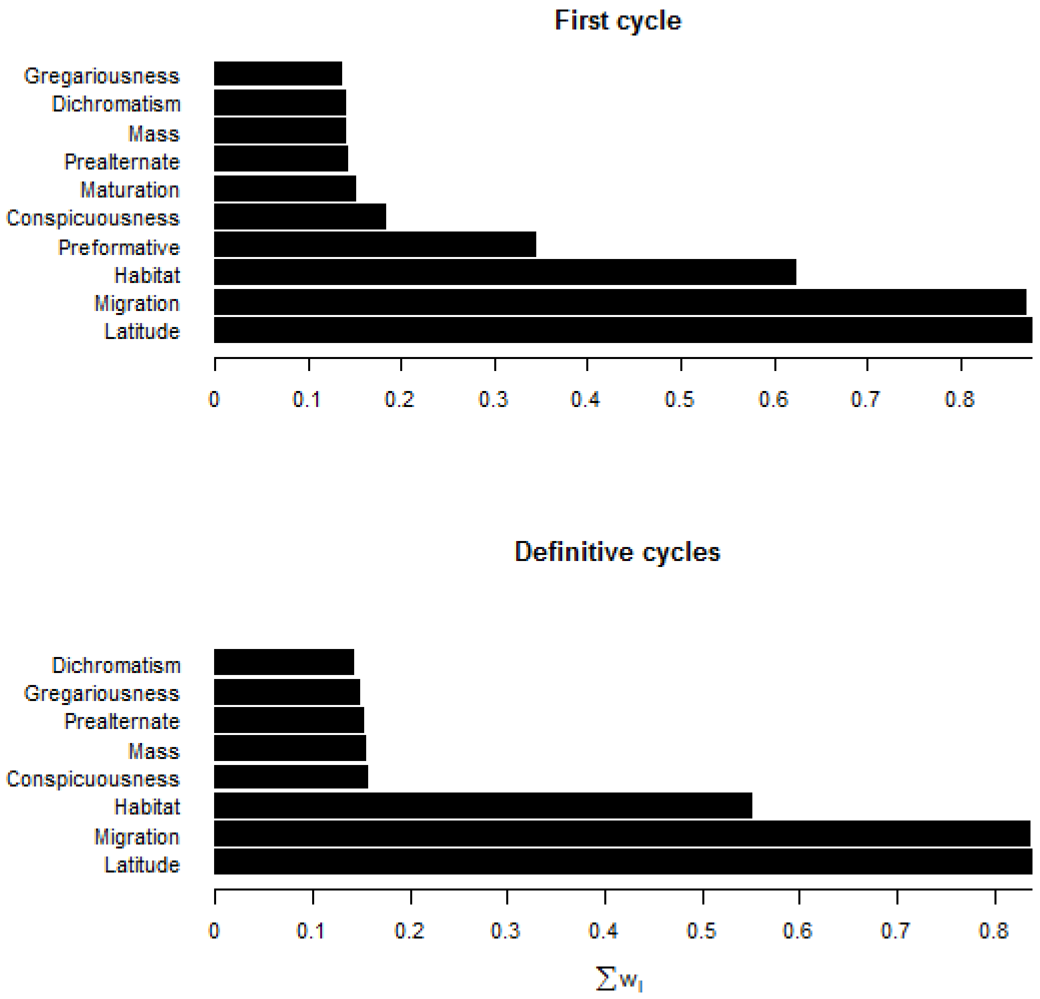


Figure S5. Relative importance of the explanatory variables for the prealternate moult based on the subset whose accumulated Akaike weights reach 95% of the total averaged models: 529 and 154 for first and definitive cycles, respectively, which corresponds to 25.8% and 30.1% model uncertainty. The scale indicates sum of Akaike weights.

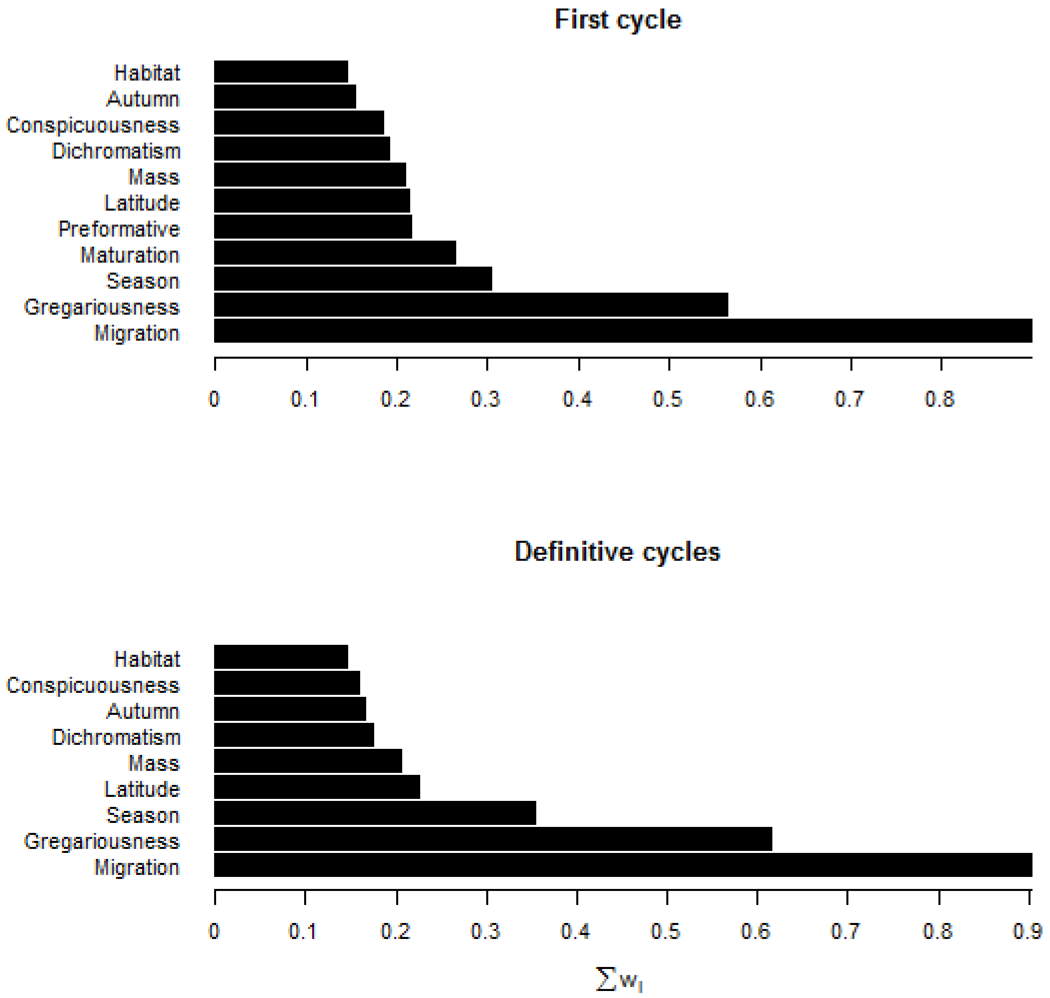


Table S5. Results of the PGLS of 11 natural history covariates on non-breeding moults. Intercepts and coefficients (adjusted standard error) with shrinkage are based on the subset of the total averaged models whose accumulated Akaike weights reached 95%.

	Intercept	**Autumn**	**Conspicuousness**	**Dichromatism**	**Gregariousness**	**Habitat**	**Latitude**	**Mass**	**Maturation**	**Migration**	**Preformative**	**Prealternate**	**Season**
Autumn first-cycle	2.74 (1.78)		0.03 (0.24)	0.00 (0.18)	0.01 (0.12)	-0.30 (0.32)	-1.04 (0.58)	-0.00 (0.09)	0.02 (0.13)	1.11 (0.62)	-0.16 (0.30)	0.00 (0.11)	
Autumn definitive cycles	1.98 (1.03)		-0.00 (0.17)	0.01 (0.16)	0.01 (0.12)	-0.23 0.28)	-0.93 (0.57)	-0.01 (0.09)		1.03 (0.64)		0.01 (0.11)	
Prealternate first-cycle	0.76 (1.04)	0.01 (0.07)	-0.04 (0.19)	-0.05 (0.21)	0.25 (0.29)	-0.01 (0.08)	0.04 (0.20)	0.03 (0.10)	0.08 (0.21)	0.59 (0.30)	-0.05 (0.15)		0.09 (0.20)
Prealternate definitive cycles	0.47 (0.80)	0.07 (0.17)	-0.11 (0.31)	-0.17 (0.37)	0.35 (0.31)	-0.05 (0.20)	0.20 (0.39)	0.13 (0.18)		0.50 (0.31)			0.32 (0.25)

Figure S6. Scatterplot of migration distance versus breeding latitude. The blue line is a polynomial smoothing line showing the increase in migration distance that takes place above 20° N.

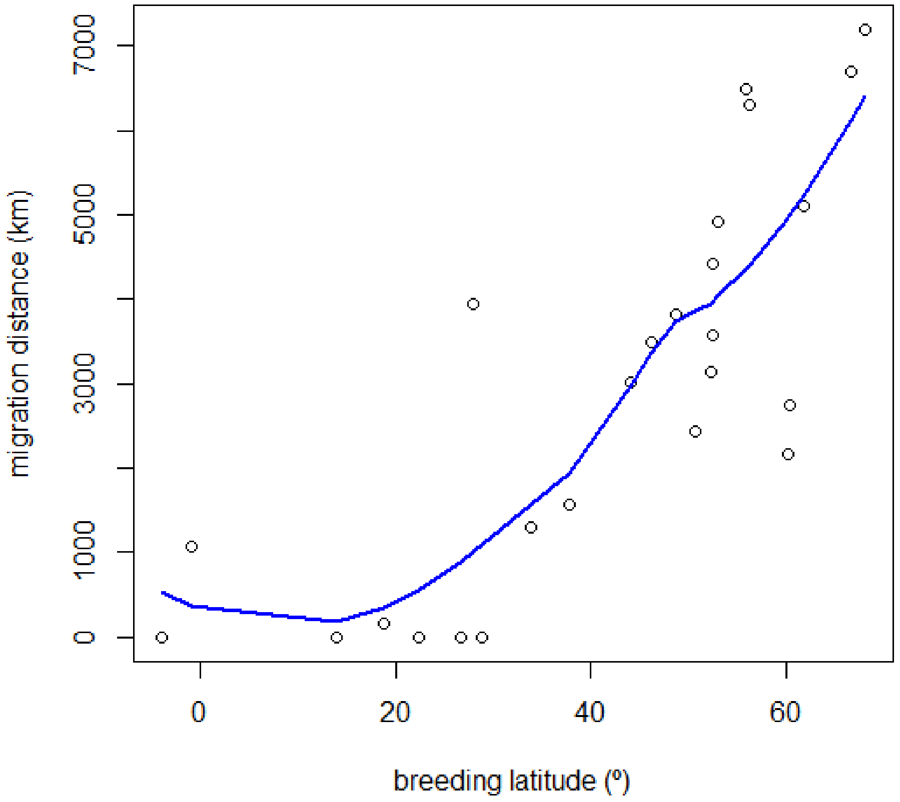


Figure S7. Phylogenetic reconstruction of non-breeding moult episodes. Black circles map changes towards absence of prealternate moult. Blank circles indicate appearance of autumn moult. Neither Slate-throated Redstart *Myioborus miniatus* nor Berthelot's Pipit *Anthus berthelotii* present non-breeding moults. The prealternate moult shows four tip losses, whereas the autumn moult shows three gains and one tip loss.

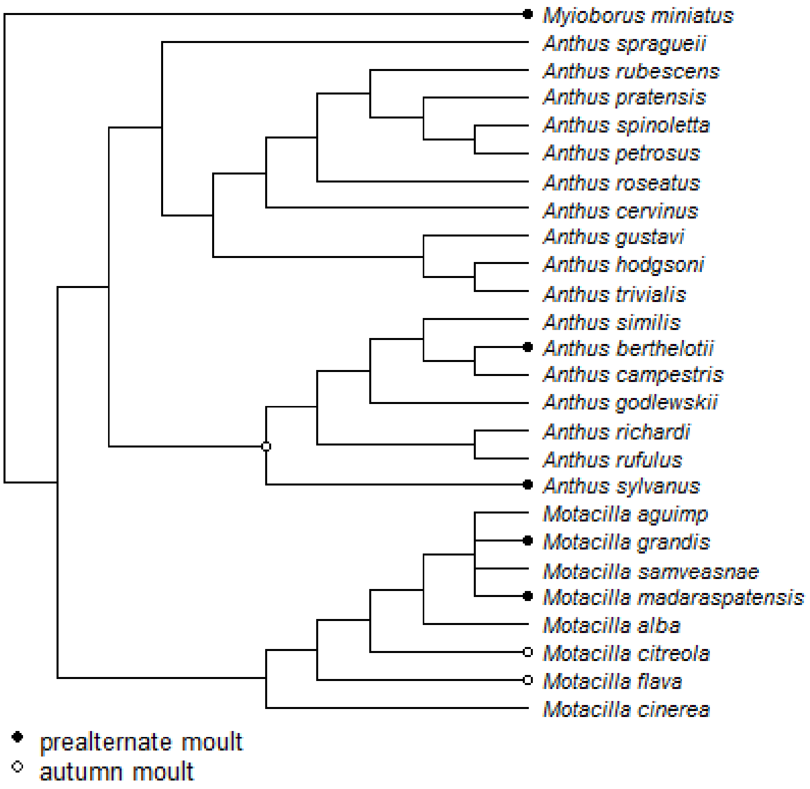
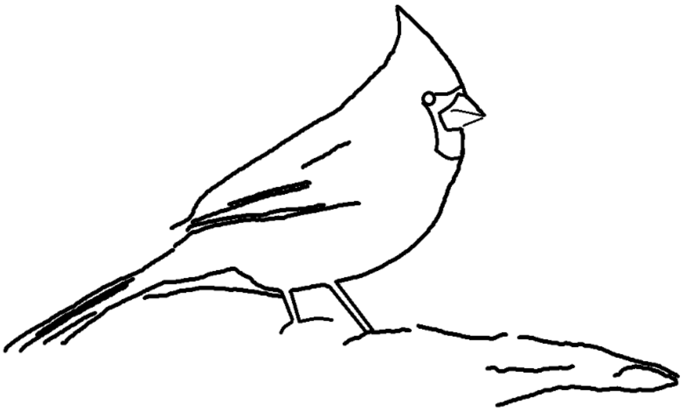


Table S6. Categories of Bayes factors used as model selection criterion in analyses of correlated evolution. These categories are based on twice the natural logarithm of the Bayes factors to have them in the same scale as the deviation and likelihood ratio tests (Kass & Raftery 1995). Bayes factors provide a summary of the evidence provided by the data in favour of any two competing hypotheses.

logBF	Evidence against H_0
0 – 2	Not worth more than a bare mention
2 – 6	Positive
6 – 10	Strong
> 10	Very strong

REFERENCES

Rohwer S. 1978. Passerine subadult plumages and the deceptive acquisition of resources: test of a critical assumption. *Condor* 80: 173–179.



Chapter 5

Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats

Santi Guallar[1,2]* Rafael Rueda-Hernández[3] & Peter Pyle[4]

1 Department of Animal Biology, University of Barcelona, Barcelona

2 Department de Vertebrats, Museu de Ciències Naturals de Barcelona, Barcelona

3 Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México DF, México.

4 Institute for Bird Populations, California, USA.

Published in: Guallar S, Rueda-Hernández R & Pyle P 2021 Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. *Ornithology* 138.

ABSTRACT

We explored adaptive factors affecting the preformative molt in the passerine family Cardinalidae and concluded that the ancestor inhabited forest habitats and underwent a partial preformative molt that included wing coverts but not primaries. Later radiations within the family appeared to be characterized by transitions from forests toward more open habitats, and such transitions also correlated positively with increased preformative molt investment, plumage signaling, and flight. While previous studies had highlighted the role of time and energy constraints in the evolution of the preformative molt in passerines, we conclude that adaptation to the physical environment has had a greater influence than constraints on the evolution of this molt in Cardinalidae. Using molt data from 430 individuals from 41 of the 51 Cardinalidae species, we tested whether social and environmental factors (delayed plumage maturation and habitat openness), as well as that of physiological and time constraints (body mass, migration distance and breeding latitude) have influenced the evolution of the preformative molt in this family. We predicted that these five factors could relate to the extent of the preformative molt in terms of energy investment, plumage signaling and flight. We also examined whether the presence of an auxiliary preformative molt correlated to the extent of the preformative molt. We found a strong phylogenetic signal for the preformative molt in Cardinalidae due to shared ancestry, with habitat openness correlating significantly with increased molt extent. We also found a very strong relationship with the auxiliary preformative molt, indicating that both episodes form part of the early life molt strategy in this family. Evolutionary histories and the environments to which each taxonomic group has adapted can diverge across passerines, and we expect that future studies will further discover the nature and strength of the evolutionary drivers of preformative molt.

INTRODUCTION

Reproduction, migration, and molt, the three major life-history events of passerines, conform to annual routines, i.e. they occur with an annual periodicity (Houston & McNamara 1999). However, the first annual cycle of passerines deviates from the routines of later cycles (of adults) because of the developmental events that take place during the early life of the individual. A characteristic trait of the early life of passerine species is the preformative molt, a molt episode unique to the first cycle (Howell *et al.* 2003), which appears to have evolved to replace weak juvenile feathers produced rapidly in the nest (Callan *et al.* 2019).

The preformative molt varies across passerine phylogeny, being restricted to body feathers in some species (e.g. *Sylvia borin*; Jenni and Winkler 1994) while involving full feather replacement in others (e.g., up to 36 species of North American passerines; Pyle 1997a). Most passerines replace some but not all wing feathers (i.e. coverts, alula, tertials, secondaries, and primaries) and these are thus particularly useful to quantify this variation, since they can be individually recognized as replaced and retained (Jenni & Winkler 1994, Pyle 1997b).

Variation in the preformative molt has raised the question as to what adaptive factors may have driven its evolution from its ancestral state. Numerous studies have tried to shed light on this question by focusing on both proximate and ultimate causes. These studies have shown a negative relation between preformative (or post-juvenile) molt extent and time constraints (Bojarinova *et al.* 1999, Kiat & Sapir 2017), as well as with energy constraints (Gosler 1991, Norman 1999). Time may become a fixed constraint for long-distance migrants, the more so as breeding latitude increases, where tighter schedules may become a major driver of molt at both individual and evolutionary scales (Figuerola & Jovani 2001, Kiat *et al.* 2019a). Physiological constraints may have also driven evolutionary change, e.g., duration of molt increases as species size increases (Rohwer *et al.* 2009). Likewise, changes in ecological factors may create selective pressures, eventually triggering evolutionary changes. For example, evolutionary adaptation to a new habitat can lead to a strong lineage diversification (Petren *et al.* 2005), potentially driving changes in the dynamics of the preformative molt (Hope *et al.* 2016, Guallar & Jovani 2020a).

Cardinalidae is a diverse monophyletic family of New World passerines, consisting of 51 species divided in 11 genera and five major clades (Klicka *et al.* 2007, Billerman *et al.* 2020; Figure 1). It shows wide habitat diversity, from forests to open areas, it occupies an ample latitudinal range throughout the Americas, and its preformative molt has been documented for 41 species of all genera, including both Neotropical migrants (e.g. Rohwer 1986, Butler *et al.* 2002) and Neotropical residents (Thompson & Leu 1995, Johnson & Wolfe 2018, Guallar & Jovani 2020b, Guallar *et al.* 2020), and covering all genera. Most of these species only replace wing coverts and perhaps 1-2 alula or tertials during their preformative molt; however, one third of them regularly replace primaries, at least the ones that form the wing tip (e.g. eccentric molts in genus *Passerina*), while species in the genus *Cardinalis* undergo complete preformative molts (Pyle 1997a; Guallar *et al.* 2009, 2020).

The Cardinalidae is also one of the passerine families with a high known frequency of auxiliary preformative molts (sensu Pyle 2008), a distinct molt episode (formerly termed "first presupplemental molt"), which has been interpreted to precede the preformative molt (Thompson & Leu 1994, Pyle 1997b, Howell *et al.* 2003). This molt is poorly understood but is reported to include most to all body plumage and some of the wing coverts (Rohwer 1986, Willoughby 1986). Within a species, only early hatched individuals may undergo this molt, which produces an ephemeral plumage that is replaced during the preformative molt. The auxiliary preformative molt may have been part of an early life strategy that interacts with the preformative molt; however, its relationship with the latter is poorly known.

We first aimed to reconstruct the ancestral state of the preformative molt within the Cardinalidae. Once obtained, we used comparative analyses to test the influence of five natural history factors on the evolution of its preformative molt: delayed plumage maturation, habitat openness, migration distance, breeding latitude and body mass. Then, we tested whether preformative molt has evolved in a correlated manner with these factors and evaluated their relative importance on the evolution of the preformative molt. Because primaries are essential for flight, we examined transition rates between replacement and retention of primaries against the phylogeny.

We specifically tested four hypotheses. The first hypothesis tackles the effect of delayed plumage maturation (Rohwer *et al.* 1980) on the preformative molt. Delayed plumage maturation and preformative molt may interact through a trade-off between sexual signaling and survival (Senar 2006). In species with selective pressure to look attractive during the first breeding season, replacing more juvenile feathers with brighter formative feathers may be beneficial, although potentially at the expense of increased aggressive interactions with older birds (Senar *et al.* 1998, Hawkins *et al.* 2012). We thus predict that both preformative molt extent and probability of replacing primaries (at least the most exposed ones) would increase as the formative plumage becomes more similar to the definitive basic plumage of older birds.

The second hypothesis states that lineages that move into new environments may evolve different molt strategies as they are exposed to different selective pressures (Sol *et al.* 2005, Hope *et al.* 2016, Iglesias-Carrasco *et al.* 2019). For example, more abrasive habitats might exert a selective pressure to invest more in feather renewal (Willoughby 1991), while more open habitats may have a similar effect by increasing temperatures and solar radiation on feathers (Pyle 1998, Kiat *et al.* 2019b). Therefore, we expect that both preformative molt extent and probability of primary molt will increase as environments become more open.

The last two hypotheses deal with constraints. First, migratory behavior and breeding latitude may have driven passerine preformative molt evolution by constraining the time to molt before migration (Figuerola & Jovani 2001, Kiat *et al.* 2019a). Analogously, favorable weather conditions during the breeding season grow shorter as latitude increases (Dawson 2008). Therefore, we would predict that species under strong time constraints before departing the breeding grounds would decrease preformative molt extent as both breeding latitude and migratory distance increase (de la Hera *et al.* 2009). Finally, time costs of molt increase as species size increases (Rohwer *et al.* 2009). Accordingly, we predict that preformative molt extent would decrease as body mass (a surrogate of size) increases.

MATERIALS AND METHODS

Molt and natural history data

We built two separate datasets, one containing molt data and a second one containing natural history and geographic information. The molt dataset contained 430 preformative molt cards, collected from captured birds and specimens, from 41 Cardinalidae species (Guallar *et al.* 2020). We excluded 10 species because of lack of molt information: one *Amaurospiza* seedeater, seven *Habia* tanagers, and two *Piranga* tanagers; all of them forest-dwelling species (Billerman *et al.* 2020). Of our 430 molt cards, 294 belonged to one recently published dataset (Guallar & Jovani 2020b), and 136 molt cards were collected from museum specimens for this study (Guallar *et al.* 2020). Molt cards contained molt state (1 replaced, 0 retained) for each of the larger 49 upper wing feathers: 8 median coverts, 10 greater coverts, 1 carpal covert, 9 primary coverts, 3 alula feathers, 3 tertials, 6 secondaries, and 9 visible primaries. Lesser wing coverts were collectively scored 1 when more than 70% of these feathers were replaced and 0 otherwise (Guallar & Jovani 2020a). Thus, sum of molt scores ranged from 0 to 50. Identification of first-year birds was based on established aging criteria: feather coloration, shape, and wear (Pyle 1997b). For species that also undergo prealternate molts (e.g., among genera *Piranga*, *Pheucticus*, and *Passerina*), we carefully evaluated formative feathers replaced on breeding or non-breeding grounds, excluding first-alternate feathers replaced in spring. Finally, we gathered presence/absence data on the auxiliary preformative molt for each species (Table S1).

For our second dataset, we extracted habitat information from Billerman *et al.* (2020), and placed our sample species into one of four broad categories based on key terms mentioned in the habitat descriptions: forest, scrub (mesic), scrub-dry (xeric), and semi-open to open habitats. These categories reflect a gradient from closed and usually cooler habitats to open and usually warmer habitats (De Frenne *et al.* 2019). Next, we collected body mass information from Guallar *et al.* (2009) and Dunning (2007). Finally, we scored delayed plumage maturation based on plumage similarity between formative and definitive basic plumage, regardless of whether the species was sexually dichromatic (sexually monochromatic species may potentially show delayed plumage maturation as well; Woodcock *et al.* 2005). We established four categories: none (1), slight (2), moderate (3), and extensive (4), reflecting whether these two plumages were essentially identical to completely different.

To complete our second dataset, we downloaded geographic ranges from BirdLife International and Handbook of the Birds of the World (2019). We computed centroid coordinates for the breeding and wintering ranges using QGIS (QGIS Development Team 2020). For species with discontinuous ranges, we calculated average centroids weighing for the area of each polygon. We calculated migration distances between centroids of the wintering and breeding ranges using the R function GeoDistanceInMetresMatrix (Rosenmai 2014), which computes geodesic distances as implemented in package Imap (Wallace 2020).

Molt extent and primary replacement

We quantified the influence of five natural history factors on the evolution of preformative molt of Cardinalidae species, using extent of wing-feather molt as the response variable. Concretely, we used three molt-extent metrics: count, relative mass and relative exposure (de la Hera *et al.* 2013, Kiat *et al.* 2019b). Count is simply the number of wing feathers replaced (it is a non-dimensional metric) computed as the sum of feather scores for one wing and ranging from 0 (no molt) to 50 (complete molt). Mass and exposure are dimensional metrics with biological meaning, as they can be conceived as proxies of investment in plumage maintenance (e.g. to keep insulation) and of plumage signaling and exposure to wear, respectively, thus allowing more explicit interpretations. Since results for all three metrics were qualitatively similar, we only showed results for the count metric, unless stated otherwise.

Since wing-feather masses for Cardinalidae species are not available, we used as a proxy a wing-feather mass model built from 82 birds from 39 Palearctic passerine species collected from traffic collisions and prey (Guallar *et al.* 2020). We weighed each upper-wing feather to the nearest 0.01 mg. Because of their small mass, lesser and median coverts were weighed as full tracts. Mass of lesser coverts was subsequently divided by 50 (the approximate number of these feathers on a passerine wing; Figure S1). Mass of each of the eight median coverts was estimated from a sample of known weights (Table S1). We calculated mean feather mass for every species (thus giving the same weight to all species), normalized species feather masses by dividing each of them by the heaviest one, and averaged all normalized species masses to obtain a mean mass per feather across species. We imputed values for the 4.9% missing feathers in our dataset using random forest predictions (Stekhoven & Buehlmann 2012, R Core Team 2019).

Increase feather exposure leads to both increased visibility and increased wear. As with wing-feather masses, wing-feather exposures for Cardinalidae species are not available. To obtain them, we created a wing-feather exposure model from photographs of 62 live birds of 62 Palearctic species (Guallar *et al.* 2020). Photographs showed individuals with folded wings in a standardized upright lateral stance, such that tertials were visible (note that tertials lay on top of the other remiges). We obtained the number of pixels of each upper-wing feather using an image processing program (GIMP 1995-2017; Table S2 and Figure S2). We divided lesser wing coverts by 50, normalized number of pixels of every wing feather by dividing each by that of the most exposed feather and averaged all normalized values to obtain mean exposure per feather across species. Both relative mass and relative exposure were computed as the sum of normalized values of replaced feathers for each of the 430 molt cards.

However, insulation and signaling are not the only functions carried out by wing feathers. Flight is an essential function that is mainly executed by the primaries. For this reason, we also used presence/absence of primary replacement to evaluate the influence of the set of natural history factors on the evolution of preformative molt of Cardinalidae.

Ancestral state reconstruction and correlated evolution

For our working phylogeny, we downloaded 10000 trees for our set of species from BirdTree.org (Jetz *et al.* 2012), derived a consensus tree with least-squares branch lengths using package phytools (Revell 2012), and forced tips to be contemporaneous (Pagel 1992). We followed Klicka *et al.* (2007) to name the five main assemblages of this family (Fig. 1). The masked clade, which contains all the genera with a facial mask (*Piranga*, *Cardinalis*, *Caryothraustes*, and the former genera *Periporphyrus* and *Rhodothraupis*); the blue clade, which contains the species showing male blue plumage (*Amaurospiza*, *Cyanocompsa*, *Cyanoloxia*, and *Passerina*), along with *Spiza*; and three monogeneric clades containing the genera *Habia* (including the former genus *Chlorothraupis*), *Granatellus*, and *Pheucticus*. To root our tree, we used Slate-throated Redstart (*Myioborus miniatus*) as the outgroup (data from Guallar & Jovani 2020).

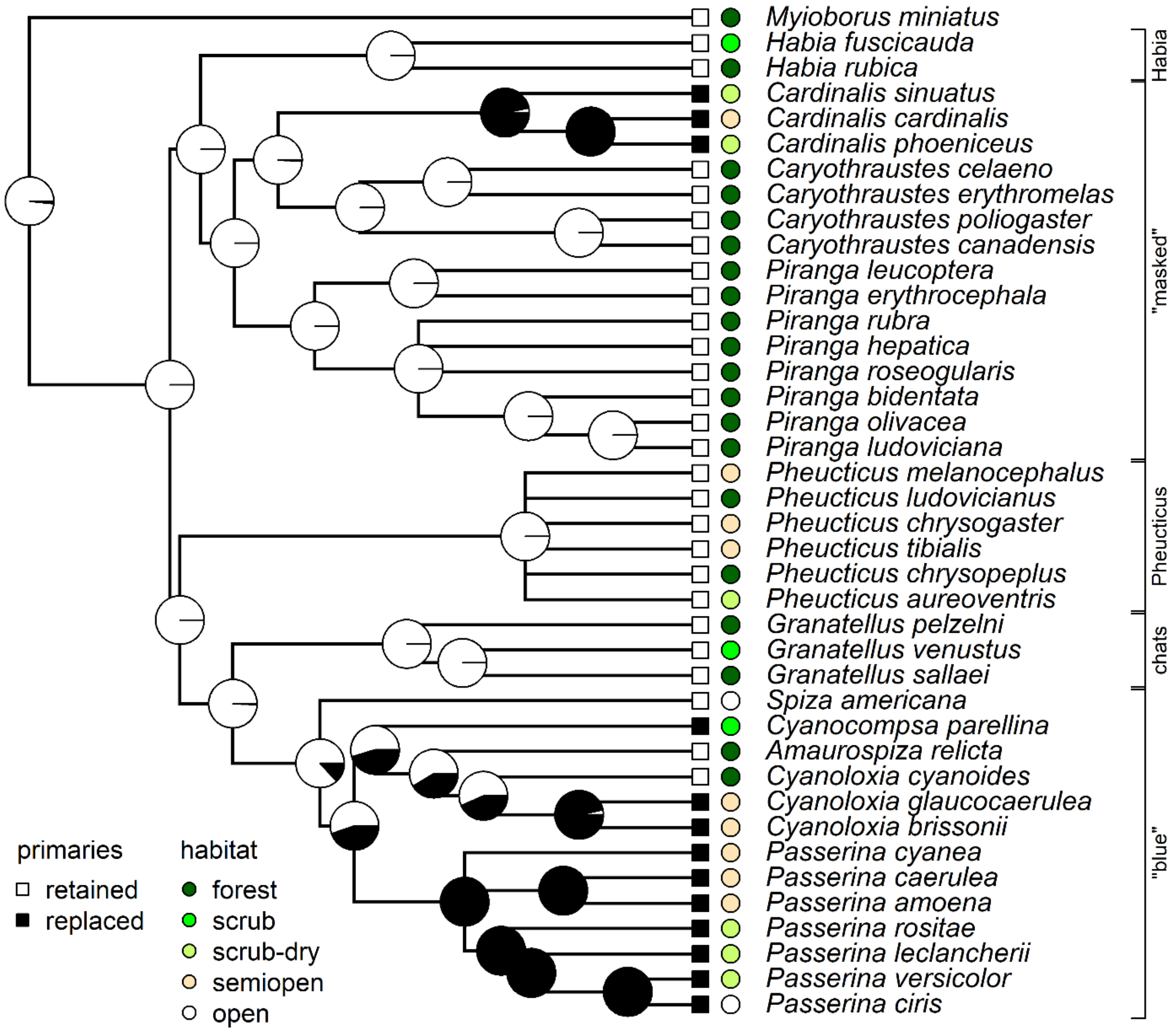
We aimed to reconstruct preformative molt evolution along the phylogenetic tree of Cardinalidae, specifically, whether the ancestral species of the family replaced primaries. We calculated state likelihoods at each node of the phylogenetic tree to determine final maximum likelihood of the ancestral state (Schluter *et al.* 1997). We resolved polytomies using the rerooting algorithm by Yang *et al.* (1995) as implemented in phytools (Revell 2012). We used the phylogenetic tree to show aggregation of similarities between these two states and habitat. We then estimated transition rates from 100 trees using fitDiscrete function as implemented in geiger (Harmon *et al.* 2008).

We employed a second batch of comparative analyses to test whether the evolution of the preformative molt in Cardinalidae (both molt extent and presence/absence of primary molt) was correlated to the evolution of each of the five natural history factors we studied, as well as presence or absence of a documented auxiliary preformative molt We used the continuous random walk model to test continuous variables and the MultiState method to test categorical variables as implemented in BayesTraits (Pagel 1999, Pagel *et al.* 2004) with default settings: MCMC analyses with 1010000 iterations (the first 10000 as burn-in period), sampled every 1000 iterations, and uniform priors (allowed for data with a strong signal).

We ensured that the acceptance rate was 20-40% indicating that chains mixed adequately. We averaged the results of 10 runs to account for randomness. We assessed evidence for correlated evolution versus evidence against it using Bayes factors, concretely the logarithmic scale proposed by Kass & Raftery (1995).

.

Figure 1. Phylogenetic reconstruction of the preformative molt of 39 Cardinalidae species. Bidtree.org does not include two of the species included in this study; Tres Marias Chat *Granatellus francescae* and Amazonian Grosbeak *Cyanoloxia rothschildii* are not split from their sister species (Red-breasted Chat *Granatellus venustus* and Blue-black Grosbeak *Cyanoloxia cyanoides*, respectively). Pie charts on internal nodes depict likelihood. Tip nodes show the association between habitat types and presence-absence of primary replacement in the preformative molt for each species. Klicka *et al.* (2007) described five major clades: (1) a masked clade (*Piranga*, *Cardinalis*, and *Caryothraustes*), (2) a "blue" clade (*Amaurospiza*, *Cyanocompsa*, *Cyanoloxia*, *Passerina*, and *Spiza*), and clades containing the genera (3) *Habia*, (4) *Granatellus*, and (5) *Pheucticus*.



Relative importance of natural history factors

Shared ancestry affects biological traits, such that trait values will be more similar in closely related than in distantly related species (Felsenstein 1985). To account for phylogenetic non-independence among molt extents in Cardinalidae, we fitted PGLS regression lines using the R function phylolm implemented in the phylolm package (Tung Ho & Ané 2014). Among the eight phylogenetic models for the error term implemented in the phylolm function, we selected the one that minimized AIC. We assessed the strength of phylogenetic non-independence using the maximum likelihood value of the scaling parameter Pagel's λ calculated with the same function. For the presence/absence of primary replacement, we fitted logistic lines using the R function phyloglm in the same R package (Tung Ho & Ané 2014).

To complement these results, we examined the relative importance of the five natural history factors on the preformative molt extent of Cardinalidae. We fitted PGLS models using the mean value of the preformative molt extent for each species as response variable, and migratory distance, mean breeding latitude, habitat, delayed plumage maturation and body mass as explanatory variables. We generated one model for each combination of explanatory variables, for a total of 32 models. We ranked the models according to their Akaike information criterion corrected for small sample size values (AICc), and calculated the relative importance of each factor based on its Akaike weight using the zero-method implemented in the R package MuMIn (Bartoń 2019, R Core Team 2019). We also ran relative importance analyses using presence/absence of primary molt as the response variable. Since phylogenetic logistic regression models are not implemented in this package, we computed Akaike weights manually for calculating relative importance of presence/absence of primary replacement.

RESULTS

Ancestral state reconstruction and correlated evolution

Our phylogenetic reconstruction fully supports a molt with no primary replacement as the ancestral state of preformative molt in Cardinalidae (likelihood = 0.999; Fig. 1). This equates with a partial molt (sensu Pyle 1997b), whereby some or all wing coverts and tertials are replaced but not primaries or secondaries. Transition rate from the ancestral state toward primary replacement was 0.0127, whereas the reversal rate was 0.0010 (ΔAICc = 1.854, weak evidence against equal rates). Replacement of primaries during the preformative molt in Cardinalidae was homogenous within genera: with one exception, congeneric species showed either primary replacement or primary retention. Interestingly, the sole exception to this pattern, Blue-black Grosbeak (*Cyanoloxia cyanoides*), is linked to a shift in habitat with respect to the other *Cyanoloxia* species (Fig. 1). More open habitats of both the masked and blue clades (sensu Klicka *et al.* 2007; Fig. 1) are linked to preformative molts that include the replacement of primaries. Notably, however, this shift occurred in neither the *Pheucticus* clade nor in *Spiza* of the blue clade.

Consistent with this result, we also found strong to very strong support for the correlated evolution of the preformative molt and habitat (Table 1). None of the other four natural history factors showed strong evidence of correlated evolution to preformative molt (although delayed plumage maturation reached positive evidence for the count and mass metrics). In view of the relevance of these results, we also reconstructed the ancestral state of habitat and found solid support for a forest-dwelling ancestor of Cardinalidae (likelihood = 0.979). Thus, character reconstruction indicates that the common ancestor was forest dwelling and that it did not replace primaries.

Only species among *Cardinalis*, *Pheucticus*, and three genera in the blue clade are known to undergo auxiliary preformative molts (Table S1). We found very strong support for the correlated evolution of the auxiliary preformative molt and the preformative molt (Table 1). Preformative molt extent was significantly larger in species with auxiliary preformative molt (mean ± SD = 35.1 ± 10.5, n = 14) than in species without it (mean ± SD = 20.7 ± 3.1, n = 25; $F_{1,37}$ = 41.23, P = 0.001; Fig. 3, Table S3 and Fig. S3). However, we found only a weak support for the correlated evolution of the auxiliary preformative molt, habitat, and presence/absence of primary molt (MultiState method: log BF = -0.18; Pagel *et al.* 2004).

Figure 2. Bivariate regression of habitat category on preformative wing-feather molt extent in Cardinalidae. Habitat categories in ascending order of openness. Open habitat category lumped in the semi-open category due to its low sample size (n = 2). Hatched line shows ordinary least-squares regression, red line depicts phylogenetically corrected regression with shaded 95% confidence intervals computed from the variance-covariance matrix as implemented in the R package evomap (Smaers & Rohlf 2016).

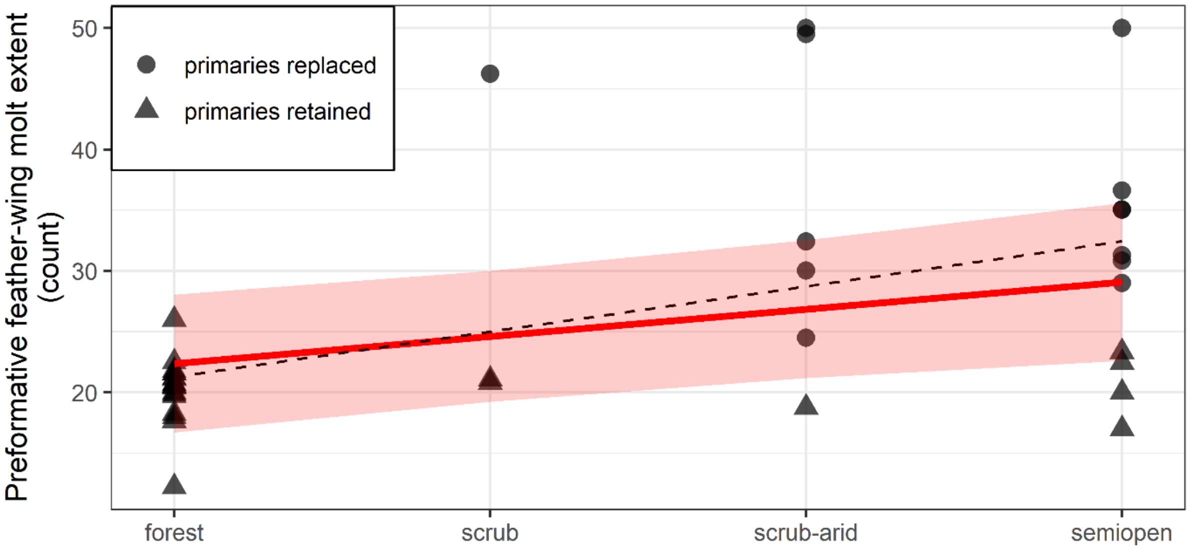


Figure 3. Relationship between preformative molt extent (count) and presence/absence of auxiliary preformative molt. Points represent mean preformative molt extent of each species. Note that available information on the presence of the auxiliary preformative molt is deficient in tropical species, hence, these results should be considered conservative; further study is required.

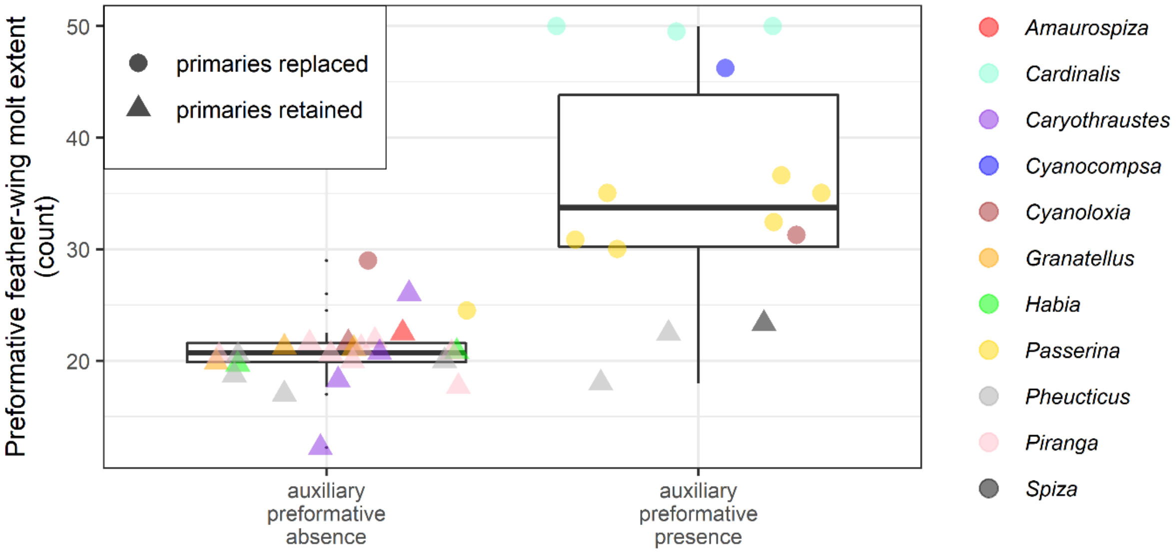


Table 1. Evidence of correlated evolution between preformative wing-feather molt and five natural-history factors, and between preformative wing-feather molt and presence/absence of auxiliary preformative molt in Cardinalidae. Results for all three metrics were consistent, although exposure evidence was mitigated. DPM = delayed plumage maturation; logBF = logarithm of Bayes factor (Kass & Raftery 1995).

	logBF	Evidence
Extent: count		
Habitat	10.72	Very strong
Migration	-0.35	Weak against
Latitude	-0.43	Weak against
DPM	2.82	Positive
Mass	0.68	Weak
Auxiliary PF	17.06	Very strong
Extent: mass		
Habitat	9.74	Strong
Migration	0.23	Weak
Latitude	0.65	Weak
DPM	4.33	Positive
Mass	0.00	Weak
Auxiliary PF	22.48	Very strong
Extent: exposure		
Habitat	5.19	Strong
Migration	-0.21	Weak against
Latitude	-0.50	Weak against
DPM	1.23	Weak
Mass	0.62	Weak
Auxiliary PF	5.52	Strong
Primary molt		
Habitat	5.00	Strong
Migration	-1.40	Weak against
Latitude	0.83	Weak
DPM	1.03	Weak
Mass	-0.41	Weak against
Auxiliary PF	1.29	Weak

Relative importance of natural history factors

The best fit for PGLS regression lines was achieved by the early burst model for the count and mass metrics (Table S4), which allows the rate of evolution to slow through time, and is consistent with a rapid diversification of clades as they enter new adaptive zones, i.e. adaptive radiation (Simpson 1945). However, it was indistinguishable from the Brownian motion model since ΔAICc < 2 (Burnham & Anderson 2002). It was the opposite for the exposure metric (now indistinguishable from the Early Burst model since ΔAICc < 2; Table S4), and consistent with random evolution of signaling across the family (which does not exclude natural selection; Hansen & Martins 1996, Harmon 2019). We found a phylogenetic signal $\lambda = 1$, which implies very strong phylogenetic dependence among related species likely due to phylogenetic inertia.

Based on these analyses, we conclude that habitat was the most important factor explaining preformative molt extent for all three extent metrics, and the only one reaching statistical significance, i.e. with an estimated coefficient whose confidence interval did not overlap with zero (Table 2). Preformative molt extent increased toward more open habitats (Fig. 2; Table S5), and (more weakly) with longer migration distances, increased breeding latitude, and heavier body mass. On the other hand, molt extent decreased as formative plumage increasingly differed from the definitive plumage (Table 2). In support of the weak effect of migration distance, we also did not find significant differences between the preformative molt extent of migratory (mean ± SD= 26.0 ± 7.0, n = 13) and non-migratory species of the family Cardinalidae (mean ± SD= 25.8 ± 10.8, n = 26; $F_{1,37}$= 0.002, P = 0.964; Table S6).

Results for the presence/absence of primary molt analyses were congruous with those for extent: probability of molting primaries increased as habitat becomes more open. Body mass had a negative effect as predicted by our hypothesis on increasing time costs with increasing body size, albeit it was not significant.

Table 2. Results of the PGLS analysis of five natural history factors on three preformative wing-feather molt extent metrics and presence/absence of primary molt in Cardinalidae. 95% confidence intervals (CI) based on 100 bootstrapped samples. To make raw count directly comparable with mass and extent, we normalized this metric to range between 0 and 100. Relative importance (RI) obtained from averaging the 32 models that can be fitted from the combination of the five natural history factors. Values based on the subset of models whose accumulated Akaike weights reached 95% of the total averaged models. Coefficients for the presence/absence of primary molt based on univariate models due to poor convergence of the multivariate model.

	Coefficient	CI	P	RI
Extent: count				
Habitat	3.558	0.118 - 5.825	**0.033**	0.829
Migration	0.001	-0.001 - 0.002	0.606	0.252
Latitude	0.067	-0.120 - 0.219	0.499	0.274
DPM	-1.179	-6.528 - 4.683	0.701	0.209
Mass	0.022	-0.243 - 0.397	0.913	0.173
Extent: mass				
Habitat	6.018	1.184 - 9.887	**0.016**	0.924
Migration	0.001	-0.003 - 0.005	0.628	0.219
Latitude	0.053	-2.530 - 0.324	0.717	0.214
DPM	-1.524	-8.700 - 6.193	0.739	0.195
Mass	0.046	-0.390 - 0.562	0.878	0.181
Extent: exposure				
Habitat	6.470	2.885 - 10.145	**0.008**	1.000
Migration	-0.001	-0.004 - 0.002	0.708	0.197
Latitude	0.009	-0.127 - 0.357	0.546	0.223
DPM	-4.069	-0.104 - 2.241	0.290	0.319
Mass	-0.164	-0.579 - 0.275	0.517	0.227
Primary molt				
Habitat	1.576	0.803 - 2.554	**0.005**	1.000
Migration	-0.014	-0.566 - 0.838	0.944	0.385
Latitude	-0.074	-0.914 - 0.766	0.739	0.397
DPM	-0.320	-1.369 - 0.298	0.309	0.333
Mass	-0.489	-1.729 - 0.387	0.241	0.321

DISCUSSION

Our analyses on the evolution of the preformative molt in the family Cardinalidae have yielded two main findings. First, they indicate that the ancestor of Cardinalidae was a forest-dwelling species whose preformative molt did not include primaries. Second, habitat has been the main force driving preformative molt evolution in Cardinalidae. Transitions from forests toward more open habitats correlated positively to preformative molt investment and exposure, which also involved the replacement of primaries in most genera (Table 1, Figs. 1-2).

Although more than half of the extant species of Cardinalidae continue to inhabit forests, several species have adapted to more open habitats along their evolutionary history. According to Klicka *et al.* (2007), diversification of the five main Cardinalidae clades occurred very early in the history of the family (Fig. 1), consistent with the best-adjusted model, the early burst model. However, this early radiation did not imply a transition to open habitats, except within the blue clade.

Species may colonize new habitats in one of three ways: through dispersal to a new area, extinction of competitors, or the evolution of a new trait or set of traits that allow them to interact with the environment in a new way (Simpson 1945). Our results suggest that transition from the ancestral forest habitat toward open habitats has triggered the increase in preformative molt extent within Cardinalidae, particularly in the evolution of primary replacement. Primaries could be under selection pressure to be replaced during the preformative molt in open-habitat species because these have more pointed wings (Keast 1996; Guallar *et al.* 2009, 2020), leaving juvenile primaries more exposed and therefore prone to degrade faster, which would reduce flight efficiency (Weber *et al.* 2010). Again, increased wear and insolation on more exposed outer than inner primaries may add to aerodynamic reasons to explain the evolution of eccentric molts in Cardinalidae species occurring in open habitats (Pyle 1998; Fig. 1).

Overall, none of the 21 forest-dwelling species in our study replaces primaries during the preformative molt, while 13 of 20 non-forest dwellers do (Fig. 1). Thus, one single transition outside forest habitats may have occurred in the masked clade associated with the origin of genus *Cardinalis*. Both the *Granatellus* and the *Pheucticus* assemblages contain non-forest species but none of these species undergoes primary replacement during the preformative molt (Fig. 1). Absence of transition toward replacement of primaries could occur, for example, because of phylogenetic inertia (phylogenetic signal $\lambda = 1$) or because these species developed other behavioral or physiological solutions to cope with the new physical environment.

The picture gets more complex within the blue clade. This assemblage holds the largest number of species that replace primaries during their preformative molt. However, Dickcissel (*Spiza americana*), which branched off early in the blue clade (Klicka *et al.* 2007), does not replace primaries despite inhabiting completely open areas. The remaining species of the blue clade inhabit open areas, with only *Amaurospiza* seedeaters and two of the four *Cyanoloxia* species inhabiting forests. This suggests a basal transition outside forest habitats, with eventual reversions in the latter two genera and a parallel reversion to the ancestral preformative molt state (retention of primaries).

Thus, both the analyses of correlated evolution and of relative importance consistently showed habitat as the main evolutionary force driving preformative molt extent of Cardinalidae. The influence of habitat has been associated with variation in preformative molt both within and among passerine species (Willoughby 1991, 2007; Guallar *et al.* 2016). Several elements of habitats may affect feather integrity and cause plumage abrasion: cluttered or rough vegetation such as those of xeric scrub (Willoughby 1991), the interaction of open habitats with higher temperatures in the tropics (Kiat & Izhaki 2016), or exposure to direct sunlight typical of open habitats (Bergman 1982, Pyle 1998). Contrastingly, we did not find strong support for delayed plumage maturation, migration distance, breeding latitude, or body mass to have a noticeable influence on the evolution of the preformative molt extent in this family.

Delayed plumage maturation is closely related to sexual and social factors (Senar 2006). Despite the pervasive presence of sexual dichromatism in Cardinalidae (only two *Caryothraustes* species are sexually monochromatic; Billerman *et al.* 2020), we did not find a significant effect of delayed plumage maturation on the preformative molt in Cardinalidae. If anything, we found a negative effect opposite to our hypothesis prediction (Table 1), likely driven by the unexpected presence of delayed plumage maturation in species undergoing extensive preformative molts. Thus, while the complete preformative molt in species with advanced plumage maturation like those in the genus Cardinalis was predictable under our first hypothesis, species with nearly as extensive preformative molts showed delayed plumage maturation (e.g. the entire *Passerina* and *Cyanocompsa* genera; Figs. 1 and 3). This may reflect the heterogeneous strategies underlying delayed plumage maturation, which include species with first-cycle males mimicking the female plumage to reduce aggressive interactions with adult males during winter, but also to deceive them during the breeding season (Rohwer 1986, Senar 2006).

Like delayed plumage maturation, none of the variables associated with constraints showed a significant influence on the evolution of the preformative molt in Cardinalidae (Tables 1 and 2). Although considered a crucial factor in the evolution of molt strategies of Palearctic passerines (Figuerola & Jovani 2001, Kiat *et al.* 2019a), migration distance was uncorrelated to preformative molt extent in Cardinalidae. This discrepancy may have arisen because of different environmental scenarios associated with different evolutionary trajectories, and consequently different evolutionary drivers (Rohwer *et al.* 2005, Ydenberg *et al.* 2007). However, we also suggest that this difference may be one of interpretation. The "post-juvenile" molt in Palearctic studies has largely been defined as molt on the breeding grounds prior to migration, whereas here we assume that the preformative molt strategy has evolved (sensu Humphrey & Parkes 1959) to include molts that are suspended for migration and completed at stopover locations (e.g., Young 1991, Rohwer *et al.* 2005, Pyle *et al.* 2009) or on the winter grounds (Pyle 1997b, Pyle *et al.* 2018). Preformative molt extent may be influenced by an increase in solar exposure with longer migrations, long-distance migrants being exposed to more sun on an annual basis than those that remain on or closer to northern breeding grounds, because solar radiation increases toward the tropics (Pyle 1998, Mueller 2013). Analogously to open-habitat species, primaries could be under selection pressure to be replaced during the preformative molt in long-distance-migrants, because these species need to maximize the aerodynamic properties of primaries to maximize efficiency during the migratory flight (Weber *et al.* 2010).

Finally, the very strong positive correlation between documented presence of an auxiliary preformative molt and extent of the preformative molt provides evidence of their being two elements of the same early-life molt strategy (Howell *et al.* 2003). This view receives further support by the fact that auxiliary preformative molt is not correlated with habitat. Ephemeral, auxiliary formative plumage likely provides some benefits, for example, replacing weak juvenile feathers for migration while allowing for males to remain in a cryptic plumage until the preformative molt (Rohwer 1986, Rohwer *et al.* 2005, Rohwer 2013), and this could help explain the direct relation between presence of auxiliary preformative molt and extensive preformative molts (Figure 3, Figure S3). On the other hand, the weak correlation between this molt episode and habitat does not support a relationship between it and increased exposure to harsh vegetation or insolation. Confirmation of these results will require more documentation for the presence or absence of this molt in all species of Cardinalidae.

This study presents a comparative and functional perspective of the evolution of the preformative molt in a passerine family endemic to the American continent. Our findings indicated the existence of a strong phylogenetic signal and have pinpointed the importance of the physical environment on the evolution of the first-cycle molt strategies, at least in this passerine family. Although our results do not support those of previous analyses indicating the influence of time constraints on the evolution of early life molt strategies (Kiat & Izhaki 2016), such analyses should be expanded in future studies to additional passerine families once large databases on preformative molt extent are built. Considering that the evolutionary histories and the environments to which each taxonomic group has adapted can diverge across passerines, we expect that future studies will find differences in the nature and strength of evolutionary drivers of their preformative molt.

ACKNOWLEDGEMENTS

We wish to thank for their assistance and access to specimen collections: Maureen Flannery, California Academy of Sciences, San Francisco; Carla Cicero, Museum of Vertebrate Zoology, Berkeley; Dr. Adolfo Navarro and M.C. Fanny Rebón of the Museo de Zoología Alfonso Herrera, Dr. Patricia Escalante and M.C. Marco Gurrola of the Colección Nacional de Aves, Mexico City. Special thanks to the following: Sergi Fernández for access to natural history information; Roger Jovani for helpful discussion; Kaspar Delhey for sharing his code to calculate transition rates.

REFERENCES

Bartoń K 2019. MuMIn: multi-model inference. R package v 1.43.15. https://CRAN.R-project.org/ package=MuMIn

Bergman G 1982. Why are the wings of *Larus f. fuscus* so dark? *Ornis Fenn.* 59: 77–83.

Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS (eds) 2020. *Birds of the world.* Cornell Laboratory of Ornithology, Ithaca, NY. https://birdsoftheworld-org.proxy.birdsof theworld.org/bow/home

BirdLife International and Handbook of the Birds of the World 2019. Bird species distribution maps of the world. Version 2019.1. http://datazone. birdlife.org/species/requestdis.

Bojarinova JG, Lehikoinen E, Eeva T 1999. Dependence of postjuvenile molt on hatching date, condition and sex in the Great Tit. *J. Avian Biol.* 30: 437–446.

Burnham KP, Anderson DR 2002. *Model selection and multimodel inference: a practical information-theoretic approach,* 2nd ed. Springer, New York.

Butler LK, Donahue MG, Rohwer S 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): Age effects, aerodynamics, and conservation implications. *Auk* 119: 1010–1023.

Callan LM, La Sorte FA, Martin TE, Rohwer VG 2019. Higher nest predation favors rapid fledging at the cost of plumage quality in nestling birds. *Amer. Nat.* 193: 717–724.

Dawson A 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Phil. Trans. R. Soc. B* 363: 1621–1633.

de la Hera I, Diaz JA, Perez-Tris J, Telleria JL 2009. A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. *J. Avian Biol.* 40: 461–465.

de la Hera I, Reed TE, Pulido F, Visser ME 2013. Feather mass and winter moult extent are heritable but not associated with fitness-related traits in a long-distance migratory bird. *Evol. Ecol.* 27: 1199–1216.

De Frenne P, Zellweger F, Rodríguez-Sánchez F, Scheffers BR, Hylander K, Luoto M, Vellend M, Verheyen K, Lenoir J 2019. Global buffering of temperatures under forest canopies. *Nature Ecol. Evol.* 3: 744–749.

Dunning JB 2007. *CRC Handbook of avian body masses, 2nd ed*. CRC Press, Boca Raton, FL.

Felsenstein J 1985. Phylogenies and the comparative method. *Amer. Nat.* 125: 1–15.

Figuerola J, Jovani R 2001. Ecological correlates in the evolution of moult strategies in Western Palearctic passerines. *Evol. Ecol.* 15: 183–192.

Gosler AG 1991. On the use of greater covert moult and pectoral muscle as measures of condition in passerines. *Bird Study* 38: 1–9.

Guallar S, Jovani R 2020a. Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. *Ibis* 162: 778–786.

Guallar S, Jovani R 2020b. Dataset. (doi:10.6084/m9.figshare.9896516)

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A 2009. *Paseriformes del Occidente de México: morfometría, datación y sexado.* Museu de Ciències Naturals de Barcelona, Barcelona.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2016. Molt strategies of ten Neotropical forest passerine species. *Wilson J. Ornith.* 128: 543–555.

Guallar S, Rueda-Hernández R, Pyle P 2021. Data from: Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. *Ornithology* 138.

Hansen TF, Martins EP 1996. Translating between microevolutionary process and macroevolutionary patterns: the correlation structure of interspecific data. *Evolution* 50: 1404–1417.

Harmon LJ 2019. Phylogenetic comparative methods: learning from trees. EcoEvoRxiv, 20 May 2019. https://doi.org/10.32942/osf.io/e3xnr

Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24: 129–131.

Hawkins GL, Hill GE, Mercadante A 2012. Delayed plumage maturation and delayed reproductive investment. *Biol. Rev.* 87: 257–274.

Hope SF, Stabile FA, Butler LK 2016. Urban living alters moult dynamics in a passerine. *J. Avian Biol.* 47: 304–311.

Houston AI, McNamara JM 1999. *Models of adaptive behaviour.* Cambridge University Press, Cambridge.

Howell SNG, Corben C, Pyle P, Rogers DI 2003. The first basic problem: a review of molt and plumage homologies. *Condor* 105: 635–653.

Humphrey, P. S., K. C. Parkes 1959. An approach to the study of molts and plumages. *Auk* 76: 1–31.

Iglesias-Carrasco M, Duchêne DA, Head ML, Møller AP, Cain K 2019. Sex in the city: sexual selection and urban colonization in passerines. *Biol. Lett.* 15: 20190257.

Jenni L, Winkler R 1994. *Molt and ageing of European passerines*. Academic Press, London.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO 2012. The global diversity of birds in space and time. *Nature* 491: 444–448.

Johnson EI, Wolfe JD 2018. *Molt in Neotropical birds: life history and aging criteria.* Studies in Avian Biology 51. CRC Press, Boca Raton, FL.

Kass RE, Raftery AE 1995. Bayes factors. *J. Amer. Stat. Assoc.* 90: 773–795.

Keast A 1996. Wing shape in insectivorous passerines inhabiting New Guinea and Australian rain forests and eucalypt forest / eucalypt woodlands. *Auk* 113: 94–104.

Kiat Y, Izhaki I 2016. Why renew fresh feathers? Advantages and conditions for the evolution of complete post-juvenile moult. *J. Avian Biol.* 47: 47–56.

Kiat Y, Sapir N 2017. Age-dependent modulation of songbird summer feather molt by temporal and functional constraints. *Amer. Nat.* 189: 184–195.

Kiat Y, Izhaki I, Sapir N 2019a. The effects of long-distance migration on the evolution of moult strategies in Western-Palearctic passerines. *Biol. Rev.* 94: 700–720.

Kiat Y, Vortman Y, Sapir N 2019b. Feather moult and bird appearance are correlated with global warming over the last 200 years. *Nature Comm.* 10: 2540.

Klicka J, Burns K, Spellman GM 2007. Defining a monophyletic Cardinalini: a molecular perspective. *Mol. Phyl. Evol.* 45: 1014–1032.

Mueller RW 2013. Solar irradiance, global distribution. In *Solar energy*. (Richter C, Lincot D, Gueymard CA, eds.). Springer, New York.

Norman SC 1999. Biometrics and post juvenile moult in the Goldcrest *Regulus regulus*. *Ring. Migr.* 19: 175–180.

Pagel M 1992. A method for the analysis of comparative data. *J. Theor. Biol.* 156: 431–442.

Pagel M 1999. Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.

Pagel M, Meade A, Barker D 2004. Bayesian estimation of ancestral character states on phylogenies. *Syst. Biol.* 53: 673–684.

Petren K, Grant PR, Grant BR, Keller LF 2005. Comparative landscape genetics and the adaptive radiation of Darwin's finches: the role of peripheral isolation. *Mol. Ecol.* 14: 2943–2957.

Pyle P 1997a. Molt limits in North American passerines. *North Amer. Bird Bander* 22: 49–90.

Pyle P 1997b. *Identification Guide to North American Birds. Part I Columbidae to Ploceidae.* Slate Creek Press, Bolinas, CA.

Pyle P 1998. Eccentric first-year molt patterns in certain Tyrannid flycatchers. *Western Birds* 29: 29–35.

Pyle P 2008. *Identification Guide to North American Birds. Part II.* Slate Creek Press, Point Reyes Station, CA.

Pyle P, Leitner WA, Lozano-Angulo L, Avilez-Teran F, Swanson H, Gómez-Limón E, Chambers MK 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. *Condor* 111: 583–590.

Pyle P, Saracco JF, DeSante DF 2018. Evidence of widespread movements from breeding to molting grounds by North American landbirds. *Auk Orn. Adv.* 135: 506–520.

QGIS Development Team 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team 2019. R: A language and environment for statistical computing v3. 6. 1. R Foundation for Statistical Computing, Vienna.

Revell LJ 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Meth. Ecol. Evol.* 3: 217–223.

Rohwer S 1986. A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. *Auk* 103: 281–292.

Rohwer S 2013. Molt intensity and conservation of a molt migrant (*Passerina ciris*) in northwestern Mexico. *Condor* 115: 421–433.

Rohwer S, Fretwell SD, Niles DM 1980. Delayed maturation in Passerine plumages and the deceptive acquisition of resources. *Amer. Nat.* 115: 400–437.

Rohwer S, Butler LK, Froehlich DR, Greenberg R, Marra PP 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. In *Birds of Two Worlds: The Ecology and Evolution of Migration* (Greenberg R, Marra PP eds.). Johns Hopkins University Press, Baltimore.

Rohwer S, Ricklefs RE, Rohwer VG, Copple MM 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biol.* 7: 1246.

Rosenmai P 2014. Calculating a distance matrix for geographic points using R. https://eurekastatistic s.com/calculating-a-distance-matrix-for geograp hic-points-using-r/

Schluter D, Price T, Mooers AØ, Ludwig D 1997. Likelihood of ancestor states in adaptive radiation. *Evolution* 51: 1699–1711.

Senar JC 2006. Color diplays as intrasexual signals of aggression and dominance, p. 87–136. In *Bird Coloration: Function and Evolution* (Hill GE, McGraw KJ eds.). Harvard University Press, Cambridge, MS.

Senar JC, Copete JL, Martin AJ 1998. Behavioural and morphological correlates of variation in the extent of postjuvenile moult in the Siskin Carduelis spinus. *Ibis* 140: 661–669.

Simpson GG 1945. The Principles of Classification and a Classification of Mammals. *Bull. Amer. Mus. Nat. Hist.* 85.

Smaers JB, Rohlf FJ 2016. Testing species' deviations from allometric predictions using the phylogenetic regression. *Evolution* 70: 1145–1149.

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Nat. Acad. Sci.* 102: 5460–5465.

Stekhoven DJ, Buehlmann P 2012. MissForest - non-parametric missing value imputation for mixed-type data. *Bioinformatics* 28: 112–118.

Thompson CW, Leu M 1994. Determining homology of molts and plumages to address evolutionary questions: A rejoinder regarding Emberizid finches. *Condor* 96: 769–782.

Thompson CW, Leu M 1995. Molts and plumages of orange-breasted buntings (*Passerina leclancherii*) : implications for theories of delayed plumage maturation. *Auk* 112: 1–19.

Tung Ho LS, Ané C 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Syst. Biol.* 63: 397–408.

Wallace JR 2020. lmap: interactive mapping v 1. 32. https://cran.r-project.org/web/packages/lma p/lmap.pdf

Weber TP, Kranenbarg S, Hedenström A, Waarsing JH, Weinans H 2010. Flight feather shaft structure of two warbler species with different moult schedules: a study using high-resolution X-ray imaging. *J. Zool.* 280: 163–170.

Willoughby EJ 1986. An unusual sequence of molts and plumages in Cassin's and Bachman's sparrows. *Condor* 88: 461–472.

Willoughby EJ 1991. Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proc. West. Found. Vert. Zool.* 4: 247–286.

Willoughby EJ 2007. Geographic variation in color, measurements, and molt of the Lesser Goldfinch in North America does not support subspecific designation. *Condor* 109: 419–436.

Woodcock EA, Rathburn MK, Ratcliffe LM 2005. Achromatic plumage reflectance, social dominance and female mate preference in Black-capped chickadees (*Poecile atricapillus*). *Ethology* 111: 891–900.

Yang Z, Kumar S, Nei M 1995. A new method for inference of ancestral nucleotide and amino acid sequences. *Genetics* 141: 1641–1650.

Ydenberg RC, Butler RW, Lank DB 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. *J. Avian Biol.* 38: 523–529.

Young BE 1991. Annual molt and interruption of the fall migration for molting in Lazuli Buntings. *Condor* 93: 236–250.

SUPPLEMENTARY INFORMATION

Table S1. Species names and associated natural history information used in this study. DPM = delayed plumage maturation (1 = none, 2 = slight, 3 = moderate, 4 = extensive). Primary molt (PM) and auxiliary preformative (aPF) molt are presence/absence data. Information for Nearctic species on the latter episode extracted from Pyle (1997b).

Latin name	English name	Habitat	Mass (g)	Migration (km)	DPM	Latitude (º)	aPF	PM	Synonyms
Pheucticus chrysopeplus	Yellow Grosbeak	forest	75.9	0	3	21.118474	0	0	
Pheucticus tibialis	Black-thighed Grosbeak	semiopen	62.3	0	2	9.531165	0	0	
Pheucticus chrysogaster	Golden Grosbeak	semiopen	55.8	0	3	-8.346485	0	0	
Pheucticus aureoventris	Black-backed Grosbeak	scrub-dry	49	880	4	-18.566268	0	0	
Pheucticus ludovicianus	Rose-breasted Grosbeak	forest	42	4299	4	48.044080	1	0	
Pheucticus melanocephalus	Black-headed Grosbeak	semiopen	45.5	1967	4	40.888574	1	0	
Granatellus venustus	Red-breasted Chat	scrub	11.1	0	4	19.2100271	0	0	
Granatellus francescae	Tres Marias Chat	scrub-dry	9.9	0	4	21.558557	0	0	*Granatellus venustus*
Granatellus sallaei	Gray-throated Chat	forest	11.2	0	3	18.2461694	0	0	
Granatellus pelzelni	Rose-breasted Chat	forest	26.3	0	3	-2.98181274	0	0	
Spiza americana	Dickcissel	open	14.7	4040	3	39.972085	1	0	
Passerina cyanea	Inidigo Bunting	semiopen	28.7	1915	4	39.162198	1	1	
Passerina caerulea	Blue Grosbeak	semiopen	15.5	2002	4	34.254125	1	1	
Passerina amoena	Lazuli Bunting	semiopen	20	2302	4	43.031897	1	1	
Passerina rositae	Rose-bellied Bunting	scrub-dry	13.2	0	4	16.612092	0	1	
Passerina leclancherii	Orange-breasted Bunting	scrub-dry	12.5	0	4	18.322753	1	1	
Passerina versicolor	Varied Bunting	scrub-dry	15.9	644	4	25.122893	1	1	
Passerina ciris	Painted Bunting	open	16.2	1731	4	32.241282	1	1	
Cyanocompsa parellina	Blue Bunting	scrub	13.1	0	4	18.8298015	1	1	
Amaurospiza relicta	Slate-blue Seedeater	forest	13.1	0	4	18.3667759	0	0	*Amaurospiza concolor*
Cyanoloxia cyanoides	Blue-black Grosbeak	forest	32.5	0	4	11.1680564	0	0	
Cyanoloxia rothschildii	Amazonian Grosbeak	forest	24.8	0	4	-3.65613983	0	0	*Cyanoloxia cyanoides*
Cyanoloxia brissonii	Ultramarine Grosbeak	semiopen	27.5	0	4	-19.4359239	1	1	*Cyanocompsa brissonii*
Cyanoloxia glaucocaerulea	Glaucuous-blue Grosbeak	semiopen	18.2	735	4	-29.7829783	0	1	
Habia fuscicauda	Red-throated Ant-Tanager	scrub	38	0	4	16.637223	0	0	
Habia rubica	Red-crowned Ant-Tanager	forest	32.5	0	4	-6.966514	0	0	
Piranga roseogularis	Rose-throated Tanager	forest	24	0	4	18.9259574	0	0	
Piranga erythrocephala	Red-headed Tanager	forest	18.32	0	4	21.592919	0	0	
Piranga leucoptera	White-winged Tanager	forest	36.6	0	3	3.795284	0	0	
Piranga olivacea	Scarlet Tanager	forest	28.2	4825	3	41.720508	0	0	
Piranga rubra	Summer Tanager	forest	29.2	1985	4	33.472758	0	0	
Piranga bidentata	Flame-colored Tanager	forest	33.7	0	4	20.7573468	0	0	
Piranga ludoviciana	Western Tanager	forest	28.1	1695	3	48.953968	0	0	
Piranga hepatica	Hepatic Tanager	forest	39.2	100	4	32.5016091	0	0	includes *Piranga lutea*

Table S1 (cont.)

Latin name	English name	Habitat	Mass (g)	Migration (km)	DPM	Latitude (o)	aPF	PM	Synonyms
Cardinalis cardinalis	Northern Cardinal	semiopen	42.6	100	1	34.8565633	1	1	
Cardinalis phoeniceus	Vermilion Cardinal	scrub-dry	35	0	1	10.9550030	1	1	
Cardinalis sinuatus	Pyrrhuloxia	scrub-dry	35.2	0	1	28.2555012	1	1	
Caryothraustes poliogaster	Black-faced Grosbeak	forest	41.8	0	2	15.6434785	0	0	
Caryothraustes canadensis	Yellow-green Grosbeak	forest	34.5	0	2	-0.7442601	0	0	
Caryothraustes celaeno	Crimson-collared Grosbeak	forest	60	0	4	22.5160982	0	0	*Rhodothraupis celaeno*
Caryothraustes erythromelas	Red-and-black Grosbeak	forest	48	0	4	1.44481776	0	0	*Periporphyrus erythromelas*
Myioborus miniatus	Slate-throated Whitestart	forest	7.83	0	3	9.52509163	0	0	

Chapter 6

Partial or complete? The evolution of post-juvenile moult strategies in passerine birds

Kaspar Delhey[1], Santi Guallar[2], Rafael Rueda Hernández[3], Mihai Valcu[1], Daiping Wang[1] & Bart Kempenaers[1]

1 Max Planck Institute for Ornithology, Seewiesen, Germany

2 Department de Vertebrats, Museu de Ciències Naturals de Barcelona, Barcelona

3 Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México DF, México.

Published in: Delhey K, Guallar S, Rueda-Hernández R, Valcu M, Wang D & Kempenaers B 2020 Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. *J. Anim. Ecol.* 89: 2896-2908.

ABSTRACT

Moulting strategies in birds have evolved to avoid overlap with, or prepare for, other demanding parts of the annual cycle, such as reproduction or migration. When moulting for the first time after leaving the nest, young birds replace their typically poor-quality plumage during the post-juvenile moult. The extent of this moult varies between species from partial (not all feathers are moulted) to complete. Earlier studies that aimed to explain this variation were restricted to Western Palearctic birds and focused almost exclusively on constraints. These studies suggest that in most species a complete post-juvenile moult may not be possible simply because young birds do not have the same access to resources as adults, unless environmental conditions are favourable. We expanded the spatial and taxonomic scope to >1300 passerine species from across the world and considered not only the role of constraints on moult, but also the importance of selective pressures favouring a complete moult. Thus, we test whether complete post-juvenile moult is more prevalent in species where nest-grown feathers are presumably of poor quality (shorter nestling period), that live in environments that foster quick plumage degradation (open habitats, high insolation and humidity), and where males are under strong sexual selection. Our data reveal that 24% of species carry out a complete post-juvenile moult, and that this trait has a strong phylogenetic signal. Complete moult is more common in species that inhabit warmer regions and open habitats, show no delayed plumage maturation, and have higher levels of sexual dichromatism (indicating strong sexual selection). Neither the presumed quality of the nest-grown plumage, nor living in regions with high insolation correlates with complete moult. In conclusion, the evolution of complete post-juvenile moult not only depends on whether birds can perform a complete moult (i.e. suitable environmental conditions) but also on the strength of selection associated with the need of a complete moult. In particular, the necessity to keep the plumage in good condition in challenging environments, and the benefits associated with producing adult-like plumage colours to attract mates or deter rivals, seem to play an important role.

INTRODUCTION

Feathers are an essential feature of birds, fulfilling a variety of key functions, such as flight, thermoregulation, communication, and camouflage. They are also extremely complex integumentary appendages composed of keratin which, when fully grown, are dead structures that deteriorate over time. This requires their regular replacement through moults. Moulting is considered an energetically expensive process that involves substantial physiological changes and often affects the performance of the plumage, hampering flight or reducing insulation (Newton 2009). Hence, variation among species in the timing, speed, sequence, and extent of moult has been shaped by natural selection (a) to coincide with periods when resource availability is high (Barta *et al.* 2006), (b) to avoid interference with other demanding life-history events such as reproduction and migration (Newton 2009) and (c) to ensure that the plumage is in optimal shape for these events (Kiat 2018). As a result, in most bird species, moult episodes follow a predictable sequence during their annual and life cycles (Barta *et al.* 2006).

In most passerine species, adults replace the entire plumage at least once per year, and this moult – which is referred to as prebasic or post-nuptial moult – generally takes place shortly after breeding (Jenni & Winkler 1994, Howell *et al.* 2003). For young birds, the first moult after leaving the nest is the preformative or post-juvenile moult (Jenni & Winkler 1994, Howell *et al.* 2003). Juvenile individuals commonly have plumage of lower quality than that of adults (Fogden 1972, Callan *et al.* 2019) and to successfully face the challenges of early independent life their feathers will most likely need to be replaced (Kiat and Izhaki 2016, Kiat and Sapir 2018). However, this moult is also challenging, because young birds are not as proficient as adults at obtaining food and evading predators (Heise & Moore 2003, Hoy *et al.* 2015, Naef-Daenzer & Gruebler 2016). It is no surprise then that in the majority of passerine birds the first moult leading into adulthood is partial. Commonly, most of the body plumage is replaced, but varying numbers of wing and tail feathers are retained. Nevertheless, a sizeable proportion of species carry out a complete post-juvenile moult (Ginn & Melville 1983, Jenni & Winkler 1994, Pyle 1997), raising the question why not all species follow this strategy. To answer this question, we need to identify not only the constraints and costs that prevent a complete moult, but also the factors that favour a complete post-juvenile moult and establish how these vary across species.

One important constraint limiting the occurrence of complete post-juvenile moult is simply the time available for moulting. Accordingly, previous analyses (Kiat & Izhaki 2016) show that complete -post-juvenile moult is more prevalent among (a) smaller and medium-sized species compared to larger ones, because larger species moult more slowly (Rohwer *et al.* 2009), and (b) resident species, presumably because migratory species have less time to moult before departing to their wintering grounds. These time constraints should be most marked for species living in highly seasonal environments, where favourable conditions for moulting deteriorate rapidly after the summer. Furthermore, (Kiat & Izhaki 2016) show that complete post-juvenile moult is more common at lower latitudes, where temperatures are higher and seasonality lower. The type of resources exploited also matter since species that feed on highly seasonal resources such as insects and other invertebrates are less likely to show complete post-juvenile moult than seed-eating species (Kiat & Izhaki 2016). The latter presumably have a more stable food supply, especially towards the end of summer and autumn when moulting takes place (Barta *et al.* 2006, Faccio 2018). These recent efforts exploring the evolution of moult strategies are largely restricted to passerines that occur in temperate regions and it remains to be shown whether environmental constraints can explain the occurrence of complete post-juvenile moult in a more diverse sample of species.

While resource availability may lead to a partial post-juvenile moult in many species (Kiat & Izhaki 2016), species with ecological and life-history characteristics that require a highly functional post-juvenile plumage will be under stronger selection to moult the entire juvenile plumage. Because the post-juvenile moult replaces the plumage grown in the nest, species in which nest-grown feathers are of poorer quality –such as species with a short developmental time in the nest (Callan *et al.* 2019)– should be more likely to perform a complete moult. Indeed, previous studies showed that Western Palearctic species with a complete post-juvenile moult grew poorer-quality plumage in the nest (Kiat & Izhaki 2016, Kiat & Sapir 2018). In addition, a complete post-juvenile moult should be more likely in species that live in environmental conditions that foster feather degradation. Feathers degrade rapidly by being exposed to sunlight (Test 1940, Bergman 1982). Hence, species that are more exposed to strong sunshine, such as those that live in open environments and in regions with high levels of insolation should be more likely to have a complete post-juvenile moult. Feathers also degrade due to keratinolytic bacteria, which are more active in humid and warm conditions (Burtt & Ichida 2004). Thus, species living in these conditions should also be more likely to evolve complete post-juvenile moult.

Furthermore, the occurrence of complete post-juvenile moult may be linked to the intensity of sexual selection. A complete post-juvenile moult eliminates the differences in feather wear and coloration between new and old feathers that characterise first-year birds in species with partial post-juvenile moult. Such subtle cues of age –when available– may be used by conspecifics to gauge the age of a rival or potential mate (Crates *et al.* 2015). Age is an important determinant of breeding success in many species (Cleasby & Nakagawa 2012), with older males being preferred as mates and better at competing for resources (Brooks and Kemp 2001). It could thus be hypothesized that in species in which males are under strong sexual selection, juvenile birds should be more likely to have evolved complete post-juvenile moult to conceal their age and display the most elaborate colours possible during their first breeding season (Kiat *et al.* 2019). This effect however, should mainly apply to species where the plumage of first-year males resembles that of older males, because a complete post-juvenile moult would make no difference in species where young males clearly differ from older males, that is, in species with delayed plumage maturation (Hawkins *et al.* 2012). Moreover, species with delayed plumage maturation are often under stronger sexual selection (Beauchamp 2003), and thus statistically accounting for delayed plumage maturation is essential to assess the effects of sexual selection intensity on the extent of post-juvenile moult.

Here, we undertake a large-scale analysis of the evolutionary and ecological correlates of complete post-juvenile moult in passerine birds. We collated information on the extent of post-juvenile moult (partial vs. complete) for the species of passerine birds that inhabit three well-known avifaunas (Western Palearctic, Nearctic and Australasia) and we complemented this survey with information from the primary literature on species from other regions. Following the two key hypotheses that the extent of post-juvenile moult is shaped by constraints and by variation in selective pressures associated with plumage performance, we predict that complete post-juvenile moult should be more prevalent in: (1) species that are less time-constrained, such as smaller species that are resident or migrate short distances; (2) species that live in environments with less seasonal fluctuation of resources such as tropical regions; (3) species that exploit less-seasonal resources (seed-based diet); (4) species with short developmental periods in the nest, that fledge with lower-quality plumage, (5) species that live where feather deterioration is more rapid, i.e. in open habitats and regions with high levels of insolation or rainfall (which promote the activity of feather-degrading bacteria); and (6) species that are under strong sexual selection, such that males may benefit from achieving similar coloration to adults during their first year (species with reduced delayed plumage maturation).

MATERIALS AND METHODS

Post-juvenile moult scoring and species included

We scored each species of passerine with available moult data mentioned in the three main regional handbooks where information on moult is consistently listed (Birds of the Western Palearctic, BWP (Cramp & Simmons 1977), Birds of North America Online, BNA (Poole 2005) and the Handbook of Australian, New Zealand and Antarctic Birds, HANZAB (Marchant & Higgins 1990). We complemented and updated this dataset with information from the primary literature (see the Data sources section) and from own unpublished field data. In total we compiled data for n = 1593 taxa.

Species for which we could obtain moult data were classified into the following categories: (1) complete post-juvenile moult, species that moult all feathers during the post-juvenile moult; (2) partial post-juvenile moult, species that moult some but not all feathers (including species classified as having incomplete, partial and limited post-juvenile moult; Pyle 1997, Johnson & Wolfe 2017); and (3) partial or complete post-juvenile moult, species where some individuals or populations show complete and some partial post-juvenile moult. Migratory species that initiate their post-juvenile moult in the breeding area and complete it after arriving in the wintering grounds (e.g. many Hirundinidae) were included as having a complete post-juvenile moult, following the classification provided in our sources. However, the strategy of completing the post-juvenile moult in the wintering quarters is hard to distinguish from that of species which undergo a partial post-juvenile moult, but then perform a complete nuptial (pre-breeding) moult in their wintering grounds (e.g. many *Acrocephalus* sp.). In our first classification these species were assigned to the partial post-juvenile moult category, because post-juvenile and nuptial moult were considered as separate moulting events. However, given the difficulty of separating moult events in some cases (Jenni & Winkler 1994), and the fact that from a functional point of view all these species perform a complete moult before their first breeding season, we computed a new response variable (complete moult before first breeding: yes/no). Species were considered to have a complete moult before the first breeding season if they had either a complete post-juvenile moult or if we had evidence that they performed a complete nuptial moult. We note that the extent of nuptial moult is often not well-known. Nevertheless, using this new response variable allowed us to assess whether results differed compared to the original post-juvenile moult classification. For each species, we also estimated data quality by recording whether or not the moult type assessment was based on limited data (usually reported in text by indicating that limited information was available and/or that only few specimens have been examined).

After classifying moult patterns, we matched the scientific names used in our moult data sources with the species names used by our source of phylogenetic information: www.birdtree.org (Jetz *et al.* 2012). After matching species names, we ended up with 94 species for which we had more than one source of information on post-juvenile moult, and the classification agreed for 81 species. In the remaining cases, we either used the more recent or comprehensive source (n = 2 species), or we assigned “complete or partial” (n = 11 species for which one source assigned one population as having complete post-juvenile moult and another source assigned a different population as having partial post-juvenile moult). This resulted in a final sample of 1315 species for which we had data on post-juvenile moult.

Explanatory variables

Variables based on distribution ranges. We used distribution ranges (as vectorized polygons) from Birdlife International (http://datazone.birdlife.org/) and overlapped these with raster layers of annual mean temperature (BIOCLIM BIO 1, resolution 0.0083 decimal degrees), annual precipitation (BIOCLIM BIO12, 0.0083 decimal degrees), and mean annual insolation, the amount of solar energy received by a given surface (W/m^2, 0.25 decimal degrees). Annual mean temperature and annual precipitation were obtained from (Karger *et al.* 2017) while insolation was obtained by averaging monthly estimates for the years 2006 to 2019 obtained from https://neo.sci.gsfc.nasa.gov/. Using the function ‘exact_extract’ from the R package ‘exactextractr’ (Baston 2020) we averaged climatic and insolation values for all raster cells covered by a species’ distribution. We computed climatic and insolation estimates separately for the breeding and year-round distribution ranges and for the non-breeding distribution range of migratory species. Subsequently, we averaged data for the breeding or year-round resident and non-breeding distribution to obtain overall estimates for the entire species distribution. This procedure may not be entirely accurate when quantifying the climate experienced by migratory species, because they do not experience the winter in their breeding grounds. Therefore, climatic variables may be biased in migratory species, particularly in long-distance migrants. To determine whether this potential bias drives some of the climatic effects that we detect (see results), we re-ran analyses excluding long-distance migrants (species with migratory distances > 2000 km; Dufour *et al.* 2020). Finally, we computed absolute latitude as the distance in degrees between the centroid of each species’ breeding or year-round resident distribution (avoiding the non-breeding distribution) and the equator using function “sf_centroid” from the package “sf” (Pebesma 2018). This information was available for 1311 species.

Other explanatory variables. (a) Body mass (log10-transformed, n = 1287 species) was obtained mainly from Dunning (2008) and (Wilman *et al.* 2014) as collated by (Mcqueen *et al.* 2019). (b) Migration distance (in km, data for n = 1315 species), obtained from (Dufour *et al.* 2020) (variable called “distance_quanti_ALL” in their dataset). In this dataset migration distance was missing for 10 resident species and these were assigned migration distance of 0 (Dufour *et al.* 2020). (c) Diet, the percentage of the diet composed by seeds, obtained from Wilman *et al.* (2014) (data for n = 1315 species). (d) Length of the nestling period (in days, n = 860 species), collated from the Handbook of the Birds of the World (Del Hoyo 1992, HBW) and Cooney *et al.* (2020). (e) Habitat openness (n = 1311 species). Based on the habitat use data from Birdlife International (http://datazone.birdlife.org/) we assigned each major habitat used by each species an openness score that varies from 1 (forests) to 4 (coastal and marine environments) and averaged these scores for each species. For more details on the scores assigned to each type of habitat, see suppl. material. (f) Sexual dichromatism, as an estimator of the strength of sexual selection on males, scored based on scanned book plates from the HBW. Sexual dichromatism was computed for each species as the average difference in Red-Green-Blue (RGB) values between males and females across nine plumage patches as described in (Mcqueen *et al.* 2019) (n = 1293 species). Book plates provide good approximations of colour variation measured directly on museum specimens (Dale *et al.* 2015, Delhey *et al.* 2019). (g) Delayed plumage maturation (n = 1297 species), scored on a three- level scale (0 = species where first-year males are identical or very similar to second-year adult males, 1 = species where first-year individuals are similar but on average less ornamented than second-year males, and 2 = species which have a clearly distinct first-year plumage and often take several years to reach adult plumage).

Statistical analyses

All analyses were carried out within the R statistical environment (R Development Core Team 2019). We used the package btw (Griffin 2018) to interact with the program BayesTraits V3 (http://www.evolution.rdg.ac.uk/BayesTraitsV3.0.2/BayesTraitsV3.0.2.html) from within R. We used the Multistate module in BayesTraits to estimate the rates of evolutionary shifts between the different types of post-juvenile moult using maximum likelihood across a sample of 100 phylogenies. We considered two alternative transition models: a model where gains of complete post-juvenile moult happen at a different rate than losses, and a model where both rates are set to be equal. We compared the performance of both models using a likelihood-ratio test. As BayesTraits allows polymorphic traits, species with both partial and complete post-juvenile moult were considered polymorphic. All other analyses require binary traits and hence we classified all species with partial/complete post-juvenile moult as being able to carry out a complete moult.

We quantified the phylogenetic signal of post-juvenile moult using Fritz & Purvis' D for binary traits (Fritz & Purvis 2010) using the function phylo.d from the R package caper (Orme *et al.* 2018) computed across 100 phylogenies (see below for justification). D values close to 0 indicate a strong phylogenetic signal as expected from a Brownian motion type of evolution (equivalent to lambda = 1 for a continuous trait), while values close to 1 indicate random evolutionary patterns (essentially little phylogenetic signal, equivalent to lambda = 0 for a continuous trait; Fritz & Purvis 2010). We also used a permutation procedure implemented in the same function (1000 permutations) to test whether values of D are statistically different from 0 and 1. For visual purposes, we also reconstructed ancestral states for the different types of post-juvenile moult using stochastic mapping across 100 phylogenies as implemented by function 'make.simmap' in the package phytools (Revell 2012) using the model that allows different rates for gains and losses (the best supported model identified by BayesTraits, see results).

To quantify the associations between our explanatory variables and the occurrence of complete post-juvenile moult we used logistic phylogenetic regression (Ives & Garland 2010) as implemented in the function phyloglm from the package phylolm (Tung Ho & Ané 2014). The phylogenetic structure in the residual distribution is estimated and corrected by the parameter alpha, which reflects the overall rate of transition between binary states. Small values of alpha (close to zero) correspond to stronger phylogenetic effects (Ives & Garland 2010). All models were run across a sample of 100 phylogenies (see justification below) using the Ericsson backbone obtained from www.birdtree.org (Jetz *et al.* 2012) to account for phylogenetic uncertainty. These phylogenetic supertrees include nearly all bird species and have been obtained using available genetic data in combination with taxonomic information to randomly place species without genetic data using a birth-death polytomy resolver (Rabosky 2015). Based on simulations, Rabosky (2015) suggested that this random placement of species may bias comparative analyses by reducing the phylogenetic signal in trait data. However, this conclusion was based on simulations with closely related groups of species, within taxonomic families, and Rabosky (2015) suggests that biases should be much less marked if the analyses are focused on taxonomically broad and sparse datasets. Given that our data include most passerine families with relatively sparse sampling within families, we expect biases to be minor. Moreover, most of the species included in our samples have been placed in the phylogeny using genetic data (n = 1176 species).

In each case, results from the 100 models were summarised using Rubin's rules (Nakagawa & de Villemereuil 2019). This approach enabled us to compute average estimates, their standard errors, associated test statistics (t-values), degrees of freedom and p-values that incorporate phylogenetic uncertainty adjusting for sample sizes (Nakagawa & de Villemereuil 2019). We also computed “relative efficiency” which reflects, for each parameter, the efficacy of the process of accounting for phylogenetic uncertainty by comparing the used number of phylogenies with the theoretical efficacy achieved by using an infinite number of phylogenies. This value varies between 0 and 1 and achieving values above 0.99 is recommended (Nakagawa & de Villemereuil 2019). We achieved this level with 100 phylogenies for all models and parameters, adequately capturing phylogenetic uncertainty in our analyses. In some cases (see Tables S1-S14) a few models (all < 108) failed to converge and were discarded, but relative efficiency values were still > 0.99.

Because some of the explanatory variables had missing values, sample sizes differed between datasets. We therefore compiled two main datasets. For Dataset 1 (n = 1266 species), we subset the data to include: body mass, latitude, temperature, precipitation, insolation, habitat openness, delayed plumage maturation, sexual dichromatism and migration distance. For Dataset 2 (n = 860 species) we included the variables mentioned above plus time nestlings spent in the nest. For each dataset, we ran models including each explanatory variable as sole predictor and one model with all variables together. However, we could not fit all covariates in the same model due to high levels of collinearity between latitude and temperature (r = -0.83), latitude and insolation (r = 0.60) and temperature and insolation (r = 0.77). We therefore fitted three alternative models: one with latitude, one with temperature, and one with insolation. Finally, we re-ran these three multivariate models for a subset of dataset 1, eliminating species for which moult information was more limited (n = 245) to check whether results changed.

All explanatory variables were centred and scaled. For all models we computed two values of R2 using function R2.lik from the package rr2 (Ives and Li 2018). This function compares the likelihood of the focal model with a null model. We compared it to two different null models: (1) a simple logistic regression without covariates and without accounting for the effect of phylogeny, and (2) a phylogenetic logistic regression without covariates. Thus, the first R^2 value should quantify the effects of both covariates and phylogeny (equivalent to R^2 conditional), while the second estimates the contribution of covariates independent of phylogeny (equivalent to R^2 marginal).

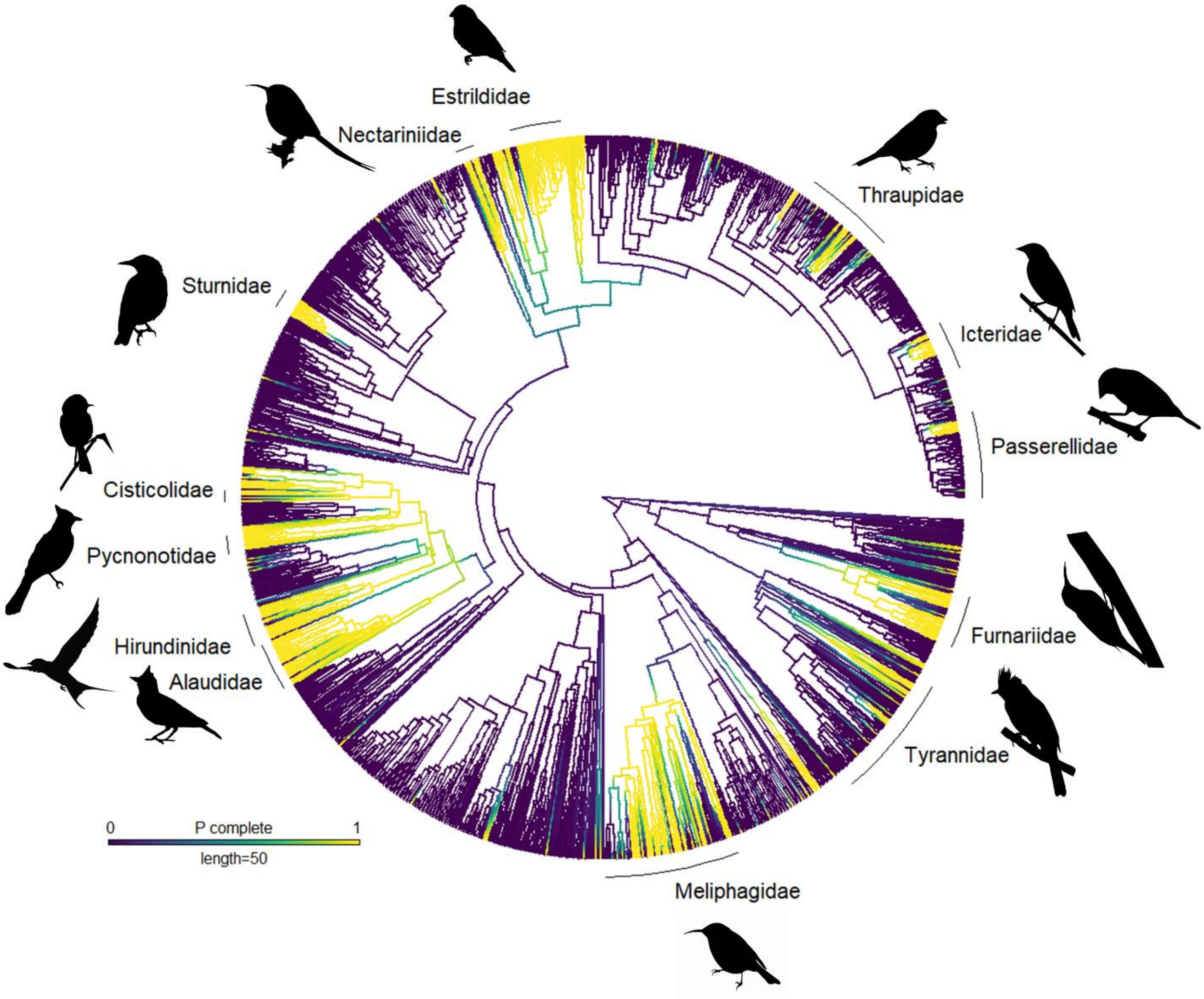
RESULTS

We obtained information on post-juvenile moult for 1315 species belonging to 83 of the 97 families of passerine birds. Of those, 214 species (16.3%) had complete post-juvenile moult, 105 (8.0%) had partial or complete post-juvenile moult and 996 (75.7%) had partial post-juvenile moult. The occurrence of complete post-juvenile moult was much more common in certain bird families than in others (Fig. 1). The phylogenetic signal for binary traits D averaged 0.014 across 100 phylogenies (range: -0.015 to 0.046), which is indicative of a strong phylogenetic structure. Permutation tests indicated that values of D were not significantly different from 0 (Brownian motion, average P = 0.48, range: 0.37–0.58), but were always significantly different from 1 (random pattern, all P < 0.001).

The analysis of transition rates between states suggests that transitions from partial to complete post-juvenile moult occurred at a much lower rate (average: 0.0084, range: 0.007–0.01) than the reverse (average: 0.024, range: 0.019–0.03), and the model allowing different transition rates was better supported than the equal-rates model (likelihood-ratio test across all phylogenies, mean $\chi^2 = 26.98$, all P < 0.001). This analysis also revealed that the most likely state at the root of the phylogeny was partial post-juvenile moult (probability of root being partial moult, average 0.85, range: 0.75–0.92). Similarly, stochastic mapping also suggests that the ancestral trait for passerines was partial post-juvenile moult, and that complete post-juvenile moult has been gained independently multiple times and often lost (Fig. 1, e.g. Alaudidae, Hirundinidae, Furnariidae, etc.). On average, across the 100 stochastic mapping reconstructions and phylogenies, shifts from partial to complete happened 98 times and from complete to partial 88 times.

Logistic phylogenetic regressions using the most complete dataset (dataset 1, n = 1266, of which 313 species are classified as having complete post-juvenile moult), revealed that complete post-juvenile moult is more prevalent in: (a) species found at lower latitudes (Fig. 2C, L), in warm (Fig. 2D, L), and wet regions (Fig. 2G, L), (b) species that inhabit open habitats (Fig. 2F, L), (c) species where first-year males resemble adults in appearance (species without delayed plumage maturation, Fig. 2J, L), and (d) species with higher levels of sexual dichromatism (Fig 2I, L). Full model results are provided in Tables S1-S3.

Figure 1. Phylogenetic distribution of post-juvenile moult types for 1315 species of passerine birds. Ancestral state reconstruction based on 100 stochastic mappings on one example phylogeny (for the purpose of illustration), where the colour palette represents ancestral trait reconstruction depicting the probability of having complete post-juvenile moult (yellow = 1). Intermediate colour values represent uncertainty surrounding the location of evolutionary transitions in the phylogeny. Silhouettes (retrieved from www.phylopic.org) represent some selected families with high prevalence of complete post-juvenile moult. The length of the colour palette represents 50 million years on the phylogeny.



Smaller species, and species that feed on seeds were more likely to have complete post-juvenile moult, but these effects were generally not statistically significant (Fig. 2L). There were no statistically significant effects of insolation or migration distance (Fig. 2L). The phylogenetic signal was strong in all cases, as indicated by the small values of alpha (0.02-0.03, see Tables S1–S14). Multivariate models accounted for ~54% of the variation in post-juvenile moult type (multivariate models with latitude or temperature, R^2conditional = 0.54), but most of this is due to shared phylogenetic history. The explanatory variables together explained 12-14% of the variation in moult pattern. Out of the three multivariate models tested, the one with latitude had the lowest AICc value (860, Table S1), followed by the model with temperature (AICc = 864, Table S2) and the insolation model (AICc = 873, Table S3). Fitting explanatory variables as single predictor variables yielded qualitatively similar effects, but these were not always statistically significant (e.g. sexual dichromatism, Fig. 2L, Table S4). Restricting the dataset to include species for which there also was information on the length of the nestling period (dataset 2, n = 860, of which 213 species with complete post-juvenile moult), revealed that species with fast-growing nestlings were not more likely to have complete post-juvenile moult (Fig. 2K, L, full model results are shown in Tables S5-S7).

We assessed the robustness of our results through three additional analyses: (a) using an alternative moult classification, (b) excluding species where moult data are more limited, and (c) excluding long-distance migratory species to assess whether potential inaccuracies in the computation of their climatic variables is driving climatic effects in the analyses. (a) We used an alternative classification of moult by scoring whether there is complete moult before first breeding regardless of moult type. This analysis shows similar results (Tables S8-S10), except for the migration distance effect, which becomes statistically significant, suggesting that a complete moult before the first breeding season is more likely in species with longer migration distances. (b) We eliminated species for which moult information was based on limited information (n = 1021 species, 245 species excluded). The results were similar (Tables S11-S13), except for the sexual dichromatism effect, which became statistically non-significant. (c) We excluded long-distance migratory species to assess the effect of potential inaccuracies in the climatic variables. However, the effects of temperature and rainfall did not change (Table S14), suggesting that our conclusions are robust.

DISCUSSION

Our survey across >1300 species, which includes members of most families of passerines, revealed that nearly 25% of the species have at least some individuals or populations that carry out a complete post-juvenile moult. Ancestral trait reconstructions indicate that complete post-juvenile moult has been gained and lost multiple times and is highly phylogenetically conserved (Fig. 1A). Our comparative analyses identified several ecological, environmental, and life-history predictors that together account for >10% of the variation in the extent of the post-juvenile moult (considered as a binary trait: partial versus complete; Figs. 2). Our results show an increased prevalence of complete moult in warm, favourable environmental conditions with low resource seasonality, confirming earlier work (Kiat & Izhaki 2016), and indicating the importance of constraints. However, our study also indicates the important roles of plumage degradation and visual signalling, highlighting the selective pressures that favour complete post-juvenile moult (Fig. 3).

We hypothesised that lower-quality juvenile plumage and conditions that foster rapid plumage degradation should constitute strong selective factors favouring a complete post-juvenile moult. The quality of plumage in young birds varies greatly and is positively correlated with the time they spend in the nest (Callan *et al.* 2019). However, our data clearly show that species with shorter nestling periods are not more likely to have a complete post-juvenile moult (Fig. 2), despite their presumed poorer quality plumage. This is surprising given that previous work detected clear associations between feather quality and post-juvenile moult (Kiat & Izhaki 2016; Kiat & Sapir 2018). By necessity, i.e. due to data availability, we used a proxy of feather quality (nestling period) rather than feather quality itself and this could have weakened our inference. Moreover, it is possible that the direction of causation is reversed, meaning that increased quality of nest-grown plumage is an evolutionary response to partial post-juvenile moult (Kiat & Sapir 2018). Rigorous tests of these ideas, that allow general conclusions beyond Western Palearctic species (Kiat & Izhaki 2016; Kiat & Sapir 2018), will require more data on feather quality.

Plumage degradation is continuous and starts already in the nest, in part through the action of feather-degrading bacteria (Azcárate-García *et* *al.* 2020), which are more active and prevalent in warm and humid environments (Burtt & Ichida 2004). Accordingly, we found that both temperature and, to a lesser extent, precipitation correlated positively with the likelihood of complete post-juvenile moult (Fig. 2). Our study thus suggests that increased risk of feather degradation may favour the evolution of complete post-juvenile moult. Feathers also degrade through exposure to sunlight (Test 1940, Bergman 1982, Surmacki *et al.* 2011), and our analyses revealed that species living in open environments, which are more exposed to sunlight, are more likely to have a complete post-juvenile moult (Fig. 2K). Following this logic, we also expected that species living in regions with higher levels of solar radiation would be more likely to undergo a complete post-juvenile moult. However, this was not the case: the effect of insolation was positive but clearly not statistically significant (Fig. 2). Because the effect of insolation may apply mainly to species living in open habitats, we further tested for a positive interaction between insolation and habitat openness, but the interaction was negative and not statistically significant (t = -1.045, P = 0.29).

Figure 2. Boxplots (A-K) of raw data without phylogenetic correction showing differences between species with partial and complete post-juvenile moult, and a forest plot (L) depicting effects and 95%CIs of explanatory variables included in the phylogenetic logistic regression models. Because there were many missing values in one covariate (nestling period) we carried out the analyses on two datasets: dataset 1 (n = 1266 species), included all covariates except for the duration of the nestling period, and dataset 2 (n = 860 species) which also included nestling period. In addition, due to collinearity, latitude, insolation, and annual mean temperature could not be included in the same model and were fitted in three separate models. Full model results and output can be found in Tables S1-S7. Boxplots show median and interquartile ranges and outliers (black dots); in the forest plots 95%CIs that do not overlap 0 correspond to statistically significant effects (P < 0.05).

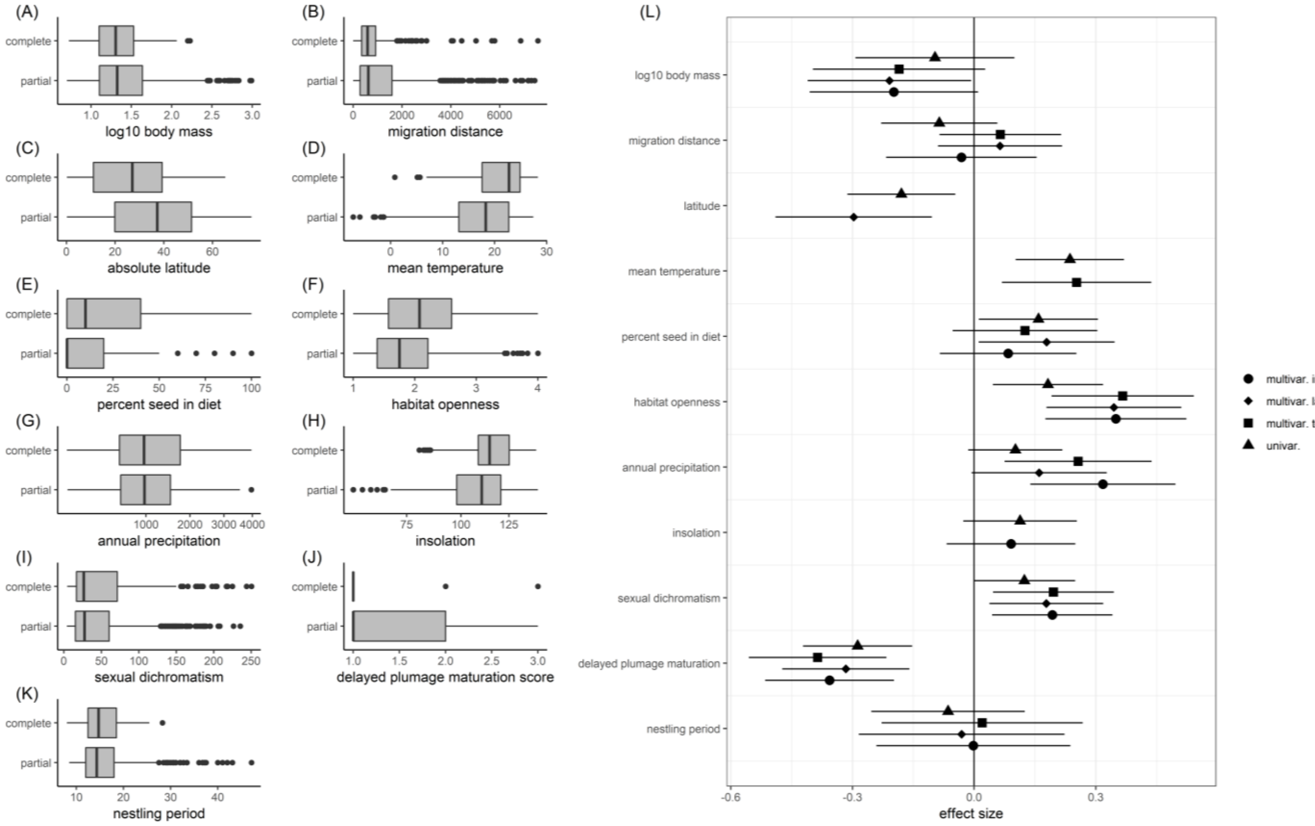
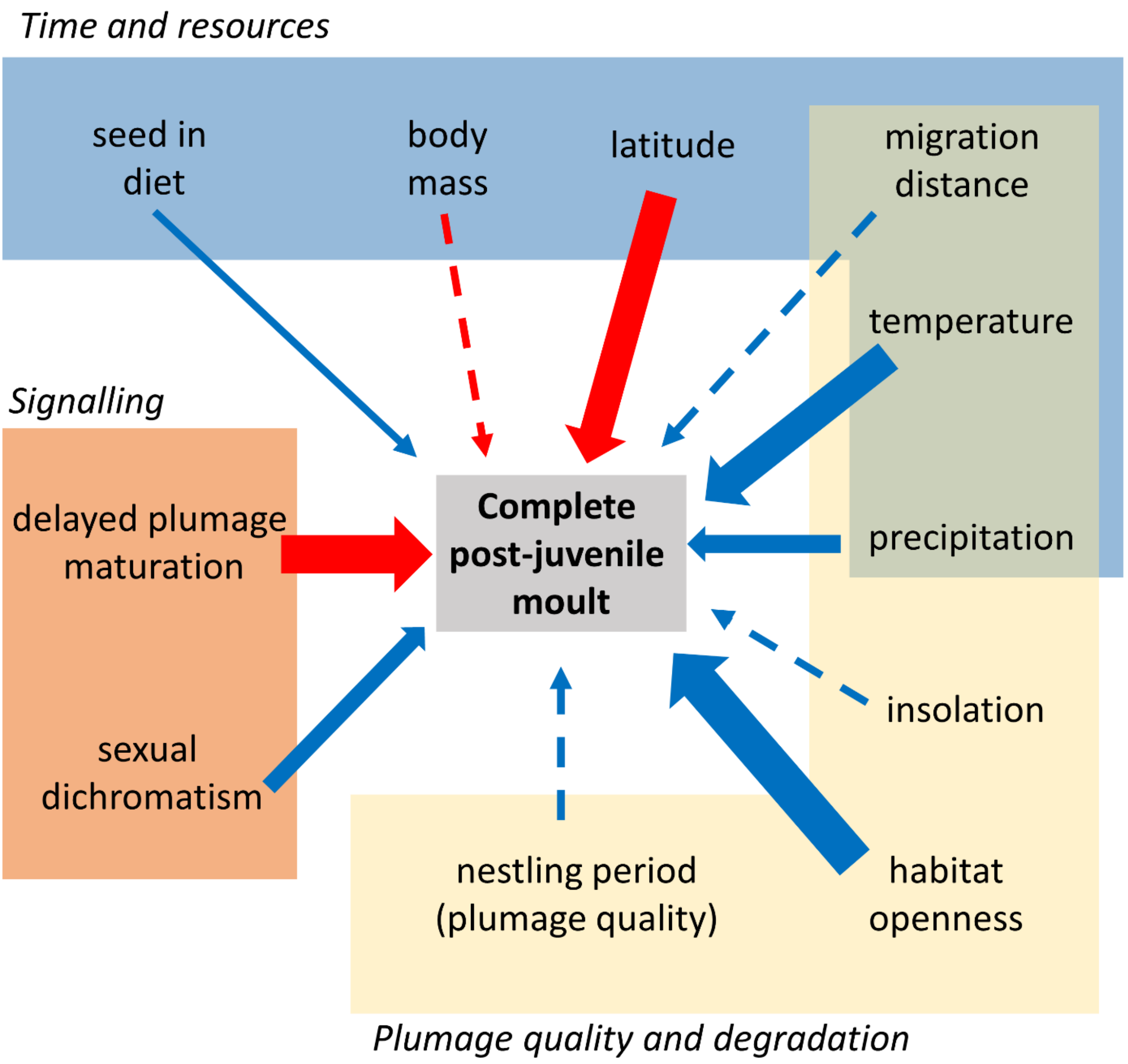


Figure 3. Summary of effects associated with complete post-juvenile moult in passerine birds. Arrow thickness represent the strength of the effect (blue positive effects, red negative effects) and dashed lines represent non-significant effects based on Fig. 2L. Effects have been grouped into three broad categories: constraints imposed by available time and food resources (light blue), selective forces associated with plumage quality and degradation (light yellow) and selective forces associated with the ornamental signalling functions of plumage (orange).



Alternatively, the association between complete post-juvenile moult and habitat openness may not only be caused by faster feather degradation in open habitats, but also because birds inhabiting such environments rely more on their flying abilities to escape predators, display (Menezes & Santos 2020) or forage, than species living in closed environments (Guallar *et al.* 2009). A complete post-juvenile moult would ensure a less worn plumage ready to cope with these challenges during their first year.

The lack of an insolation effect was unexpected, in particular, because insolation strongly correlated with temperature and latitude (see Materials and Methods), two covariates that are linked to complete post-juvenile moult in previous (Kiat & Izhaki 2016) and in our analyses (Fig. 2). Latitudinal gradients in the prevalence of complete post-juvenile moult have been interpreted as evidence that warmer, tropical climates with lower seasonality impose less stringent temporal constraints on post-juvenile moult, because environmental conditions do not deteriorate as rapidly as in temperate regions after the summer (Kiat & Izhaki 2016). Our results are consistent with this interpretation, as are studies of intraspecific variation in moult extent, which reveal that individuals from populations living at lower latitudes and in warmer regions often show more extensive post-juvenile moults (Ginn & Melville 1983, Christmas *et al.* 1989, Jenni & Winkler 1994, Rockey 2016, Chabot *et al.* 2018). Furthermore, Kiat *et al.* (2019) showed that the extent of post-juvenile increased over time in several species of passerines, most likely as a result of climate warming. Warmer or milder climatic conditions allow for earlier breeding (one of the best-documented effects of climate change; Scheffers *et al.* 2016), resulting in earlier fledging which leads to an earlier start of the post-juvenile moult. Both correlational and experimental data show that birds that start moulting earlier in the year moult slower and achieve more extensive post-juvenile moults (Rymkevich & Bojarinova 1996, Serra *et al.* 2007, Ryzhanovskiy 2017).

Our results provide macro-evolutionary support for the hypothesis that time constraints constitute an important factor explaining variation in the completeness of post-juvenile moult. We also predicted that species that eat mostly seeds –a resource that should decline less rapidly in late summer than insects or fruit– should be more likely to evolve complete post-juvenile moult (Kiat & Izhaki 2016). While the effect was in the predicted direction, it was not statistically significant in all models (Fig. 2). Two other factors associated with time constraints, namely body size (large species moult slower; Rohwer *et al.* 2009) and migration distance (long-distant migrants are under stronger time constraints; Kiat & Izhaki 2016, Kiat & Sapir 2017) did not show statistically significant effects (Fig. 2). While the body mass effect was in the expected direction (negative), the effect of migration distance tended to be positive in the multivariate models (Fig. 2L). Thus, rather than acting as a constraint, longer migration distances tend to favour the evolution of complete post-juvenile moult. One possibility is that species that migrate farther require plumage in top condition to complete their journeys, and this should apply to flight feathers in particular. Hence, we further tested this idea by focusing on whether species moult all primaries during their post-juvenile moult (obviously all species with complete post-juvenile moult all primaries, but 97 species with partial post-juvenile moult do so as well). Repeating the analyses in Fig. 2 using complete primary moult (no/yes) as response variable revealed that the effect of migration distance was clearly not statistically significant. However, the effect of migration distance became statistically significant when we used an alternative moult classification that indicated whether or not a species carries out a complete moult before their first breeding season (either a complete post-juvenile moult or a complete nuptial moult; Tables S8-S10). We note that the main difference between the two moult classifications stems from the fact that many long-distance migratory species that carry out only a partial post-juvenile moult, perform a complete nuptial moult in their tropical wintering grounds. A complete moult in these species might be more likely because of favourable conditions (reduced constraints; Kiat & Sapir 2018), while new plumage may be advantageous to successfully complete the spring migration (selective advantage). Thus, although the effect is not clear in all analyses, our results suggest that migration distance may play a role in shaping moult strategies during the first year.

Beyond the constraints imposed by the available resources (food and time) and the feather-degradation potential of the environment, our results also suggest that the signalling functions of the plumage may have played a role in the evolution of complete post-juvenile moult. One of the strongest predictors of complete post-juvenile moult was the occurrence of delayed plumage maturation (DPM), whereby species with DPM were less likely to have a complete post-juvenile moult (Fig. 2). In species with DPM, first-cycle males differ markedly in coloration from older males, and these young males usually have lower mating success or forego reproduction entirely but benefit from reduced aggressive interactions with older males (Senar *et al.* 1998, Greene *et al.* 2000, Hawkins *et al.* 2012). If there is less pressure to look attractive in the first breeding season, replacing all juvenile feathers (often differently coloured from the adult plumage) during the post-juvenile moult may not be beneficial, and hence sexual selection on the extent of post-juvenile moult would be relaxed. In some species, a partial post-juvenile moult may also provide a flexible mechanism for individuals to signal lower status in the same way as DPM, but allowing other –presumably higher-quality individuals– to achieve a more extensive moult and more adult-like plumage, possibly at the expense of increased aggression by older males (Senar *et al.* 1998, López *et al.* 2005).

In species without DPM, on the other hand, first-year males may benefit from erasing any subtle cues of age (e.g. moult limits, the differences between old and newly moulted feathers), associated with partial post-juvenile moult. Resembling adults may be more important if the potential rewards are high, for instance, when sexual selection on males is stronger. Indeed, we found that sexual dichromatism –a proxy for the intensity of sexual selection on male birds (Dunn *et al.* 2001, Dale *et al.* 2015)– correlates positively with the likelihood of a complete post-juvenile moult (Fig.

2). Because the effects of sexual selection intensity should be more marked in species without DPM, one could also predict a negative interaction between DPM and sexual dichromatism. However, our analyses do not support this idea: the interaction term was positive and not statistically significant ($t = 1.16$, $P = 0.24$). Thus, the effects of DPM and of sexual dichromatism seem largely independent of each other, although the sexual dichromatism effect is only statistically significant after accounting for the effects of DPM and other covariates (Fig. 2L).

Consistent with the hypothesis that sexual selection affects moult, males moult more extensively than females in many (Jenni & Winkler 1994, Senar *et al.* 1998, Bojarinova *et al.* 1999, Illera & Atienza 2002, Crates *et al.* 2015, Kiat *et al.* 2019) but not all (Jenni & Winkler 1994, Kiat *et al.* 2019, Pérez-Granados 2020) species with partial post-juvenile moult. This suggests that stronger sexual selection on males, may have led to sexual dimorphism in moult extent. Thus, we could envision a scenario where strong sexual selection favours more extensive post-juvenile moult, possibly because moulting more feathers signals higher quality (Gosler 1991, Vagasi *et al.* 2012, Minias and Iciek 2013, Pagani-Núñez & Hernández-Gómez 2013, Minias *et al.* 2015, but see Crates *et al.* 2015). Within species, individuals that moult earlier in the season usually moult more slowly and more extensively (Rymkevich & Bojarinova 1996, Serra *et al.* 2007, Ryzhanovskiy 2017), which in turn may produce both higher-quality plumage (Dawson *et al.* 2000) and more colourful feathers (Serra *et al.* 2007, Ferns & Hinsley 2008, Griggio *et al.* 2009). As a consequence, strong directional selection on ornamental plumage may result in complete post-juvenile moult in males, and also in females, either due to genetic correlation or through sexual or social selection acting directly on females (Tobias *et al.* 2012). Puzzlingly, the extent of post-juvenile moult increased more in females than in males in response to historical climate warming trends, at least in a few sexually dichromatic species (Kiat *et al.* 2019), suggesting that moult in females may be more sensitive to environmental variation. Finally, while many species develop their first-year plumage colours during the post-juvenile moult, some species do so in a different moulting event, referred to as the nuptial or pre-breeding moult. Interestingly, species that change into breeding colours by means of a nuptial moult show remarkable parallels with those that undergo a complete post-juvenile moult: nuptial moult is also more prevalent in species with more marked sexual dichromatism (Mcqueen *et al.* 2019).

In sum, our analyses show that a combination of multiple, fundamentally different mechanisms, explain sizeable amounts of variation (>10%) in the extent of post-juvenile moult between species (Fig. 3). Our results clearly highlight that constraints faced by young birds during their first independent moult (time, food) are important, but are not the only factors that determine whether a species undergoes a complete post-juvenile moult. Variation between species in the strength of natural and sexual selection acting on functional or ornamental roles of plumage have important effects as well, and suggests that the extent of post-juvenile moult is not simply the outcome of a best-of-a-bad-job situation. In particular, we provide evidence for the surprisingly strong effects of delayed plumage maturation and sexual selection, which seem to have pervasive effects shaping the evolution of different types of moult in birds (Figuerola & Jovani 2001, Peters *et al.* 2013, Mcqueen *et al.* 2019).

ACKNOWLEDGEMENTS

We are indebted to the following colleagues that assisted with securing information on post-juvenile moult: Hyun-Young Nam (Migratory Bird Centre, Korea National park Research Institute, Wonju, Korea), Chang-Yong Choi (College of Agriculture and Life Sciences, Seoul National University Seoul, Korea), Noboru Nakamura (Bird Migration Research Centre, Yamashina Institute for Ornithology Japan), and Marc Herremans (Natuurpunt, Mechelen, Belgium). We thank the associate editor, two anonymous reviewers and Y. Kiat for constructive comments. The authors declare no conflicts of interest.

REFERENCES

Azcárate-García M, González-Braojos S, Díaz-Lora S, et al 2020. Interspecific variation in deterioration and degradability of avian feathers: the evolutionary role of microorganisms. *J. Avian Biol.* 51: e02320.

Barta Z, Houston AI, McNamara JM, Welham RK, Hedenström A, Weber TB, Feró O 2006. Annual routines of non-migratory birds: Optimal moult strategies. *Oikos* 112: 580–593.

Baston D 2020. exactextractr: Fast Extraction from Raster Datasets using Polygons. R package version 0.2.1.

Beauchamp G 2003. Delayed maturation in birds in relation to social foraging and breeding competition. *Evol. Ecol. Res.* 5: 589–596.

Bergman G 1982. Why are the wings *Larus f. fuscus* so dark? *Ornis Fenn.* 59: 77–83.

Bojarinova JG, Lehikoinen E, Eeva T 1999. Dependence of postjuvenile moult on hatching date, condition, and sex in the Great Tit. *J. Avian Biol.* 30: 437–446.

Brooks R, Kemp DJ 2001. Can older males deliver the good genes? *Trends Ecol. Evol.* 16: 308–313.

Burtt EH, Ichida JM 2004. Gloger's Rule, Feather-Degrading Bacteria, and Color Variation Among Song Sparrows. *Condor* 106: 681–686.

Callan LM, La Sorte FA, Martin TE, Rohwer VG 2019. Higher nest predation favors rapid fledging at the cost of plumage quality in nestling birds. *Amer. Nat.* 193: 717–724.

Chabot AMYA, Hobson KA, Craig S, Lougheed SC 2018. Moult in the Loggerhead Shrike *Lanius ludovicianus* is influenced by sex, latitude and migration. *Ibis* 160: 301–312.

Christmas SE, Christmas TJ, Parr AJ 1989. Geographical variation in greater covert moult in first winter Coal Tits *Parus ater*. *Bird Study* 36: 88–90.

Cleasby IR, Nakagawa S 2012. The influence of male age on within-pair and extra-pair paternity in passerines. *Ibis* 154: 318–324.

Cooney CR, Sheard C, Clark AD, Healy SD, Liker A, Street SE, Troisi CA, Thomas GH, Székely T, Hemmings N, Wright AE 2020. Ecology and allometry predict the evolution of avian developmental durations. *Nature Comm.* 11: 2383.

Cramp S, Simmons KEL 1977. *Handbook of the birds of Europe, the Middle East and North Africa: The birds of the Western Palearctic.* Oxford University Press, Oxford.

Crates RA, Sheldon BENC, Garroway CJ 2015. Causes and consequences of individual variation in the extent of post-juvenile moult in the blue tit *Cyanistes caeruleus* (Passeriformes: Paridae). *Biol. J. Linn. Soc.* 116: 341–351.

Dale J, Dey C, Delhey K, Kempenaers B, Valcu M 2015. The effects of life-history and social selection on male and female plumage coloration. *Nature* 527: 367–370.

Dawson A, Hinsley SA, Ferns PN, Bonser RHC, Eccleston L 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proc. Biol. Sci. B* 267: 2093–2098.

Delhey K, Dale J, Valcu M, Kempenaers B 2019. Reconciling ecogeographical rules: rainfall and temperature predict global colour variation in the largest bird radiation. *Ecol. Lett.* 22: 726–736.

Dufour P, Descamps S, Chantepie S, Renaud J, Guéguen M, Schiffers K, Thuiller W, Lavergne S 2020. Reconstructing the geographic and climatic origins of long-distance bird migrations. *J. Biogeogr.* 147: 1–12.

Dunn PO, Whittingham LA, Pitcher TE 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55: 161–75.

Dunning JBJ 2008. *CRC Handbook of avian body masses,* 2nd ed. CRC Press Taylor & Francis Group, Boca Raton, FL.

Faccio MS 2018. Tropical frugivorous birds molt and breed in relation to the availability of food resources. *Ornitol. Neotrop.* 29: S11–S18.

Ferns PN, Hinsley SA 2008. Carotenoid plumage hue and chroma signal different aspects of individual and habitat quality in tits. *Ibis* 150: 152–159.

Figuerola J, Jovani R 2001. Ecological correlates in the evolution of moult strategies in Western Palearctic passerines. *Evol. Ecol.* 15: 183–192.

Fogden MPL 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114: 307–343.

Fritz SA, Purvis A 2010. Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conserv. Biol.* 24: 1042–1051.

Ginn HB, Melville DS 1983. *Moult in birds.* British Trust for Ornithology, The Nunnery, Thetford.

Gosler AG 1991. On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the Great Tit *Parus major*. *Bird Study* 38: 1:9.

Greene E, Lyon BE, Muehter VR, Ratcliffe L, Oliver SJ, Boag PT 2000. Disruptive sexual selection for plumage coloration in a passerine bird. *Nature* 407: 1000–1003.

Griffin RH 2018. btw: Run BayesTraitsV3 from R. R package version 2.0.

Griggio M, Serra L, Licheri D, Campomori M, Pilastro A 2009. Moult speed affects structural feather ornaments in the blue tit. *J. Evol. Biol.* 22: 782–792.

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A 2009. *Paseriformes del Occidente de México: morfometría, datación y sexado.* Museu de Ciències Naturals de Barcelona, Barcelona.

Hawkins GL, Hill GE, Mercadante A 2012. Delayed plumage maturation and delayed reproductive investment. *Biol. Rev*. 87: 257–274.

Heise CD, Moore FR 2003. Age-related differences in foraging efficiency, molt, and fat deposition of gray catbirds prior to autumn migration age-related differences in foraging efficiency, molt, and fat deposition of Gray Catbirds prior to autumn migration. *Condor* 105: 496–504.

Howell SNG, Corben C, Pyle P, Rogers DI 2003. The first basic problem: a review of molt and plumage homologies. *Condor* 105: 635–653.

Hoy SR, Petty SJ, Millon A, Whitfield DP, Marquiss M, Davison M, Lambin X 2015. Age and sex-selective predation moderate the overall impact of predators. *J. Anim. Ecol.* 84: 692–701.

Illera JC, Atienza JC 2002. Determinacion del sexo y la edad en la Tarabilla Canaria *Saxicola dacotiae* mediante el estudio de la muda. *Ardeola* 49: 273–281.

Ives AR, Garland T 2010. Phylogenetic logistic regression for binary dependent variables. *Syst. Biol.* 59: 9–26.

Ives AR, Li D 2018. rr2: An R package to calculate R^2s for regression models. *J. Open Source Soft.* 3: 1028.

Jenni L, Winkler R 1994. *Moult and ageing of European passerines.* Academic Press, London.

Jetz W, Thomas GHH, Joy JBB, Mooers AO 2012. The global diversity of birds in space and time. *Nature* 491: 444–448.

Johnson EI, Wolfe JD 2018. *Molt in Neotropical birds: life-history and aging criteria*. Taylor & Francis, Boca Raton, FL.

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M 2017. Climatologies at high resolution for the Earth's land surface areas. *Sci. Data* 4: 1–20.

Kiat Y 2018. Divergent rectrix moult: the implications and conditions of moult sequence. *J. Avian Biol.* 2018: e01609.

Kiat Y, Izhaki I 2016. Why renew fresh feathers? Advantages and conditions for the evolution of complete post-juvenile moult. *J. Avian Biol.* 47: 47–56.

Kiat Y, Sapir N 2017. Age-dependent modulation of songbird summer feather molt by temporal and functional constraints. *Amer. Nat.* 189: 184–195.

Kiat Y, Sapir NIR 2018. Life-history trade-offs result in evolutionary optimization of feather quality. *Biol. J. Linn. Soc.* 125: 613–624.

Kiat Y, Vortman Y, Sapir N 2019. Feather moult and bird appearance are correlated with global warming over the last 200 years. *Nat. Commun.* 10: 2540.

López G, Figuerola J, Varo N, Soriguer R 2005. White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed. *Ardea* 93: 237–244.

Marchant S, Higgins PJ 1990. Handbook of Australian, New Zealand and Antarctic birds. Volumes 5–7. Oxford University Press, Melbourne.

Mcqueen A, Kempenaers B, Dale J, Valcu M, Emery ZT, Dey CJ, Peters A, Delhey K 2019. Evolutionary drivers of seasonal plumage colours: colour change by moult correlates with sexual selection, predation risk and seasonality across passerines. *Ecol. Lett.* 22: 1838–1849.

Menezes JCT, Santos ESA 2020. Habitat structure drives the evolution of aerial displays in birds. *J. Anim. Ecol.* 89: 482–493.

Minias P, Iciek T 2013. Extent and symmetry of post-juvenile moult as predictors of future performance in Greenfinch *Carduelis chloris*. *J. Ornithol.* 154: 465–468.

Minias P, Włodarczyk R, Surmacki A, Iciek T 2015. Silver spoon effects on plumage quality in a passerine bird. *R. Soc. Open Sci.* 2: 140459.

Naef-Daenzer B, Gruebler MU 2016. Post-fledging survival of altricial birds: ecological determinants and adaptation. *J. Field Ornithol.* 87: 227–250.

Nakagawa S, de Villemereuil P 2019. A general method for simultaneously accounting for phylogenetic and species sampling uncertainty via Rubin' s rules in comparative analysis. *Syst. Biol.* 68: 632–641.

Newton I 2009. Moult and plumage. *Ring. Migr.* 24: 220–226.

Orme D, Freckleton R, Thomas G, Petzoldt T Fritz S, Isaac N, Pearse W 2018. caper: comparative analyses of phylogenetics and evolution in R. R package version 1.0.1.

Pagani-Núñez E, Hernández-Gómez S 2013. Extent of post-juvenile moult in wintering Common Chiffchaffs *Phylloscopus collybita* is related to indices of individual quality. *Rev. Cat. Orn.* 29: 35–42.

Pebesma E 2018. Simple features for R: standardized support for spatial vector data. *R J.* 10: 439–446.

Pérez-Granados C 2020. Post-juvenile and post-breeding moult of the Black Wheatear *Oenanthe leucura* in south-eastern Spain: slowed down due to climatic aridity? *Ardea* 108: 21–29.

Peters A, Kingma SA, Delhey K (2013) Seasonal male plumage as a multi-component sexual signal: Insights and opportunities. Emu 113:232–247. doi: 10.1071/MU12083

Poole A ed. 2005. The birds of North American online: http://bna.birds.cornell.edu/BNA/ Cornell Laboratory of Ornithology, Ithaca, NY.

Pyle P (1997) *Identification guide to North American birds. Part I.* Slate Creek Press, Bolinas, CA

R Development Core Team (2019) R: A language and environment for statistical computing.

Rabosky DL (2015) No substitute for real data : A cautionary note on the use of phylogenies from birth – death polytomy resolvers for downstream comparative analyses. Evolution (N Y) 69:3207–3216. doi: 10.1111/evo.12817

Revell LJ 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3: 217–223.

Rockey WL 2016. Preformative molt adjustment in phenologically divergent populations of the Lesser Goldfinch (*Spinus psaltria*). *Wilson J. Ornithol.* 128: 70–74.

Rohwer S, Ricklefs RE, Rohwer VG, Copple MM 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biol.* 7: e1000132.

Rymkevich TA, Bojarinova JG 1996. Variation in the extent of postjuvenile moult in the Great Tit near Lake Ladoga (Russia). *Bird Study* 43: 47–59.

Ryzhanovskiy VN 2017. Completeness of seasonal molting in passerine birds (Aves, Passeriformes) in northwestern Siberia. *Contemp. Probl. Ecol.* 10: 502–510.

Scheffers BR, De Meester L, Bridge TCL, *et al.* 2016. The broad footprint of climate change from genes to biomes to people. *Science* 354: aaf7671.

Senar JC, Copete JL, Martin AJ 1998. Behavioural and morphological correlates of variation in the extent of postjuvenile moult in the Siskin *Carduelis spinus*. *Ibis* 140: 661–669.

Serra L, Griggio M, Licheri D, Pilastro A 2007. Moult speed constrains the expression of a carotenoid-based sexual ornament. *J. Evol. Biol.* 20: 2028–2034.

Surmacki A, Siefferman L, Yuan H-W 2011. Effects of sunlight exposure on carotenoid-based and structural coloration of the Blue-tailed Bee-eater. *Condor* 113: 1–8.

Test H 1940. Effects of natural abrasion and oxidation on the coloration of flickers. *Condor* 42: 76–80.

Tobias JA, Montgomerie R, Lyon BE 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Phil. Trans. R. Soc. B* 367: 2274–2293.

Tung Ho LS, Ané C 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Syst. Biol.* 63: 397–408.

Vagasi CI, Pap PL, Vincze O, Benkö Z, Marton A, Barta Z 2012. Haste makes waste but condition matters: molt rate-feather quality trade-off in a sedentary songbird. *PLoS One* 7: e40651.

Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* 95: 2027–2027.

SUPPLEMENTARY INFORMATION

Scoring habitat openness

We used the habitat classification from Birdlife International (http://datazone.birdlife.org/) to obtain all habitat types used by each species. Habitat types (habitat_class variable) were assigned an openness score as follows:

“Forest” = 1

“Shrubland” = 2

“Savanna” = 2

"Grassland" = 3

"Wetlands (inland)" = 3

"Artificial/Aquatic & Marine" = 3

"Marine Intertidal" = 4 except subclasses "Mangrove Submerged Roots" and "Salt Marshes (Emergent Grasses)" = 3

"Marine Coastal/Supratidal" = 4

"Rocky areas (e.g. inland cliffs, mountain peaks)" = 4

"Desert" = 4

"Marine Neritic" = 4

"Caves and Subterranean Habitats (non-aquatic)" = 1

"Introduced vegetation" = 2

"Marine Oceanic" = 4

"Artificial/Terrestrial" & habitat subclass="Arable Land" = 3

"Artificial/Terrestrial" & habitat subclass="Pastureland" = 3

"Artificial/Terrestrial" & habitat subclass="Plantations" = 2

"Artificial/Terrestrial" & habitat subclass="Rural Gardens" = 2

"Artificial/Terrestrial" & habitat subclass="Subtropical/Tropical Heavily Degraded Former Forest" = 1

"Artificial/Terrestrial" & habitat subclass="Urban Areas" = 2

For each species, we average openness scores across all environments used to obtain a single score per species. Note that this was done for all bird species listed at http://datazone.birdlife.org/ and we subset to our study species afterwards. This is why there are some categories above that hardly occur among passerines (e.g. caves, marine oceanic, etc.).

Table S1. Multivariate models with latitude, dataset 1. We report Akaike's Information Criterion, AIC = 859.6; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal $R^2 = 0.14$ and for the whole model, conditional $R^2 = 0.54$; n = 1266 and number of phylogenies used, n phy. = 98 (in some cases < 100, because a few models did not converge).

Variable	**Estimate**	**SE**	**t**	**P**
Intercept	-1.183	0.381	-3.103	0.0019
Latitude	-0.297	0.098	-3.018	0.0026
Annual precipitation	0.160	0.085	1.888	0.0591
Habitat openness	0.345	0.085	4.061	0.0000
Percent seed in diet	0.179	0.085	2.092	0.0365
Migration distance	0.064	0.078	0.817	0.4138
log10 body mass	-0.209	0.103	-2.030	0.0424
Delayed plumage maturation	-0.316	0.080	-3.958	0.0001
Sexual dichromatism	0.178	0.071	2.491	0.0128

Table S2. Multivariate models with temperature, dataset 1. We report Akaike's Information Criterion, AIC = 864.59; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal $R^2 = 0.13$ and for the whole model, conditional $R^2 = 0.54$; n = 1266 and number of phylogenies used, n phy. = 99 (in some cases < 100, because a few models did not converge).

Variable	**Estimate**	**SE**	**t**	**P**
Intercept	-1.266	0.373	-3.396	0.0007
Mean temperature	0.253	0.094	2.692	0.0072
Annual precipitation	0.256	0.092	2.774	0.0056
Habitat openness	0.366	0.090	4.091	0.0000
Percent seed in diet	0.126	0.091	1.379	0.1681
Migration distance	0.065	0.076	0.846	0.3981
log10 body mass	-0.185	0.108	-1.707	0.0878
Delayed plumage maturation	-0.386	0.087	-4.460	0.0000
Sexual dichromatism	0.195	0.076	2.574	0.0101

Table S3. Multivariate models with insolation, dataset 1. We report Akaike's Information Criterion, AIC = 873.3; an estimate of phylogenetic effects, alpha = 0.03 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.12 and for the whole model, conditional R^2 = 0.53; n = 1266 and number of phylogenies used, n phy. = 99 (in some cases < 100, because a few models did not converge).

Variable	**Estimate**	**SE**	**t**	**P**
Intercept	-1.260	0.381	-3.305	0.0010
Insolation	0.091	0.081	1.123	0.2616
Annual precipitation	0.318	0.091	3.479	0.0005
Habitat openness	0.350	0.089	3.939	0.0001
Percent seed in diet	0.084	0.086	0.975	0.3296
Migration distance	-0.031	0.095	-0.332	0.7403
log10 body mass	-0.198	0.106	-1.870	0.0616
Delayed plumage maturation	-0.356	0.081	-4.397	0.0000
Sexual dichromatism	0.193	0.076	2.548	0.0109

Table S4. Multivariate models with latitude, dataset 2. We report Akaike's Information Criterion, AIC = 566.47; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.15 and for the whole model, conditional R^2 = 0.57; n = 860 and number of phylogenies used, n phy. = 99 (in some cases < 100, because a few models did not converge).

Variable	**Estimate**	**SE**	**t**	**P**
Intercept	-1.206	0.453	-2.664	0.0077
Latitude	-0.274	0.116	-2.356	0.0186
Annual precipitation	0.059	0.109	0.542	0.5879
Habitat openness	0.356	0.101	3.514	0.0004
Percent seed in diet	0.127	0.108	1.173	0.2411
Migration distance	-0.065	0.107	-0.605	0.5452
log10 body mass	-0.247	0.138	-1.783	0.0747
Delayed plumage maturation	-0.441	0.122	-3.616	0.0004
Sexual dichromatism	0.164	0.091	1.795	0.0727
Nestling period	-0.031	0.129	-0.237	0.8123

Table S5. Multivariate models with temperature, dataset 2. We report Akaike's Information Criterion, AIC = 566.78; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.15 and for the whole model, conditional R^2 = 0.57; n = 860 and number of phylogenies used, n phy. = 95 (in some cases < 100, because a few models did not converge).

Variable	**Estimate**	**SE**	**t**	**P**
Intercept	-1.171	0.438	-2.673	0.0075
Mean temperature	0.190	0.095	2.009	0.0445
Annual precipitation	0.201	0.087	2.319	0.0204
Habitat openness	0.372	0.101	3.691	0.0002
Percent seed in diet	0.114	0.096	1.186	0.2356
Migration distance	-0.155	0.094	-1.657	0.0975
log10 body mass	-0.287	0.133	-2.163	0.0305
Delayed plumage maturation	-0.399	0.094	-4.231	0.0000
Sexual dichromatism	0.208	0.085	2.435	0.0149
Nestling period	0.020	0.126	0.157	0.8755

Table S6. Multivariate models with insolation, dataset 2. We report Akaike's Information Criterion, AIC = 569.24; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.15 and for the whole model, conditional R^2 = 0.57; n = 860 and number of phylogenies used, n phy. = 100 (in some cases < 100, because a few models did not converge).

Variable	**Estimate**	**SE**	**t**	**P**
Intercept	-1.078	0.453	-2.381	0.0172
Insolation	0.089	0.085	1.041	0.2981
Annual precipitation	0.237	0.088	2.690	0.0072
Habitat openness	0.325	0.095	3.406	0.0007
Percent seed in diet	0.117	0.096	1.226	0.2201
Migration distance	-0.167	0.089	-1.869	0.0616
Log10 body mass	-0.252	0.128	-1.976	0.0482
Delayed plumage maturation	-0.366	0.088	-4.137	0.0000
Sexual dichromatism	0.180	0.083	2.175	0.0296
Nestling period	-0.002	0.122	-0.015	0.9879

Table S7. Univariate models. For each model we report Akaike's Information Criteria (AIC), an estimate of the strength of phylogenetic effects (alpha, lower values indicate stronger phylogenetic effects), R^2 values for explanatory variables only (marginal R^2) and for the model as a whole (R^2, explanatory variables and phylogenetic effects), the number of species included (n) and the number of phylogenies used (n phy., sometimes < 100 because a few models failed to converge).

Variable	Estimate	SE	t	P	AIC	alpha	Marginal R^2	R^2	n	n phy
Intercept	-1.069	0.474	-2.257	0.0240	908.46	0.03	0.05	0.50	1266	100
Habitat openness	0.182	0.069	2.628	0.0086					1266	100
Intercept	-0.923	0.468	-1.973	0.0485	928.35	0.03	0.02	0.48	1266	100
Migration distance	-0.086	0.073	-1.176	0.2410					1266	100
Intercept	-0.776	0.602	-1.290	0.1972	614.07	0.02	0.01	0.50	860	99
Nestling period	-0.064	0.097	-0.665	0.5060					860	99
Intercept	-0.860	0.508	-1.694	0.0903	922.97	0.03	0.03	0.48	1266	100
Annual precipitation	0.102	0.059	1.717	0.0860					1266	100
Intercept	-0.996	0.457	-2.180	0.0292	925.81	0.03	0.02	0.48	1266	100
Insolation	0.113	0.071	1.586	0.1142					1266	100
Intercept	-0.986	0.464	-2.123	0.0337	915.78	0.03	0.04	0.49	1266	100
Latitude	-0.179	0.068	-2.645	0.0082					1266	100
Intercept	-0.907	0.487	-1.862	0.0626	927.60	0.03	0.02	0.48	1266	99
log10 body mass	-0.097	0.100	-0.965	0.3347					1266	99
Intercept	-0.984	0.455	-2.162	0.0307	909.91	0.03	0.04	0.49	1266	100
Mean temperature	0.236	0.068	3.465	0.0005					1266	100
Intercept	-0.967	0.507	-1.908	0.0564	910.80	0.03	0.04	0.49	1266	100
Percent seed in diet	0.159	0.075	2.116	0.0344					1266	100
Intercept	-0.897	0.503	-1.782	0.0747	923.06	0.03	0.03	0.48	1266	100
Sexual dichromatism	0.124	0.064	1.937	0.0528					1266	100
Intercept	-1.099	0.538	-2.041	0.0412	890.48	0.02	0.07	0.51	1266	100
Delayed plumage maturation	-0.287	0.069	-4.188	0.0000					1266	100

Table S8. Multivariate models with latitude, dataset 1 but using as dependent variable the presence/absence of complete moult before the first breeding seasons (either complete post-juvenile moult or complete nuptial moult). We report Akaike's Information Criterion, AIC = 943.65; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.13 and for the whole model, conditional R^2 = 0.54; n = 1266 and number of phylogenies used, n phy. = 99 (in some cases < 100, because a few models did not converge).

Variable	Estimate	SE	t	P
Intercept	-0.817	0.357	-2.286	0.0223
Latitude	-0.437	0.102	-4.293	<0.0001
Annual precipitation	0.023	0.082	0.284	0.7763
Habitat openness	0.258	0.078	3.291	0.001
Percent seed in diet	0.133	0.083	1.602	0.1094
Migration distance	0.378	0.084	4.501	<0.0001
log10 body mass	-0.146	0.098	-1.488	0.1369
Delayed plumage maturation	-0.207	0.07	-2.934	0.0034
Sexual dichromatism	0.122	0.071	1.725	0.0849

Table S9. Multivariate models with temperature, dataset 1 but using as dependent variable the presence/absence of complete moult before the first breeding seasons (either complete post-juvenile moult or complete nuptial moult). We report Akaike's Information Criterion, AIC = 947.73; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.12 and for the whole model, conditional R^2 = 0.54; n = 1266 and number of phylogenies used, n phy. = 99 (in some cases < 100, because a few models did not converge).

Variable	Estimate	SE	t	P
Intercept	-0.818	0.351	-2.33	0.0198
Mean temperature	0.344	0.083	4.128	<0.0001
Annual precipitation	0.174	0.073	2.394	0.0167
Habitat openness	0.222	0.075	2.963	0.0031
Percent seed in diet	0.194	0.077	2.507	0.0122
Migration distance	0.29	0.069	4.206	<0.0001
log10 body mass	-0.112	0.094	-1.189	0.2343
Delayed plumage maturation	-0.261	0.068	-3.852	0.0001
Sexual dichromatism	0.152	0.066	2.322	0.0202

Table S10. Multivariate models with insolation, dataset 1 but using as dependent variable the presence/absence of complete moult before the first breeding seasons (either complete post-juvenile moult or complete nuptial moult). We report Akaike's Information Criterion, AIC = 960.58; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2= 0.11 and for the whole model, conditional R^2= 0.53; n = 1266 and number of phylogenies used, n phy. = 100 (in some cases <100, because a few models did not converge).

Variable	Estimate	SE	t	P
Intercept	-0.823	0.364	-2.26	0.0239
Insolation	0.179	0.073	2.458	0.0141
Annual precipitation	0.283	0.077	3.692	0.0002
Habitat openness	0.262	0.076	3.458	0.0005
Percent seed in diet	0.083	0.083	0.999	0.318
Migration distance	0.228	0.069	3.306	0.001
log10 body mass	-0.118	0.094	-1.247	0.2125
Delayed plumage maturation	-0.286	0.069	-4.163	<0.0001
Sexual dichromatism	0.155	0.067	2.316	0.0206

Table S11. Multivariate models with latitude, using dataset 1 but eliminating species with limited information on moult data. We report Akaike's Information Criterion, AIC = 619.95; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.12 and for the whole model, conditional R^2 = 0.58; n = 1021 and number of phylogenies used, n phy. = 99 (in some cases <100, because a few models did not converge).

Variable	Estimate	SE	t	P
Intercept	-0.967	0.499	-1.940	0.0526
Latitude	-0.237	0.104	-2.277	0.0230
Annual precipitation	0.115	0.082	1.392	0.1640
Habitat openness	0.282	0.092	3.077	0.0022
Percent seed in diet	0.138	0.083	1.655	0.0981
Migration distance	0.059	0.079	0.748	0.4547
log10 body mass	-0.172	0.104	-1.649	0.0992
Delayed plumage maturation	-0.252	0.079	-3.200	0.0014
Sexual dichromatism	0.097	0.071	1.364	0.1726

Table S12. Multivariate models with temperature, using dataset 1 but eliminating species with limited information on moult data. We report Akaike's Information Criterion, AIC = 620.51; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.12 and for the whole model, conditional R^2 = 0.58; n = 1021 and number of phylogenies used, n phy. = 97 (in some cases < 100, because a few models did not converge).

Variable	Estimate	SE	t	P
Intercept	-0.957	0.512	-1.871	0.0615
Mean temperature	0.199	0.091	2.198	0.0283
Annual precipitation	0.201	0.083	2.413	0.0159
Habitat openness	0.271	0.094	2.887	0.0041
Percent seed in diet	0.100	0.081	1.232	0.2181
Migration distance	0.050	0.066	0.761	0.4466
log10 body mass	-0.162	0.106	-1.531	0.1257
Delayed plumage maturation	-0.250	0.079	-3.180	0.0015
Sexual dichromatism	0.082	0.068	1.208	0.2271

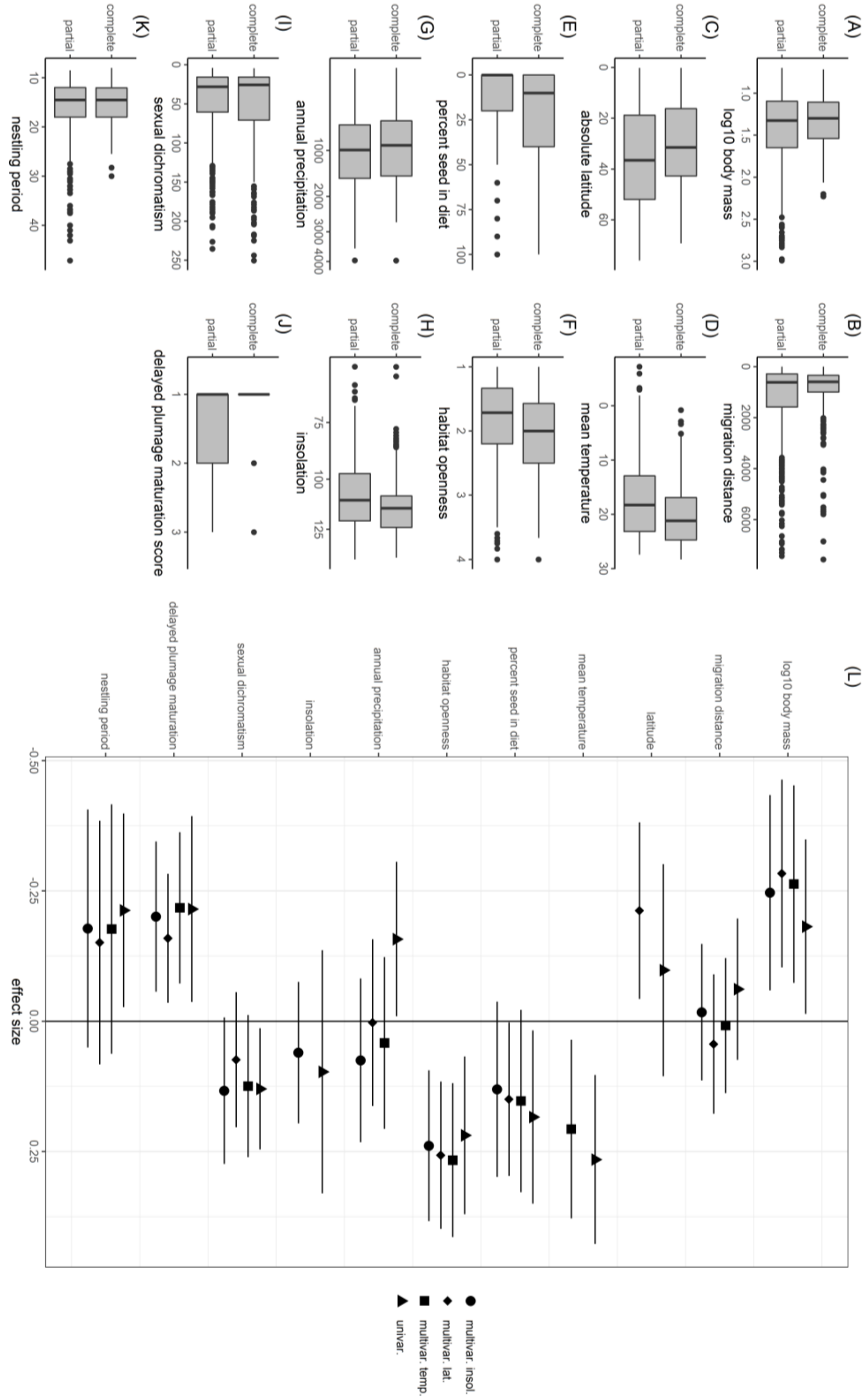
Table S13. Multivariate models with insolation, using dataset 1 but eliminating species with limited information on moult data. We report Akaike's Information Criterion, AIC = 627.26; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.11 and for the whole model, conditional R^2 = 0.57; n = 1021 and number of phylogenies used, n phy. = 98 (in some cases <1 00, because a few models did not converge).

Variable	Estimate	SE	t	P
Intercept	-0.880	0.553	-1.592	0.1119
Insolation	0.090	0.077	1.160	0.2463
Annual precipitation	0.232	0.109	2.134	0.0348
Habitat openness	0.249	0.100	2.479	0.0140
Percent seed in diet	0.075	0.080	0.934	0.3502
Migration distance	-0.054	0.096	-0.557	0.5788
log10 body mass	-0.161	0.104	-1.553	0.1205
Delayed plumage maturation	-0.230	0.086	-2.675	0.0080
Sexual dichromatism	0.088	0.073	1.196	0.2320

Table S14. Multivariate models with insolation, using dataset 1 but eliminating long distance migratory species. We report Akaike's Information Criterion, AIC = 772.29; an estimate of phylogenetic effects, alpha = 0.02 (lower values reflect stronger phylogenetic effects); R^2 values for covariates, marginal R^2 = 0.14 and for the whole model, conditional R^2 = 0.54; n = 1059 and number of phylogenies used, n phy. = 90 (in some cases < 100, because a few models did not converge).

Variable	**Estimate**	**SE**	**t**	**P**
Intercept	-1.141	0.373	-3.055	0.0022
Mean temperature	0.268	0.093	2.893	0.0038
Annual precipitation	0.249	0.089	2.792	0.0052
Habitat openness	0.296	0.09	3.277	0.0011
Percent seed in diet	0.199	0.089	2.243	0.0249
Migration distance	0.193	0.069	2.808	0.005
log10 body mass	-0.181	0.109	-1.658	0.0974
Delayed plumage maturation	-0.362	0.089	-4.08	<0.0001
Sexual dichromatism	0.235	0.079	2.986	0.0028

Figure S1. Boxplots (A-K) of raw data without phylogenetic correction showing differences between species with partial and complete of primaries during the post-juvenile moult, and a forest plot (L) depicting effects and 95%CIs of explanatory variables included in the phylogenetic logistic regression models. Because there were many missing values in one covariate (nestling period) we carried out the analyses on two datasets: dataset 1 (n = 1266 species), included all covariates except for the duration of the nestling period, and dataset 2 (n = 860 species) which also included nestling period. In addition, due to collinearity, latitude, insolation and annual mean temperature could not be included in the same model and were fitted in three separate models. Boxplots show median and interquartile ranges and outliers (black dots); in the forest plots 95%CIs that do not overlap 0 correspond to statistically significant effects (P < 0.05).



Data Sources

Alström P, Mild K 2003. *Pipits and wagtails of Europe, Asia and North America. Identification and systematics*. Christopher Helm, London.

Barshep Y, Manu SA 2013. Breeding phenology and moult of the endemic Bannerman's Weaver *Ploceus bannermani*. *Ostrich* 84: 231–233.

Botero-Delgadillo E, Bayly N, Gómez-Montes C 2012. Ciclos de muda en *Diglossa albilatera* Thraupidae. y evidencia de un patrón en la adquisición del dicromatismo sexual en el género *Diglossa*. *Bol SAO* 22: 10–16.

Craig A 1996. The annual cycle of wing-moult and breeding in the Wattled Starling *Creatophora cinerea*. *Ibis* 138: 448–454.

Diaz A, Hernández F 2018. Muda preformativa excéntrica en un espécimen de colección de la Tangara azul y amarilla *Pipraeidaea bonariensis darwinii*, Bonaparte 1983. AVES: Thraupidae. *Biol* 16: 273–279.

Dickey DR, Van Rossem AJ 1938. The birds of El Salvador. *Zool. Ser. Field Museum Nat. Hist.* 23.

DuVal EH 2005. Age-based plumage changes in the lance-tailed manakin: a two-year delay in plumage maturation. *Condor* 107: 915–920.

Eyckerman R, Cuvelier D 1982. The moult of some bird species on Mount Cameroon. *Malimbus* 4: 1–4.

Ganpule P 2019. Field identification of Sand Lark Alaudala raytal and Lesser/Asian Short-toed Lark *Alaudala rufescens/cheleensis*: An unacknowledged pitfall. *Indian Birds* 15: 97–111.

Gómez C, Botero-Delgadillo E, Bayly NJ, et al 2012. Documentando estrategias de muda en aves Neotropicales: ejemplos de la Sierra Nevada de Santa Marta, Colombia. *Ornitol. Neotrop.* 23: 129–138.

Gauci C, Sultana J 1979. Moult of the Sardinian Warbler. *Il-Meril* 20: 1–13.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2014. Moult topography and its application to the study of partial wing-moult in two neotropical wrens. *Ibis* 156: 311–320.

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A 2009. *Paseriformes del Occidente de México: morfometría, datación y sexado*. Museu de Ciències Naturals de Barcelona, Barcelona.

Guallar SX, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2018. Preformative wing molt in 23 Neotropical resident passerine species. *Ornitol. Neotrop.* 29: 3–10.

Guallar SX, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2016. Molt strategies of ten neotropical forest passerine species. *Wilson J. Ornithol.* 128: 543–555.

Hartley I, McGowan P 1991. Moult and biometrics in five birds endemic to Palawan, Philippines. *Forktail* 6: 74–77.

Hernández A 2012. Molt patterns and sex and age criteria for selected landbirds of southwest Colombia. *Ornitol. Neotrop.* 23: 215–223.

Herremans M 1999. Biannual complete moult in the Blacklchested *Prinia Prinia flavicans*. *Ibis* 141: 115–124.

Howell SNG, Lewington I, Russell W 2014. Rare birds of North America. Princeton University Press, Princeton, NJ.

Howell SNG, Webb S 1995. *A guide to the birds of Mexico and northern Central America*. Oxford University Press, Oxford.

Johnson EI, Wolfe JD 2017. *Molt in Neotropical Birds: life-history and aging criteria*. Taylor & Francis, Boca Raton, FL.

Kamtaeja S, Suwannapoom C, Sitasuwan N, Chomdej S 2015. Moult in the Stripe-throated Bulbul, *Pycnonotus finlaysoni*, sexual differences and timing. *CHIANG MAI J. Sci.* 42: 339–348.

Kawaji, N, Hirokawa J. 1998. Complete post-juvenile moult of the Asian Stubtail *Urosphena squameiceps*. *Bull. Japan Bird Band. Assoc.* 13: 1–7.

Kennedy JJ, Heavyside J, Jankowski JE, Scholer MN 2018. Molt patterns and sexing and aging criteria for ten species of high elevation landbirds from southeastern Peru. *Ornitol. Neotrop*. 29:63–73.

Kiat Y, Izhaki I 2015. Post-juvenile moult in Graceful *Prinia Prinia gracilis*. *Ring. Migr.* 30: 7–11.

King J 1972. Postnuptial and postjuvenal molt in Rufous-collared Sparrows in northwestern Argentina. *Condor* 74: 5–16.

Mallet-Rodrigues F, Castiglioni GDA, Gonzaga LP 1995. Muda e seqüência de plumagens em *Ramphocelus bresilius* na restinga de Barra de Maricá, estado do Rio de Janeiro Passeriformes: Emberizidae. *Ararajuba* 3: 88–93.

Nakamura H 1979. Summer Concentration and Moult in the Oriental Greenfinch *Carduelis sinica*. *Japanese J. Ornithol.* 28: 1–27.

Okahisa Y, Morimoto G, Takagi K, Ueda K 2013. Effect of pre-breeding moult on arrival condition of yearling male Narcissus Flycatchers *Ficedula narcissina*. *Bird Study* 60: 140–144.

Park S-Y, Seo S-G, Nam H-Y, Cho S-Y, Jin K-S SJ-Y 2019. *Moult and ageing of passerines.* Korea National Park Research Institute, Wonju.

Paxton EH, McLaughlin R, Levins S, et al 2016. *Aging and sexing guide to the forest birds of Hawai ʻi Island*. Technical Report HCSU-079, Hilo, Hawaii.

Pinilla J 2001. How does the extent of a partial moult vary? Some data for melodious warblers *Hippolais polyglotta* in central Iberia. *Ardeola* 48: 81–84.

Prys-Jones RP 1982. Molt and weight of some land-birds on Dominica, West Indies. *J. Field Ornithol.* 53: 352–362.

Pyle P 1997. *Identification guide to North American birds. Part I*. Slate Creek Press, Bolinas, CA.

Pyle P, Engilis A, Kelt DA, Pyle P 2015. *Manual for ageing and sexing birds of Bosque Fray Jorge National Park and northcentral Chile, with notes on range and breeding seasonality*. Special Publication of the Occasional Papers of the Museum of Natural Science.

Pyle P, Kayano K, Tranquillo K, et al 2017. *Manual for ageing and sexing landbirds of American Samoa, with notes on molt and breeding seasonality.* The Institute for Bird Populations, Point Reyes Station, CA.

Pyle P, Mcandrews A, Veléz P, Wilkerson RL, Siegel RB, DeSante DF 2004. Molt patterns and age and sex determination of selected southeastern Cuban landbirds. *J. Field Ornithol.* 75: 136–145.

Radley P, Crary AL, Bradley J, Carter C, Pyle P 2011. Molt patterns, biometrics, and age and gender classification of landbirds on Saipan, Northern Mariana Islands. *Wilson J. Ornithol.* 123: 588–594.

Round PD, Nimnuan S, Phothieng D, Chunkao K 2014. Moult in the Asian Pied Starling *Sturnus contra floweri* population of Thailand. *Forktail* 30: 28–33.

Round PD, Rumsey SJ 2003. Habitat use, moult and biometrics in the Manchurian Reed Warbler *Acrocephalus tangorum* wintering in Thailand. *Ring. Migr.* 21: 215–221.

Ryder TB, Durães R 2005. It's not easy being green: using molt and morphological criteria to age and sex green-plumage manakins Aves: Pipridae. *Ornitol. Neotrop.* 16: 481–491.

Salewski V, Altwegg R, Erni B, Falk KA, Bairlein F, Leisler B 2004. Moult of three Palaearctic migrants in their West African winter quarters. *J Ornithol.* 145: 109–116.

Smith C, Walker LK, Ewen JG 2015. Age and sex criteria for the hihi *Notiomystis cincta*. with additional details on moult patterns. *Notornis* 62: 135–142.

Svensson L 1992. *Identification guide to European passerines*, 2nd ed. L. Svensson, Stockholm.

Tórrez MA, Arendt WJ 2016. *La muda en especies de aves de Nicaragua.* UCA Publicaciones, Managua.

Ursino C, Facchinetti C, Reboreda JC 2012. Preformative molt in brood parasitic screaming *Molothrus rufoaxillaris* and shiny *M. bonariensis* cowbirds. *Ornitol. Neotrop.* 23: 163–171.

Vega-Cortés NA 2017. Identificación de los eventos de muda y reproducción en aves passeriformes y su relación con las épocas climáticas, en el bosque seco tropical del norte del Tolima. University of Tolima, Ibagué-Tolima, Colombia

Vellenga RE 1980. Moults of the satin bowerbird *Ptilonorhynchus violaceus*. *Emu* 80: 49–54.

Ward P 1969. The annual cycle of the Yellow-vented bulbul *Pycnonotus goiavier* in a humid equatorial environment. *J. Zool.* 157: 25–45.

Willoughby EJ 1971. Biology of larks Aves: Alaudidae. in the central Namib Desert. *African Zool.* 6: 133–176.

Wolfe JD, Chandler RB, King DI 2009a. Molt patterns, age, and sex criteria for selected highland Costa Rican resident landbirds. *Ornitol. Neotrop.* 20: 451–459.

Wolfe JD, Pyle P, Ralph CJ 2009b. Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican resident landbirds. *Wilson J. Ornithol.* 121: 556–567.

Yamagishi S 1982. Age determination in the Bull-headed Shrike *Lanius bucephalus* based on buff-tips of greater primary coverts. *J. Yamashina Inst. Ornithol.* 14: 96–102.

Yamashina Y, *et al.* 1980. *A natural history of Japanese birds*. Shuppan Kagaku

.

GENERAL DISCUSSION

1. Main contributions

This section synthesizes the main findings presented in the previous six chapters, which relate to the three study areas of this thesis: variation, regulation, and evolution (Fig. 1). Next sections of this general discussion will tackle the implications, limitations, and future studies.

1.1 Variation

The main novelty of this thesis is the recognition of the final molt phenotype as a potential target of natural selection and its formal use in quantitative analyses. This element had been relegated to play a descriptive role for its use as ageing tool (Shirihai *et al.* 2001, Guallar *et al.* 2009, Jenni &Winkler 2020b). However, variation of the final molt phenotype contains a wealth of information that is underused in traditional approaches. For example, analyzing raw data on final molt phenotype variation has unraveled a more precise picture of how post-juvenile molt has diverged along the passerine phylogeny than by using the traditional dichotomy between partial and complete molt (see Chapter 1). Network analysis of final wing-feather molt phenotypes has shown that the structure of this variation is nested, indicating an underlying rank of importance among wing feathers (see Chapter 2). The only mechanism previously suggested to explain the formation of the final molt phenotype was based on differential investment in feather tracts during the nestling and fledgling periods, whereby nestlings grow feathers of contrasting quality within their wing: the fluffiest juvenile feathers are later replaced by adult-type post-juvenile feathers, whereas the sturdiest ones are retained throughout the entire first annual cycle (Pap *et al.* 2007, 2008; de la Hera *et al.* 2010a). The underlying rank of feather importance proposed in Chapter 2 expands this scope to the feather level, providing a tangible model to test hypotheses on the regulation and evolution of the final molt phenotype.

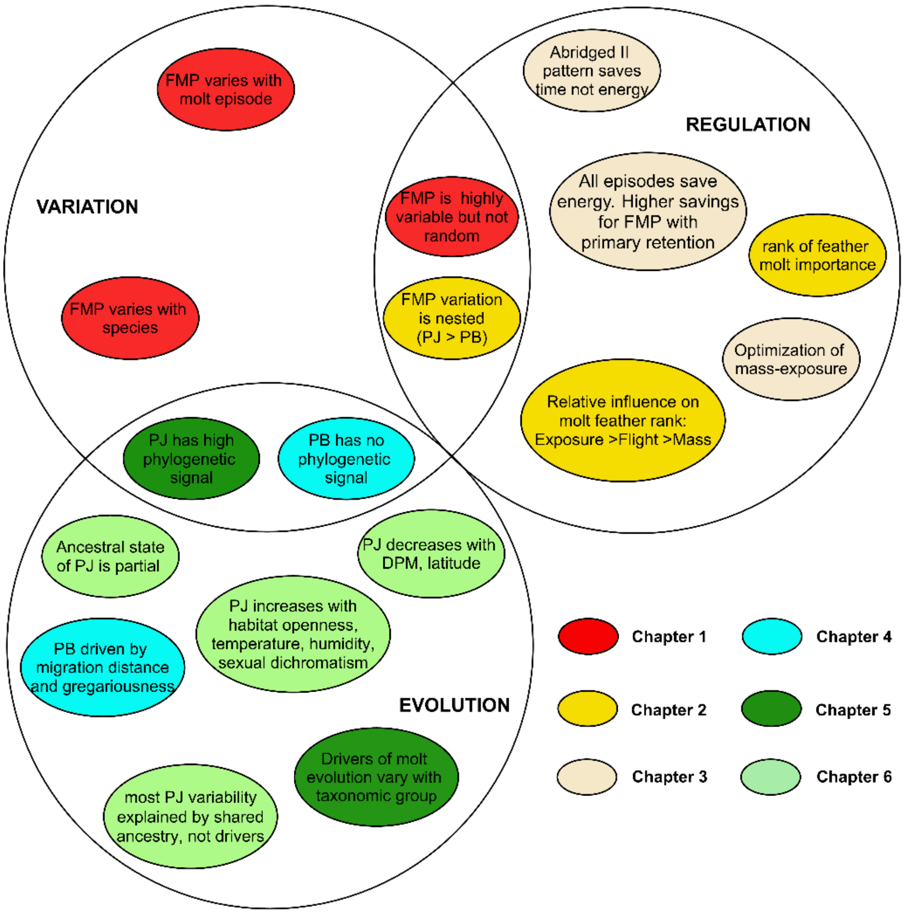
1.2 Regulation

This thesis shows that the formation of the final molt phenotype is not a random process, i.e. some phenotypes are much frequently found among individuals than expected by chance, while most of the potential phenotypes are never found in nature. Despite arguably being a trivial result, it has deep implications, the main one being the existence of mechanisms of molt control. Non-randomness could arise in partial molts if feathers differed in their costs and benefits of being molted, leading to a molt priority rank. The main prediction of this hypothesis is the existence of a nested relationship among final molt phenotypes. Support for this hypothesis is a novel contribution of this thesis. Moreover, deviations from perfect nestedness found in Chapter 2, especially for the pre-breeding molt, strongly suggest that there is more than one rank of feather importance, or even that there are other kinds of underlying mechanisms of molt control to be discovered.

Different molt ranks can arise in association with the adjustment of different plumage functions (through molt) for the upcoming life-history stage (e.g. from crypsis to sexual attractiveness in late winter or early spring). Since every feather carries out different functions, there must be differences in performance among final molt phenotypes that can be targeted by different selective forces in each life-history stage. This automatically raises questions about what plumage functions are targeted by the final molt phenotype and to what extent. To answer this question, performance of the final molt phenotype must be quantified. In Chapter 2, two plumage traits linked to the three main plumage functions (i.e. insulation, signaling, and flight) are used with this aim: (1) individual feather exposure, which is directly associated with insulation and signaling, and (2) length-corrected mass of primaries which correlates to bending stiffness, a mechanical property of feathers associated with the generation of thrust (de la Hera et al. 2010a, 2020). Regression of these two proxies along with mass of the replaced plumage (a proxy of molt cost) on the rank of feather replacement showed that exposure has a larger influence than either contribution to flight or mass of replaced plumage across species.

The individual's final investment in a partial molt must balance costs and benefits under the concrete time and energy constraints it faces. A possible optimization target of natural selection is maximizing overall plumage area while minimizing energy invested in feather synthesis. Chapter 3 shows support for this hypothesis, although the optimization is achieved via energy saving, since empirical values were lower than expected by chance in 96% cases, whereas area was (contrary to expectations) higher than expected by chance in only 12% cases.

Figure 1. Map of the thesis' main results per chapter. DPM Delayed plumage maturation, FMP final molt phenotype, PB pre-breeding molt, PJ post-juvenile molt. Some findings were obtained from independent approaches, including phylogenetic signal of post-juvenile and pre-breeding molts (Chapters 1, 4, 5, and 6), drivers and ancestral state of post-juvenile molt (Chapter 5 and 6), and non-randomness of final molt phenotype (Chapters 1 and 2).



1.3 Evolution

The evolution of molt had been approached from a Palearctic standpoint thus far (Svensson & Hedenström 1999, Figuerola & Jovani 2001, Hall & Tullberg 2004, de la Hera *et al.* 2010b, Kiat & Izhaki 2016), focusing on the role of time constraints and two macroecological characteristics of the avifauna of this region: migration and seasonality. By expanding the geographic scope to other continents, this thesis provides novel insights on passerine molt evolution. The fact that most passerine species living in Neotropical forests undergo partial post-juvenile molts instead of the complete molts predicted by hypotheses based on time constraints (Gómez *et al.* 2012, Guallar *et al.* 2009, 2016, 2018, 2021; Kennedy *et al.* 2018, Johnson & Wolfe 2018) motivated the inclusion of environmental factors in phylogenetic analyses on the last three chapters of this thesis. Results from these analyses clearly indicate that ontogenetic, climate, and habitat factors have played an even more important role than time constraints in shaping the evolution of the post-juvenile molt in passerines. Further, drivers of molt evolution vary with molt episode and taxonomic group. Thus, the evolution of the pre-breeding molt in Motacillidae strongly correlates with the species' social environment (see Chapter 4). All this variation shows that molt is an adaptive trait linked to the natural history of each species. However, most of the variation found for the post-juvenile molt is explained by shared ancestry, as corroborated by its high phylogenetic signal, suggesting a strong bond with conserved plumage functions.

2. Implications

Since feathers differ in their size, shape, and function, their replacement has different costs and benefits that must be balanced when the individual does not have unlimited time and resources to replace all its plumage. In addition, higher order effects arise when groups of feathers interact, for example creating wing gaps or forming wing-patches. Altogether, the set of feathers that an individual replaces during a molt episode (i.e. its final molt phenotype) potentially has survival and reproduction consequences that can be targeted by selection forces.

The phylogenetic signal and the enormous among-species variability of the final molt phenotype suggest that selection forces have also shaped the regulatory mechanisms of passerine molt, thus increasing adaptation to each species physical and social environment. Since environmental conditions may vary throughout the species lifecycle, it comes as no surprise that the main commonality shared among passerine molt variation, regulation, and evolution is their covariation with molt episode, expressed both at individual and species level.

2.1 Variation

Passerine final molt phenotype variation shows a nested organization that likely arises from a rank of feather-molt importance, which reflects the balance between costs and benefits of molting each feather under variable constrained scenarios. Differences among molt episodes, however, cause a deviation from perfect nestedness. This deviation shows that constraints have not been the only factor underlying formation of the final molt phenotype. Specifically, the large nestedness deviation of the pre-breeding molt suggests diversification of factors among and within species leading to different underlying molt ranks (nestedness decreases when final molt phenotypes produced by different molt ranks are analyzed together). This is supported by the lack of phylogenetic signal found in Chapters 1 and 4, which could be associated with labile functions, such as signaling social and sexual information. Contrastingly, the high phylogenetic signal of the post-juvenile molt suggests higher homogeneity of functions across species, which have modified final molt phenotypes during speciation to adapt to new environmental pressures.

Variation of the final molt phenotype pervades the whole order Passeriformes. However, they conform to certain rules of similarity, which allow to classify them in a reduced number of groups. These so-called molt patterns occur at distinct frequencies among molt episodes, lending additional support to the hypothesis that functions vary with molt episode. Moreover, molt pattern variation varies greatly among species for a given molt episode, ranging from species with fairly homogenous molt episodes (e.g. post-juvenile molt of Parulidae species living in forests; Pyle 1997) to species with highly heterogenous ones (e.g. pre-breeding molt of trans-Saharan *Sylvia* warblers; Shirihai *et al.* 2001). The biological significance and the physiological implications of this variation remain to be studied, although one trivial reason is to confer flexibility in front of unforeseeable constraints. Thus, many species present abridged phenotypes (see molt pattern description in Chapter 1) associated with the molt episode during which the complete plumage renewal takes place (e.g. Spotted Flycatcher *Muscicapa striata*; Svensson 1992).

2.2 Regulation

Molt regulation is necessarily a complex task because it coordinates the multiple elements of the active molt (see 1.2 in General Introduction). Partial molts, somehow contra intuitively, ad complexity to the regulation of the process, since it affects the control of other molt elements (e.g. sequence among tracts) and requires control over an extra element, the final molt phenotype. Moreover, birds face the problem of how to achieve an optimal balance between cost saving and plumage functionality.

The strong deviation from randomness of the final molt phenotype provides an indirect assessment of the efficiency of its regulatory mechanisms. Despite these mechanisms remain elusive at tissue level, the rules that govern formation of the final molt phenotype are likely largely based on ranks of feather importance that are only manifested during partial molts. The concrete order of feathers within these ranks immediately prompts the search on its causal factors. These factors must be linked to morphological feather traits that channel the costs of replacing each feather counterbalanced by the benefits obtained from the function they furnish. Unfortunately, information on the morphological and functional properties of individual feathers are still very incomplete.

The fact that individual feather exposure has a larger influence than mass and flight contribution on the priority of feather replacement across species and episodes has multiple implications. On one hand, individual feather exposure is positively correlated to feather degradation. However, type of deterioration depends on a variety factors, including anatomical position (e.g. dorsal insolation is higher than ventral), life-history stage (e.g. nest building and incubation may accelerate mechanical abrasion), sex (e.g. females are more prone to degrade their ventral plumage during incubation), or habitat (e.g. birds living in dense vegetation are less likely affected by solar irradiation than by friction with leaves and branches). On the other hand, individual feather exposure is also directly linked to signaling, such that the most exposed feathers are also those that may convey more information to conspecifics. Analogously, signaling may depend on numerous factors, including behavior (e.g. signaling badges may be actively displayed), environment (e.g. badge coloration may interact with habitat shadiness), sex (badges may signal sexual information), or age (e.g. young birds may prioritize crypsis over showy badges).

Despite mass appears to be less influential than feather exposure to explain ranks of feather importance, passerine molt is strongly linked to energy-saving strategies. Final molt phenotypes are significantly lighter than expected by chance, which suggests that saving energy is a catch-all strategy to keep flexible budgets to provide for contingencies. In this sense, phenotypes that do not include primaries save more energy than those that include them. This might be so because primaries are essentially involved in flight, and their replacement prioritizes the efficiency of this function over energy saving. Thus, eccentric phenotypes typical of the post-juvenile molt of many passerine species prioritize the largest primaries that form the wingtip not the innermost light primaries. The reason behind this prioritization is obscure, although it may have arisen as a solution to reduce flight losses during remex molt, a strategy that could have been selected to reduce predation risk of inexperienced birds in species that need to replace the feathers forming the wingtip during the post-juvenile molt. This view is further supported by the fact that eccentric phenotypes are extremely infrequent in adults (Wolfe & Pyle 2011). Many eccentric phenotypes are heavier than expected but abridged II phenotypes are systematically heavier. These phenotypes correlate to shorter molt duration (Kiat & Izhaki 2017), highlighting the importance of saving time in some contexts.

Diversification of ranks of feather importance among molt episodes, as well as further diversification within the pre-breeding molt, complicates identification and quantification of the underlying causal factors. Undoubtedly, differences among species' life-histories and plumage traits other than mass, exposure, and contribution to flight (e.g. pigmentation) have influenced the rank of feather importance. In any case, all this complexity reveals that regulation of the final molt phenotype is highly flexible, with exogenous and endogenous factors likely involved throughout the whole regulatory pathway, starting from genotype expression. Both the components of this pathway and the ultimate causes that have maintained its flexibility remain a mystery.

2.3 Evolution

Reconstruction of the ancestral state of the post-juvenile molt indicates that this was most likely partial. Therefore, the ancestor of passerines encountered conditions in which costs and risks outweighed the benefits of molting its whole plumage. These conditions could have been imposed by time and energy constraints, especially if this ancestor lived at high latitudes or carried out long migrations (Svensson & Hedenström 1999, Kiat & Izhaki 2016). However, other contexts could have favored a partial post-juvenile molt. For example, mild physical environments where plumage would deteriorate at a slow rate (e.g.

forest strata comprised between canopy and understory where solar irradiance is low and vegetation thin and soft; Hardy *et al.* 2004, Mazzotti *et al.* 2019) and social systems where immature birds benefit from signaling this condition (e.g. to reduce aggressive interactions with older males; Senar *et al.* 1998, López *et al.* 2005).

Subsequent transitions from partial to complete post-juvenile molt likely occurred as new species encountered conditions in which the benefits of undergoing a complete post-juvenile outweighed its costs and risks. Mapping the presence/absence of primary replacement during the post-juvenile molt on the phylogenetic tree within the family Cardinalidae suggests that some of these conditions may have appeared as forest species colonized open environments. Open habitats associate with harsher vegetation and stronger solar radiation (Willoughby 1991), which may select for a more durable plumage, and therefore the complete molt of the juvenile plumage. Incidentally, transition rates from complete to partial post-juvenile molt are higher than the reverse, which shows that the complete post-juvenile molt is more instable than the partial one. This is further supported by the presence of abridged and eccentric phenotypes in species with an essentially complete post-juvenile molt (see Fig. 3 of Chapter 1). Transitions from partial to complete post-juvenile molt highly positively correlate to plumage maturation displayed by the bird during its first year of life, which indicates that these transitions not only arise as an adaptive response to the physical environment but also because of changes in life-history traits of species.

The high phylogenetic signal of the post-juvenile molt found in Chapters 1, 5, and 6 shows that differences among species heavily depend on their phylogenetic distance. The post-juvenile molt serves a quite homogenous purpose throughout the order Passeriformes: the challenge of passing from the juvenile to the post-juvenile stage. This homogeneity may have arisen because of two groups of phylogenetic constraints: (1) highly conserved plumage traits across passerines, such as follicle size (Rohwer *et al.* 2009), feather shape, relative feather size, and feather arrangement (see Chapter 3), and (2) shared nidicolous super-fast development, that includes the production of a short-live juvenile plumage (Moreno & Soler 2011).

Nevertheless, other feather traits may vary widely among species independently of their phylogenetic distance, and even within species throughout their annual cycle. For example, feather coloration can vary profoundly between the wintering and breeding periods. Coloration is strongly associated with signaling functions, including signaling sexual attractiveness (Hill 1991, Hill & McGraw 2006, Dias *et al.* 2016). The low phylogenetic signal found for the pre-breeding molt suggests a correlation to labile functions which would be consistent with the faster character divergence associated with functions largely driven by sexual selection (Andersson 1994, Dunn *et al.* 2015, Harrison *et al.* 2015). A second group of functions could be signaled via final molt phenotype, including dominance (Leitão *et al.* 2015). Thus, the influence of gregariousness on the evolution of the pre-breeding molt phenotype in Motacillidae suggests that, beside natural and sexual selections, social selection also may play a role in the evolution of passerine molt.

Drivers of molt evolution may vary among life-history stages, although some may be shared. For example, migration has been identified as one of the main predictors of passerine molt strategies (Svensson & Hedenström 1999, Figuerola & Jovani 2001, Hall & Tullberg 2004). However, it is unclear the mechanisms through which migration may affect molt. Larger migration distances may increase feather fatigue (Weber *et al.* 2005), thus having a direct influence. On the other hand, migration distance may act indirectly decreasing plumage quality via time constraints (Hall & Fransson 2000, de la Hera *et al.* 2009a) or increasing exposure to solar radiation and number of daylight hours. Some molt episodes may evolve to cope with the extra plumage deterioration that migration may cause (Terrill *et al.* 2020). The interaction among molt episodes remains largely unclear, although some of them may tandem, forming a sort of molt syndrome, as is apparently the case of the auxiliary episode undergone by many Cardinalidae species during their early life. Other molt episodes that could tandem are the restricted molt undergone by some migratory Palearctic species and the complete molt that undergo during their migration or upon arrival in their wintering areas (Bensch *et al.* 1991, Hedenström *et al.* 1993).

3. Limitations

This section describes perceived limitations during the development of this thesis in terms of data and approach, and details how these limitations have been faced or need to be considered when drawing conclusions from the thesis.

3.1 Data

As Bridge (2011) already pointed out, paucity of descriptive molt data is pervasive (see 2.1 in General Introduction). Even basic aggregated species-level information is unavailable for most bird species. For instance, only ca. 17% species worldwide have reliable data on whether the post-juvenile molt is partial or complete (Chapter 6). Figures are much lower for individual-level data reporting final molt phenotypes (Chapters 4 and 5), with the added problem that data on most “covered” species consists of only one to a few molt cards (Gualiar *et al.* 2018, 2021). In addition, there is a strong geographical bias in favor of the Palaearctic and Nearctic zoogeographical regions (Svensson 1992, Pyle 1997). Lack of data from the Afrotropical and Indomalayan regions is dramatic, and the Neotropical and Australasian regions still are far from being well covered, especially the former (Marchant *et al.* 1990, Johnson & Wolfe 2018). This thesis has contributed to alleviate this data deficiency issue gathering original data on final molt phenotypes, specifically 6007 individuals belonging to 508 species. Importantly, 195 are Neotropical species, from which no molt data existed or were very scarce. Using these data, Chapters 4 to 6 have shown that time constraints are just one among the multiple factors that may drive passerine molt evolution. Thus, ontogenetic, social, climate, and habitat factors have played an even more important role than in shaping the evolution of the post-juvenile and pre-breeding molt episodes.

A most-welcome initiative would be the creation of a worldwide repository of molt cards. By centralizing as much as possible final molt phenotype information would boost molt studies, saving time and financial resources to gather information that may already exist but remains in oblivion and scattered all over the world.

Limitations of the method used for gathering final molt phenotype deserve a separate comment. Identification of the different generations of feathers on a plumage after a partial molt episode is an interpretative task that depends on the observer’s expertise (in general but also with each species), the species (e.g. *Empidonax* flycatchers are much harder to score than *Setophaga* or some *Sylvia* warblers; see Fig. A1 in Appendix 2 of Chapter 2) and factors such as molt episode (e.g. it is much easier to score pre-breeding than post-juvenile feathers in European Pied Flycatcher) or study material (e.g. live captures, photographs, or study specimens). These are (implicitly) acknowledged sources of uncertainty on bird molt research, but there is still a lack of sound studies on the repeatability of this measure among and within observers, species, and feather tracts. More importantly, a major unsolved caveat of passerine molt research is the lack of an objective method to measure the age of individual feathers and thus to contrast the current method based on visual identification of molt generations against a much precise and objective approach. However, this has been achieved for molt studies in owls by measuring the natural degradation of porphyrins on their feathers using UV light (Weidensaul *et al.* 2011), bringing hope to develop similar methods for other bird groups.

Overall, the intrinsic and variable level of subjectivity associated with final molt phenotype data (e.g. species, feather tracts) have produced errors that may have affected results and conclusions in this thesis, especially regarding nestedness analyses in Chapter 2. However, note that the noise introduced by data subjectivity would likely decrease nestedness, therefore making results from these analyses conservative. Departures from perfect nestedness could arguably result also from noise; however, they have been interpreted in this thesis as indicative of the existence of different underlying rules of molt (see demonstration in Fig. A2 in Appendix 2). There are two reasons behind this interpretation. First, analyses were done using unique final molt phenotypes, i.e. repeated identical final molt phenotypes were used only once in the analyses. While this does not exclude the possibility that all identical molt phenotypes shared the same subjectivity error, it certainly lowers the odds. Second, note that there are deviations from nestedness that are shared across molt phenotypes. This is revealed by the presence of black cells in the lower right triangle in Fig. 3 (expected to be white in a perfectly nested pattern), and the presence of white cells on the upper left triangle (expected to be black in a perfectly nested pattern). An example of both situations is provided by T1 and T2 tertial feathers on the left panel of Fig. 3.

In summary, while recording final molt phenotypes is a major unsolved issue in bird molt research, there are strong reasons to sustain that the conclusions of this thesis drawn from molt phenotype data are sound.

3.2 Approach

Despite each chapter of this thesis is self-consistent, some approach heterogeneities across chapters merit comment. Environmental and natural history variables have not been homogenously defined across the whole thesis. For example, area of renewed plumage has been defined at feather level in Chapter 2 (i.e. percentage feather exposed), whereas it has been defined at plumage level in Chapter 3 (percentage plumage exposed). This explains the apparent contradiction between the relative importance results in Chapter 2 (exposure is more important than mass) and the role of mass and exposure as possible optimization target in Chapter 3 (observed mass lower than predicted by chance, the opposite for exposure).

Heterogeneity in the treatment of two variables reflects the need to adapt to the different nuances of the objectives set in each chapter of this thesis. First, plumage maturation has been defined to reflect temporal progress of maturation in Chapter 4, whereas in Chapters 5 and 6 reflects degree of maturation of the post-juvenile plumage. Second, habitat openness has been codified in four categories through Chapters 4 to 6, although classification of habitat types differs among them because of the range of habitats associated with the group of birds studied in each chapter. Finally, dichromatism was measured using a subjective score in Chapter 4 because it had not been published an objective method yet, whereas it was already measured using an objective score in Chapter 6 (overall coloration; Dale *et al.* 2015).

Another group of shortcomings associates with some variables that only capture a part of the information that should convey. For example, the flight index devised in Chapter 2 only relates to thrust, leaving out the other major forces involved in flight (i.e. drag and lift). Exposure in chapters 2, 3, and 5 has been defined on the folded wing, leaving out the information associated with the open wing (e.g. abrasion caused by friction with vegetation during flight). Future studies should consider the use of multivariate approaches to these complex variables.

Finally, definition of some variables may miss the relevant information and/or the target of selection forces. For example, temperature, precipitation, and insolation in Chapter 6 are just an approximation of the climate and irradiation that migrant species may experience since averages the annual values for the winter and the breeding periods, which may vary wildly for long-distance migratory species. In Chapter 6, nestling phase duration may not capture the relevant information targeted by selection forces during evolution, which is the quality of the juvenile plumage. Juvenile plumage quality may be heterogenous since passerine birds (all?) can allocate resources differentially to feather tracts (de la Hera *et al.* 2010a, 2020), so that nestling phase duration (especially if differences are small, as occurs among small to medium sized passerines) may not correlate to overall plumage quality: nestlings can allocate more resources to those feathers destined to last long, like remiges, and grow fluffy short-lived feathers (Butler *et al.* 2008). Redefinition of these variables in future studies may yield more meaningful results and more robust conclusions.

4. Synthesis

The final molt phenotype of passerines deviates strongly from randomness despite its astonishing variation. This variation fits an overall nested structure, although degree of nestedness varies among molt episodes, being very high for the post-juvenile molt and low for the pre-breeding molt. This heterogeneity is likely due to the existence of more than one rank of feather importance, especially within the latter episode, and suggests flexibility of the regulatory mechanisms of molt. These differences are paralleled by the differences in phylogenetic signal: very high for the post-juvenile molt and very low for the pre-breeding molt. This is probably linked to the fact that each molt episode serves different functions, being the pre-breeding ones of more labile nature at an evolutionary scale. However, the low variation explained by phylogenetic models suggests that variation of the final molt phenotype is constrained by morphological, physiological, and functional features shared among species (i.e. phylogenetic constraints), at least for the post-juvenile molt. Although limited, exogenous factors have shaped the evolution of passerine molt, likely through the action of selective forces acting on the differential performance of the final molt phenotype. The interplay between conserved phylogenetic constraints and adaptation to the changing individual and environmental contexts fuels the regulation and evolution of the final molt phenotype.

This thesis may help rethink two concepts about molt. First, molt consists of two main components: an active process which yields a molt output that has been likely shaped during evolution to fine-tune adaptation to the environment. For this reason, the set of feathers replaced after a molt episode (i.e. the final molt phenotype) may be the final objective of regulatory mechanisms. Second, selection forces may target molt elements (see 1.2 in General Introduction) from both the process and the output, varying in intensity with species and molt episode. Thus, the final molt phenotype may have relatively less importance than sequence or intensity of remex replacement in soaring birds, while sequence or the investment in feather synthesis may have little importance during the pre-breeding partial molt of some passerine species whereas coloration, and/or symmetry of the final molt phenotype may be the relevant targets of mate selection (e.g. de Heij *et al.* 2011).

Direct evidence of the final molt phenotype as target of natural selection has not been demonstrated yet, and some studies even challenge this possibility. Thus, lack of relationship between feather mass and extent of pre-breeding molt and fitness-related traits in European Pied Flycatcher, and the non-significant effect of post-juvenile molt extent on reproductive success in Blue Tit *Cyanistes caeruleus*, suggest a minor role of the final molt phenotype (de la Hera *et al.* 2013, Crates *et al.* 2015). However, results from the former study are not consistent with an experimental study on the same species that identifies the size of the white wing-patch (which is replaced during the pre-breeding molt) as target of sexual selection (de Heij *et al.* 2011). This discrepancy may arise for several reasons, including insufficiently sampled variation (study birds were too similar) and use of an incorrect target (feather mass and extent may not be an important objective during the pre-breeding molt in this species). Some findings in this thesis suggest that the final molt phenotype has an adaptive nature, like the prevalent energy-saving strategy (Chapter 3) or its correlation with environmental drivers (Chapters 5 and 6).

5. Concluding remarks and future directions

Understanding any biological process requires reliable descriptive data and robust methods that allow inferring the laws that explain it. This usually recommends a multi-angle approach, and the study of molt can be tackled from its evolutionary history within the avian class to its expression in an individual bird. To have the widest possible overview of molt, this thesis has intended to provide answers to three fundamental questions: variation (what), regulation (how), and evolution (why). Specifically, this thesis has focused on the variation of the final molt phenotype of passerines to investigate the underlying mechanisms of molt regulation and the factors shaping molt evolution along the phylogeny.

Bridge (2011) exposed three large gaps in our understanding of molt: data deficiency, physiology, and interaction with flight. One decade later these gaps are still far from being adequately covered (Table 1). Moreover, this list fell short of being exhaustive, not even for the largest gaps. Indeed, evolution and relation with fitness have begun to be explored in the last decade, and especially molt genetics remains in total darkness. Additionally, it is worth noting that the poor knowledge we have on the interaction between molt and flight should be generalized to most plumage functions. Paucity of information on both the behavioral and physical functions of individual feathers (or plumage areas) and their seasonal dynamics hampers the task of interpreting molt strategies. Thus, molting certain wing feathers in late winter likely relate to a change of function (e.g. from insulation to sexual attractiveness; Terrill *et al.* 2020), restitution of mechanical properties (Weber *et al.* 2005), or signaling individual quality during a period of depletion of food resources (Sherry *et al.* 2005, Danner *et al.* 2015).

Table 1. Molt studies in five fields and four methodological approaches. Blanks indicate categories without published studies, ☑ categories covered by many studies, ☐ categories with very few published studies (example references are provided below). This thesis provides a morphological, physiological, and evolutionary perspective using descriptive and hypothesis testing approaches based on the final molt phenotype (red background).

	Theoretical	Descriptive	Hypothesis testing	Experimental
Evolution	☑	☐(2)	🟥 ☑	
Genetics			☐(3)	
Physiology	☐(1)	☑	🟥 ☑	☑
Morphology		🟥 ☑	🟥 ☑	☐(4)
Ecology		☑	☑	☐(5)

(1) Miller (1941); (2) Descriptive evolution refers to paleontological studies: Kiat *et al.* 2020, (3) de la Hera *et al.* (2013), Saino *et al.* (2013); (4) Bridge (2008), de Heij *et al.* (2011), Kiat (2018); (5) Senar *et al.* (2002).

Other questions seem far off mainstream molt studies and will not likely be tackled in the next years. Theoretical and experimental approaches are the most neglected ones, while genetics is the most neglected field of study (Table 1). Future studies on the genetics of molt could shed light on its regulation, help settle the ongoing issue on molt homologies (Howell *et al.* 2003), and unravel how molt episodes integrate in the annual molt cycle.

This thesis has settled the scene for some studies to be carried out in the short term in order to fill important gaps in our understanding of bird molt: 1) the drivers of molt evolution in other passerine families; 2) the interaction between the final molt phenotype and remaining molt elements, especially possible trade-offs with plumage quality; 3) the relationship between feather properties (including second-order properties like wing-patches), plumage functions, and final molt phenotype, including seasonal interactions; 4) the variation of mechanisms of molt control, and how they have evolved (Fig. 3).

CONCLUSIONS

1. The final molt phenotype (set of feathers that a bird replaces in a molt episode) is an essential element of bird molt but has been seldom studied. It is extremely variable among individuals but less than would be expected if feathers were replaced at random. The final molt phenotype is also highly variable among species, showing a strong phylogenetic signal for the post-juvenile molt in passerines.
2. Variation of the final molt phenotype largely follows a nested organization across passerines, although degree of nestedness is high in the post-juvenile molt and moderate in the pre-breeding molt. This nested organization strongly suggests the existence of an underlying rule of molt control based on a rank of feather importance. Individual feather exposure and less so individual feather mass and contribution to flight seem to be relevant variables related to the rank of feather importance.
3. For any given molt extent, empirical partial molt phenotypes save more energy than expected for molt phenotypes generated at random. Further, they optimize the exposed area of wing plumage for any given investment in feather synthesis. The extent of these facts varies among molt episodes.
4. Multiple constraints and environmental factors have shaped the evolution of molt. Thus, completeness in the post-juvenile molt of passerines has been largely shaped by delayed plumage maturation, habitat openness, temperature, and latitude. However, the strength of the specific drivers varies among taxonomic groups. For example, habitat openness is the most influential driver in the evolution of the post-juvenile molt in the family Cardinalidae.
5. Contrasting with the strong phylogenetic signal of the post-juvenile molt, the pre-breeding molt lacks phylogenetic signal, indicating an association with rapidly evolving functions. Thus, gregariousness is the second most influential evolutionary driver of the pre-breeding molt in the family Motacillidae.
6. The ancestral state of the post-juvenile molt in passerines is a partial molt. Transition rates from partial to complete molt are three times lower than the reverse. The complete molt has been independently gained multiple times (and more often lost) throughout the passerine phylogenetic tree.
7. The very strong correlated evolution between the post-juvenile and the pre-supplemental molt episodes indicates that they form part of the early life molt strategy of some passerine families.

REFERENCES

Achache Y, Sapir N, Eimelech Y 2018. Hovering hummingbird wing aerodynamics during the annual cycle. II. Implications of wing feather moult. *R. Soc. open Sci.* 5: 71766.

Alström P, Mild K 2003. *Pipits and wagtails of Europe, Asia and North America.* Identification and systematics. Christopher Helm, London.

Amman GA 1937. Number of contour feathers of *Cygnus* and *Xanthocephalus*. *Auk* 54: 201–202.

Amezian M, Cortes J, Thompson I, Bensusan K, Perez C, Louah A, Aziz El Agbani M, Qninba A 2010. Complete moult of an undescribed resident taxon of the Reed Warbler *Acrocephalus scirpaceus / baeticatus* complex in the Smir marshes, Northern Morocco. *Ardea* 98: 225–234.

Andersson M 1994. *Sexual selection*. Princeton Univ. Press, Princeton, NJ.

Azcárate-García M, González-Braojos S, Díaz-Lora S, et al 2020. Interspecific variation in deterioration and degradability of avian feathers: the evolutionary role of microorganisms. *J. Avian Biol.* 51: e02320.

Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J 2004. Phylogeny and diversification of the largest avian radiation. *Proc. Nat. Acad. Sci.* 1010: 11040–11045.

Barshep Y, Underhill LG, Balachandran S, Pearson DJ 2013. Conditions on the non-breeding areas affect primary moult strategy of the Curlew Sandpiper *Calidris ferruginea*. *Ardea* 101: 13–22.

Barta Z, Houston AI, McNamara J, Welham RK, Hedenström A, Weber TP, Feró O 2006. Annual routines of non-migratory birds: optimal moult strategies. *Oikos* 112: 580–593.

Barta Z, McNamara J, Houston AI, Weber TP, Hedenström A, Feró O 2008. Optimal moult strategies in migratory birds. *Phil. Trans. R. Soc. Lond. B* 363: 211–229.

Battley PF 2006. Consistent annual schedules in a migratory shorebird. *Biol. Lett.* 2: 517–520.

Ben-Hamo M, Downs CJ, Burns DJ, Pinshow B 2017. House sparrows offset the physiological trade-off between immune response and feather growth by adjusting foraging behavior. *J. Avian Biol.* 48: 837–845.

Bensch S, Grahn M 1993. A new method for estimating individual speed of molt. *Condor* 95: 305–315.

Bensch S, Hasselquist D, Hedenström A, Ottosson U 1991. Rapid moult among Palaearctic passerines in West Africa- an adaptation to the oncoming dry season? *Ibis* 133: 47–52.

Bergman G 1982. Why are the wings of *Larus f. fuscus* so dark? *Ornis Fenn.* 59: 77–83.

Bock WJ 2000. Explanatory history of the origin of feathers. *Amer. Zool*. 40: 478–485.

Bojarinova JG, Lehikoinen E, Eeva T 1999. Dependence of postjuvenile molt on hatching date, condition and sex in the Great Tit. *J. Avian Biol.* 30: 437–446.

Braune BM, Gaskin DE 1987. A mercury budget for the Bonaparte's Gull during autumn moult. *Ornis Scand.* 18: 244–250.

Bridge ES 2004. The effects of intense wing molt on diving in alcids and potential influences on the evolution of molt patterns. *J. Exp. Biol.* 207: 3003–3014.

Bridge ES 2006. Influences of morphology and behavior on wing-molt strategies in seabirds. *Mar. Orn.* 34: 7–19

Bridge ES 2008. How does imping affect wing performance. *J. Wildlife Rehab.* 29: 4–9.

Bridge ES 2011. Mind the gaps, what's missing in our understanding of feather molt. *Condor* 113: 1–4.

Bridge ES, Voelker G, Thompson CW, Jones AW, Baker AJ 2007. Effects of size and migratory behavior on the evolution of wing molt in terns (Sternae): a phylogenetic-comparative study. *Auk* 124: 841–856.

Bustnes JO, Folstad I, Erikstad KE, Fjeld M, Miland ØO, Skaare JU 2002. Blood concentration of organochlorine pollutants and wing feather asymmetry in Glaucous Gulls. *Funct. Ecol.* 16: 617–622.

Butler LK, Rohwer S, Speidel MG 2008. Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. *J. Avian Biol.* 39: 629–639.

Buttemer WA, Nicol SC, Sharman A 2003. Thermoenergetics of pre-moulting and moulting kookaburras (*Dacelo novaeguineae*): they're laughing. *J. Comp. Physiol. B* 173: 223–230.

Buttemer WA, Addison BA, Astheimer LB 2015. Lack of seasonal and moult-related stress modulation in an opportunistically breeding bird, the white-plumed honeyeater (*Lichenostomus penicillatus*). *Horm. Behav.* 76: 34-40.

Buttemer WA, Bauer S, Emmenegger T, Dimitriov D, Peev S, Hahn S 2019. Moult-related reduction of aerobic scope in passerine birds*. J. Comp. Physiol. B* 189: 463–470.

Carney RM, Tischlinger H, Shawkey MD 2020. Evidence corroborates identity of isolated fossil feather as a wing covert of *Archaeopteryx*. *Sci. Reports* 10: 15593.

Chai P 1997. Hummingbird hovering energetics during moult of primary flight feathers. *J. Exp. Biol.* 200: 1527–1536.

Chmura HE, Meddle SL, Wingfield JC, Hahn T 2017. Effects of a social cue on reproductive development and pre-alternate molt in seasonally breeding migrant and resident female songbirds (*Zonotrichia leucophrys*). *J. Exp. Bioo.* 220: 2947–2956.

Clark CJ, Kirschel ANG, Hadjioannou L, Prum RO 2016. Smithornis broadbills produce loud wing song by aeroelastic flutter of medial primary wing feathers. *J. Exp. Biol.* 219: 1069–1075.

Cooper NW, Murphy MT, Redmond LJ, Dolan AC 2009. Density-dependent age at first reproduction in the eastern kingbird. *Oikos* 118: 413–419.

Coppack T, Tindemans I, Czisch M, van der Linden A, Berthold P, Pulido F 2008. Can long distance migratory birds adjust to the advancement of spring by shortening migration distance? The response of the pied flycatcher to latitudinal photoperiodic variation. *Glob. Change Biol.* 14: 2516–2522.

Crates RA, Sheldon BC, Garroway CJ 2015. Causes and consequences of individual variation in the extent of post-juvenile moult in the blue tit *Cyanistes caeruleus* (Passeriformes: Paridae). *Biol. J. Linn. Soc.* 116: 341–351.

Crossin GT, Dawson A, Phillips RA, Trathan PN, Gorman KB, Adlard S, Williams TD 2012. Seasonal patterns of prolactin and corticosterone secretion in an Antarctic seabird that moults during reproduction. *Gen. Comp. Endocrinol.* 175: 74–81.

Cyr NE, Wikelski M, Romero LM 2008. Increased energy expenditure but decreased stress responsiveness during molt. *Physiol. Biochem. Zool.* 81: 452–462.

Czirják GA, Pap PL, Vágási CI, Giraudeau M, Mureşan C, Mirleau P, Heeb P 2013. Preen gland removal increases plumage bacterial load but not that of feather-degrading bacteria. *Naturwissenschaften* 100: 145–151.

Dale J, Dey CJ, Delhey K, Kempenaers B, Valcu M 2015. The effects of life history and sexual selection on male and female plumage colouration. *Nature* 527: 367–370.

Danner RM, Greenberg RS, Danner JE, Walters JR 2015. Winter food limits timing of pre-alternate moult in a short-distance migratory bird. *Funct. Ecol.* 29: 259–267.

Dawson A 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starlings *Sturnus vulgaris*. *Ibis* 146: 493–500.

Dawson A 2005. The effect of temperature in photoperiodically regulated gonadal maturation, regression and moult in starlings – potential consequences of climate change. *Funct. Ecol.* 19: 995–1000.

Dawson A 2006. Control of molt in birds: association with prolactin and gonadal regression in starlings. *Gen. Comp. Endocr.* 147: 314–322.

Dawson A 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Phil. Trans. R. Soc. B* 363: 1621–1633.

Dawson A, Hinsley SA, Ferns PN, Bonser RHC, Eccleston L 2000. Rate of moult affects feather quality, a mechanism linking current reproductive effort to future survival. *Proc. R. Soc. B* 267: 2093–2098.

de Heij ME, Gustafsson L, Brommer JE 2011. Experimental manipulation shows that the white wing patch in Collared Flycatchers is a male sexual ornament. *Ecol. Evol.* 1: 546–555.

de la Hera I, Pérez-Tris J, Tellería JL 2009a. Migratory behaviour affects the trade-off between feather growth rate and feather quality. *Biol. J. Linn. Soc.* 97: 98–105.

de la Hera I, Díaz, JA, Pérez-Tris J, Tellería JL 2009b. A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. *J. Avian Biol.* 40: 461−465.

de la Hera I, Pérez-Tris J, Tellería JL 2010a. Migratory behavior and differential resource allocation between wing and tail feathers in a passerine bird. *Auk* 127: 647−652.

de la Hera I, Pérez-Tris J, Tellería JL 2010b. Relationships among timing of moult, moult duration and feather mass in long-distance migratory passerines. *J. Avian Biol.* 41: 609−614.

de la Hera I, Schaper SV, Díaz JA, Pérez-Tris J, Bensch S, Tellería JL 2011. How much variation in the molt duration of passerines can be explained by the growth rate of tail feathers? *Auk* 128: 321−329.

de la Hera I, DeSante DF, Milá B 2012. Feather growth rate and mass in Nearctic passerines with variable migratory behavior and molt pattern. *Auk* 129: 222−230.

de la Hera I, Reed TE, Pulido F, Visser ME 2013. Feather mass and winter moult extent are heritable but not associated with fitness-related traits in a long-distance migratory bird. *Evol. Ecol.* 27: 1199–1216.

de la Hera I, Pérez-Tris J, Tellería JL 2015. Adventitious feather replacement favours a more rapid regeneration of primaries over rectrices in two passerine bird species. *Ibis* 157: 883–887.

de la Hera I, Hernández-Téllez I, Pérez-Rigueiro J, Pérez-Tris J, Rojo FJ, Tellería JL 2020. Mechanical and structural adaptations to migration in the flight feathers of a Palaearctic passerine. *J. Evol. Biol.* 33: 979–989.

del Hoyo J, Elliott A, Sargatal J 1992–2002. *Handbook of the birds of the world. Volumes 1-7*. Lynx Edicions, Barcelona.

del Hoyo J, Elliott A, Christie D 2003–2013. *Handbook of the birds of the world. Volumes 8-17*. Lynx Edicions, Barcelona.

Delius JD 1988. Preening and associated comfort behavior in birds. *Ann. N. Y. Acam. Sci.* 525: 40–55.

deGraw WA, Kern MD 1985. Changes in the blood and plasma volume of Harris' sparrows during postnuptial molt. *Comp. Biochem. Physiol.* 81A: 889–893.

Demongin L 2016. Identification guide to birds in the hand. Laurent Demongin.

Dias RI, Manica L, Gressler D, Bell JA, Fecchio A 2016. Plumage coloration, body condition and immunological status in Yellow-billed Cardinals (*Paroaria capitata*). *Ethol. Ecol. Evol.* 28: 462-476.

Dietz MW, Daan S, Masman D 1992. Energy requirements for molt in the kestrel *Falco tinnunculus*. *Physiol. Zool.* 65: 1217–1235.

Dietz MW, Rogers KG, Piersma T 2013. When the seasons don't fit: speedy molt as a routine carry-over cost of reproduction. *PLoS One* 8: e53890.

Dittmann DL, Demcheck DK 2006. Contributions to our knowledge of molt in the Calliope Hummingbird. *Birding* 38: 32–40.

Dolnik VR, Gavrilov VM 1979. Bioenergetics of molt in the Chaffinch (*Fringilla coelebs*). *Auk* 96: 253–264.

Dunn PO, Armenta JK, Whittingham LA 2015. Natural and sexual selection act on different axes of variation in avian plumage color. *Sci. Adv.* 1: e1400155.

Dvořák R 2016. Aerodynamics of bird flight. *EPJ Web of Conferences* 114: 01001.

Dwight J 1900. The sequence of plumages and moults of the passerine birds of New York. *Ann. N.Y. Acad. Sci.* 13: 73–360.

Earnst SL 1992. The timing of wing molt in Tundra Swans: energetic and non-energetic constraints. *Condor* 94: 847–856.

Echeverry-Galvis MA, Hau M 2013. Flight performance and feather quality: paying the price of overlapping moult and breeding in a tropical highland bird. *PLoS One* 8: e61106.

Edwards AE 2008. Large-scale variation in flight feather molt as a mechanism enabling biennial breeding in albatrosses. *J. Avian Biol.* 39: 144–151.

Edwards AE, Rohwer S 2005. Large-scale patterns of molt activation in the flight feathers of two albatross species. *Condor* 107: 835–848.

Ellis DH, Lish JW, Kéry M, Redpath SM 2006. Short-term oscillations in avian molt intensity: evidence from the golden eagle *Aquila chrysaetos*. *J. Avian Biol.* 37: 642–644.

Ellis VA, Merrill L, Wingfield JC, O'Loghlen AL, Rothstein SI 2012. Changes in immunocompetence and other physiological measures during molt in Brown-headed Cowbirds (*Molothrus ater*). *Auk* 129: 231–238.

Ellis DH, Rohwer VG, Rohwer S 2017. Experimental evidence that a large raptor can detect and replace heavily damaged flight feathers long before their scheduled moult dates. *Ibis* 159: 217–220.

Ericson PGP, Christidis L, Cooper A, Irestedt M, Jackson J, Johansson US, Norman JA 2002. A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc. Biol. Sci. B* 269: 235–241.

Ewart DN, Lanyon WE 1970. The first prebasic molt of the Common Yellowthroat (Parulidae). *Auk* 87: 362–363.

Ferns PN, Hinsley SA 2004. Immaculate tits: head plumage pattern as an indicator of quality in birds. *Anim. Behav.* 67: 261–272.

Ferns PN, Hinsley SA 2010. How blue are British tits? Sex, age and environmental effects. *Bird Study* 57: 315–329.

Figuerola J, Jovani R 2001. Ecological correlates in the evolution of moult strategies. *Evol. Ecol.* 15: 183–192.

Filardi CE, Rohwer S 2001. Life history implications of complete and incomplete primary molts in pelagic cormorants. *Condor* 103: 555–569.

Fox AD, Kahlert J 1999. Adjustments to nitrogen metabolism during wing moult in Greylag Geese *Anser anser*. *Funct. Ecol.* 13: 661–669.

Fox AD, Kahlert J 2005. Changes in body mass and organ size during wing moult in non-breeding graylag geese *Anser anser*. *J. Avian Biol.* 36: 538–548.

Fry CH 1969. Structural and functional adaptation to display in the Standard-winged Nightjar *Macrodipteryx longipennis*. *J. Zool.* 157: 19–24.

Gargallo G 1996. Evidence for partial prenuptial moult in adult and first-year Penduline Tits *Remiz pendulinus*. *Bird Study* 43: 157–163.

Gargallo G 2013. Feather selection and replacement patterns demonstrate that Goldfinches *Carduelis carduelis* fix postjuvenile moult extent prior to moult initiation. *J. Ornithol.* 154: 219–230.

Gerken M, Afnan R, Dörl J 2006. Adaptive behaviour in chickens in relation to thermoregulation. *Arch.Geflügelk.* 70: 199–207.

Gienapp P, Merilä J 2010. Genetic and environmental effects on a condition-dependent trait: feather growth in Siberian jays. *J. Evol. Biol.* 23: 715–723.

Ginn HB, Melville DS 1983. *Moult in birds (BTO guide)*. British Trust for Ornithology, Tring.

Gómez C, Botero-Delgadillo E, Bayly NJ, Moreno MI, Páez CA 2012. Documentando estrategias de muda en aves neotropicales: ejemplos de la Sierra Nevada de Santa Marta, Colombia. *Ornitol. Neotropical* 23: 129–138.

Gow EA, Stutchbury BJM 2013. Understanding sex differences in parental effort in a migratory songbird: examining a sex-specific trade-off between reproduction and molt. *Condor* 115: 640–649.

Griggio M, Serra L, Licheri D, Campomori C, Pilastro A 2009. Moult speed affects structural feather ornaments in the blue tit. *J. Evol. Biol.* 22: 782–792.

Gromadzka J 1989. Breeding and wintering areas of Dunlin migrating through southern Baltic. *Ornis Scand.* 20: 132–144.

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A 2009. *Paseriformes del Occidente de México: morfometría, datación y sexado.* Museu de Ciències Naturals de Barcelona, Barcelona.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2014. Moult topography and its application to the study of partial wing-moult in two neotropical wrens. *Ibis* 156: 311–320.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2016. Molt strategies of ten Neotropical forest passerine species. *Wilson J. Ornith.* 128: 543–555.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P 2018. Preformative wing molt in 23 Neotropical resident passerine species. *Ornitol. Neotropical* 29: S3–S10.

Guallar S, Rueda-Hernández R, Pyle P 2021. Preformative molt in Neotropical Cardinalidae. *Ornithol. Res*. 29: https://doi.org/10.1007/s43388-020-00024-z.

Gunderson AR 2008. Feather-degrading bacteria: a new frontier in avian and host-parasite research? *Auk* 125: 972–979.

Gwinner E 2003. Circannual rhythms in birds. *Curr. Opin. Neurobiol.* 13: 770–778.

Hahn TP, Swingle J, Wingfield JC, Ramenofsky M 1992. Adjustments of the prebasic molt schedule in birds. *Ornis Scand.* 23: 314–321.

Hall KSS, Fransson T 2000. Lesser Whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. *J. Avian Biol.* 31: 583–587.

Hall KSS, Tullberg BS 2004. Phylogenetic analyses of the diversity of moult strategies in Sylviidae in relation to migration. *Evol. Ecol.* 18: 85–105.

Hardy JP, Melloh R, Koenig G, Marks D, Winstral A, Pomeroy JW, Link T 2004. Solar radiation transmission through conifer canopies. *Agric. For. Meteorol.* 126: 257-270.

Harrison PW, Wright AE, Zimmer F, Dean R, Montgomery SH, Pointer MA, Mank JE 2015. Sexual selection drives evolution and rapid turnover of male gene expression. *Proc. Nat. Acad. Sci.* 112: 4393–4398.

Haukioja E 1971. Flightlessness in some moulting passerines in Northern Europe. *Ornis Fenn.* 48: 101–116.

Hazlerigg DG, Lincoln GA 2011. Hypothesis: cyclical histogenesis is the basis of circannual timing. *J. Biol. Rhythms* 26: 471–485.

Hedenström A, Sunada S 1999. On the aerodynamics of moult gaps in birds. *J. Exp. Biol.* 202: 67–76.

Hedenström A, Bensch S, Hasselquist D, Lockwood M, Ottosson U 1993. Migration, stopover and moult of the Great Reed Warbler *Acrocephalus arundinaceus* in Ghana, West Africa. *Ibis* 135: 177–180.

Hegyi G, Laczi M, Boross N, Jablonszky M, Kötel D, Krenhardt K, Marko G, Nagy G, Rosivall B, Szász E, Garamszegy LZ, Török J 2018. When to measure plumage reflectance: a lesson from Collared Flycatchers *Ficedula albicollis*. *Ibis* 161: 27–34.

Herremans M 2006. Identification and occurrence of a biannual complete molt. *Acta Zool. Sin.* 52(Suppl): 448–450.

Herremans M, Berghman L, Decuypere E, Vandesande F 1993. Immunocytochemical demonstration of progesterone and estrogen receptors in feathers and skin of adult hens. *Acta Biol. Hung.* 44: 353–366.

Hill GE 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature* 350: 337–338.

Hill GE, McGraw KJ eds. 2006. *Bird Coloration, Volume 2: Function and Evolution*. Harvard University Press, Cambridge, MA.

Ho LST, Ané C 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Syst. Biol.* 63: 397–408.

Howell SNG 2010. *Molt in North American birds. Peterson field guides*. Houghton Mifflin Harcourt, New York.

Howell SNG, Corben C, Pyle P, Rogers DI 2003. The first basic problem: a review of molt and plumage homologies. *Condor* 105: 635–653.

Hoye BJ, Buttemer WA 2011. Inexplicable inefficiency of avian molt? Insights from an opportunistically breeding arid-zone species, *Lichenostomus penicillatus*. *PLoS One* 6: e16230.

Humphrey PS, Parkes KC 1959. An approach to the study of molt and plumages. Auk 76: 1–31.

Irestedt M, Jønsson KA, Fjeldså J, Christidis L, Ericson PGP 2009. An unexpectedly long history of sexual selection in birds-of-paradise. *BMC Evol. Biol.* 9: 235.

Jenni L, Winkler R 2020a. *The biology of molt in birds*. Helm, London.

Jenni L, Winkler R 2020b. *Molt and ageing of European passerines.* 2nd ed. Academic Press, London.

Jenni L, Ganz K, Milanesi P, Winkler R 2020. Determinants and constraints of feather growth. *PLoS One* 15: e0231925.

Jenni-Eiermann S, Helfenstein F, Vallat A, Glauser G, Jenni L 2015. Corticosterone: effects on feather quality and deposition into feathers. *MMethods Ecol. Evol.* 6: 237–246.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO 2012. The global diversity of birds in space and time. *Nature* 491: 444–448.

Johnson EI, Wolfe JD 2018. Molt in Neotropical birds: life history and aging criteria. CRC Press, Boca Raton, FL.

Jovani R, Rohwer S 2017. Fault bars in bird feathers: mechanisms, and ecological and evolutionary causes and consequences. *Biol. Rev.* 92: 1113–1127.

Karell P, Brommer JE, Ahola K, Karstinen T 2013. Brown tawny owls moult more flight feathers than grey ones. *J. Avian Biol.* 44: 235–244.

Kemp AC 1995. *The hornbills: Buceratiformes*. Oxford University Press, Oxford.

Kennedy JJ, Heavyside J, Jankowskii JE, Scholer MN 2018. Molt patterns and sexing and aging criteria for ten species of high elevation landbirds from southeastern Peru. *Ornitol. Neotropical* 29: S63–S73.

Kennerley P, Pearson D 2010. *Reed and bush warblers*. Christopher Helm, London.

Kiat Y 2017. Divergent primary moult—A rare moult sequence among Western Palaearctic passerines. *PLoS One* 12: e0187282.

Kiat Y 2018. Divergent rectrix moult the implications and conditions of moult sequence. *J. Avian Biol.* 49: jav-01609.

Kiat Y, Izhaki I 2016. Why renew fresh feathers? Advantages and conditions for the evolution of complete post-juvenile moult. *J. Avian Biol.* 47: 47–56.

Kiat Y, Izhaki I 2017. Non-moulted primary coverts correlate with rapid primary moulting. *J. Avian Biol.* 48: 380–386.

Kiat Y, Izhaki I 2021. Split moult time constraints or endogenous strategy. *Ibis* 163: https://doi.org/10.1111/ibi.12897.

Kiat Y, Sapir N 2017. Age-dependent modulation of songbird summer feather molt by temporal and functional constraints. *Amer. Nat.* 189: 184–195.

Kiat Y, Sapir N 2018. Life-history trade-offs result in evolutionary optimization of feather quality. *Biol. J. Linn. Soc.* 125: 613–624.

Kiat Y, Izhaki I, Sapir N 2016. Determinants of wing-feather moult speed in songbirds. *Evol. Ecol.* 30: 783–795.

Kiat Y, Izhaki I, Sapir N 2019a. The effects of long-distance migration on the evolution of moult strategies in Western-Palearctic passerines. *Biol. Rev.* 94: 700–720.

Kiat Y, Vortman Y, Sapir N 2019b. Feather moult and bird appearance are correlated with global warming over the last 200 years. *Nature Comm.* 10: 2540.

Kiat Y, Balaban A, Sapir N, O'Connor JK, Wang M, Xu X 2020. Sequential molt in a feathered dinosaur and implications for early paravian ecology and locomotion. *Current Biol.* 30: 1–6.

Klicka J, Burns K, Spellman GM 2007. Defining a monophyletic Cardinalini: a molecular perspective. *Mol. Phyl. Evol.* 45: 1014–1032.

Knopf FL 1974. Schedule of presupplemental molt of white pelicans with notes on the bill horn. *Condor* 77: 356–359.

Kuenzel WJ 2003. Neurobiology of molt in avian species. *Poultry Sci.* 82: 981–991.

Laesser J, van Wijk RE 2018. Postponed moult of primary coverts untangles the ageing of Wrynecks *Jynx torquilla*. *Ring. Migr.* 32: 87–103.

Langston NE, Rohwer S 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. Oikos 76: 498–510.

Lee S-I, Kim J, Park H, Jabłoński PG, Choi H 2015. The function of the alula in avian flight. *Sci. Reports* 5: 9914.

Leitão AV, Ferreira AC, Funghi C, Trigo S, Mota PG 2015. Evidence for multiple functions in a sexually selected ornament. *Anim. Behav.* 110: 155–161.

Lewis SA, Furness RW 1991. Mercury accumulation and excretion in laboratory reared black-headed gull *Larus ridibundu*s chicks. *Arch. Env. Contam. Toxicol.* 21 :316–320.

Lind J 2001. Escape flight in moulting Tree Sparrows (*Passer montanus*). *Funct. Ecol.* 15: 29-35.

Lind J, Jakobsson S 2001. Body building and concurrent mass loss: flight adaptations in tree sparrows. *Proc. R. Soc. B* 268: 1915–1919.

Lindström Å, Daan S, Visser GH 1994. The conflict between moult and migratory fat deposition: a photoperiodic experiment with Bluethroats. *Anim. Behav.* 48: 1173–1181.

Long JA, Schouten P 2008. *Feathered dinosaurs: the origin of birds*. CSIRO Press, Melbourne.

López G, Figuerola J, Varo N, Soriguer R 2005. White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed. *Ardea* 93: 237–244.

Lovette IJ, Pérez-Emán JL, Sullivan JP, Banks RC, Fiorentino I, Córdoba-Córdoba S, Echeverry-Galvis M, Barker FK, Burns KJ, Klicka J, Lanyon SM, Bermingham E 2010. A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). *Mol. Phyl. Evol.* 57: 753–770.

Lucas AM, Stettenheim PR 1972. *Avian anatomy, integument*. Agricultural Handbook 362. US Department of Agriculture, Washington DC.

Lustick S 1970. Energy requirements of molt in cowbirds. *Auk* 87: 742–746.

MacArthur RH, Wilson EO 2001. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

MacDougall-Shackleton SA, Stevenson TJ, Watts HE, Pereyra ME, Hahn TP 2009. The evolution of photoperiod response systems and seasonal GnRH plasticity in birds. *Integr. Comp. Biol.* 49: 580–589.

Maderson PFA, Hillenius WJ, Hiller U, Dove CC 2009. Towards a comprehensive model of feather regeneration. *J. Morphol.* 270: 1166–1208.

Maddison WP, Maddison DR 2001. Mesquite: a modular system for evolutionary analysis. version 0.98. http://mesquiteproject.org

Marchant S, Higgins PJ 1990. *Handbook of Australian, New Zealand and Antarctic birds*. Oxford University Press, Melbourne.

Masman D, Daan S 1987. The allocation of energy in the annual cycle of the kestrel, *Falco tinnunculus*. In Bird DA ed. *The ancestral Kestrel*, pp 124–136. Raptor Res. Found. Inc. and Macdonald Raptor Res. Center of McGill Univ. State. Anne de Bellevue, Quebec.

Marzal A, Ashgar M, Rodríguez L, Reviriego M, Hermosell IG, Balbontín J, García-Longoria L, de Lope F, Bensch S 2013. Co-infections by malaria parasites decrease feather growth but not feather quality in house martin. *J. Avian Biol.* 44: 437–444.

Mazzotti G, Malle J, Barr S, Jonas T 2019. Spatially continuous characterization of forest canopy structure and subcanopy irradiance derived from handheld radiometer surveys. *J. Hydrometeorol.* 20: 1417–1433.

Meister W 1951. Changes in histological structure of the long bones of birds during the molt. *Anat. Rec.* 111: 1–21.

Miller AH 1941. The significance of molt centers among the secondary remiges in the Falconiformes. *Condor* 43: 113–115.

Møller AP, Erritzøe J, Nielsen JT 2009. Frequency of fault bars in feathers of birds and susceptibility to predation. *Biol. J. Linn. Soc.* 97: 334–345.

Moreno J, Soler JJ 2011. Sources of distinctness of juvenile plumage in Western Palearctic passerines. *Biol. J. Linn. Soc.* 102: 440-454.

Moreno J, Sanz JJ, Merino S 2001. Daily energy expenditure and cell-mediated immunity in pied flycatchers while feeding nestlings: interaction with moult. *Oecologia* 129: 492–497.

Moreno-Rueda G 2010. Experimental test of a trade-off between moult and immune response in house sparrows *Passer* domesticus. *J. Evol. Biol.* 23: 2229–2237.

Morton GA, Morton ML 1990. Dynamics of postnuptial molt in free-living mountain white-crowned sparrows. *Condor* 92: 813–828.

Mulvihill RS, Winstead RL 1997. Variation in the extent of the first prebasic wing molt of dark-eyed juncos. *J. Field Ornithol.* 68: 183–199.

Murphy ME, King JR 1990. Diurnal changes in tissue glutathione and protein pools of molting White-crowned Sparrows: the influence of photoperiod and feeding schedule. *Physiol. Zool.* 63: 1118–1140.

Murphy ME, King JR 1991. Protein intake and the dynamics of the postnuptial molt in White-crowned Sparrows *Zonotrichia leucophrys gambelii*. *Can. J. Zool.* 69: 2225–2229.

Murphy ME, King JR 1992. Energy and nutrient use during moult by white-crowned sparrows *Zonotrichia leucophrys gambelii*. *Ornis Scand.* 23: 304–313.

Murphy ME, King JR, Lu J 1988. Malnutrition during the postnuptial molt of White-crowned Sparrows: feather growth and quality. *Can. J. Zool.* 66: 1403–1413.

Murphy ME, Taruscio TG, King JR, Truitt SG 1992. Do molting birds renovate their skeletons as well as their plumages? Osteoporosis during the annual molt in sparrows. *Can. J. Zool.* 70: 1109–1113.

Naef-Daenzer B, Gruebler MU 2016. Post-fledging survival of altricial birds: ecological determinants and adaptation. *J. Field Ornithol.* 87: 227–250.

Navarro J, González-Solís J 2007. Experimental increase of lying costs in a pelagic seabird: effect on foraging strategies, nutritional state and chick condition. *Oecologia* 151: 150–160.

Newton I 1966. The moult of the bullfinch *Pyrrhula pyrrhula*. *Ibis* 108: 41–67.

Newton I 1967. Feather growth and moult in some captive finches. *Bird Stud*y 14: 10–24.

Newton I 1968. The moulting seasons of some finches and buntings. *Bird Study* 15: 84–92.

Newton I 1989. *Lifetime reproduction in birds.* Academic Press, London.

Newton I 2011. Migration within the annual cycle: species, sex and age differences. *J. Ornithol.* 152: 169–185.

Nicolai B 1968. Die isolierte Frühmauser der Farbmerkmale des Kopfgefieders bei *Uraeginthus granatinus* und *U. ianthinogaster* (Estrildidae). *Z. Tierpsychol.* 25: 854–861.

Niese RL, Tobalske BW 2016. Specialized primary feathers produce tonal sounds during flight in rock pigeons (*Columba livia*). *J. Exp. Biol.* 219: 2173–2181.

Nilsson J-Å, Svensson E 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proc. R. Soc. B* 263: 711–714.

Noskov GA, Rymkevich TA, Iovchenko IP 1999 Intraspecific variation of molt adaptive significance and ways of realisation. In Adams NJ, Slotow RH eds. *Proceedings of the 22nd International Ornithological Congress Durban*, pp 544–563. BirdLife South Africa, Johannesburg.

Noskov GA, Rymkevich TA, Smirnov EN 2018. Postjuvenile Moult in the Common Crossbill (*Loxia curvirostra curvirostra*): photoperiodic regulation and its role in synchronization of the annual cycle. *Biol. Bull.* 45: 718–731.

Oschadleus HD, Osborne T 2005. Chestnut Weaver *Ploceus rubiginosus* biometrics and primary moult in Namibia. *Ostrich* 76: 206–211.

Pageau C, Tonra CM, Shaikh M, Flood NJ, Reudink MW 2020. Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines. *Biol. Lett.* 16: 20200155.

Pagel M, Meade A, Barker D 2004. Bayesian estimation of ancestral character states on phylogenies. *Syst. Biol.* 53: 673–684.

Pap PL, Barta Z, Tökölyi J, Vágási CI 2007. Increase of feather quality during moult: a possible implication of feather deformities in the evolution of partial moult in the great tit *Parus major*. *J. Avian Biol.* 38: 471–478.

Pap PL, Vágási CI, Czyrják GA, Barta Z 2008. Diet quality affects postnuptial molting and feather quality of the house sparrow (*Passer domesticus*): interaction with humoral immune function? *Can. J. Zool.* 86: 834–842.

Pap PL, Vágási CI, Bărbos L, Marton A 2013. Chronic coccidian infestation compromises flight feather quality in house sparrows *Passer domesticus*. *Biol. J. Linn. Soc.* 108: 414–428.

Paradis E, Claude J, Strimmer K 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20: 289–290.

Park S-Y, Seo S-G, Nam H-Y, Cho S-Y, Jin KS, Song JY 2019. *Moult and ageing of passerines*. Bird Research Center, Korea National Park Research Institute, Wonju.

Péczely P 1992. Hormonal regulation of feather development and moult on the level of feather follicles. *Ornis Scand.* 23: 346–354.

Pérez-Granados C, Calleja JA, Seoane J, Fernández-Tizón M, Vigalondo B, Meléndez L, Kiat Y 2021. Time available for moulting shapes inter- and intra-specifc variability in post-juvenile moult extent in wheatears (genus *Oenanthe*). *J Ornithol.* 162: doi.org/10.1007/s10336-020-01826-0.

Peters A, Astheimer LB, Boland CRJ, Cockburn A 2000. Testosterone is involved in acquisition and maintenance of sexually selected male plumage in Superb Fairy-Wrens, *Malurus cyaneus*. *Behav. Ecol. Sociobiol.* 47: 438–445.

Pinilla J 2001. How does the extent of a partial moult vary? Some data for Melodious Warbler *Hippolais polyglotta* in central Iberia. *Ardeola* 48: 81–84.

Pirrello S, Pilastro A, Serra L 2015. Nest-dwelling ectoparasites influence the start and duration of the first pre-basic moult in the European starling *Sturnus* vulgaris. *J. Avian Biol.* 46: 412–418.

Pitocchelli J, Piatt JF, Carter HR 2003. Variation in plumage, molt, and morphology of the Whiskered Auklet (*Aethia pygmaea*) in Alaska. *J. Field Ornithol.* 74: 90–98.

Podlaszczuk O, Włodarczy R, Janiszewski T, Kaczmarek K, Minias P 2017. When moult overlaps migration: moult-related changes in plasma biochemistry of migrating common snipe. *PeerJ* 5: e3057.

Portugal SJ, Green JA, Butler PJ 2007. Annual changes in body mass and resting metabolism in captive barnacle geese (*Branta leucopsis*): the importance of wing moult. *J. Exp. Biol.* 210: 1391–1397.

Portugal SJ, Thorpe SKS, Green JA, Myatt JP, Butler PJ 2009. Testing the use/disuse hypothesis: pectoral and leg muscle changes in captive barnacle geese *Branta leucopsis* during wing moult. *J. Evol. Biol.* 212: 2403–2410.

Portugal SJ, Butler PJ, Green JA, Cassey P 2011. Indications of phenotypic plasticity in moulting birds: captive birds reveal adaptive changes in mineralisation of their long bones during wing moult. *J. Ornithol*. 152: 1055–1061.

Proctor NC, Lynch PJ 1993. *Manual of ornithology.* Yale University Press, New Haven, CT.

Prum RO, Williamson S 2001. Theory of the growth and evolution of feather shape. *J. Exp. Zool.* 291: 30–57.

Prum RO, Berv JS, Dornburg A, Field DJ, Townsend JP, Lemmon EM, Lemmon AR 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* 526: 569–573.

Prŷs-Jones RP 1991. The occurrence of biannual primary molt in passerines. *Bull. Brit. Orn. Club* 111: 150–152.

Pyle P 1997. Identification guide to North American birds. Part I. Slate Creek Press, Bolinas, CA.

Pyle P 1998. Eccentric first-year molt patterns in certain Tyrannid flycatchers. *Western Birds* 29: 29–35.

Pyle P 2013. Evolutionary implications of synapomorphic wing-molt sequences among falcons (Falconiformes) and parrots (Psittaciformes). *Condor* 115: 593–602.

Pyle P (in prep.) Examination of images from Macaulay Library to determine avian molt strategies: A

case study on eight species of North American hummingbirds. *Ornithology* 138.

Pyle P, Kayano K, Tranquillo K, Murphy K, Wilcox B, Arcilla N 2017. *Manual for ageing and sexing landbirds of American Samoa, with notes on molt and breeding seasonality*. Special Publication of The Institute for Bird Populations, Point Reyes Station, CA.

Rayner JMV, Swaddle JP 2000. Aerodynamics and behavior of take-off and molt in birds. In Domenici P, Blake RW eds. *Biomechanics in animal* behaviour, pp 125–157. BIOS Scientific Publishers, Oxford.

Redfern CPF, Alker PJ 1996. Plumage development and post-juvenile moult in the Sedge Warbler *Acrocephalus schoenobaenus*. *J. Avian Biol.* 27: 157–163.

Remisiewicz M, Tree AJ, Underhill LG, Taylor PB 2010. Rapid or slow moult? The choice of a primary moult strategy by immature Wood Sandpipers *Tringa glareola* in southern Africa. *J. Ornithol.* 151: 429–441.

Revell LJ 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3: 217–223.

Rohwer S, Rohwer VG 2013 How do birds adjust the time required to replace their flight feathers. *Auk* 130: 699–707.

Rohwer S, Rohwer VG 2018. Breeding and multiple waves of primary molt in Common ground-doves of coastal Sinaloa. *PeerJ* 6: e4243.

Rohwer S, Wang L-K 2010. A quantitative analysis of flight feather replacement in the moustached tree swift *Hemiprocne mystacea*, a tropical aerial forager. *PLoS One* 5: e11586.

Rohwer S, Ricklefs RE, Rohwer VG, Copple MM 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biol.* 7: e1000132.

Rohwer S, Fox AD, Daniel T, Kelly JF 2015. Chronologically sampled flight feathers permits recognition of individual molt-migrants due to varying protein sources. *PeerJ* 3: e743.

Ross, JD, Kelly JF, Bridge ES, Engel MH, Reinking DL, Boyle WA 2015. Pallid bands in feathers and associated stable isotope signatures reveal effects of severe weather stressors on fledgling sparrows. *PeerJ* 3: e814.

Rymkevich TA, Bojarinova JG 1996. Variation in the extent of postjuvenile moult in the Great Tit near Lake Ladoga (Russia). *Bird Study* 43: 47–59.

Ryzhanovsky VN 2013. Photoperiodic conditions during molting of the Indian Pied Wagtail (*Motacilla alba dukhunensis*) and location of its winter habitats. *Biol. Bull.* 40: 414–417.

Saino N, Romano M, Caprioli M, Fasola M, Lardelli R, Micheloni P, Scandolara C, Rubolini D, Gianfranceschi L 2013. Timing of molt of barn swallows is delayed in a rare *Clock* genotype. *PeerJ* 1: e17.

Schieltz PC, Murphy ME 1997. The contribution of insulation changes to the energy cost of avian molt. *Can. J. Zool.* 75: 396–400.

Seddon N, Botero CA, Tobias JA, Dunn PO, MacGregor HEA, Rubenstein DR, Uy JAC, Weir JT, Whittingham LA, Safran RJ 2013. Sexual selection accelerates signal evolution during speciation in birds. *Proc. R. Soc. B* 280: 20131065.

Selander RK 1958. Age determination and molt in the Boat-tailed Grackle. Condor 60: 355–376.

Senar JC, Copete JL, Martin AJ 1998. Behavioural correlates of variation in the extent of postjuvenile molt in the Siskin *Carduelis spinus*. *Ibis* 140: 661–669.

Senar JC, Domènech J, Uribe F 2002. Great tits (*Parus major*) reduce body mass in response to wing area reduction, a field experiment. *Behav. Ecol.* 13: 725–727.

Senar JC, Domènech J, Camerino M 2005. Female Siskins choose mates by the size of the yellow wing stripe. *Behav. Ecol. Sociobiol.* 57: 465–469.

Serra L, Pirrello S, Licheri D, Griggio M, Pilastro A 2010. Sex-dependent response of primary moult to simulated time constraints in the rock sparrow *Petronia petronia*. *J. Avian Biol.* 41: 327–335.

Sherry TW, Johnson MD, Strong AM 2005. Does winter food limit populations of migratory birds? In Greenberg R, Marra PP eds. *Birds of two worlds: the ecology and evolution of temperate-tropical migration.* John Hopkins University Press, Baltimore, MD.

Shirihai H, Helbig A, Gargallo G 2001. Sylvia *warblers*. Christopher Helm, London.

Shugart GW, Rohwer S 1996. Serial descendent primary molt or Staffelmauser in Black-crowned Night-Herons. *Condor* 98: 222–233.

Sibley CG, Ahlquist JE 1990. *Phylogeny and classification of birds: a study in molecular evolution*. Yale University Press, New Haven, CT.

Sieburth D, Pyle P 2018. Evidence for a prealternate molt-migration in the Rufous Hummingbird and its implications for the evolution of molts in Apodiformes. *Auk* 135: 495–505.

Slessers M 1970. Bathing behavior of land birds. *Auk* 87: 91–99.

Stresemann E, Stresemann V 1966. Die Mauser der Vögel. *J. Orrnithol.* 107: 1–445.

Strinella E, De Faveri A, Artese C, Catoni C 2015. Timing and duration of moult in relation to weather conditions in four montane passerine species at the Gran Sasso, Central Italy. *Ring. Migr.* 30: 67–74.

Stutchbury BJM, Gow EA, Done T, MacPherson M, Fox JW, Afanasyev V 2011. Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proc. R. Soc. B* 278: 131–137.

Sutton GM 1935. The juvenal plumage and postjuvenal molt in several species of Michigan sparrows. *Cranbrook Inst. Sci.* 3: 1–36.

Svensson L 1992. *Identification guide to European passerines*, 4th ed. Stockholm, L. Svensson.

Svensson E, Hedenström A 1999. A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: Sylviidae). *Biol. J. Linn. Soc.* 67: 263–276.

Swaddle JP, Witter MS 1997. The effects of molt on the flight performance, body mass, and behavior of European starlings, *Sturnus vulgaris*. *Can. J. Zool.* 75: 1135–1146.

Swaddle JP, Williams EV, Rayner JMV 1999. The effect of simulated flight feather moult on escape take-off performance in starlings. *J. Avian Biol.* 30: 351–358.

Taruscio TG, Murphy ME 1995. 3-Methylhistidine excretion by molting and non-molting sparrows. *Comp. Biochem. Physiol.* 111A: 397–403.

Terrill RS 2020. Simultaneous wing molt as a catalyst for the evolution of flightlessness in birds. *Amer. Nat.* 196: 775–784.

Terrill RS, Seeholzer GF, Wolfe JD 2020. Evolution of breeding plumages in birds. A multiple-step pathway to seasonal dichromatism in New World warblers. *Ecol. Evol.* 10: 9223–9239.

Thompson CW, Leu M 1995. Molts and plumages of orange-breasted buntings (*Passerina leclancherii*): implications for theories of delayed plumage maturation. *Auk* 112: 1–19.

Tökölyi J, Bókony V, Barta Z 2008. Seasonal colour change by moult or by the abrasion of feather tips: a comparative study. *Biol. J. Linn. Soc.* 94: 711–721.

Tomotani BM, Muijres FT, Koelman J, Casagrande S, Visser ME 2018a. Simulated moult reduces flight performance but overlap with breeding does not affect breeding success in a long-distance migrant. *Funct. Ecol.* 32: 389–401.

Tomotani BM, van der Jeugd H, Gienapp P, de la Hera I, Pilzecker J, Teichmann C, Visser ME 2018b. Climate change leads to differential shifts in the timing of annual cycle stages in a migratory bird. *Glob. Change Biol.* 24: 823–835.

Tomotani BM, Muijres FT 2019. A songbird compensates for wing molt during escape flights by reducing the molt gap and increasing angle of attack. *J. Exp. Biol.* 222: 1–11.

Tonra CM, Marini KLD, Marra PP, Germain RR, Holberton RL, Reudink MW 2014. Color expression in experimentally regrown feathers of an overwintering migratory bird: implications for signaling and seasonal interactions. *Ecol. Evol.* 4: 1222–1232.

Tucker VA 1991. The effect of molting on the gliding performance of a Harris' Hawk (*Parabuteo unicinctus*). *Auk* 108: 108–113.

Vágási C, Pap PL, Barta Z 2010. Haste makes waste: accelerated molt adversely affects the expression of melanin-based and depigmented plumage ornaments in house sparrows. *PLoS One* 5: e14215.

Vágási C, Pap PL, Vincze O, Benkö Z, Marton A, Barta Z 2012. Haste makes waste but condition matters: molt rate-feather quality trade-off in a sedentary songbird. *PLoS One* 7: e40651.

van der Jeugd HP, Eichhorn G, Litvin KE, Stahl J, Larsson K, van der Graaf AJ, Drent RH 2009. Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Glob. Change Biol.* 15: 1057–1071.

Vega Rivera JH, McShea WJ, Rappole JH, Haas CA 1999. Postbreeding movements and habitat use of adult wood thrushes in northern Virginia. *Auk* 116: 458–466.

Vergara P, Martínez-Padilla J, Fargallo JA 2013. Differential maturation of sexual traits: revealing sex while reducing male and female aggressiveness. *Behav. Ecol.* 24: 237–244.

Vézina F, Gustowska A, Jalvingh KM, Chastel O, Piersma T 2009. Hormonal correlates and thermoregulatory consequences of molting on metabolic rate in a northerly wintering shorebird. *Physiol. Biochem. Zool.* 82: 129–142.

Videler JJ 2005. *Avian flight*. Oxford University Press, Oxford.

Wang X, Clarke JA 2015. The evolution of avian wing shape and previously unrecognized trends in covert feathering. *Proc. R. Soc. B* 282: 20151935.

Watt DJ, Ralph CJ, Atkinson CT 1984. The role of plumage polymorphism in dominance relationships of the White-throated Sparrow. *Auk* 101: 110–120.

Weber TP, Borgudd J, Hedenström A, Persson K, Sandberg G 2005. Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species. *Biol. Lett.* 1: 27–30.

Weber TP, Kranenbarg S, Hedenström A, Waarsing JH, Weinans H 2010. Flight feather shaft structure of two warbler species with different moult schedules: a study using high-resolution X-ray imaging. *J. Zool.* 280: 163–170.

Weidensaul CS, Colvin BA, Brinker DF, Huy JS 2011. Use of ultraviolet light as an aid in age classification of owls. *Wilson J. Ornithol.* 123: 373–377.

Wetmore A 1936. The number of contour feathers in passeriform and related birds. *Auk* 53: 159–169.

Wiersma P, Muñoz-Garcia A, Walker A, Williams JB 2007. Tropical birds have a slow pace of life. *Proc. Nat. Acad. Sci.* 104: 9340–9345.

Williams EV, Swaddle JP 2003. Moult, flight performance and wingbeat kinematics during take-off in European starlings *Sturnus vulgaris*. *J. Avian Biol.* 34: 371–378.

Williamson K 1972. Reversal of normal moult sequence in the Spotted Flycatcher. *British Birds* 65: 50–51.

Willoughby EJ 1986. An unusual sequence of molts and plumages in Cassin's and Bachman's sparrows. *Condor* 88: 461–472.

Willoughby EJ 1991. Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proc. West. Found. Vert. Zool.* 4: 247–286.

Willoughby EJ 2007. Geographic variation in color, measurements, and molt of the Lesser Goldfinch in North America does not support subspecific designation. *Condor* 109: 419–436.

Wingfield JC 2008. Organization of vertebrate annual cycles; implications for control mechanisms. *Phil. Trans. R. Soc. B* 363: 425–441.

Wolfe JD, Pyle P 2011. First evidence for eccentric prealternate molt in the Indigo Bunting: possible implications for adaptive molt strategies. *Western Birds* 42: 257–262.

Young DA, Boag DA 1982. Changes in physical condition of male Mallards (*Anas platyrhynchos*) during molt. *Can. J. Zool.* 60: 3220–3226.

Zann R 1985. Slow continuous wing-moult of Zebra Finches *Poephila guttata* from southern Australia. *Ibis* 127: 184–196.

Zeidler K 1966. Untersuchungen über Flügelbefiederung und Mauser des Haussperlings (*Passer domesticus* L.). *J. Ornithol.* 107: 113–153.

Zenatello M, Serra L, Baccetti N 2002. Trade-offs among body mass and primary molt patterns in migrating black terns *Chlidonias nigra*. *Ardea* 90: 411–420.

Zuberogoitia I, Gil JA, Martínez JE, Erni B, Aniz B, López-López P 2016. The flight feather moult pattern of the bearded vulture (*Gypaetus barbatus*). *J. Ornithol.* 157: 209–217.

Zuberogoitia I, Zabala J, Martínez JE 2018. Moult in birds of prey: a review of current knowledge and future challenges for research. *Ardeola* 65: 183–207.

ANNEXES: Published articles

Chapter 1 contains the article first published on 10 November 2019 **Guallar S, Jovani R 2020. Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. *Ibis* 162: 778–786. https://doi.org/10.1111/ibi.12798**

IBIS
BOU international journal of avian science
Ibis (2020), **162**, 778–786 doi: 10.1111/ibi.12798

Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny

SANTI GUALLAR[1]* & ROGER JOVANI[2]
[1] *Department of Animal Biology, University of Barcelona, Av. Diagonal 643, Barcelona, 08028*
[2] *Department of Evolutionary Ecology, Estación Biológica de Doñana, CSIC, Americo Vespucio s/n., 41092, Seville, Spain*

Passerine wing-feather moult has been studied historically in terms of its intensity, duration, timing and extent. However, little is known about variation of wing-moult phenotypes (i.e. the identity of moulted wing feathers in a given individual) within species, among moult episodes and in relation to passerine phylogeny. Here we studied 5373 wing-moult cards from 285 Holarctic and 155 Neotropical passerine species. Variation of moult phenotypes, although high, was far below that expected by chance, and the same phenotypes were repeated among individuals within and among species, suggesting the existence of shared mechanisms of moult control. We successfully classified moult phenotypes according to nine moult patterns described in the literature and found an uneven distribution between the preformative and the prealternate moult. Moult patterns were phylogenetically conserved for the preformative but not for the prealternate moult. Our results suggest differential seasonal control of bird moult with preformative moults being associated with (evolutionarily conserved) somatic demands, whereas prealternate moults are probably associated with (rapidly evolving) signalling functions.

Keywords: moult patterns, moult signatures, seasonal expression.

Feather evolution eventually led to feathered wings, and these to bird flight, becoming a key innovation in the evolution of tetrapods. The concomitant evolution of feather moult was essential to maintain function of these dead, keratin structures that are prone to degradation by biotic (e.g. lice and bacteria; Goldstein *et al.* 2004, Vas *et al.* 2008) as well as abiotic factors (e.g. mechanical abrasion, sunlight; Lennox & Rowlands 1969, Surmacki *et al.* 2011). Within species, the study of bird moult ecology and its evolution has largely focused on the reasons for individual variation of moult extent (i.e. quantity of replaced feathers), such as body condition (Gosler 1994) or time available for moulting (Bojarinova *et al.* 1999, Kiat & Izhaki 2017), and the overlap with energetically costly activities such as breeding and migration (Hemborg *et al.* 2001, Podlaszczuk *et al.* 2016). Among species, moult research has focused on differences in moult speed, duration, extent, location, and sequence as a result of the interaction of moult with specific traits such as body size (Rohwer *et al.* 2009), sexual dichromatism (Figuerola & Jovani 2001), migratory behaviour (de la Hera *et al.* 2010) and environmental factors (Dawson 2008).

Wing-feather moult phenotypes

Much less attention has been paid to moult phenotypes, in other words the identity of feathers replaced by an individual bird in a given moult episode. Thus, the proximate and ultimate reasons explaining exactly which feathers are replaced, and why these differ among species, among individuals within species and among moult episodes, are poorly understood. This is surprising for two reasons. First, different wing feathers may have very

*Corresponding author.
Email: sguallar@yahoo.com
Twitter: @SANTIGUA

different functions, e.g. status signalling by greater coverts, stall delay by alula feathers, lift by primaries. Secondly, the identity of retained and replaced feathers has been recorded for decades in moult cards (Ginn & Melville 1983), being summarized in wing diagrams showing the proportion of individuals in a given species replacing each feather (or feather track) as an age determination tool (Jenni & Winkler 1994, Gualla r *et al.* 2009). However, moult cards have been largely neglected as a resource for studying the evolution of bird moult, even though these cards are for individual birds on which natural selection operates, and record data feather-by-feather, thus accounting for the distribution of functions across the wing.

Here, we focus on the wing-feather moult of passerines, arguably the bird order whose moult has been most thoroughly studied. Passerines moult in a scheduled and periodical fashion, replacing the whole plumage at least once a year (Jenni & Winkler 1994). Full plumage renewal generally occurs right after breeding, during the prebasic moult (Humphrey & Parkes 1959). However, many species undergo additional, partial moult episodes (Svensson 1992, Jenni & Winkler 1994, Pyle 1997a). These include the preformative moult of young birds (equivalent to the post-juvenile moult; Jenni & Winkler 1994), which replaces their juvenile plumage soon after fledging (Howell *et al.* 2003), and the prealternate moult of older birds (equivalent to the pre-breeding moult; Jenni & Winkler 1994), which takes place after the prebasic moult and before the onset of the breeding season (typically in the wintering grounds for migratory species; Humphrey & Parkes 1959).

We accrued a large dataset of individual moult phenotypes by gathering moult cards for birds whose moult had finished from literature and original data. First, we explored variation of moult phenotypes across individuals, species and moult episodes. Then, we tested whether moult phenotypes are random sets of replaced feathers for any given moult extent.

Phenotypic variation and moult signatures

The study of moult phenotype variation is challenging and has been little addressed to date. Here, we tackled the complexity of moult phenotype variation by using a literature review of the so-called moult patterns, which are labels given in order to group similar moult phenotypes. Applying this approach, we aimed to explore three aspects related to the ecology and evolution of moult phenotypes in passerines.

First, we explored whether individuals of a species during a given moult episode showed different moult patterns. As endogenous (e.g. physical condition) and exogenous (e.g. available time) factors may vary among individuals, we expected that moult phenotypes may reflect these differences and could be classified in different moult patterns.

Secondly, we examined differences in the frequency of moult patterns between moult episodes across species. Although basic plumage requirements prioritized in each moult episode are poorly understood, they may differ strongly. For instance, the preformative moult has been related to somatic performance (Middleton 1986, Minias & Iciek 2013), whereas the prealternate moult may also meet signalling functions (Fig. S1), such as social status (Guallar & Figuerola 2016) and sexual attractiveness, at least in species in which this episode takes place just before the breeding season (Lantz & Karubian 2016).

We also studied the frequency distribution of moult patterns from every species and moult episode (hereafter, moult signatures), then mapped these moult signatures to bird phylogeny and calculated their phylogenetic signal in both the preformative and the prealternate moult.

METHODS

Moult phenotypes

Moult cards of finished moults were retrieved from published sources and mist-netted birds from Holarctic and Neotropical bird species (Table S1). Moult state (1 replaced, 0 retained) was scored for each individual upper wing-feather, except for lesser wing coverts, which were collectively scored 1 when more than 70% of the feathers were replaced and 0 otherwise (assessment of the percentage of replaced lesser coverts is rather imprecise; to account for this fact, we defined a value high enough to indicate that nearly the whole tract was moulted). For standardization purposes, the 10th primary of species with nine visible primaries was given the same moult score as the ninth primary (Hall 2005). We removed 47 moult cards with no wing feathers replaced (or with only < 70% of lesser coverts replaced). Thus, moult extent can range in this study from 1 to 51 (lesser coverts = 1, median coverts = 8, greater coverts = 10, carpal covert = 1, primary coverts = 9, alula = 3, tertials = 3, secondaries = 6, primaries = 10).

Although moult is conceived to be a non-random process due to the differential properties (e.g. shape, mass, position) of each feather and its associated function, as far as we know this hypothesis has never explicitly been tested. The total number of potential moult phenotypes (i.e. combinations of replaced feathers) is 2^{51}–1. The number of potential moult phenotypes differs for each moult extent; for example, there are 51 combinations when moulting one wing feather, but 1275 when moulting two. Thus, for each individual in our dataset we simulated new moult phenotypes of the same moult extent, but randomizing the identity of replaced feathers. Then, we tested whether feathers are moulted randomly by comparing the number of repeated moult phenotypes across individuals between observed and simulated moult phenotypes. If moult is a non-random process, some moult phenotypes would be more repeated than expected by chance.

Phenotypic variation and moult signatures

We reviewed the existing literature for passerine wing-moult patterns. The term moult pattern is rather vague and it has been applied to refer to features as diverse as duration (Newton & Rothery 2005), sequence of replacement (Edelstam 1984), intensity (Hall & Fransson 2000), timing (Marini & Durães 2001) and interaction of moult with other stages of the annual cycle (Giunchi *et al.* 2008). Here, we restricted the definition of moult pattern to 'classes' of observed wing-moult phenotypes (e.g. Pyle 1997b, Pinilla 2001). We then searched for the term 'moult pattern' used in this way in the specialized literature and classified the wing-moult cards in our dataset according to the currently proposed moult patterns we found.

Determination of moult homologies is an unsettled issue, with basic questions such as number of annual episodes undergone by a species still under debate (e.g. Howell *et al.* 2003, Piersma 2004, Thompson 2004, Willoughby 2004). We used two working criteria to define our moult episodes: (1) preformative moult as the first moult episode during which the juvenile plumage is replaced (e.g. in the case of non-migratory *Acrocephalus* warblers, the preformative moult is complete, whereas it is partial for migratory species of the genus); (2) prealternate moult as the main moult episode during the non-breeding period (e.g. many species in Laniidae and Phylloscopidae show two non-breeding moult episodes, but the prealternate moult is the more extensive of the two episodes).

For each species and moult episode (preformative and prealternate), we calculated the proportion of moult phenotypes classified in each moult pattern (i.e. moult signatures). We then used hierarchical clustering with Bray–Curtis distances to group species with similar moult signatures (Fig. S2). We applied the complete linkage method because it tends to maximize dissimilarities between clusters and yield more balanced clusters (James *et al.* 2013). Given the lower abundance of prealternate moult cards in our dataset, we only included species with at least 19 moult cards for the preformative moult and at least 10 moult cards for the prealternate moult. Some species may moult more than once between the prebasic moult and before the onset of the breeding season. In these cases, we only included moult phenotypes from the most extensive of these moults as the prealternate moult (e.g. the late winter moult of Parulidae or the late autumn moult of Acrocephalidae; Salewski *et al.* 2004, Guallar *et al.* 2009).

To test for the phylogenetic signal of moult signatures, we downloaded 1000 trees for each set of bird species from birdtree.org (Jetz *et al.* 2012). Then we derived majority rule consensus trees computing mean length branches using 'phytools' (Revell 2012). From these, we estimated phylogenetic signals for moult signatures within each moult episode. Because this variable is categorical, we could not use Pagel's lambda or other methods based on continuous variables. Instead, we adopted the permutation approach proposed by Maddison and Slatkin (1991) (R code available at https://github.com/juliema/publications/tree/master/BrueeliaMS; Bush *et al.* 2016, R Core Team 2017). Specifically, we randomized the tree tips 999 times and compared the scores for each randomization with the empirical score. Statistical significance indicates both phylogenetic conservation and deviation from randomness. Because *P*-values vary slightly among permutation tests, we averaged *P*-values from 10 runs.

RESULTS

Moult phenotypes

We gathered a dataset of 5456 moult cards of birds which had finished moult (Guallar & Jovani 2019), discarding 83 moult cards either because of null extent or because they were assigned to an anomalous pattern (i.e. those that could not be assigned to any of the nine moult patterns defined in Table 1; Table S2). The final dataset used in the analyses consisted of 5373 moult cards from 440 passerine species (285 Holarctic and 155 Neotropical), 2297 of which came from unpublished sources (Table S1). In total, 4085 moult cards were preformative, 1141 prealternate and 147 belonged to other moult episodes.

Moult phenotypes covered the whole moult extent range (i.e. from 1 to 51). In total, 20.5% of the (unique) moult phenotypes occurred at least twice in the dataset, contrasting with only 0.6% of the simulated ones (Chi-square test $\chi^2 = 672.1$, $P < 0.0001$; Figs S3 & S4). In terms of individual moult phenotypes, 73.9% were repeated by at least one other individual, but this only occurred in 1.5% of the randomly simulated moult phenotypes (Chi-square test $\chi^2 = 4081.0$, $P < 0.0001$; Fig. S3).

Table 1. Summary of published passerine wing-feather moult patterns.

Pattern	Description	Reference(s)
Abridged I	Complete moult aborted within secondaries: 1–6 secondaries retained.Example: Prebasic moult of Blue Bunting *Cyanocompsa parellina*.	Mead and Watmough (1976) and Norman (1991)
Abridged II	Complete moult in which primary coverts are retained.Example: Preformative moult of Graceful Prinia *Prinia gracilis*.	Pyle (1998) and Kiat and Izhaki (2017)
Complete	Full feather replacement following a highly conserved moult sequence in passerines: start at primary 1, replacement of primaries accompanied by respective primary coverts. It can be halted at any point and resumed later on (suspension) or not (arrest).Example: Preformative moult of House Sparrow *Passer domesticus*.	Zeidler (1966)
Eccentric	Retention of a variable number of (largely inner) primaries and (largely outer) secondaries, and most to all primary coverts.Example: Preformative moult of *Passerina* buntings.	Winkler and Jenni (1987) and Pyle (1998)
General	Replacement of secondary (i.e. lesser, median and greater) coverts. Tertials are replaced only if secondary coverts are moulted. There is a prioritization from leading to trailing edge of wing: filling of an entire feather tract before proceeding with the next.Example: Preformative moult of *Turdus* thrushes.	Pyle (1997b) and Guallar *et al.* (2014)
Proximal	Same as the general pattern but tertials (and adjacent inner secondaries) can be replaced with retention of outer secondary coverts. From leading to trailing edge of the wing: prioritization of feathers closer to the body before finishing replacement of anterior tracts.Example: Preformative moult of *Henicorhina* wood-wrens.	Pyle (1997b) and Guallar *et al.* (2014)
Inverted	Replacement of inner secondaries and secondary coverts. Prioritization of feathers closer to the body from trailing to leading edge of the wing: tertials, secondaries and greater coverts over median and lesser coverts (the latter at low percentages).Example: Prealternate moult of some trans-Saharan migrants (e.g. European Pied Flycatcher *Ficedula hypoleuca*), and of residents of arid habitats (e.g. *Peucaea* sparrows).	Jenni and Winkler (1994) and Guallar *et al.* (2018)
Limited	Replacement of lesser and median coverts; might include the carpal covert. Prioritization of feathers from leading to trailing edge of the wing and from inner to outer feathers.Example: Preformative moult of dippers *Cinclus* spp., nuthatches *Sitta* spp., treecreepers *Certhia* spp. or kinglets *Regulus* spp.	Jenni and Winkler (1994) and Pyle (1997a)
Reduced	Replacement of one to a few tertials and/or greater coverts. Strongly asymmetrical moults are considered accidental.Example: 'winter' moult of some *Myiarchus* flycatchers, presupplemental ('spring') moult of Melodious Warbler *Hippolais polyglotta*.	Pinilla (2001) and Guallar *et al.* (2018)

Traditional nomenclature based on moult extent refers to these patterns as complete and partial moults (from limited to extensive).

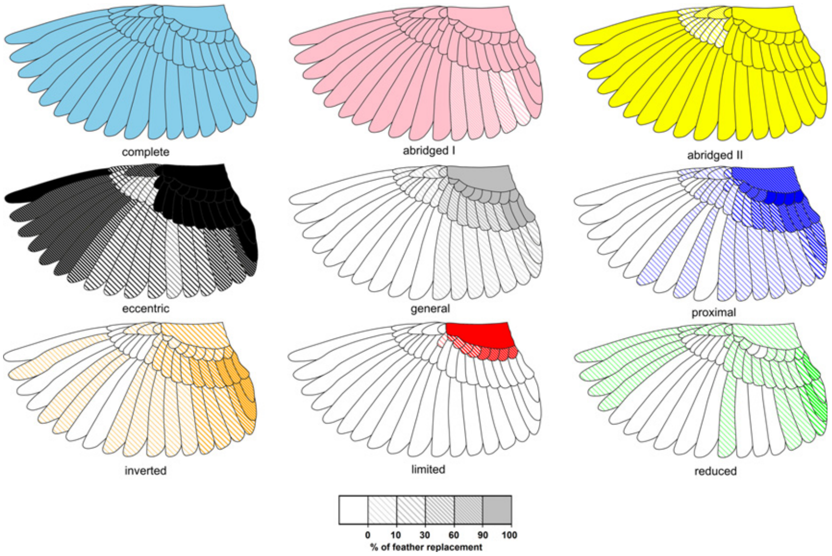


Figure 1. Frequency of feather replacement by moult pattern. Definitions of moult patterns can be found in Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

Phenotypic variation and moult signatures

We retrieved 14 potential moult patterns from the literature, of which we retained only nine (Fig. 1, Table 1, Table S3). Note that the complete moult pattern includes arrested and suspended moults (i.e. birds that stopped a normal complete moult; Stresemann & Stresemann 1966, Norman 1991). Thus, under this definition, the complete moult pattern also comprises partial moult phenotypes. Interestingly, 99.1% of the moult phenotypes in our dataset were unequivocally classified using Table 1. Only 48 moult phenotypes (comprising 27 species) could not be classified and might either belong to minority yet undescribed moult patterns or be simply considered as anomalies (Table S2).

Moult signatures differed strongly between moult episodes (G test $G_8 = 1889.7$, $P < 0.001$, Fig. 2). The preformative moult was dominated by the general pattern (Table 1), whereas the prealternate episode was dominated by the complete pattern (Table 1), with the rest of the patterns more evenly distributed.

Species differed strongly in their moult signatures for both the preformative and the prealternate moults (Fig. 3, Fig. S2). Moult signatures were phylogenetically conserved for the preformative moult ($P < 0.001$) and were more independent from phylogeny for the prealternate moult ($P = 0.158$, Fig. 3, Fig. S5).

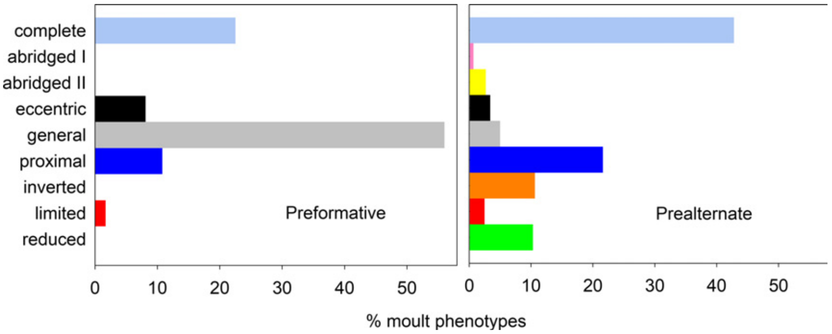


Figure 2. Frequency of moult patterns (Table 1) in the preformative and the prealternate episodes, calculated as the mean percentage of moult cards per species and pattern. Bar colours follow Figure 1. [Colour figure can be viewed at wileyonlinelibrary.com]

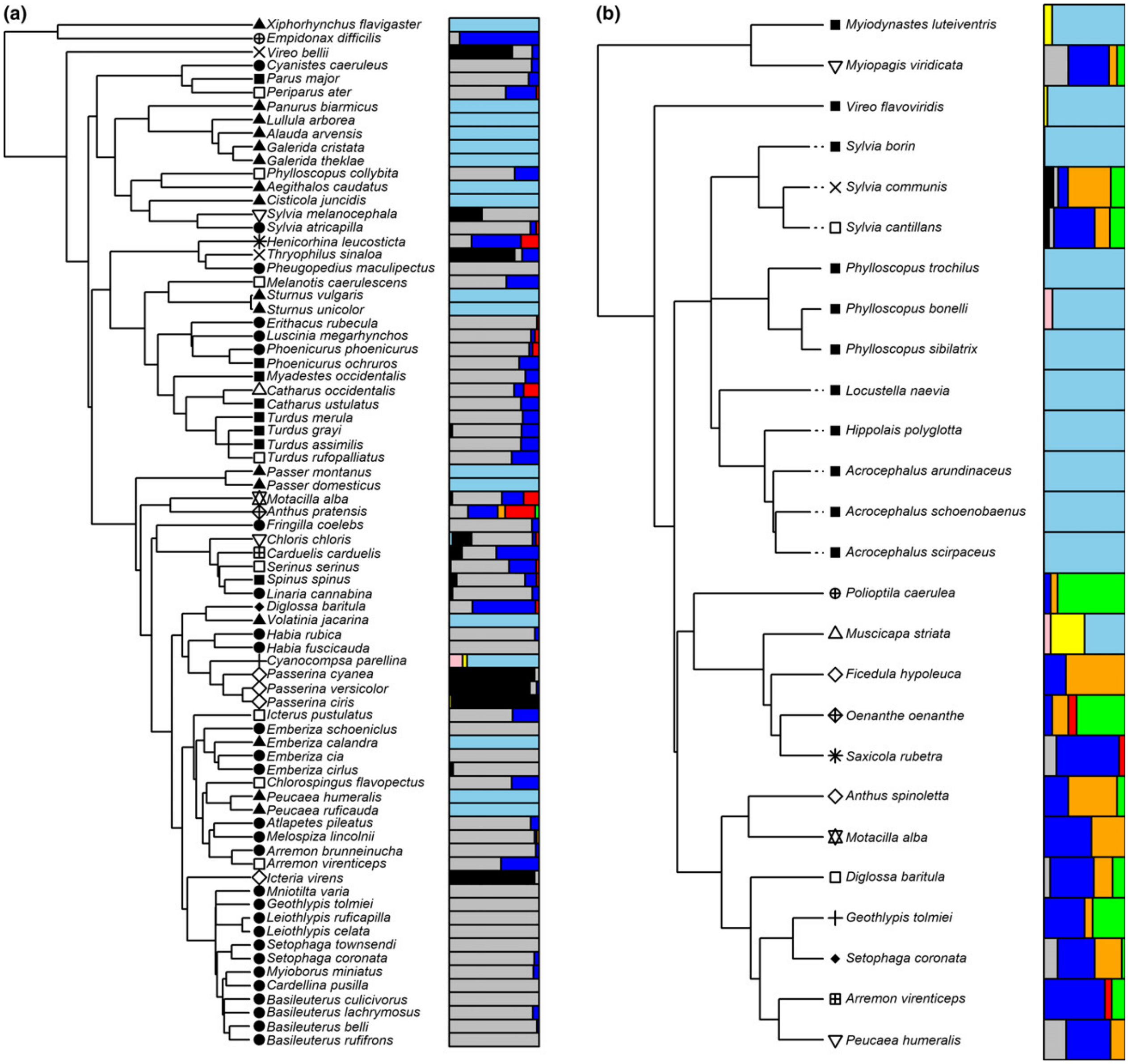


Figure 3. Phylogenetic trees of moult signatures: barplots show the proportion of moult cards following each moult pattern defined in Table 1. Symbols on the branch tips indicate group membership obtained through cluster analysis of similarity among moult signatures: 15 groups for the preformative moult and 13 for the prealternate moult (Fig. S2). (a) Preformative moult (n = 76 species, 24 families). (b) Prealternate moult (n = 26 species, 12 families). Bray–Curtis distances among species' pattern signatures were 0.57 and 0.67, respectively. Note the homogeneous pattern signatures within Phylloscopidae and Acrocephalidae. Colour of moult patterns follows Figure 1. [Colour figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Moult phenotypes

We have shown that the identity of replaced feathers is far from random. In fact, more than 70% of moult phenotypes are repeated at least twice in the dataset, compared to the 1.5% expected by chance (Fig. S3b). In other words, individuals often share exactly the same combination of replaced feathers, which is extremely unlikely by chance alone. Moreover, most of these repeated moult phenotypes were shared by individuals of different species and families (Fig. S2b). Therefore, passerine moult is largely a non-random process, suggesting strongly that moult is governed by some underlying rules shared across the whole order (Jenni & Winkler 1994, Kiat *et al.* 2019). These rules could, for example, be based on inherent ranks of feather-moult, energy investment or plumage exposure.

Phenotypic variation and moult signatures

The preformative moult of fledglings showed less moult pattern variation than the prealternate moult of older birds during the non-breeding season (Fig. 2). This suggests that plumage requirements of young passerines are less diverse between species than the demands affecting the prealternate moult. A possible explanation is that the prealternate moult associates with plumage signalling functions in sexual contexts, as evidenced by the higher prevalence of prealternate moults in sexually dimorphic passerines (Omland & Lanyon 2000). More generally, the larger pattern variation in the prealternate moult might reflect more diverse plumage functions (dominance status or sexual attractiveness) and are highly species-specific (Andersson 1983). Feather tracts involved in sexual signalling may vary among species, e.g. greater coverts in Eurasian Siskin *Spinus spinus* (Senar *et al.* 2005), and greater coverts and tertials in European Pied Flycatcher *Ficedula hypoleuca* (Heij *et al.* 2011; Fig. S1). The strong homogeneity and low variation in the prealternate moult signatures of Phylloscopidae and Acrocephalidae are of note, suggesting that signalling is not important in these two families (Fig. 3). Interestingly, the 11 species with the lowest prealternate moult signature variation are sexually monochromatic (filled squares, Fig. 3; Fig. S2). These results suggest that moult patterns allow passerines to adapt to changing seasonal requirements.

Although moult patterns are shared across species and between moult episodes, species differed strongly in their moult signatures. Nevertheless, closely related species tended to show more similar moult signatures. Our data suggest that this similarity is greater in the preformative than in the prealternate moult (Fig. 3). Accordingly, only the preformative moult showed a statistically significant phylogenetic signal. This is also consistent with the larger moult pattern variation shown in the prealternate moult, which may be correlated to the more labile evolution of sexually dimorphic plumages (Omland & Lanyon 2000). Phylogenetic conservation of preformative moult signatures further suggests that the underlying mechanisms of moult control have been shaped by natural selection, which have evolved in coordination with other key traits such as flight ability (Swaddle & Witter 1997, Pérez-Tris & Tellería 2001) and camouflage (Berggren *et al.* 2004).

We thank Javier Quesada of the Museum of Natural Sciences in Barcelona and Begoña Adrados of EBD-CSIC in Seville for assistance and access to specimen collections. We are grateful to László Garamszegi, Alejandro González Voyer and Peter Pyle for their helpful comments. The manuscript benefitted from the comments of Yosef Kiat and one anonymous reviewer. This is contribution no. 313 from Ottenby Bird Observatory. We thank Javier Blasco Zumeta, British Trust for Ornithology, Carnegie Museum of Natural History's Powdermill Avian Research Center, Marcel Gahbauer of McGill Bird Observatory, Marc Illa, Stephen Menzie, Prof. David Norman of Merseyside Ringing Group, Peter Pyle, and Margaret Rhode for permission to use moult data.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.9896516.

REFERENCES

Andersson, M. 1983. On the functions of conspicuous seasonal plumages in birds. *Anim. Behav.* **31**: 1262–1264.

Berggren, Å., Armstrong, D.P. & Lewis, R.M. 2004. Delayed plumage maturation increases overwinter survival in North Island robins. *Proc. R. Soc. Lond. B* **271**: 2123–2130.

Bojarinova, J.G., Lehikoinen, E. & Eeva, T. 1999. Dependence of postjuvenile molt on hatching date, condition and sex in the Great Tit. *J. Avian Biol.* **30**: 437–446.

Bush, S.E., Weckstein, J.D., Gustafsson, D.R., Allen, J., DiBlasi, E., Shreve, S.M., Boldt, R., Skeen, H.R. & Johnson, K.P. 2016. Unlocking the black box of feather louse diversity: a molecular phylogeny of the hyper-diverse genus *Brueelia*. *Mol. Phylogenet. Evol.* **94**: 737–751.

Dawson, A. 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philos. Trans. R. Soc. B* **363**: 1621–1633.

Edelstam, C. 1984. Patterns of moult in large birds of prey. *Ann. Zool. Fenn.* **21**: 271–276.

Figuerola, J. & Jovani, R. 2001. Ecological correlates in the evolution of moult strategies. *Evol. Ecol.* **15**: 183–192.

Ginn, H.B. & Melville, D.S. 1983. *Moult in Birds (BTO guide)*. Tring: British Trust for Ornithology.

Giunchi, D., Caccamo, C. & Pollonara, E. 2008. Pattern of wing moult and its relationship to breeding in the Eurasian Stone-curlew *Burhinus oedicnemus*. *Ardea* **96**: 251–260.

Goldstein, G., Flory, K.R., Browne, B.A., Majid, S., Ichida, J.M. & Burtt, E.H., Jr. 2004. Bacterial degradation of black and white feathers. *Auk* **121**: 656–659.

Gosler, A.G. 1994. Mass-change during moult in the Great Tit *Parus major*. *Bird Study* **41**: 146–154.

Guallar, S. & Figuerola, J. 2016. Factors influencing the evolution of moult in the nonbreeding season: insights from the family Motacillidae. *Biol. J. Linn. Soc.* **118**: 774–785.

Guallar, S. & Jovani, R. 2019. https://doi.org/10.6084/m9.figshare.9896516

Guallar, S., Santana, E., Contreras, S., Verdugo, H. & Gallés, A. 2009. *Paseriformes del Occidente de México: Morfometría, Datación y Sexado*. Barcelona: Museu de Ciències Naturals de Barcelona.

Guallar, S., Ruiz-Sánchez, A., Rueda-Hernández, R. & Pyle, P. 2014. Moult topography and its application to the study of partial wing-moult in two neotropical wrens. *Ibis* **156**: 311–320.

Guallar, S., Ruiz-Sánchez, A., Rueda-Hernández, R. & Pyle, P. 2018. Preformative wing molt in 23 Neotropical resident passerine species. *Orn. Neotrop.* **29**: S3–S10.

Hall, K.S.S. 2005. Do nine-primaried passerines have nine or ten primary feathers? The evolution of a concept. *J. Ornithol.* **146**: 121–126.

Hall, K.S.S. & Fransson, T. 2000. Lesser-whitethroats under time constraint moult more rapidly and grow shorter wing feathers. *J. Avian Biol.* **31**: 583–587.

de Heij, M.E., Gustafsson, L. & Brommer, J.E. 2011. Experimental manipulation shows that the white wing patch in Collared Flycatchers is a male sexual ornament. *Ecol. Evol.* **1**: 546–555.

Hemborg, C., Sanz, J.J. & Lundberg, A. 2001. Effects of latitude on the trade-off between reproduction and moult: a long-term study with Pied Flycatcher. *Oecologia* **129**: 206–212.

de la Hera, I., Pérez-Tris, J. & Tellería, J.L. 2010. Relationships among timing of moult, moult duration and feather mass in long-distance migratory passerines. *J. Avian Biol.* **41**: 609–614.

Howell, S.N.G., Corben, C., Pyle, P. & Rogers, D.I. 2003. The first basic problem: a review of molt and plumage homologies. *Condor* **105**: 635–653.

Humphrey, P.S. & Parkes, K.C. 1959. An approach to the study of molt and plumages. *Auk* **76**: 1–31.

James, G., Witthen, D., Hastie, T. & Tibshirani, R. 2013. *An Introduction to Statistical Learning with Applications in R*. New York: Springer Science+Business Media.

Jenni, L. & Winkler, R. 1994. *Moult and Ageing of European Passerines*. London: Academic Press.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. 2012. The global diversity of birds in space and time. *Nature* **491**: 444–448.

Kiat, Y. & Izhaki, U. 2017. Non-moulted primary coverts correlate with rapid primary moulting. *J. Avian Biol.* **48**: 380–386.

Kiat, Y., Izhaki, O. & Sapir, N. 2019. The effects of long-distance migration on the evolution of moult strategies in Western-Palearctic passerines. *Biol. Rev.* **94**: 700–720.

Lantz, S.M. & Karubian, J. 2016. Male Red-backed Fairywrens appear to enhance a plumage-based signal via adventitious molt. *Auk* **133**: 338–346.

Lennox, F.G. & Rowlands, R.J. 1969. Photochemical degradation of keratins. *Photochem. Photobiol.* **9**: 359–367.

Maddison, W.P. & Slatkin, M. 1991. Null models for the number of evolutionary steps in a character on a phylogenetic tree. *Evolution* **45**: 1184–1197.

Marini, M.Â. & Durães, R. 2001. Annual patterns of molt and reproductive activity of passerines in South-Central Brazil. *Condor* **103**: 767–775.

Mead, C.J. & Watmough, B.R. 1976. Suspended moult of trans-Saharan migrants in Iberia. *Bird Study* **23**: 187–196.

Middleton, A.L.A. 1986. Seasonal changes in plumage structure and body composition of the American Goldfinch *Carduelis tristis*. *Can. Field Nat.* **100**: 545–549.

Minias, P. & Iciek, T. 2013. Extent and symmetry of post-juvenile moult as predictors of future performance in Greenfinch *Carduelis chloris*. *J. Ornith.* **154**: 465–468.

Newton, I. & Rothery, P. 2005. The timing, duration and pattern of moult and its relationship to breeding in a population of the European Greenfinch *Carduelis chloris*. *Ibis* **147**: 667–679.

Norman, S.C. 1991. Suspended split-moult systems – an alternative explanation for some Palearctic migrants. *Ring. Migr.* **12**: 135–138.

Omland, K.E. & Lanyon, S.M. 2000. Reconstructing plumage evolution in orioles (*Icterus*): repeated convergence and reversal patterns. *Evolution* **54**: 2119–2133.

Pérez-Tris, J. & Tellería, J.L. 2001. Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. *J. Avian Biol.* **32**: 207–213.

Piersma, T. 2004. Understanding evolution of plumages and other cyclic avian life-history phenomena: role for an improved molt terminology. *Condor* **106**: 196–198.

Pinilla, J. 2001. How does the extent of a partial moult vary? Some data for Melodious Warbler *Hippolais polyglotta* in central Iberia. *Ardeola* **48**: 81–84.

Podlaszczuk, O., Kamiński, M., Włodarczy, R., Kaczmarek, K., Janiszewski, T. & Minias, P. 2016. Plumage quality mediates a life-history trade-off in a migratory bird. *Front. Zool.* **13**: 47.

Pyle, P. 1997a. *Identification Guide to North American birds. Part I: Columbidae to Ploceidae*. Bolinas: Slate Creek Press.

Pyle, P. 1997b. Molt limits in North American passerines. *North Am. Bird Bander* **22**: 49–89.

Pyle, P. 1998. Eccentric first-year molt patterns in certain Tyrannid flycatchers. *Western Birds* **29**: 29–35.

R Core Team 2017. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Revell, L. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223.

Rohwer, S., Ricklefs, R.E., Rohwer, V.G. & Copple, M.M. 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biol.* **7**: e1000132.

Salewski, V., Altwegg, R., Erni, B., Falk, K.H., Bairlein, F. & Leisler, B. 2004. Moult of three Palaearctic migrants in their West African winter quarters. *J. Ornithol.* **145**: 109–116.

Senar, J.C., Domènech, J. & Camerino, M. 2005. Female Siskins choose mates by the size of the yellow wing stripe. *Behav. Ecol. Sociobiol.* **57**: 465–469.

Stresemann, E. & Stresemann, V. 1966. Die Mauser der Vögel. *J. Ornithol.* **107**: 1–337.

Surmacki, A., Liu, M., Mercadante, A. & Hill, G.E. 2011. Effect of feather abrasion on structural coloration in male Eastern Bluebirds *Sialia sialis*. *J. Avian Biol.* **42**: 514–521.

Svensson, L. 1992. *Identification Guide to European Passerines*, 4th edn. Stockholm: L. Svensson.

Swaddle, J.P. & Witter, M.S. 1997. The effects of molt on the flight performance, body mass, and behaviour of European Starlings (*Sturnus vulgaris*): an experimental approach. *Can. J. Zool.* **75**: 1135–1146.

Thompson, C.W. 2004. Determining evolutionary homologies of molts and plumages: a commentary on Howell et al. (2003). *Condor* **106**: 199–206.

Vas, Z., Csörgő, T., Møller, A.P. & Rózsa, L. 2008. The feather holes on the Barn Swallow *Hirundo rustica* and other small passerines are probably caused by *Brueelia* spp. lice. *J. Parasitol.* **94**: 1438–1440.

Willoughby, E.J. 2004. Molt and plumage terminology of Howell et al. (2003) still may not reflect homologies. *Condor* **106**: 191–196.

Winkler, R. & Jenni, L. 1987. Weitere Indizien für ‘sektorale’ Handschwingenmauser bei jungen Singvögeln. *J. Ornithol.* **128**: 243–246.

Zeidler, K. 1966. Untersuchungen über Flügelbefiederung und Mauser des Haussperling *Passer domesticus*. *J. Ornithol.* **107**: 113–153.

Received 28 April 2019;
revision accepted 4 November 2019.
Associate Editor: Javier Pérez-Tris.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. European Pied Flycatcher after prealternate moult.

Figure S2. Cluster analysis of moult signatures per episode.

Figure S3. Distribution of repeated moult phenotypes.

Figure S4. (a) Accumulation curve of unique moult phenotypes in the dataset. (b) Frequency of repeated moult phenotypes.

Figure S5. Frequency of evolutionary transitions for the moult signatures in two moult episodes obtained from Maddison & Slatkin tests.

Table S1. Data sources.

Table S2. Moult anomalies in the dataset.

Table S3. Justification of moult pattern selection.

Chapter 2 contains the article published online on 26 September 2020 **Guallar S, Jovani R 2020. Moult nestedness and its imperfections: insights to unravel the nature of passerine wing-feather moult rules. *J. Avian Biol.* 51: e02553. https://doi.org/10.1111/jav.02553**

JOURNAL OF
AVIAN BIOLOGY

Article

Moult nestedness and its imperfections: insights to unravel the nature of passerine wing-feather moult rules

Santi Guallar and Roger Jovani

S. Guallar (https://orcid.org/0000-0002-1121-1968) ✉ (sguallar@yahoo.com), Dept de Vertebrats, Museu de Ciències Naturals de Barcelona, Barcelona. – R. Jovani (https://orcid.org/0000-0002-8693-9742), Dept of Evolutionary Ecology, Estación Biológica de Doñana, CSIC, Spain.

Journal of Avian Biology
2020: e02553
doi: 10.1111/jav.02553

Subject Editor: Javier Pérez-Tris
Editor-in-Chief: Jan-Åke Nilsson
Accepted 21 September 2020

Passerine moult shows two well-known although intriguing characteristics: 1) a varying subset of wing feathers are retained during certain moult episodes, and 2) the identity of the replaced feathers is not random. However, the rules that underlie these moult features are largely unknown. Non-randomness could arise under time and energy constraints if feathers differed in their importance, such that they could be ordered following a hypothetical moult rank. This rule predicts a nested relationship among wing-feather moult phenotypes, where phenotypes of smaller extent would consist of subsets of the wing feathers replaced in phenotypes of larger extent. Here, we analysed a dataset of 3909 preformative and prealternate moult phenotypes from 434 Holarctic and Neotropical passerine species. We found that passerine wing-feather moult was nested (nodf=84.31). However, systematic imperfections in the nestedness pattern led us to test whether the existence of different feather moult ranks may increase nestedness in homogeneous subsets of moult phenotypes. We tested this hypothesis between moult episodes and found that nestedness increased for the preformative moult (nodf=90.99) and decreased for the prealternate moult (nodf=67.28). We further analysed the adaptive meaning of different moult ranks associated with feather mass, feather exposure and feather contribution to flight. Overall, these three feather traits explained 53.74% of the variation in the priority of wing-feather replacement, with exposure having a stronger explanatory power than the other two traits. Our findings provide a first model to interpret variation of wing-feather moult phenotypes in passerines, and outlines the relevance of season for passerine moult, suggesting a dynamic link between moult expression and plumage requirements.

Keywords: control rules, moult episodes, moult phenotypes, network analysis, Passeriformes, phylogenetic constraints

Introduction

Bird plumage performs multiple functions thanks to evolutionary feather diversification and specialization. To maintain plumage functionality, feathers have to be moulted, but birds often do not perform a complete moult, leading to individual variation in moult phenotypes (i.e. different sets of moulted feathers in a given bird after a given

NORDIC SOCIETY OIKOS

www.avianbiology.org

moult episode). A recent study based on 5373 wing-moult phenotypes from 285 Holarctic and 155 Neotropical passerine species, showed that moult phenotypes were highly variable, but many were repeated much more often than expected by chance (Gullar and Jovani 2020a). This, along with the long known interspecific differences in the priority of wing-feather moult (Jenni and Winkler 1994), shows that birds do not moult feathers at random (formally tested in Guallar and Jovani 2020a). Moult phenotypes differed between the preformative moult of young birds (equivalent to the postjuvenile moult; Jenni and Winkler 1994), which replace their juvenile plumage soon after fledging (Howell et al. 2003), and the prealternate moult of older birds (equivalent to the prebreeding moult; Jenni and Winkler 1994), which takes place after the prebasic moult (equivalent to the postbreeding moult; Jenni and Winkler 1994) and before the onset of the breeding season (typically in the wintering grounds for migratory species; Humphrey and Parkes 1959). Moreover, closely related species showed similar frequencies of moult phenotypes within the preformative and the prealternate moult episodes (Guallar and Jovani 2020a), with a large percentage of the variation among species due to shared ancestry (Delhey et al. 2021). Altogether, this suggests a complex scenario created by the interplay between seasonal variation, the adaptive value of moult phenotypes and the constraints imposed by evolutionary history. Despite the enormous variation of moult, moult phenotypes within and among species for each episode are highly predictable, claiming for the existence of both adaptive and evolutionarily constrained mechanisms of moult control. However, our understanding of the nature of both the rules governing the moult process and their physiological mechanisms is in its infancy.

One potential rule of moult control could consist of determining the identity of feathers to be moulted by the extent of moult, that is, some wing feathers would be replaced even in very restricted moults, while others would only be replaced in very extensive moults. This would be analogous to a to-do list in which tasks are carried out in strict descendant order of importance. Feathers to be replaced during a moult episode could be prioritised according to their cost to be produced, their exposure to abrasion and/or their functional contribution to flight. In any case, regardless of the factors that drive this prioritisation, a process based on this feather-moult priority principle would lead to a nested relationship among wing-feather moult phenotypes: phenotypes of smaller extent consisting of subsets of those feathers replaced in phenotypes of larger extent (Fig. 1).

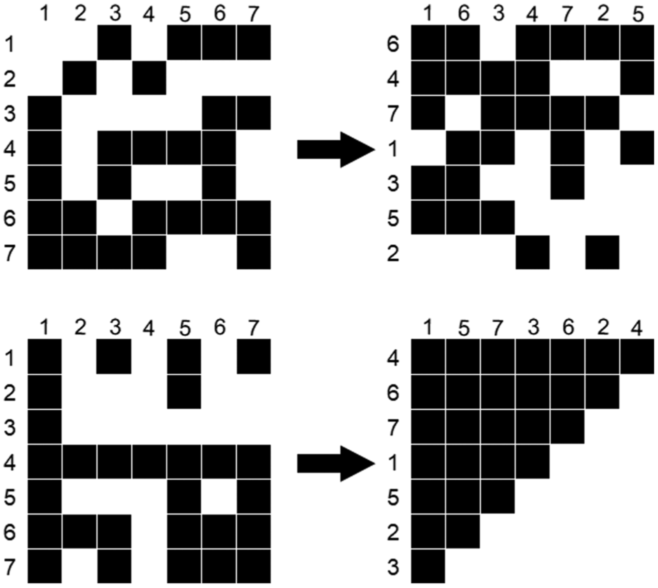


Figure 1. Left column: two hypothetical sets of seven moult cards, each of seven feathers. In both sets, 28 feathers were replaced (black squares). Every row corresponds to the moult card of one individual bird. Right column: same data presented in descending order of both replaced feathers (i.e. moult extent) and number of birds replacing each feather (i.e. frequency of replacement). The top set does not show nestedness, whereas the bottom set shows a perfect nestedness. Nestedness implies that birds moulting fewer feathers always replace a subset of the feathers moulted by birds showing larger moult extents. Note that moult cards in the bottom set could result from a shared strategy of moult whereby birds show a decreasing preference of moult for feathers 1, 5, 7, 3, 6, 2 and 4. Thus, feather one has the highest priority, being replaced when no other feather is replaced. On the other hand, feather four has the lowest priority, being only replaced if and only if all other feathers are also replaced.

Here, we first tested whether passerines share a unique feather-moult priority list. Nevertheless, current knowledge on wing-feather moult phenotypes suggests the potential existence of different ways of moulting. Thus, it has been proposed that wing-feather moult phenotypes reflect the diversification of plumage moult requirements among species and between preformative and prealternate moult episodes (Guallar and Jovani 2020a). The underlying mechanisms of moult control may vary between moult episodes to allow this diversification, ultimately producing different priority lists. Accordingly, we tested the hypothesis that moult episodes present different wing-feather moult ranks. This hypothesis predicts a decrease in overall nestedness when phenotypes from different moult episodes are pooled.

Given that we found a strong nestedness in our moult dataset, we further studied why some feathers had a higher moult priority than others (i.e. why some feathers are replaced during a given moult episode even when only some few feathers are replaced). Several factors may influence order among wing feathers in a moult priority list. We hypothesise that this order is the result of a trade-off between the costs and benefits associated with moulting each wing feather. To cast some light on the causes that influence the position of each wing feather in the moult priority list defined in our moult dataset, we investigated three feather traits that may potentially influence it:

1) Mass. The energy required to synthesize a feather is proportional to its mass Lindström et al. (1993). Therefore,

the heavier is a feather the higher the cost to replace it, and hence (all else being equal) its probability of replacement should be lower.

2) Exposure. Wing feathers do not endure a uniform degradation, some are more exposed to mechanical abrasion and solar radiation than others are (e.g. secondaries are nearly hidden in the folded wing; Bergman 1982, Flinks and Salewski 2012). Assuming that more exposed feathers wear off faster, the more exposed the feather the higher the benefit to replace it, and hence (all else being equal) its probability of replacement should be higher.
3) Contribution to flight. Passerines have wings with low aspect ratios adapted to flapping flight. Thrust and lift are provided by the remiges (particularly by the 10 primaries, which are longer than the six secondaries; Dvořák 2016), with a smaller contribution by three tertials and three alula feathers (Møller 1991, Lee et al. 2015). Coverts largely contribute to reduce drag, but also contribute to lift by creating camber (Shyy et al. 2013). Replacement of wing feathers imposes an aerodynamic loss along with an increase of predation risk during the period of active moult (Slagsvold and Dale 1996), which might be greater in unexperienced individuals (Martin et al. 2018). However, this is an ambivalent factor because fresh feathers would allow greater flight efficiency once moult is finished. Thus, feathers with larger contribution to flight would imply a higher replacement cost during the moulting period, but higher benefits afterwards, making difficult to predict the overall fitness outcome.

In summary, the goals of this study were threefold: to test for the nested nature of passerine wing-feather moult phenotype variation, to test whether passerine wing-feather moult phenotypes are the result of more than one moult rank of wing feathers after grouping by moult episode, and to investigate the role of wing-feather mass, exposure, and contribution to flight on moult priority rank across moult episodes.

Material and methods

More detailed methods can be found in the Supplementary information.

Data

Moult

We used 3909 moult cards from our recently published dataset (Guallar and Jovani 2020b). Of these, 3455 belonged to the preformative episode and 454 to the prealternate episode from 434 passerine species (279 Holarctic and 155 Neotropical). Moult cards, which are the formal procedure to record moult phenotypes, contained moult state (1 replaced, 0 retained) for each of the larger 50 upper wing feathers (8 median coverts, 10 greater coverts, one carpal covert, nine primary coverts, three alula feathers, three tertials, six secondaries, 10 primaries; Supplementary information). Lesser wing coverts were collectively scored 1 when more than 70% of these feathers were replaced and 0 otherwise. Thus, moult extent ranged from 1 to 51.

Mass

We weighted the feathers of one wing from 86 birds belonging to 43 Palearctic passerine species (range = 1–13, mean = 2.0 individuals per species). We calculated mean feather mass for each feather of every species, so that each species had the same weight on the final calculation. We averaged feather masses across species, and normalised values dividing by the mass of the heaviest feather.

Exposure

Exposure deals with abrasion produced by direct friction with vegetation, and by direct insolation. It also deals with signalling, since the most exposed feathers are the most visible ones. We used photographs of 62 live birds from 62 Palearctic species. We obtained the number of pixels visible in the picture for each of the upper-wing feathers using an image-processing program (<www.gimp.org>). Next, we normalised every feather by the most exposed one, and obtained a mean value per feather across species. This approach yields the exposure of each feather in relation to the whole folded wing, regardless of the feather portion that is actually exposed. To address this effect, we corrected the normalised feather-exposure values by their corresponding normalised masses obtained previously.

Contribution to flight

As far as we know, the individual wing-feather contribution to thrust, lift and drag has never been quantified. Here, we tentatively propose a hybrid index based on the correlation between mass-corrected length of primaries and bending stiffness, which is an important mechanical feather property to generate thrust (Dawson 2005, de la Hera et al. 2010a, 2020). We expand this approach to secondaries and tertials. Thus, we measured primary length from 196 ringed birds from 29 Palearctic species, and length of secondaries from 29 wings displayed in <https://www.featherbase.info/de/home> from the same 29 species. We averaged individual remex lengths per species and divided each of them by the corresponding average remex mass for that species. We normalised remex index by dividing each of them by the remex with the highest index. Then, we averaged feather values across species. We finally assigned constant values to alula feathers and wing coverts. These feathers are not implied in thrust generation, therefore their contribution to flight cannot be measured in the same scale than remiges. For this reason, we gave them arbitrary low values: 0.01 to wing coverts and lesser alula, 0.03 to medial alula and 0.06 to greater alula.

Analyses

Nestedness

Frequency of moult phenotypes varied enormously, while some were extremely common throughout species and episodes (e.g. complete phenotype), others were very rare. This natural bias is exacerbated by the fact that some species were much more sampled than others. As a compromise to deal with both over and under-representation biases, we first removed 46 anomalous moult phenotypes that did not match any of the nine currently defined moult patterns (Guallar and Jovani 2020a), and then collapsed our dataset discarding all identical moult cards so that we only retained the unique ones. Thus prepared, the input matrix contained wing feathers in columns and 1082 unique moult cards in rows. We computed the nodf metric to estimate degree of nestedness (Almeida-Neto et al. 2008), as implemented in R package *vegan* (Oksanen et al. 2019, <www.r-project.org>). This metric quantifies the overlap of 1's (moulted feathers) from right to left columns and from bottom to top rows of the input matrix, and the marginal totals between all pairs of columns and all pairs of rows. It takes values from 0 to 100, 50 being the value of a pure random pattern, values below 50 indicating anti-nested patterns (e.g. checkerboard patterns; Almeida-Neto et al. 2008), and values close to 100 indicating perfect nestedness. We tested whether the nestedness of the input matrix and of each moult pattern deviated from randomness by randomising the identity of the feathers moulted by each individual, but maintaining the number of moulted feathers (COL null model implemented in ANINHADO; Guimarães and Guimarães 2006).

Moult nestedness would indicate that birds replacing fewer feathers would moult a subset of the feathers replaced by birds moulting more feathers. From a feather viewpoint, this means that there is one (top priority) feather moulted even if no other feather is replaced, while other (low priority) feathers are only moulted if many other feathers (of higher priority) are also replaced. In other words, the most parsimonious rule behind moult nestedness would be the existence of a feather moult priority.

Feather traits

Using R package *randomForest* (Liaw and Wiener 2002), we fitted a random-forest model to test the overall and relative contribution of the three feather traits (mass, exposure and contribution to flight) to explain the frequency of replacement of each wing feather across species, computed as the proportion of moult cards in which each feather was moulted.

In addition, to assess the relevance of feather traits to the wing feather moult priority, we sorted the columns of the input matrix (feathers) for the nestedness analysis in descendant order for each of these variables. As for the frequency of replacement, we ordered moult phenotypes (rows) in descendant order of moult extent. Thus, a feather trait that determined the priority of wing feather moult would show a nestedness value closer to the maximum possible. Note that the maximum nestedness expected when ordering columns according to one feather trait was equal to the nodf obtained sorting the input matrix by frequency of wing-feather replacement (columns) and extent (rows) in descendant order.

We also explored the variation of nestedness among the three influential feather traits between moult episodes to test the consistency of the main results. To carry out these analyses, we selected the 404 unique moult cards assigned to the prealternate moult and 708 assigned to the preformative moult. We discarded other moult episodes due to low sample sizes.

Results

Priority of feather replacement showed a peak on the proximal secondary coverts (i.e. greater, median and lesser coverts), decreasing towards distal secondary coverts and alula (Fig. 2a). On the other hand, remiges showed a centrifugal pattern: priority of replacement increased from the minimum found in the central remiges toward tertials, and primaries that form the wing tip. Primary coverts and central remiges had the lowest frequencies of feather replacement (Fig. 2a).

We found a high nestedness associated with the whole dataset of unique moult phenotypes (Fig. 3). Nestedness of the complete dataset (nodf = 84.31) deviated significantly from randomness (95% CI expected by random: nodf = 58.63–59.68), and was intermediate between the higher nestedness of the preformative moult episode and the lower nestedness of the prealternate ($nodf_{PF} = 90.99$, $nodf_{PA} = 67.28$; Fig. 3). Results were nearly identical when nestedness was calculated for the subset of 72 species with both preformative and prealternate moult cards ($nodf_{PF} = 91.30$, $nodf_{PA} = 66.63$). Nestedness calculated for each moult episode separately deviated from the expected nestedness according to their sample size, i.e. from random subsets with the same number of moult phenotypes taken from the complete dataset (Fig. 4).

Mass showed a gradual decrease from coverts towards the primaries that form the wing tip (Fig. 2b). Exposure peaked on the tertials and primaries that form the wing tip, with a secondary focus on the medial greater coverts (Fig. 2c). Contribution to flight showed a similar pattern to mass, with a somewhat more abrupt decrease (Fig. 2d). Overall, wing-feather mass, exposure and contribution to flight explained together 53.74% of the observed variation in the priority of wing-feather replacement across species. Exposure showed a larger predictive strength to explain priority of wing-feather replacement than the other two traits (Table 1).

Nestedness analyses confirmed these results: we found similar nestedness values when we ordered wing feathers according to each of these three traits ($nodf_{mass} = 79.05$, $nodf_{exposure} = 82.35$, $nodf_{flight} = 73.90$; Table 2). Interestingly, these nestedness values based on ranking feathers according to a single feather trait were not far from the maximum nestedness that could be obtained with this dataset, i.e. after ordering feathers according to their frequency of replacement (nodf = 84.31; Fig. 3). Similar results were found when repeating these analyses by moult episode (Table 2), with the preformative moult showing consistently greater nestedness values than the prealternate moult (Fig. 4).

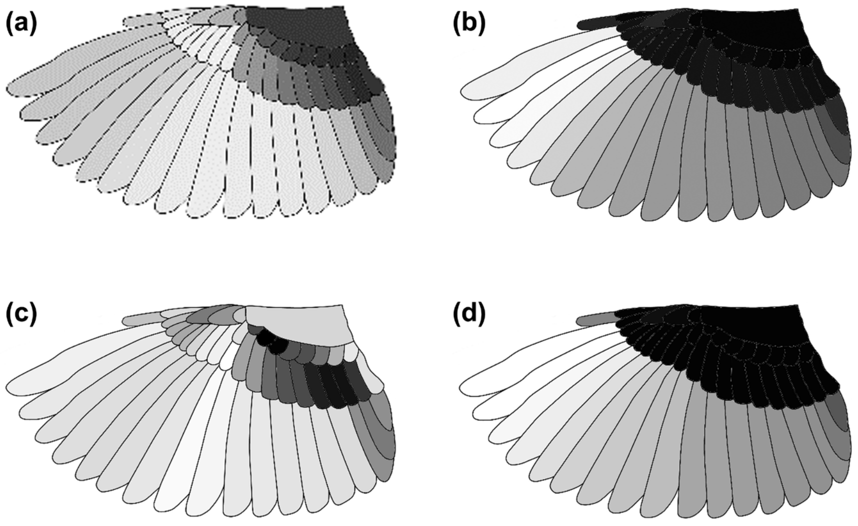


Figure 2. Predicted probabilities of replacement of each wing feather according to four factors. (a) Priority of wing feather replacement for 1082 unique passerine moult cards. (b) Priority of wing feather replacement based on the normalised mass obtained from 86 birds (43 species). (c) Priority of wing feather replacement based on the normalised wing feather exposure obtained from 62 birds (62 species). (d) Priority of wing feather replacement based on the normalised wing feather contribution to flight obtained from 196 birds (29 species); here, we considered that priority of replacement was proportional to the cost during the moulting period not to the benefits gained after this period. Percentage shades vary from white (0%) to black (100%). See Material and methods for details.

Discussion

Even before wing-feather replacement diagrams became popular in bird moult research, it was implicitly assumed a strong relationship between moult extent and the increasing probability of replacement of a given wing feather (Richter 1972, Jenni and Winkler 1994, Gargallo et al. 2009). However, even studies that mentioned the existence of such moult rule have been always restricted to within-moult episodes and individual species (Jenni and Winkler 1994, Gargallo 2013). Here, we explicitly tested for the first time the hypothesis that passerines moult their wing feathers following a defined rank, concretely, the existence of a nested arrangement of moulted wing feathers across 3909 moult cards from 434 passerine species.

We did find such a nested relationship among passerine moult phenotypes: birds moulting fewer feathers replaced a subset of the feathers moulted by birds with larger wing-moult extents. The high nestedness we found is remarkable given that we analysed a large and diverse dataset (nodf = 84.31). However, we also found many imperfections graphically detected as black cells below the diagonal and white cells above the diagonal (Fig. 1, 3, Supplementary information). Deviations from perfect nestedness (especially in the prealternate moult; nodf = 67.28) further suggested that either a mixture of different lists of moult priorities or a combination of these rank-based lists with other rules of moult control can be at play. The European pied flycatcher *Ficedula hypoleuca* may be a good example to illustrate this because it undergoes contrasting partial preformative and prealternate moult episodes. The preformative moult includes all lesser coverts, and usually all median coverts and 1–3 inner greater coverts; on the other hand, the prealternate moult includes few lesser and 4–5 inner median coverts, usually 5–7 inner greater coverts, all tertials, and usually 1–2 inner secondaries (Jenni and Winkler 1994). The nestedness of both episodes are high: $\text{nodf}_{PF} = 82.34$ (n = 12), $\text{nodf}_{PA} = 84.18$ (n = 48). However, the nestedness for both episodes together is lower (nodf = 71.72). This reduction is expected when lumping two moult ranks of wing feathers (Supplementary information), and strongly suggests a link between seasonal diversification of plumage requirements and priority of feather moult. Insightfully, the prealternate moult of the European pied flycatcher includes the wing feathers with white marks (de la Hera et al. 2013).

The existence of rank lists controlling wing-feather moult immediately arises the question about their biological meaning, and particularly whether it has an adaptive basis. Moult may be strongly driven by phylogenetic history, since dinosaurian ancestors of birds already showed sequential feather replacement 50 million years ago (Kiat et al. 2020). Analogously, shared phylogenetic history may have played a decisive role on phenotypic diversity. Thus, both the preformative and the prealternate moults show a large phylogenetic signal (Guallar and Jovani 2020a), with many ecological factors explaining a small proportion of the observed variation (Delhey et al. 2021), while important evolutionary transitions such as habitat shifts likely explaining adaptive changes in moult (Guallar et al. 2021). This evolutionary balance likely requires the interaction of multiple factors, both adaptive and non-adaptive. Thus, wing-feather mass, exposure and contribution to flight explained around 54% of the observed variation in the priority of feather moult, suggesting the adaptive value of feather moult priority lists. While the greater prediction power of exposure provides an interesting

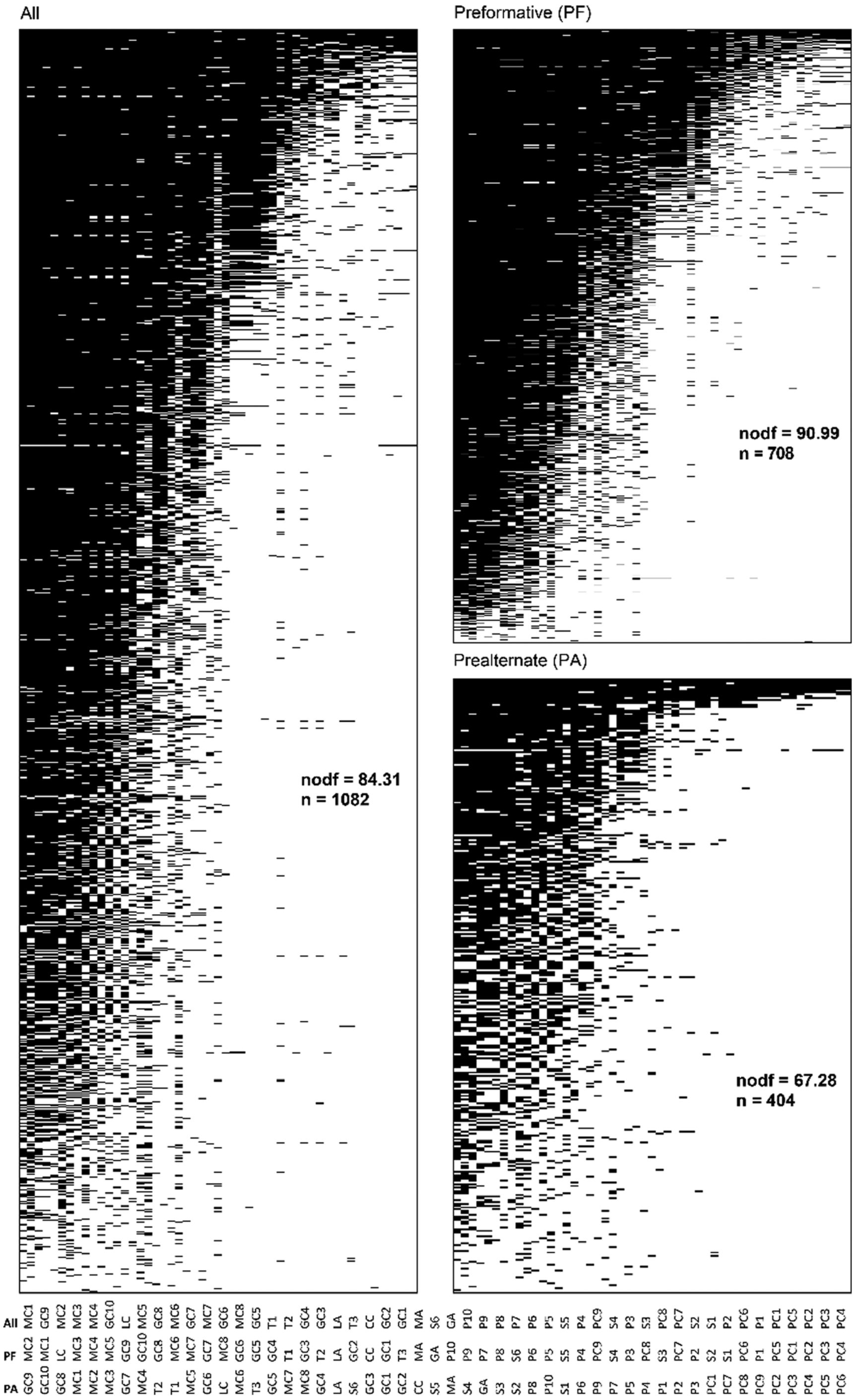


Figure 3. Nestedness plots for the overall dataset and for the two moult episodes separately. Unique wing-moult phenotypes are shown in rows and feathers in columns. Each dash indicates the replacement of a given feather. The matrix is ordered to maximise nestedness: phenotypes are ordered by moult extent and feathers by frequency of replacement across moult phenotypes. For illustrative purposes, feather moult ranks (i.e. feather identity on the x-axis of each panel) are shown on the bottom. Notice that total sample size is smaller than the sum of sample sizes per episode because some unique wing-moult phenotypes are shared by both episodes.

insight, the fact that 46% of the observed variation remained unexplained indicates that other factors have also driven the evolution of moult priority lists. One such factor could be the adaptive differential investment in feather tracts during the nestling and fledging periods (Pap et al. 2007, de la Hera et al. 2010b).

Our study provides a conceptually (and quantitative) solid model of moult control that can be used to contrast empirical

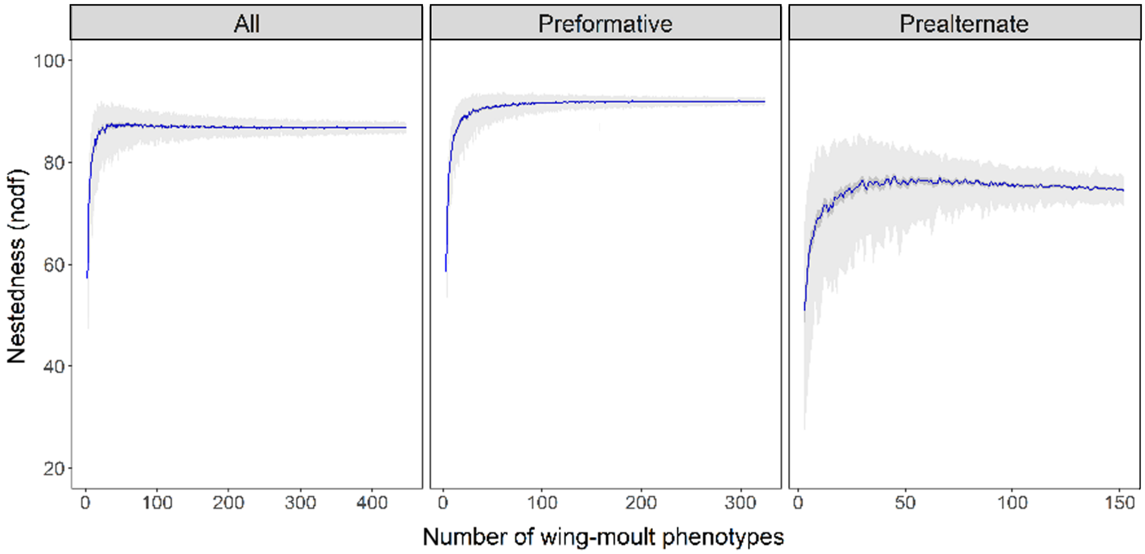


Figure 4. Variation of the expected nestedness for unique moult phenotypes. Blue lines show the bootstrapped mean nestedness obtained from random resamples (i.e. extraction of different number of random rows from Fig. 3); dark grey areas show the 95% bootstrapped interval of the mean; light grey areas show 95% bootstrapped interval of 500 random resamples. Notice that uncertainty on the measure of prealternate nestedness was higher than uncertainty of preformative nestedness. Interestingly, mean nestedness decreased with increasing number of moult phenotypes. This effect is very slight in the preformative moult (peak nodf = 92.10, total nodf = 90.99), but more apparent in the prealternate moult (peak nodf = 77.38, total nodf = 67.28). Mean and bootstrapped intervals estimated using the R library *bayesboot* (Bååth 2016).

moult data. Overall, our results strongly suggest the existence of rank lists underlying the control of passerine wing-feather moult, while deviations from perfect nestedness suggest that other rules of moult control might be in operation and/or the existence of different moult priority lists within moult episodes (Supplementary information). We further suggest that nestedness is the physiological system of moult control evolutionarily conserved in the order Passeriformes given their anatomical constraints and the central role that moult plays in their natural history. Moreover, the imperfections that we found may have arisen as a consequence of the diversification of plumage requirements across passerine species and moult episodes, which might have generated new feather moult priorities and even new mechanisms of moult control along their evolution.

Our approach, borrowed from the study of ecological systems, is adequate to the study of moult phenotypes because it relates moult extent and feather identity (which feathers are actually replaced), thus allowing to establish a relationship among feathers as moult extent increases and providing insight into the underlying rules of moult control. More classical approaches, such as the use of moult patterns allow to categorise the variation of moult phenotypes and also suggest the existence of heterogeneity in the moult process (Supplementary information), although they do not inform about the intrinsic relationships among moult phenotypes. Future studies on this topic should enlarge the number of species sampled (this study comprises around 7% of the approximately 6000 extant passerine species), use new and improved metrics to tackle the influence of plumage functions (including those not treated here, such as thermoregulation or signalling). Future research would also benefit from adding more plumage traits (e.g. feather area, pigmentation), and exploring alternative rules of control not based on lists of priorities.

Table 1. Feature importance obtained from a random forest analysis of wing-feather mass, exposure and contribution to flight on the frequency of wing-feather replacement observed in a dataset of 1082 unique moult phenotypes from preformative and prealternate moults. The method is based on the permutation importance method (Strobl et al. 2008, Breiman and Cutler 2019). Importance values do not sum up to one, the essential is the relative predictive strengths of the features.

Feather trait	Importance
Exposure	0.0458
Contribution to flight	0.0277
Mass	0.0256

Acknowledgements – Marina Moreno, Walo Moreno and Laura Gangoso for collecting wings. Constructive comments by two

Table 2. Nestedness for the whole dataset and separately for the preformative and prealternate moult episodes after ordering feathers according to three feather traits.

Feather trait	All	Preformative	Prealternate
Exposure	82.35	88.65	62.64
Mass	79.04	86.02	58.32
Contribution to flight	73.89	83.22	54.14

anonymous referees and Javier Pérez-Tris considerably improved this study.

Authors' contributions

Santiago Guallar: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Resources (lead); Software (lead); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Roger Jovani**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Methodology (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Conflicts of interest – The authors declare that they have no conflicts of interest.

Permits – Permits were granted by the Spanish regional administration Consejería de Medio Ambiente, Caza y Patrimonio, Cabildo de Lanzarote (permit ES-000687/2015), and Departament de Territori i Sostenibilitat. Generalitat de Catalunya (permit SF/0229/2019).

Transparent Peer Review

The peer review history for this article is available at https://publons.com/publon/10.1111/jav.02553

Data availability statement

Data available from the Figshare at: <https://dx.doi.org/10.6084/m9.figshare.12782153.v1> (Guallar and Jovani 2020c).

References

Almeida-Neto, M., Guimarães, P., Guimarães Jr, P. R., Loyola, R. D. and Ulrich, W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. – Oikos 117: 1227–1239.

Bååth, R. 2016. bayesboot: an implementation of Rubin's (1981) Bayesian bootstrap. R package ver. 0.2.1. – <https://CRAN.R-project.org/package=bayesboot>

Bergman, G. 1982. Why are the wings of *Larus f. fuscus* so dark? – Ornis Fennica 59: 77–83.

Breiman, L. and Cutler., A. 2019. Random forests – classification manual. – <http://www.math.usu.edu/~adele/forests/>

Dawson, A. 2005. The scaling of primary flight feather length and mass in relation to wing shape, function and habitat primary flight feather length and mass. – Ibis 147: 283–292.

de la Hera, I., Hedenström, A., Pérez-Tris, J. and Tellería, J. L. 2010a. Variation and mechanical properties of feathers of blackcap *Sylvia atricapilla* in relation to migration. – J. Avian Biol. 41: 342–347.

de la Hera, I., Pérez-Tris, J. and Tellería, J. L. 2010b. Migratory behavior and differential resource allocation between wing and tail feathers in a passerine bird. – Auk 127: 647–652.

de la Hera, J., Reed, T. E., Pulido, F. and Visser, M. E. 2013. Feather mass and winter moult extent are heritable but not associated with fitness-related traits in a long-distance migratory bird. – Evol. Ecol. 27: 1199–1216.

de la Hera, I., Hernández-Téllez, I., Pérez-Rigueiro, P., Pérez-Tris, J., Rojo, F. J. and Tellería, J. L. 2020. Mechanical and structural adaptations to migration in the flight feathers of a Palaearctic passerine. – J. Evol. Biol. 33: 979–989.

Delhey, K., Guallar, S., Rueda-Hernández, R., Valcu, M., Wang, D. and Kempenaers, B. 2021. Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. – J. Anim. Ecol. 90: <http://dx.doi.org/10.1111/1365-2656.13354>.

Dvořák, R. 2016. Aerodynamics of bird flight. – EPJ Web of Conferences 114: 01001.

Flinks, H. and Salewski, V. 2012. Quantifying the effect of feather abrasion on wing and tail lengths measurements. – J. Ornithol. 153: 1053–1065.

Gargallo, G. 2013. Feather selection and replacement patterns demonstrate that goldfinches *Carduelis carduelis* fix postjuvenile moult extent prior to moult initiation. – J. Ornithol. 154: 219–230.

Guallar, S. and Jovani, R. 2020a. Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. – Ibis 162: 778–786.

Guallar, S. and Jovani, R. 2020b. Data from: Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. – Figshare, <http://dx.doi.org/10.6084/m9.figshare.9896516>.

Guallar, S. and Jovani, R. 2020c. Data from: Moult nestedness and its imperfections: insights to unravel the nature of passerine wing-feather moult rules. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.k6djh9w42>.

Guallar, S., Rueda-Hernández, R. and Pyle, P. 2021. Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. – Ornithology 138: in press.

Guallar, S., Santana, E., Contreras, S., Verdugo, H. and Gallés, A. 2009. Paseriformes del Occidente de México: morfometría, datación y sexado. – Museu de Ciències Naturals de Barcelona.

Guimarães, P. R. and Guimarães, P. 2006. Improving the analyses of nestedness for large sets of matrices. – Environ. Model. Softw. 21: 1512–1513.

Howell, S. N. G., Corben, C., Pyle, P. and Rogers, D. I. 2003. The first basic problem: a review of molt and plumage homologies. – Condor 105: 635–653.

Humphrey, P. S. and Parkes, K. C. 1959. An approach to the study of molt and plumages. – Auk 76: 1–31.

Jenni, L. and Winkler, R. 1994. Moult and ageing of European passerines. – Academic Press.

Kiat, Y., Balaban, A., Sapir, N., O'Connor, J. K., Wang, M. and Xu, X. 2020. Sequential molt in a feathered dinosaur and implications for early paravian ecology and locomotion. – Curr. Biol. 30: 1–6.

Lee, S-I., Kim, J., Park, H., Jabłoński, P. G. and Choi, H. 2015. The function of the alula in avian flight. – Sci. Rep. 5: 9914.

Liaw, A. and Wiener, M. 2002. Classification and regression by randomForest. – R News 2: 18–22.

Lindström, A., Visser, G. H. and Daan, S. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. – Phys. Zool. 66: 490–510.

Martin, T. E., Tobalske, B., Riordan, M. M., Case, S. B. and Dial, K. P. 2018. Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. – Sci. Adv. 4: eaar1988.

Møller, A. P. 1991. Influence of wing and tail morphology on the duration of song flight in skylarks. – Behav. Ecol. Sociobiol. 28: 309–314.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. and Wagner, H. 2019. Vegan: community ecology package. R package ver. 2.5-6. – <http://cran.us.r-project.org>.

Pap, L., Barta, Z., Tökölyi, J. and Vágási, C. I. 2007. Increase of feather quality during moult: a possible implication of feather deformities in the evolution of partial moult in the great tit *Parus major*. – J. Avian Biol. 38: 471–478.

Richter, A. 1972. Zum umfang der jugendmauser am flügel der amsel *Turdus merula*. – Ornithol. Beob. 69: 1–16.

Shyy, W., Aono, H., Kang, C-K. and Liu, H. 2013. An introduction to flapping wing aerodynamics. – Cambridge Univ. Press.

Slagsvold, T. and Dale, S. 1996. Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced molt. – Ecology 77: 462–471.

Strobl, C., Boulesteix, A., Kneib, T., Augustin, T. and Zeileis, A. 2008. Conditional variable importance for random forests. – BMC Bioinform. 9: 307.

Chapter 4 contains the article first published on 5 February 2016 **Guallar S, Figuerola J 2016. Factors influencing the evolution of moult in the non-breeding season: insights from the family Motacillidae.** ***Biol. J. Linn Soc.*** **116: 774–785. https://doi.org/10.1111/bij.12784**

The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2016, **118**, 774–785. With 3 figures.

Factors influencing the evolution of moult in the non-breeding season: insights from the family Motacillidae

SANTIAGO GUALLAR[1]* and JORDI FIGUEROLA[2]

[1]*Galanthus, Carretera de Juià, 46, Celrà, Girona, 17460, Spain*
[2]*Department of Wetland Ecology, Estación Biológica de Doñana, CSIC, Avda. Américo Vespucio, s/n, 41092, Sevilla, Spain*

Received 19 October 2015; revised 9 December 2015; accepted for publication 9 December 2015

The number of moults per annual cycle and their final spatial pattern (i.e. topography) show high interspecific variation in the order Passeriformes. Factors behind this variability remain obscure, especially for variability in spatial pattern among species. Here, we explored the relative influence of ten ecological, ontogenetic, social and sexual factors on the evolution of autumn moult (feather replacement largely undertaken by migratory species, which is not necessarily an independent episode within their moult cycle) and prealternate moult among Northern Hemisphere species of the family Motacillidae using phylogenetically controlled analyses, ancestral state reconstruction and analyses of correlated evolution. The results strongly support the presence of prealternate moult and absence of autumn moult as ancestral states in this family. A high rate of change between related species indicates phylogenetic independence among prealternate moult patterns and examined factors. Migration distance and gregariousness are the most important factors influencing prealternate moult evolution, and point toward natural selection and sociality as the most important evolutionary drivers of prealternate moult in Motacillidae. Breeding latitude, seasonal plumage change, winter plumage conspicuousness, sexual dichromatism, plumage maturation and extent of preformative moult show a minor influence, and suggest that ontogeny and sexual selection may have played a limited role in shaping prealternate moult in Motacillidae. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **118**, 774–785.

KEYWORDS: autumn moult – gregariousness – moult strategies – moult topography – pipits – prealternate moult – wagtails.

INTRODUCTION

Moult is the process that allows the maintenance and adjustment of plumage functionality throughout the annual cycle (Jenni & Winkler, 1994). A high amount of variability in moult strategy within and among species (Svensson, 1992; Pyle, 1997a, b) is achieved through many elements that integrate a species' moult strategy (Barta *et al.*, 2006): topography (the spatial configuration of the replaced feathers after a moult; Gualllar *et al.*, 2014), energetic requirements, feather quality, number and timing of moults per cycle, intensity, duration and order of replacement. Moult strategies may affect survival and fitness (Holmgren & Hedenström, 1995), and have probably evolved in response to shifts in natural history and environmental parameters (Rohwer *et al.*, 2009; Pap *et al.*, 2015).

Until now, most studies have emphasized the evolution of the preformative and definitive prebasic moults (equated to the postjuvenile and postnuptial moults, respectively; terminology follows Howell *et al.*, 2003), while other moults have received less attention. The presence of a single moult within the annual cycle, the prebasic moult, is the ancestral state in passerines, and the addition of the prealternate moult (equivalent to the prenuptial moult) is considered an autapomorphy with multiple independent evolutionary origins (Figuerola & Jovani, 2001; Howell *et al.*, 2003). The prealternate moult is largely undertaken by migratory species before departing their wintering grounds. However, the existence of other moult episodes is controversial. In particular, the replacement of feathers upon arrival at the winter grounds – usually in early autumn – is rarely

---

*Corresponding author. E-mail: sguallar@yahoo.com acknowledged as an independent episode (Howell *et al.*, 2003; Newton, 2008: 305–306). Autumn feather replacement of migratory passerines has been routinely reported in their winter grounds (Shirihai, Helbig & Gargallo, 2001; Alström & Mild, 2003; Guallar *et al.*, 2009), but it usually involves only body feathers, suggesting the end of a previous 'true' moult episode, suspended or not (birds may migrate while still replacing part of their body plumage, even the juvenal one, which may affect aerodynamics; Butler, Donahue & Rohwer, 2002). Some migratory species are known to suspend their prebasic/preformative moult until they finish migration (e.g. Alström & Mild, 2003), although some clearly have an autumn moult episode (e.g. *Passerina* buntings and Bell's Vireo *Vireo bellii*; Guallar *et al.*, 2009). Regardless, autumn moulting may constitute an individual- or species-level strategy to cope with tight complex annual cycles (Wingfield, 2008). Besides taking place outside the breeding grounds, prealternate and autumn moults neither overlap in time nor interact directly with reproduction. For these reasons, we categorize them as 'non-breeding moults'. Migration is a strong selective factor that influences the evolution of non-breeding moult strategies (Svensson & Hedenström, 1999; Figuerola & Jovani, 2001), but other factors may also affect the timing and duration of moult. For example, depletion of food resources and presence of predators may affect the schedule of primary moult (Voelker & Rohwer, 1998; Rohwer, Butler & Froehlich, 2005; Ydenberg, Butler & Lank, 2007), and moult duration is related to wing size (Bridge *et al.*, 2007; Rohwer *et al.*, 2009).

Evolution of moult may have not only been affected by natural selection, but also by sexual selection (Simpson & Campbell, 2013). Birds use different plumage characteristics for mate choice (Zahavi, 1997), and the emergence of the prealternate moult in a species annual cycle could have been targeted by sexual selection to produce a brighter plumage during the mating season (Figuerola & Jovani, 2001; Peters, 2007). The extent of the preformative moult may also serve as an indicator of health status (Senar, Copete & Martin, 1998; López *et al.*, 2005).

For these reasons, natural and sexual selection appear to be drivers of moult evolution. Here, we use phylogenetically controlled comparative analyses to evaluate the relative influence of different ecological, social and sexual factors on the evolution of non-breeding moult among species of the family Motacillidae, which has a well-documented and highly diverse natural history (Cramp, 1988; Alström & Mild, 2003). We focused on the 25 of the 31 species of this family breeding in the Northern Hemisphere with published descriptions of non-breeding moult.

We test six hypotheses on the potential factors mentioned above. First, migratory behaviour may have favoured the evolution of non-breeding moults. If this is the case we can expect more extensive non-breeding moults as migratory distance increases. This hypothesis has already received support from previous studies analysing the number, seasonality and extent of moult in some European passerines (Svensson & Hedenström, 1999; Figuerola & Jovani, 2001) although it has not been tested for the autumn moult. One mechanism proposed to explain this effect is a reduction in feather quality induced by time constraints (de la Hera, Pérez-Tris & Tellería, 2009) arising from ever tighter moult schedules, so that birds have less time available to grow high-quality feathers (Hall & Fransson, 2000; Dawson, 2004). Species under strong time constraints before departing the breeding grounds tend to present more moult episodes and more extensive ones than those that do not face time constraints (Holmgren & Hedenström, 1995). Exposure to increased solar radiation in winter grounds as migration distance increases is also thought to explain this effect (Bergman, 1982; Figuerola & Jovani, 2001).

Latitude may have influenced the evolution of non-breeding moult episodes as well. This second hypothesis suggests that time for moult is constrained by climatic conditions at northern latitudes (Dawson, 2008). According to this hypothesis, species breeding at higher latitudes may experience increasing time constraints and may grow lower quality feathers (Hall & Fransson, 2000; Kiat & Izhaki, 2016) which they would tend to renew as soon as possible after departing the breeding grounds. Consequently, autumn moult will be more frequent and also will tend to be more extensive in these species. Extreme time constraints before migration would tend to cause very reduced prebasic or preformative moults (Barta *et al.*, 2006). However, sexual selection would not exert pressure on this moult in Motacillidae, as autumn moult in species of this family does not involve changes in coloration, and autumn plumage is overridden by the prealternate moult before the onset of the breeding season.

The third hypothesis states that the prealternate moult may have evolved to allow plumage coloration changes. Seasonal changes can be achieved through wear (e.g. in Common Reed Bunting *Emberiza schoeniclus*; Cramp & Perrins, 1994) and photo-oxidation (e.g. in Common Linnet *Carduelis cannabina*; Blanco *et al.*, 2005), but most species achieve them through moult. The prealternate moult may become more extensive to allow larger plumage changes. The same effect could be found in conspicuous species to allow the acquisition of brighter alternate plumages. Note that seasonal changes in plumage coloration are not necessarily associated with sexual dichromatism (e.g. Water Pipit *Anthus spinoletta*).

The fourth hypothesis posits that the evolution of prealternate moults may have been driven by sexual selection. Moult is an energetically costly process (Murphy, 1996), and as such may honestly signal physical condition; therefore, individuals with more extensive prealternate moult may have an advantage as potential breeding mates. Sexual selection also predicts more extensive prealternate moult as sexual dichromatism becomes greater: species with sexual marks restricted to an area of the body – such as the eyebrow of Blue-gray Gnatcatcher *Polioptila caerulea* (Guallar *et al.*, 2009) – would tend to replace fewer feathers than species with overall dichromatic plumage such as Summer Tanager *Piranga rubra* (Pyle, 1997a, b). Here, we test the second prediction of this hypothesis: the influence of dichromatism on moult evolution.

The fifth hypothesis posits that social selection may have influenced the evolution of non-breeding moults through the acquisition of new functions such as status signalling. Gregarious species display badges of status (Tibbets & Safran, 2009; Chaine *et al.*, 2013) and their signal phenotype probably expresses other aspects of their social environment (Dey, Dale & Quinn, 2014), which can be mediated through non-breeding moults. This hypothesis predicts more extensive non-breeding moults in more gregarious species (probably associated with higher social complexity).

Finally, the sixth hypothesis posits that ontogenetic factors may have contributed to shaping non-breeding moults. Plumage maturation is delayed in first-cycle individuals of many species until the prealternate moult (Rohwer, Fretwell & Niles, 1980; Hill, 1996). This delay may have selected for a more extensive first prealternate moult in order to acquire an alternate plumage as similar to the definitive alternate plumage as possible. Partial preformative moults could have influenced non-breeding moult evolution, as plumage gaps should be filled and formative feathers of potentially lower quality (Butler, Rohwer & Speidel, 2008; Echeverry-Galvis & Hau, 2013) are replaced as soon as possible.

MATERIAL AND METHODS

DATASET AND PHYLOGENETIC RELATIONSHIPS

We obtained information on moult strategies, plumage characteristics, gregariousness, habitat occurrence and latitudinal distribution of Motacillidae of the Northern Hemisphere from Alström & Mild (2003; see Supporting information, Table S1, Data S1). When intraspecific variation in the variable of interest exists, we discarded infrequent values and calculated the arithmetic mean of the remaining ones. We completed gaps on gregariousness using information from Étchecopar & Hüe (1983) and Ali & Ripley (1993).

We visually scored dichromatism, conspicuousness and seasonal plumage change for each species using illustrations in Alström & Mild (2003). To reduce subjectivity, we averaged the scores of three observers for each of these variables.

We included body mass as a surrogate of size (data from Dunning, 2007). Because no information on body mass of the recently described Mekong Wagtail *Motacilla samveasnae* is available, we took it as the mean of White Wagtail *Motacilla alba* and African Pied Wagtail *Motacilla aguimp*, due to the similarity to these two species (see Diagnosis in Duckworth *et al.*, 2001).

Species range maps were downloaded from BirdLife International and NatureServe (2014). Migration distance was computed as the kilometres between the centroid of the wintering range and the centroid of the breeding range using QGIS (QGIS Development Team, 2015). Centroids were weighted by the area of polygons. Latitudinal distances between the breeding and wintering centroids were calculated using Geographic Distance Matrix Generator (Ersts, 2015).

We created four categories of mass and breeding latitude from the computation of three quartiles on our dataset (Supporting information, Table S1). Likewise, we created three categories of migration distance by computing two quartiles for migratory species and added a fourth category for non-migrant species. The purpose of using the same scale for all covariates was to allow direct comparisons among the model estimates.

For our working phylogeny we downloaded 10 000 trees for our set of species from birdtree.org (Jetz *et al.*, 2012), and then derived a consensus tree, assigned all internode branches equal to 1 and forced tips to be contemporaneous (Pagel, 1992). We used Slate-throated Redstart *Myioborus miniatus* as the outgroup (data from Guallar *et al.*, 2009).

To check sensitivity to phylogeny, we replicated all our analyses using published phylogenetic trees for this family (Voelker, 1999; Alström & Ödeen, 2002). As results only show minor differences, we included our replicates in the Supporting Information (Figs S4, S5, Table S5).

INFLUENCE OF NATURAL HISTORY FACTORS

To control for the phylogenetic relationship among the sampled species we used phylogenetic generalized least squares regression (PGLS; Pagel, 1997,

1999) models as implemented in the R statistical environment (The R Foundation for Statistical Computing, 2015) and the libraries ape, geiger and nlme. The PGLS approach controls for non-independence among species by incorporating a matrix of the covariances based on their phylogenetic relationships (Martins & Hansen, 1997; Pagel, 1997, 1999).

We estimated the phylogenetic signal (λ) using the unpublished function pglm3.3.r (R. Freckleton, University of Sheffield). The phylogenetic signal represents the importance of phylogenetic correlation within the data (Freckleton, Harvey & Pagel, 2002) and varies between 0 and 1. We then tested the statistical significance of λ against theoretical values of 0 and 1 using likelihood ratio tests. Finally, λ was incorporated in the correlation structure of the PGLS models to control for the effect of phylogenetic relationship (Harvey & Pagel, 1991; Martins & Hansen, 1997).

We first explored the relative importance of nine covariates on the prealternate and the autumn moults in two sets of PGLS models: migratory strategy, mean breeding latitude, seasonal plumage coloration change (only in prealternate models as autumn moult are not associated with changes in plumage coloration), male basic plumage conspicuousness, sexual dichromatism in alternate plumage, gregariousness in the non-breeding season, non-breeding moult pattern (autumn on models with prealternate moult as response and vice versa), habitat and body mass (Supporting information, Table S1). Each set of models contains all combinations among the covariates (2048 models for the prealternate moult as response, and 512 models for the autumn moult as response).

We also investigated the possible influence of ontogeny on prealternate and autumn moults by including two age-specific covariates, plumage maturation and preformative moult, in two new sets of models. Again, each of these two sets of PGLS models contains all possible combinations among the covariates.

We ranked the models according to their Akaike information criterion corrected for small sample size (AICc) values, and calculated the relative importance of each covariate based on its Akaike weight using the zero method implemented in package MuMIn. In the zero method (Burnham & Anderson, 2002), all covariates absent from models are substituted by zeros, and estimates are obtained by averaging over all models in the top model set (Grueber *et al.*, 2011). This method is recommended in studies aiming at determining which factors have the strongest effect on the response variable (Nakagawa & Freckleton, 2011). As we standardized our covariates, we assessed their relative magnitude and direction directly. Each estimated coefficient in the average model equates to effect size of its corresponding covariate (Grueber *et al.*, 2011). We expressed parameter uncertainty by means of the estimated standard error (Burnham & Anderson, 2002), and model uncertainty as the percentage of models used to create the 95% confidence sets of models (McAlpine *et al.*, 2008).

We compared migration distance and breeding latitude among species with or without non-breeding moults, using phylogenetic ANOVA (Garland *et al.*, 1993) using the phytools package.

ANCESTRAL STATE RECONSTRUCTION AND CORRELATED EVOLUTION

We first tested for differences in transition rates between states using default settings in BayesTraits (Pagel, 1999; Pagel, Meade & Barker, 2004). The significant differences between transition rates were incorporated in subsequent analyses. Next, we checked whether the evolution of non-breeding moult was directional. Model selection was based on Bayes factors (BFs) (Kass & Raftery, 1995) .

We reconstructed the ancestral state of non-breeding moults in our replicate phylogeny (Supporting information, Fig. S1) calculating state likelihoods at each node to determine final maximum likelihood of the ancestral state (Schluter *et al.*, 1997). We dealt with the polytomy by averaging the values of the involved species (all absences for the autumn moult, two presences and two absences for the prealternate moult).

Reliable statistical inference could not be drawn for the autumn moult because of the low number of species that present it ($N = 7$). Nevertheless, we show the output of correlated evolution and relative importance analyses for this moult in the Supporting Information (Data S1).

RESULTS

Phenology of non-breeding moults in Motacillidae of the Northern Hemisphere is synthesized in Figure 1. Only four species (16%) do not show non-breeding moults, all of which are non-migratory except the Japanese Wagtail *Motacilla grandis* (a short-distance migrant). The remaining species undergo either prealternate moult or autumn plus prealternate moults (only seven species show autumn moult, 28%). There were no species that underwent only autumn moult. Alström & Mild (2003) state that in species with two non-breeding moults the same feathers are replaced in both episodes.

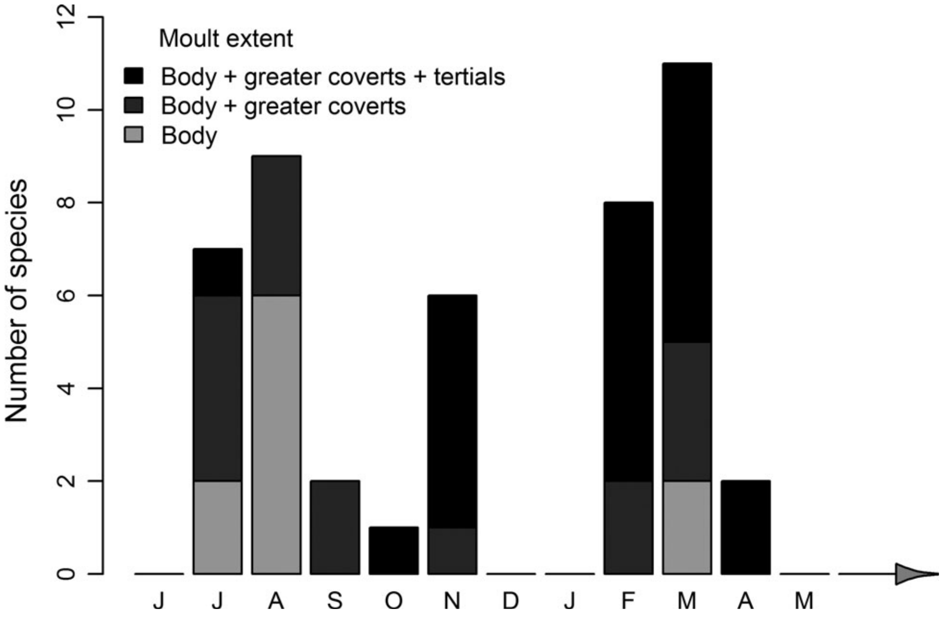


Figure 1. Annual moult cycle of Northern Hemisphere Motacillidae (prebasic moult is not shown). Preformative moult shows the widest range of moult extent values. Autumn moult takes place immediately after migration from the breeding grounds and prealternate moult before migration to the breeding grounds. It is important to bear in mind that autumn moulting could actually be the completion of suspended or protracted prebasic/preformative moults in some cases. Moult extent values were rounded to the nearest integer. Each species' moult was assigned to the second month of the period recorded by Alström & Mild (2003) because this probably coincides with moult peak (highest overlap of individuals and highest moult intensity). Prealternate moult phenology of paddyfield pipit *Anthus rufulus* and Mekong wagtail have not been documented yet and are not included here. The key refers to categories defined in Supporting Information (Table S1).

RELATIVE IMPORTANCE OF NATURAL HISTORY FACTORS

Migration distance, gregariousness and seasonal change are the most important factors influencing prealternate moult, with maturation ranking fourth in first-cycle birds (although the latter two factors with much lower relative importance values; Fig. 2). However, only migration reached statistical significance in the averaged model. Breeding latitude, sexual dichromatism, plumage conspicuousness and preformative moult had little influence. Coefficients of the covariates had the expected signs: positive for all the previously mentioned covariates except preformative moult, conspicuousness, dichromatism and habitat (Table 1). Model and parameter uncertainty are moderately high (Fig. 2, Table 1).

The phylogenetic signal $\lambda < 0.001$ for all models was significantly different from 1 (loglik > 8.43, $P < 0.004$) but not from 0 (loglik < −0.001, $P = 1$), which implies phylogenetic independence due to a very high rate of change between related species.

Species with autumn moult (mean ± SE migration distance 3158.58 ± 2064.08 km, $N = 7$) and species without it (2856.23 ± 2463.72 km, $N = 18$) did not show significant differences ($F_{1,24} = 0.08$, $P = 0.88$). We did not find significant differences between the number of migratory and non-migratory species with autumn moult (chi square test $\chi^2 = 0.30$, $P = 0.58$). Species with prealternate moult (mean ± SE migration distance = 3426.78 ± 2195.46 km, $N = 21$) undertook significantly longer migrations than species without it (389.96 ± 799.92 km, $N = 4$; $F_{1,24} = 7.26$, $P = 0.007$).

Species with autumn moult (mean ± SE breeding latitude = 35.55 ± 21.05°, $N = 7$) bred farther south than species without it (43.63 ± 19.88°, $N = 18$). Again, differences were not significant ($F_{1,24} = 0.81$, $P = 0.60$).

Migration distance did not influence the occurrence of non-breeding moults, and no differences in migratory distance were found between species with prealternate moult (3560.87 ± 2321.85 km, $N = 14$) and species with both prealternate and autumn moult (3158.58 ± 2064.08 km, $N = 7$; $F_{1,24} = 1.84$, $P = 0.21$).

ANCESTRAL STATE RECONSTRUCTION AND CORRELATED EVOLUTION

Evolutionary gains of prealternate moult were more frequent than losses (log BF = 7.88) and transitions

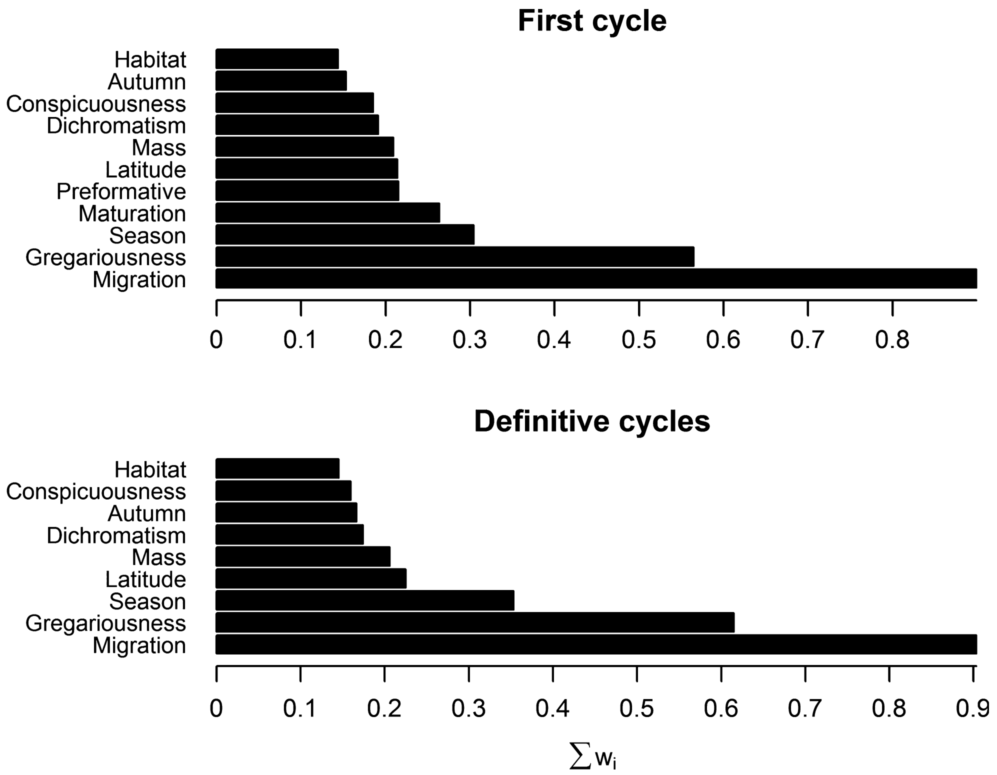


Figure 2. Relative importance of covariates used for prealternate moult models based on the subset whose accumulated Akaike weights reached 95% of the total averaged models: 529 and 154 for first and definitive cycles, respectively, which corresponds to 25.8 and 30.1% model uncertainty. The scale indicates the sum of Akaike weights.

towards autumn moult were also more frequent than losses (log BF = 2.54).

We found no support for directionality in the evolution of non-breeding moults (log BF = 0.45 for prealternate moult; log BF = 1.12 for autumn moult).

Our reconstruction of non-breeding moult strongly supports the presence of prealternate moult as an ancestral state (likelihood = 0.96) of Motacillidae breeding in the Northern Hemisphere but not autumn moult (likelihood = 0.82) (Fig. 3).

The four wagtails included in the polytomy plus the clade encompassing the seven species from Long-billed Pipit *Anthus similis* to Upland Pipit *Anthus sylvanus* contain all non-migratory species that breed in more southern latitudes (Fig. 3). Unexpectedly, the latter clade contains 71% (five) of all species with autumn moult (Fig. 3).

We found very strong support for the correlated evolution of the prealternate moult and the two most important covariates that influence it: migration and gregariousness (Table 2). Species without autumn moult have a plumage throughout the winter that is acquired in either the prebasic or the preformative moult. As the prebasic moult is always complete in this family, variation in the extent of the preformative moult might be influenced by some of these natural history factors. As 16 of the 18 species which did not present autumn moult showed winter gregariousness, we also checked the correlation between preformative moult and winter gregariousness and found a strong association (log BF = 2.65), which suggests an influence of sociality on the evolution of this moult episode.

We found a direct relationship between migration distance and breeding latitude in Motacillidae [in accordance with Outlaw & Voelker (2006) but contrasting with the results obtained from a broad taxonomic group by Figuerola & Jovani (2001); Supporting information, Fig. S7). We also found a positive but weak correlation between breeding latitude and extent of prealternate moult (log BF = 1.93). This could be an additive effect which would enhance the effect of migration distance, especially in species without autumn moult.

DISCUSSION

To examine evolutionary pressures that underlie non-breeding moult strategies, we tested multiple

Table 1. Results of PGLS analyses of ten natural history covariates on prealternate moult

	Autumn	Conspicuosness	Dichromatism	Gregariousness	Habitat	Latitude	Mass	Maturation	Migration	Preformative	Season
First cycle	0.01 (0.07)	−0.04 (0.19)	−0.05 (0.21)	0.25 (0.29)	−0.01 (0.08)	0.04 (0.20)	0.03 (0.10)	0.08 (0.21)	**0.59 (0.30)**	−0.05 (0.15)	0.09 (0.20)
Definitive cycles	0.01 (0.07)	−0.02 (0.13)	−0.03 (0.17)	0.28 (0.29)	−0.01 (0.08)	0.05 (0.20)	0.03 (0.10)		**0.61 (0.30)**		0.11 (0.21)

Coefficients (adjusted standard error) with shrinkage are based on the subset of total averaged models whose accumulated Akaike weights reached 95%. Significance is indicated by bold type. Only migration distance and gregariousness had noticeable effect sizes.

hypotheses for the evolution of non-breeding moult using broad-scale natural history information of the Motacillidae breeding in the Northern Hemisphere.

In agreement with previous studies (Svensson & Hedenström, 1999; Figuerola & Jovani, 2001), we found that migration distance is the most important factor influencing non-breeding moults. Species that undertake longer migrations are also likely to be exposed to more intense solar radiation in the wintering grounds, a factor that may increase plumage deterioration (Lennox & Rowlands, 1969; Surmacki, Sieffermann & Yuan, 2011; but see Willoughby, 1991). While the evolution of prealternate moult is highly correlated with migration distance, the occurrence of non-breeding moults was not related to migration distance.

The relationship between non-breeding moults and breeding latitude does not support the hypothesis predicting more extensive autumn moult as species breed at higher latitudes, suggesting phylogenetic inertia.

Seasonal plumage change is an important life-history trait in the annual cycle of many bird species, including Motacillidae, as it involves behavioural changes (Ruff *Philomachus pugnax* and Rock Ptarmigan *Lagopus mutus* are extreme cases; Hogan-Warburg, 1966; Montgomerie, Lyon & Holder, 2001) and physiological changes (Brush, 1990) with fitness consequences mediated by variation in predation rates (Montgomerie *et al.*, 2001) and mating success (Andersson, 1994). Seasonal change was the third most important factor but was weakly correlated to prealternate moult. This low influence on the evolution of prealternate moult is probably due to the limited seasonal plumage changes that species of this family undergo (only four of 25 species presented changes that were scored as moderate). Seasonal plumage changes may take place to a greater extent in males than in females (e.g. they are very conspicuous in the migratory species of the genus *Piranga* in the family Cardinalidae). As few sex-specific differences in moulting strategies are mentioned in the literature (Pyle 2007), it is thus not surprising that seasonal change was only weakly correlated with prealternate moult extent. It again points to the occurrence and extent of prealternate moults being driven by the need to replace feathers due to loss of functionality, at least partially. Any increase in colour change in males based on sexual selection would then have occurred after the moult had evolved in both sexes due to other factors.

In agreement with Figuerola & Jovani (2001), sexual dichromatism showed a small influence on prealternate moult. Sexual dichromatism is associated with losses of female ornamentation in other passerine families (Friedman *et al.*, 2009; Simpson,

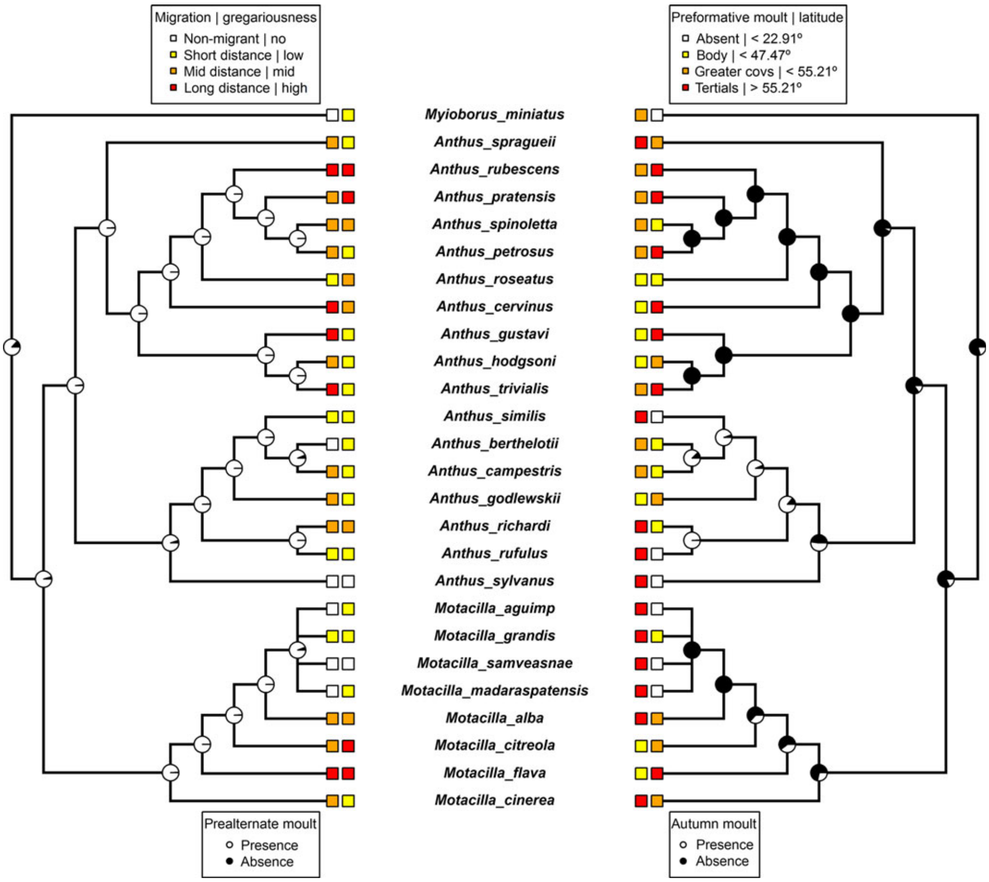


Figure 3. Phylogenetic reconstruction of non-breeding moults. Pie charts on internal nodes depict likelihood of presence/absence for prealternate moult on the left tree, and for autumn moult on the right tree. The four tip nodes depict, from left to right: migration distance, gregariousness, preformative wing-moult extent (categorization in Supporting Information, Table S1) and breeding latitude.

Table 2. Evidence of correlated evolution between prealternate moult and influential covariates

	log BF	Evidence
Conspicuousness	−0.96	Weak against
Dichromatism	2.80	Positive
Gregariousness	10.29	Very strong
Breeding latitude	1.93	Weak
Habitat	′1.17	Weak
Mass	0.70	Weak
Maturation	1.29	Weak
Migration distance	10.88	Very strong
Preformative moult	1.97	Weak
Seasonal change	1.08	Weak

Johnson & Murphy, 2015), so that prealternate moult is not necessarily linked to an increase in sexual dichromatism. Thus, sexual selection seems to have played a limited role in the evolution of prealternate moult in Motacillidae.

Sociality had a remarkable influence on the evolution of prealternate moult as shown by its very strong correlation with gregariousness and by the fact that this covariate is the second most important one explaining variation of prealternate moult. Gregariousness characterizes the winter social behaviour of many species of Motacillidae but, contrary to predictions from our hypothesis, of nine species that showed mid to high gregariousness only Yellow Wagtail *Motacilla flava* and Citrine Wagtail *Motacilla citreola* presented autumn moult. Given this, why might gregariousness exert its influence at the end of the winter period? February to April, the peak of prealternate moult in our study species (Fig. 1), coincides with depletion of food resources in many regions (Lack, 1966; Karr, 1976; Sherry, Johnson & Strong, 2005), which can influence prealternate moult (Danner *et al.*, 2015). In this context, prealternate moult (and particularly extent and feather quality) could constitute an honest signal of physical condition. Premigratory roosts (López *et al.*, 2005) also take place at the end of this period, in which signal of a higher status could be advantageous for example to claim the safest places in the roost (Beauchamp, 1999).

As expected, higher scores of delayed plumage maturation were associated with more extensive prealternate moults, and prealternate moult extent decreased with extent of preformative moult. The prealternate moult was weakly correlated with these two factors, which were the fourth and fifth most influential ones in first-cycle birds. Altogether, these ontogenetic factors do not seem to have played an important role in the evolution of prealternate moult, although preformative moult may have had a stronger influence on autumn moult (see Supporting Information, Data S1).

We have studied the effect of multiple natural history factors on the evolution of non-breeding moults in the family Motacillidae. Lack of information for many species reduces the scope of our conclusions but we can still provide insight into the fact that non-breeding moult may have evolved under different selective forces in different taxonomic groups. We found that migration distance is the most influential force in Motacillidae, although gregariousness has also been an important driver of moult evolution. However, we still lack detailed information on other essential factors that may have played an even more important role in the evolution of non-breeding moult strategies in Motacillidae, such as feather quality and variation of feather coloration throughout the year. Differences in feather quality among species and even within individual feathers (especially in nestlings) are important drivers of the extent of the preformative moult of passerines (Weber *et al.*, 2005; Kiat & Izhaki, 2016).

There was a remarkable versatility in the evolution of moult strategies as suggested by the lack of phylogenetic inertia. This capacity for rapid change highlights their adaptive character, which introduces a great deal of flexibility in the moult strategies of passerines, and also has contributed to diversification of their natural histories by taking up new functions such as social signalling under selective pressures conditioned by changes in the state of other traits. For example, the gain of a prealternate moult might subsequently be targeted by sexual selection to originate sexual dichromatism. Phylogenetic analyses may help to elucidate the selective forces at work, but the genetic basis of moult evolution remains virtually unexplored. Future research should investigate which genes are involved and how differences in gene regulation relate to different moult strategies in birds.

ACKNOWLEDGEMENTS

We are deeply grateful for the comments of Ray Danner, Peter Pyle, Stephen Winter and one anonymous reviewer. Natàlia Pérez and Marcos Pérez assisted with the covariate scoring. José Luis Copete helped with bibliography search. Alejandro González-Voyer advised on the use of BayesTraits. We are indebted to Juan José Soler for sharing with us the function pglm3.3.r.

REFERENCES

Ali S, Ripley D. 1993. *Handbook of the birds of India and Pakistan, Vol. 9, 2nd edn*. Oxford: Oxford University Press.

Alström P, Mild K. 2003. *Pipits and wagtails of Europe, Asia and North America. Identification and systematics*. London: Christopher Helm.

Alström P, Ödeen A. 2002. Incongruence between mitochondrial DNA, nuclear DNA and molecular data in the avian genus Motacilla: implications for estimates of species phylogenies. Unpublished DPhil Thesis, Uppsala University.

Andersson M. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.

Barta Z, Houston AI, McNamara JM, Welham RK, Hedenström A, Weber TP, Feró O. 2006. Annual routines of non-migratory birds: optimal moult strategies. *Oikos* **112:** 580–593.

Beauchamp G. 1999. The evolution of communal roosting in birds: origin and secondary losses. *Behavioral Ecology* **10:** 675–687.

Bergman G. 1982. Why are the wings of *Larus f. fuscus* so dark? *Ornis Fennica* **59:** 77–83.

BirdLife International and NatureServe. 2014. *Bird species distribution maps of the world*. Cambridge and Arlington, VA: NatureServe and BirdLife International.

Blanco G, Frías O, Garrido-Fernández J, Hornero-Méndez D. 2005. Environmental-induced acquisition of nuptial plumage expression: a role of denaturation of feather carotenoproteins? *Proceedings of the Royal Society of London Series B, Biological Sciences* **272:** 1893–1900.

Bridge ES, Voelker G, Thompson CW, Jones AW, Baker AJ. 2007. Effects of size and migratory behavior on the evolution of wing molt in terns (Sternae): a phylogenetic-comparative study. *Auk* **124:** 841–856.

Brush AH. 1990. Metabolism of carotenoid pigments in birds. *FASEB Journal* **4:** 2969–2977.

Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn*. New York: Springer.

Butler LK, Donahue MG, Rohwer S. 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): age effects, aerodynamics, and conservation implications. *Auk* **119:** 1010–1023.

Butler LK, Rohwer S, Speidel MG. 2008. Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. *Journal of Avian Biology* **39:** 629–639.

Chaine AS, Roth AM, Shizuka D, Lyon BE. 2013. Experimental confirmation that avian plumage traits function as multiple status signals in winter contests. *Animal Behaviour* **86:** 409–415.

Cramp S, ed. 1988. *The birds of the Western Palearctic, Vol. 5: tyrant flycatchers to thrushes*. Oxford: Oxford University Press.

Cramp S, Perrins CM, eds. 1994. *The birds of the Western Palearctic, Vol. 9: buntings and New World warblers*. Oxford: Oxford University Press.

Danner RM, Greenberg RS, Danner JE, Walters JR. 2015. Winter food limits timing of pre-alternate moult in a short-distance migratory bird. *Functional Ecology* **29:** 259–267.

Dawson A. 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starling *Sturnus vulgaris*. *Ibis* **146:** 493–500.

Dawson A. 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* **363:** 1621–1633.

Dey CJ, Dale J, Quinn JS. 2014. Manipulating the appearance of a badge of status causes changes in true badge expression. *Proceedings of the Royal Society of London Series B, Biological Sciences* **281:** 20132680.

Duckworth JW, Alstrom P, Davidson P, Evans TD, Poole CM, Setha T, Timmins RJ. 2001. A new species of wagtail from the lower Mekong basin. *Bulletin of the British Ornithologists' Club* **121:** 152–182.

Dunning JB. 2007. *CRC handbook of avian body masses, 2nd edn*. Boca Raton, FL: CRC Press.

Echeverry-Galvis MA, Hau M. 2013. Flight performance and feather quality: paying the price of overlapping moult and breeding in a tropical highland bird. *PLoS ONE* **8:** e61106. doi:10.1371/journal.pone.0061106.

Ersts PJ. 2015. *Geographic Distance Matrix Generator (v. 1.2.3)*. American Museum of Natural History, Center for Biodiversity and Conservation. Available at: http://biodiversityinformatics.amnh.org/open_source/gdmg

Étchecopar RD, Hüe F. 1983. *Les oiseaux de Chine. Passereaux*. Paris: Boubée.

Figuerola J, Jovani R. 2001. Ecological correlates in the evolution of moult strategies in Western Palearctic passerines. *Evolutionary Ecology* **15:** 183–192.

Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist* **160:** 712–726.

Friedman NR, Hofmann CM, Kondo B, Omland KE. 2009. Correlated evolution of migration and sexual dichromatism in the New World orioles (*Icterus*). *Evolution* **63:** 3269–3274.

Garland T, Dickerman AW, Janis CM, Jones JA. 1993. Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42:** 265–292.

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG. 2011. Multimodel inference in ecology and evolution challenges and solutions. *Journal of Evolutionary Biology* **24:** 699–711.

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A. 2009. *Paseriformes del Occidente de México: morfometría, datación y sexado*. Barcelona: Museu de Ciències Naturals de Barcelona.

Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P. 2014. Moult topography and its application to the study of partial wing-moult in two Neotropical wrens. *Ibis* **156:** 311–320.

Hall KSS, Fransson T. 2000. Lesser-whitethroats under time constraint moult more rapidly and grow shorter wing feathers. *Journal of Avian Biology* **31:** 583–587.

Harvey PH, Pagel MD. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.

de la Hera I, Pérez-Tris J, Tellería JL. 2009. Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. *Biological Journal of the Linnean Society* **97:** 98–105.

Hill GE. 1996. Subadult plumage in the house finch and tests of models for the evolution of delayed plumage maturation. *Auk* **113:** 858–874.

Hogan-Warburg AJ. 1966. Social behavior of the ruff (*Philomachus pugnax*). *Ardea* **54:** 108–229.

Holmgren N, Hedenström A. 1995. The scheduling of molt in migratory birds. *Evolutionary Ecology* **9:** 354–368.

Howell SNG, Corben C, Pyle P, Rogers DI. 2003. The first basic problem: a review of molt and plumage homologies. *Condor* **105:** 635–653.

Jenni L, Winkler R. 1994. *Molt and ageing of European passerines*. London: Academic Press.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. *Nature* **491:** 444–448.

Karr JR. 1976. Seasonality, resource availability, and community diversity in tropical bird communities. *American Naturalist* **110:** 973–994.

Kass RE, Raftery AE. 1995. Bayes factors. *Journal of the American Statistical Association* **90:** 773–795.

Kiat Y, Izhaki I. 2016. Why renew fresh feathers? Advantages and conditions for the evolution of complete post-juvenile moult. *Journal of Avian Biology* **47:** 47–56.

Lack D. 1966. *Population studies of birds*. Oxford: Oxford University Press.

Lennox FG, Rowlands RJ. 1969. Photochemical degradation of keratins. *Photochemistry and Photobiology* **9:** 359–367.

López G, Figuerola J, Varo N, Soriguer R. 2005. White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed. *Ardea* **93:** 237–244.

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* **149:** 646–667.

McAlpine CA, Rhodes JR, Bowen ME, Lunney D, Callaghan JG, Mitchell DL, Possingham HP. 2008. Can multiscale models of species' distribution be generalized from region to region? A case study of the koala. *Journal of Applied Ecology* **45:** 558–567.

Montgomerie R, Lyon B, Holder K. 2001. Dirty ptarmigan: behavioral modification of conspicuous male plumage. *Behavioral Ecology* **12:** 429–438.

Murphy ME. 1996. Energetics and nutrition of moult. In: Carey C, ed. *Avian energetics and nutritional ecology*. New York: Chapman Hall, 158–198.

Nakagawa S, Freckleton RP. 2011. Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behavioural Ecology and Sociobiology* **65:** 103–116.

Newton I. 2008. *The migration ecology of birds*. London: Academic Press.

Outlaw DC, Voelker G. 2006. Phylogenetic tests of hypotheses for the evolution of avian migration, a case study using the Motacillidae. *Auk* **123:** 455–466.

Pagel M. 1992. A method for the analysis of comparative data. *Journal of Theoretical Biology* **156:** 431–442.

Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* **26:** 331–348.

Pagel M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401:** 877–884.

Pagel M, Meade A, Barker D. 2004. Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology* **53:** 673–684.

Pap PL, Osváth G, Sándor K, Vincze O, Bărbos L, Marton A, Nudds RL, Vágási CI. 2015. Interspecific variation in the structural properties of flight feathers in birds indicates adaptation to flight requirements and habitat. *Functional Ecology* **29:** 746–757.

Peters A. 2007. Testosterone treatment of female Superb Fairy-wrens *Malurus cyaneus* induces a male-like prenuptial moult, but no coloured plumage. *Ibis* **149:** 121–127.

Pyle P. 1997a. *Identification guide to North American birds. Part I*. Bolinas, CA: Slate Creek Press.

Pyle P. 1997b. Molt limits in North American passerines. *North American Bird Bander* **22:** 49–89.

Pyle P. 2007. Revision of molt and plumage terminology in ptarmigan (Pashianidae: Lagopus spp.) based on evolutionary considerations. *Auk* **124:** 508–514.

QGIS Development Team. 2015. *QGIS 2.8.2 Wien*. Available at: http://qgis.org/es/site/

Rohwer S, Fretwell SD, Niles DM. 1980. Delayed maturation in Passerine plumages and the deceptive acquisition of resources. *American Naturalist* **115:** 400–437.

Rohwer S, Butler LK, Froehlich D. 2005. Ecology and demography of east–west differences in molt scheduling in Neotropical migrant passerines. In: Greenberg R, Marra PP, eds. *Birds of two worlds: the ecology and evolution of temperate-tropical migration*. Baltimore, MD: John Hopkins University Press, 87–105.

Rohwer S, Ricklefs RE, Rohwer VG, Copple MM. 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biology* **7:** e1000132.

Schluter D, Price T, Mooers AØ, Ludwig D. 1997. Likelihood of ancestor states in adaptive radiation. *Evolution* **51:** 1699–1711.

Senar JC, Copete JL, Martin AJ. 1998. Behavioural correlates of variation in the extent of postjuvenile molt in the Siskin *Carduelis spinus*. *Ibis* **140:** 661–669.

Sherry TW, Johnson MD, Strong AM. 2005. Does winter food limit populations of migratory birds? In: Greenberg R, Marra PP, eds. *Birds of two worlds: the ecology and evolution of temperate–tropical migration*. Baltimore, MD: John Hopkins University Press, 414–425.

Shirihai H, Helbig A, Gargallo G. 2001. *Sylvia warblers*. London: Christopher Helm.

Simpson JA, Campbell L. 2013. *The Oxford handbook of close relationships*. Oxford: Oxford University Press.

Simpson RK, Johnson MA, Murphy TG. 2015. Migration and the evolution of sexual dichromatism: evolutionary loss of female coloration with migration among wood-warblers. *Proceedings of the Royal Society of London Series B, Biological Sciences* **282:** 20150375.

Surmacki A, Sieffermann L, Yuan H-W. 2011. Effects of sunlight exposure on carotenoid-based and structural coloration of the Blue-tailed Bee-eater. *Condor* **113:** 590–596.

Svensson L. 1992. *Identification guide to European passerines, 4th edn*. Stockholm: L. Svensson.

Svensson E, Hedenström A. 1999. A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: Sylviidae). *Biological Journal of the Linnean Society* **67:** 263–276.

The R Foundation for Statistical Computing. 2015**.** *Version 3.2.0 (2015-04-16)*. Vienna: The R Foundation for Statistical Computing.

Tibbets EA, Safran RJ. 2009. Co-evolution of plumage characteristics and winter sociality in New and Old World sparrows. *Journal of Evolutionary Biology* **22:** 2376–2386.

Voelker G. 1999. Molecular evolutionary relationships in the avian genus *Anthus* (pipits: Motacillidae). *Molecular Phylogenetics and Evolution* **11:** 84–94.

Voelker G, Rohwer S. 1998. Contrasts in the scheduling of molt and migration in eastern and western Warbling-Vireos. *Auk* **115:** 142–155.

Weber TP, Borgudd J, Hedenström A, Persson K, Sandberg R. 2005. Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species. *Biology Letters* **1:** 27–30.

Willoughby EJ. 1991. Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proceedings of the Western Foundation of Vertebrate Zoology* **4:** 247–286.

Wingfield JC. 2008. Organization of vertebrate annual cycles: implications for control mechanisms. *Philosophical Transactions of the Royal Society of London B* **363:** 425–441.

Ydenberg RC, Butler RW, Lank DB. 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. *Journal of Avian Biology* **38:** 523–529.

Zahavi A. 1997. *The handicap principle: a missing piece of Darwin's puzzle*. Oxford: Oxford University Press.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. Consensus trees.
Figure S2. Relative importance of the explanatory variables for the autumn moult based on the subset whose accumulated Akaike weights reached 95% of the total averaged models.
Figure S3. Relative importance of the explanatory variables for the autumn moult based on the subset whose accumulated Akaike weights reached 95% of the total averaged models.
Figure S4. Relative importance of the explanatory variables for the autumn moult based on the subset whose accumulated Akaike weights reach 95% of the total averaged models: 231 and 87 for first and definitive cycles, respectively, which corresponds to 22.6 and 34.0% model uncertainty.
Figure S5. Relative importance of the explanatory variables for the prealternate moult based on the subset whose accumulated Akaike weights reach 95% of the total averaged models: 529 and 154 for first and definitive cycles, respectively, which corresponds to 25.8 and 30.1% model uncertainty.
Figure S6. Scatterplot of migration distance versus breeding latitude.
Figure S7. Phylogenetic reconstruction of non-breeding moult episodes.
Table S1. Categorization of natural history information used in analyses.
Table S2. Results of the PGLS of ten natural history covariates on autumn moult.
Table S3. Evidence of correlated evolution between autumn moult and influential covariates.
Table S4. Results of the PGLS of 11 natural history covariates on autumn moult.
Table S5. Results of the PGLS of 11 natural history covariates on non-breeding moults.
Table S6. Categories of Bayes factors used as model selection criterion in analyses of correlated evolution.
Data S1. Values of 13 covariates for 25 species of the family Motacillidae used in analyses. In a separate spreadsheet raw scores of Conspicuousness, Dichromatism and Seasonal change given by three observers.

Chapter 5 contains the article accepted on 12 August 2020 **Guallar S, Rueda-Hernández R, Pyle P 2021. Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats.** ***Ornithology*** **138*.***

Ornithology

AMERICAN ORNITHOLOGICAL SOCIETY
americanornithology.org
1400 South Lake Shore Drive

December 24, 2020

Universitat de Barcelona Facultat de Biologia
Animal Biology
Diagonal 643
Barcelona, 08028
SPAIN

Ref.: Ms. No. AUK-20-073

Dear Santi Guallar,

We congratulate you on the recent acceptance of your article “Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats” to the second-oldest ornithological journal in the world: ***Ornithology*****.** The journal is the #2 journal over the last five-year-average in the Journal Impact Factor among all the 24 ornithological journals.

Ornithology has a long history of advancing the fundamental scientific knowledge of bird species and broad biological concepts (e.g., ecology, evolution, behavior, physiology, genetics) through studies of bird species.

Your article is expected to be published online at academic.oup.com/condor and at BioOne.org in December 2020.

With kind regards,

T. Scott Sillett

T. Scott Sillett
Migratory Bird Center, Smithsonian
Smithsonian Institution
Editor-in-Chief
Ornithology

Chapter 6 contains the article published online on 26 September 2020 **Delhey K, Guallar S, Rueda-Hernández R, Valcu M, Wang D, Kempenaers B 2020. Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. *J. Anim. Ecol.* 89: 2896–2908. https://doi.org/10.1111/1365-2656.13354**

Received: 11 June 2020 | Accepted: 19 August 2020

DOI: 10.1111/1365-2656.13354

RESEARCH ARTICLE

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

Partial or complete? The evolution of post-juvenile moult strategies in passerine birds

Kaspar Delhey[1,2] | **Santiago Guallar**[3] | **Rafael Rueda-Hernández**[4] | **Mihai Valcu**[1] | **Daiping Wang**[1] | **Bart Kempenaers**[1]

[1]Max Planck Institute for Ornithology, Seewiesen, Germany

[2]School of Biological Sciences, Monash University, Clayton, Vic., Australia

[3]Department de Vertebrats, Museu de Ciències Naturals de Barcelona, Barcelona, Spain

[4]Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México DF, México

Correspondence
Kaspar Delhey
Email:kaspardelhey@gmail.com

Funding information
Max-Planck-Gesellschaft

Handling Editor: Isabella Capellini

Abstract

1. Moulting strategies in birds have evolved to avoid overlap with, or prepare for, other demanding parts of the annual cycle, such as reproduction or migration. When moulting for the first time after leaving the nest, young birds replace their typically poor-quality plumage during the post-juvenile moult. The extent of this moult varies between species from partial to complete.
2. Earlier studies, restricted to Western Palearctic birds, suggest that in most species a complete post-juvenile moult may not be possible simply because young birds are constrained by not having the same access to resources as adults, unless environmental conditions are favourable. These studies also show that complete post-juvenile moult is more common in species with poor-quality nest-grown plumage.
3. We expanded the spatial and taxonomic scope of previous studies to 1,315 species of passerines from across the world and considered both the role of constraints, plumage quality and other selective pressures favouring a complete post-juvenile moult. Thus, we test whether complete moult is more prevalent in species where nest-grown feathers are presumably of poor quality (shorter nestling period), that live in environments that foster quick plumage degradation (open habitats, high insolation and humidity), and where males are under strong sexual selection.
4. Our data reveal that 24% of species carry out a complete post-juvenile moult, and that this trait has a strong phylogenetic signal. Complete moult is more common in species that inhabit warmer regions and open habitats, show no delayed plumage maturation and have higher levels of sexual dichromatism (indicative of strong sexual selection). Neither the presumed quality of the nest-grown plumage nor living in regions with high insolation correlates with complete moult.
5. In conclusion, the evolution of complete post-juvenile moult not only depends on whether birds can perform a complete moult (i.e. suitable environmental conditions) but also on the strength of selection associated with the need of a complete moult. In particular, the necessity to keep the plumage in good condition in challenging environments and the benefits associated with producing adult-like plumage colours to attract mates or deter rivals seem to play an important role.

KEYWORDS
climate, delayed plumage maturation, moult, passeriformes, plumage colour, sexual selection

1 | INTRODUCTION

Feathers are an essential feature of birds, fulfilling a variety of key functions, such as flight, thermoregulation, communication and camouflage. They are also extremely complex integumentary appendages composed of keratin which, when fully grown, are dead structures that deteriorate over time. This requires their regular replacement through moults. Moulting is considered an energetically expensive process that involves substantial physiological changes and often affects the performance of the plumage, hampering flight or reducing insulation (Newton, 2009). Hence, variation among species in the timing, speed, sequence and extent of moult has been shaped by natural selection (a) to coincide with periods when resource availability is high (Barta et al., 2006), (b) to avoid interference with other demanding life-history events such as reproduction and migration (Newton, 2009) and (c) to ensure that the plumage is in optimal shape for these events (Kiat, 2018). As a result, in most bird species, moult episodes follow a predictable sequence during their annual and life cycles (Barta et al., 2006).

In most passerine species, adults replace the entire plumage at least once per year, and this moult—which is referred to as prebasic or post-nuptial moult—generally takes place shortly after breeding (Howell et al., 2003; Jenni & Winkler, 1994). For young birds, the first moult after leaving the nest is the preformative or post-juvenile moult (Howell et al., 2003; Jenni & Winkler, 1994). Juvenile individuals commonly have plumage of lower quality than that of adults (Callan et al., 2019; Fogden, 1972) and to successfully face the challenges of early independent life their feathers will most likely need to be replaced (Kiat & Izhaki, 2016; Kiat & Sapir, 2018). However, this moult is also challenging because young birds are not as proficient as adults at obtaining food and evading predators (Heise & Moore, 2003; Hoy et al., 2015; Naef-Daenzer & Gruebler, 2016). It is no surprise then that in the majority of passerine birds the first moult leading into adulthood is partial. Commonly, most of the body plumage is replaced, but varying numbers of wing and tail feathers are retained. Nevertheless, a sizeable proportion of species carry out a complete post-juvenile moult (Ginn & Melville, 1983; Jenni & Winkler, 1994; Pyle, 1997), raising the question why not all species follow this strategy. To answer this question, we need to identify not only the constraints and costs that prevent a complete moult but also the factors that favour a complete post-juvenile moult, and establish how these vary across species.

One important constraint limiting the occurrence of complete post-juvenile moult is simply the time available for moulting. Accordingly, previous analyses (Kiat & Izhaki, 2016) show that complete post-juvenile moult is more prevalent among (a) smaller and medium-sized species compared to larger ones because larger species moult more slowly (Rohwer et al., 2009) and (b) resident species, presumably because migratory species have less time to moult before departing to their wintering grounds. These time constraints should be most marked for species living in highly seasonal environments, where favourable conditions for moulting deteriorate rapidly after the summer. Furthermore, Kiat and Izhaki (2016) show that complete post-juvenile moult is more common at lower latitudes, where temperatures are higher and seasonality lower. The type of resources exploited also matter since species that feed on highly seasonal resources such as insects and other invertebrates are less likely to show complete post-juvenile moult than seed-eating species (Kiat & Izhaki, 2016). The latter presumably have a more stable food supply, especially towards the end of summer and autumn when moulting takes place (Barta et al., 2006; Faccio, 2018). These recent efforts exploring the evolution of moult strategies are largely restricted to passerines that occur in temperate regions and it remains to be shown whether environmental constraints can explain the occurrence of complete post-juvenile moult in a more diverse sample of species.

While resource availability may lead to a partial post-juvenile moult in many species (Kiat & Izhaki, 2016), species with ecological and life-history characteristics that require a highly functional post-juvenile plumage will be under stronger selection to moult the entire juvenile plumage. Because the post-juvenile moult replaces the plumage grown in the nest, species in which nest-grown feathers are of poorer quality—such as species with a short developmental time in the nest (Callan et al., 2019)—should be more likely to perform a complete moult. Indeed, previous studies showed that Western Palearctic species with a complete post-juvenile moult grew poorer-quality plumage in the nest (Kiat & Izhaki, 2016; Kiat & Sapir, 2018). In addition, a complete post-juvenile moult should be more likely in species that live in environmental conditions that foster feather degradation. Feathers degrade rapidly by being exposed to sunlight (Bergman, 1982; Test, 1940). Hence, species that are more exposed to strong sunshine, such as those that live in open environments and in regions with high levels of insolation should be more likely to have a complete post-juvenile moult. Feathers also degrade due to keratinolytic bacteria, which are more active in humid and warm conditions (Burtt & Ichida, 2004). Thus, species living in these conditions should also be more likely to evolve complete post-juvenile moult.

Furthermore, the occurrence of complete post-juvenile moult may be linked to the intensity of sexual selection. A complete post-juvenile moult eliminates the differences in feather wear and colouration between new and old feathers that characterize first-year birds in species with partial post-juvenile moult. Such subtle cues of age—when available—may be used by conspecifics to gauge the age of a rival or potential mate (Crates et al., 2015). Age is an important determinant of breeding success in many species (Cleasby & Nakagawa, 2012), with older males being preferred as mates and better at competing for resources (Brooks & Kemp, 2001). It could thus be hypothesized that in species in which males are under strong sexual selection, juvenile birds should be more likely to have evolved complete post-juvenile moult to conceal their age and display the most elaborate colours possible during their first breeding season (Kiat et al., 2019). This effect, however, should mainly apply to species where the plumage of first-year males resembles that of older males because a complete post-juvenile moult would make no difference in species where young males clearly differ from older males, that is, in species with delayed plumage maturation (Hawkins et al., 2012). Moreover, species with delayed plumage maturation are often under stronger sexual selection (Beauchamp, 2003), and thus statistically accounting for delayed plumage maturation is essential to assess the effects of sexual selection intensity on the extent of post-juvenile moult.

Here we undertake a large-scale analysis of the evolutionary and ecological correlates of complete post-juvenile moult in passerine birds. We collated information on the extent of post-juvenile moult (partial vs. complete) for the species of passerine birds that inhabit three well-known avifaunas (Western Palearctic, Nearctic and Australasia) and we complemented this survey with information from the primary literature on species from other regions. Following the two key hypotheses that the extent of post-juvenile moult is shaped by constraints and by variation in selective pressures associated with plumage performance, we predict that complete post-juvenile moult should be more prevalent in (a) species that are less time-constrained, such as smaller species that are resident or migrate short distances; (b) species that live in environments with less seasonal fluctuation of resources such as tropical regions; (c) species that exploit less-seasonal resources (seed-based diet); (d) species with short developmental periods in the nest, that fledge with lower-quality plumage, (e) species that live where feather deterioration is more rapid, that is, in open habitats and regions with high levels of insolation or rainfall (which promote the activity of feather-degrading bacteria) and (f) species that are under strong sexual selection such that males may benefit from achieving similar colouration to adults during their first year (species with reduced delayed plumage maturation).

2 | MATERIALS AND METHODS

2.1 | Post-juvenile moult scoring and species included

We scored each species of passerine with available moult data mentioned in the three main regional handbooks where information on moult is consistently listed [Birds of the Western Palearctic, BWP (Cramp & Simmons, 1977), Birds of North America Online, BNA (Poole, 2005) and the Handbook of Australian, New Zealand and Antarctic Birds, HANZAB (Marchant & Higgins, 1990)]. We complemented and updated this dataset with information from the primary literature (see the Data sources section) and from own unpublished field data. In total, we compiled data for $N = 1{,}593$ taxa.

Species for which we could obtain moult data were classified into the following categories: (a) complete post-juvenile moult, species that moult all feathers during the post-juvenile moult; (b) partial post-juvenile moult, species that moult some but not all feathers (including species classified as having incomplete, partial and limited post-juvenile moult; Johnson & Wolfe, 2017; Pyle, 1997) and (c) partial or complete post-juvenile moult, species where some individuals or populations show complete and some partial post-juvenile moult. Migratory species that initiate their post-juvenile moult in the breeding area and complete it after arriving in the wintering grounds (e.g. many Hirundinidae) were included as having a complete post-juvenile moult, following the classification provided in our sources. However, the strategy of completing the post-juvenile moult in the wintering quarters is hard to distinguish from that of species which undergo a partial post-juvenile moult, but then perform a complete nuptial (pre-breeding) moult in their wintering grounds (e.g. many *Acrocephalus* sp.). In our first classification, these species were assigned to the partial post-juvenile moult category because post-juvenile and nuptial moult were considered as separate moulting events. However, given the difficulty of separating moult events in some cases (Jenni & Winkler, 1994), and the fact that from a functional point of view all these species perform a complete moult before their first breeding season, we computed a new response variable (complete moult before first breeding: yes/no). Species were considered to have a complete moult before the first breeding season if they had either a complete post-juvenile moult or if we had evidence that they performed a complete nuptial moult. We note that the extent of nuptial moult is often not well known. Nevertheless, using this new response variable allowed us to assess whether results differed compared to the original post-juvenile moult classification. For each species, we also estimated data quality by recording whether or not the moult type assessment was based on limited data (usually reported in text by indicating that limited information was available and/or that only few specimens have been examined).

After classifying moult patterns, we matched the scientific names used in our moult data sources with the species names used by our source of phylogenetic information: www.birdtree.org (Jetz et al., 2012). After matching species names, we ended up with 94 species for which we had more than one source of information on post-juvenile moult, and the classification agreed for 81 species. In the remaining cases, we either used the more recent or comprehensive source ($N = 2$ species), or we assigned 'complete or partial' ($N = 11$ species for which one source assigned one population as having complete post-juvenile moult and another source assigned a different population as having partial post-juvenile moult). This resulted in a final sample of 1,315 species for which we had data on post-juvenile moult.

2.2 | Explanatory variables

2.2.1 | Variables based on distribution ranges

We used distribution ranges (as vectorized polygons) from Birdlife International (http://datazone.birdlife.org/) and overlapped these with raster layers of annual mean temperature (BIOCLIM BIO 1, resolution 0.0083 decimal degrees), annual precipitation (BIOCLIM BIO12, 0.0083 decimal degrees), mean annual insolation, and the amount of solar energy received by a given surface (W/m^2, 0.25 decimal degrees). Annual mean temperature and annual precipitation were obtained from Karger et al. (2017) while insolation was obtained by averaging monthly estimates for the years 2006–2019 obtained from https://neo.sci.gsfc.nasa.gov/. Using the function 'exact_extract' from the R package 'EXACTEXTRACTR' (Baston, 2020), we averaged climatic and insolation values for all raster cells covered by a species' distribution. We computed climatic and insolation estimates separately for the breeding and year-round distribution ranges and for the non-breeding distribution range of migratory species. Subsequently, we averaged data for the breeding or year-round resident and non-breeding distribution to obtain overall estimates for the entire species distribution. This procedure may not be entirely accurate when quantifying the climate experienced by migratory species because they do not experience the winter in their breeding grounds. Therefore, climatic variables may be biased in migratory species, particularly in long-distance migrants. To determine whether this potential bias drives some of the climatic effects that we detect (see Section 3), we re-ran analyses excluding long-distance migrants (species with migratory distances >2,000 km; Dufour et al., 2020). Finally, we computed absolute latitude as the distance in degrees between the centroid of each species' breeding or year-round resident distribution (avoiding the non-breeding distribution) and the equator using function 'sf_centroid' from the package 'SF' (Pebesma, 2018). This information was available for 1,311 species.

2.2.2 | Other explanatory variables

(a) Body mass (log$_{10}$-transformed, $N = 1,287$ species) was obtained mainly from Dunning et al. (Dunning, 2008) and Wilman et al. (2014) as collated by Mcqueen et al. (2019). (b) Migration distance (in km, data for $N = 1,315$ species) was obtained from Dufour et al. (2020) (variable called 'distance_quanti_ALL' in their dataset). In this dataset, migration distance was missing for 10 resident species and these were assigned migration distance of 0 (Dufour et al., 2020). (c) Diet, the percentage of the diet composed by seeds, obtained from Wilman et al. (2014, data for $N = 1,315$ species). (d) Length of the nestling period (in days, $N = 860$ species), collated from the Handbook of the Birds of the World (HBW; del Hoyo et al., 2018) and Cooney et al. (2020). (e) Habitat openness ($N = 1,311$ species). Based on the habitat use data from Birdlife International (http://datazone.birdlife.org/), we assigned each major habitat used by each species an openness score that varies from 1 (forests) to 4 (coastal and marine environments) and averaged these scores for each species. For more details on the scores assigned to each type of habitat, see Supporting Information. (f) Sexual dichromatism, as an estimator of the strength of sexual selection on males, scored based on scanned book plates from the HBW. Sexual dichromatism was computed for each species as the average difference in Red–Green–Blue (RGB) values between males and females across nine plumage patches as described in Mcqueen et al. (2019; $N = 1,293$ species). Book plates provide good approximations of colour variation measured directly on museum specimens (Dale et al., 2015; Delhey et al., 2019). (g) Delayed plumage maturation ($N = 1,297$ species), scored on a three-level scale (0 = species where first-year males are identical or very similar to second-year adult males, 1 = species where first-year individuals are similar but on average less ornamented than second-year males, and 2 = species which have a clearly distinct first-year plumage and often take several years to reach adult plumage).

2.3 | Statistical analyses

All analyses were carried out within the R statistical environment (R Development Core Team, 2019). We used the package BTW (Griffin, 2018) to interact with the program BayesTraits V3 (http://www.evolution.rdg.ac.uk/BayesTraitsV3.0.2/BayesTraitsV3.0.2.html) from within R. We used the Multistate module in BayesTraits to estimate the rates of evolutionary shifts between the different types of post-juvenile moult using maximum likelihood across a sample of 100 phylogenies. We considered two alternative transition models: a model where gains of complete post-juvenile moult happen at a different rate than losses, and a model where both rates are set to be equal. We compared the performance of both models using a likelihood-ratio test. As BayesTraits allows polymorphic traits, species with both partial and complete post-juvenile moult were considered polymorphic. All other analyses require binary traits and hence we classified all species with partial/complete post-juvenile moult as being able to carry out a complete moult.

We quantified the phylogenetic signal of post-juvenile moult using Fritz and Purvis' D (2010) for binary traits using the function 'phylo.d' from the R package CAPER (Orme et al., 2018) computed across 100 phylogenies (see below for justification). D values close to 0 indicate a strong phylogenetic signal as expected from a Brownian motion type of evolution (equivalent to lambda = 1 for a continuous trait), while values close to 1 indicate random evolutionary patterns (essentially little phylogenetic signal, equivalent to lambda = 0 for a continuous trait; Fritz & Purvis, 2010). We also used a permutation procedure implemented in the same function (1,000 permutations) to test whether values of D are statistically different from 0 and 1. For visual purposes, we also reconstructed ancestral states for the different types of post-juvenile moult using stochastic mapping across 100 phylogenies as implemented by function 'make.simmap' in the package PHYTOOLS (Revell, 2012) using the model that allows different rates for gains and losses (the best supported model identified by BayesTraits, see Section 3).

To quantify the associations between our explanatory variables and the occurrence of complete post-juvenile moult, we used logistic phylogenetic regression (Ives & Garland, 2010) as implemented in the function 'phyloglm' from the package PHYLOLM (Tung Ho & Ané, 2014). The phylogenetic structure in the residual distribution is estimated and corrected by the parameter alpha, which reflects the overall rate of transition between binary states. Small values of alpha (close to zero) correspond to stronger phylogenetic effects (Ives & Garland, 2010). All models were run across a sample of 100 phylogenies (see justification below) using the Ericsson backbone obtained from www.birdtree.org (Jetz et al., 2012) to account for phylogenetic uncertainty. These phylogenetic supertrees include nearly all bird species and have been obtained using available genetic data in combination with taxonomic information to randomly place species without genetic data using a birth–death polytomy resolver (Rabosky, 2015). Based on simulations, Rabosky (2015) suggested that this random placement of species may bias comparative analyses by reducing the phylogenetic signal in trait data. However, this conclusion was based on simulations with closely related groups of species, within taxonomic families, and Rabosky (2015) suggests that biases should be much less marked if the analyses are focused on taxonomically broad and sparse datasets. Given that our data include most passerine families with relatively sparse sampling within families, we expect biases to be minor. Moreover, most of the species included in our samples have been placed in the phylogeny using genetic data ($N = 1,176$ species).

In each case, results from the 100 models were summarized using Rubin's rules (Nakagawa & de Villemereuil, 2019). This approach enabled us to compute average estimates, their standard errors, associated test statistics (*t* values), degrees of freedom and *p*-values that incorporate phylogenetic uncertainty adjusting for sample sizes (Nakagawa & de Villemereuil, 2019). We also computed 'relative efficiency' which reflects, for each parameter, the efficacy of the process of accounting for phylogenetic uncertainty by comparing the used number of phylogenies with the theoretical efficacy achieved using an infinite number of phylogenies. This value varies between 0 and 1, and achieving values above 0.99 is recommended (Nakagawa & de Villemereuil, 2019). We achieved this level with 100 phylogenies for all models and parameters, adequately capturing phylogenetic uncertainty in our analyses. In some cases (see Tables S1–S14), a few models (all <10) failed to converge and were discarded, but relative efficiency values were still >0.99.

Because some of the explanatory variables had missing values, sample sizes differed between datasets. We therefore compiled two main datasets. For dataset 1 ($N = 1,266$ species), we subset the data to include the following: body mass, latitude, temperature, precipitation, insolation, habitat openness, delayed plumage maturation, sexual dichromatism and migration distance. For dataset 2 ($N = 860$ species), we included the variables mentioned above plus time nestlings spent in the nest. For each dataset, we ran models including each explanatory variable as sole predictor and one model with all variables together. However, we could not fit all covariates in the same model due to high levels of collinearity between latitude and temperature ($r = -0.83$), latitude and insolation ($r = 0.60$) and temperature and insolation ($r = 0.77$). We therefore fitted three alternative models: one with latitude, one with temperature and one with insolation. Finally, we re-ran these three multivariate models for a subset of dataset 1, eliminating species for which moult information was more limited ($N = 245$) to check whether results changed.

All explanatory variables were centred and scaled. For all models, we computed two values of R^2 using function 'R2.lik' from the package 'RR2' (Ives & Li, 2018). This function compares the likelihood of the focal model with a null model. We compared it to two different null models: (a) a simple logistic regression without covariates and without accounting for the effect of phylogeny and (b) a phylogenetic logistic regression without covariates. Thus, the first R^2 value should quantify the effects of both covariates and phylogeny (equivalent to $R^2_{\text{conditional}}$), while the second estimates the contribution of covariates independent of phylogeny (equivalent to R^2_{marginal}).

3 | RESULTS

We obtained information on post-juvenile moult for 1,315 species belonging to 83 of the 97 families of passerine birds. Of those, 214 species (16.3%) had complete post-juvenile moult, 105 (8.0%) had partial or complete post-juvenile moult and 996 (75.7%) had partial post-juvenile moult. The occurrence of complete post-juvenile moult was much more common in certain bird families than in others (Figure 1). The phylogenetic signal for binary traits D averaged 0.014 across 100 phylogenies (range: −0.015 to 0.046), which is indicative of a strong phylogenetic structure. Permutation tests indicated that values of D were not significantly different from 0 (Brownian motion, average $p = 0.48$, range: 0.37–0.58), but were always significantly different from 1 (random pattern, all $p < 0.001$).

The analysis of transition rates between states suggests that transitions from partial to complete post-juvenile moult occurred at a much lower rate (average: 0.0084, range: 0.007–0.01) than the reverse (average: 0.024, range: 0.019–0.03), and the model allowing different transition rates was better supported than the equal-rates model (likelihood-ratio test across all phylogenies, mean $\text{chi}^2 = 26.98$, all $p < 0.001$). This analysis also revealed that the most likely state at the root of the phylogeny was partial post-juvenile moult (probability of root being partial moult, average 0.85, range: 0.75–0.92). Similarly, stochastic mapping also suggests that the ancestral trait for passerines was partial post-juvenile moult, and that complete post-juvenile moult has been gained independently multiple times and often lost (Figure 1, e.g. Alaudidae, Hirundinidae, Furnariidae, etc.). On average, across the 100 stochastic mapping reconstructions and phylogenies, shifts from partial to complete happened 98 times and from complete to partial 88 times.

Logistic phylogenetic regressions using the most complete dataset (dataset 1, $N = 1,266$, of which 313 species are classified as having complete post-juvenile moult) revealed that complete post-juvenile moult is more prevalent in (a) species found at lower latitudes (Figure 2c,l), in warm (Figure 2d,l) and wet regions (Figure 2g,l), (b) species that inhabit open habitats (Figure 2f,l), (c) species where first-year males resemble adults in appearance (species without delayed plumage maturation, Figure 2j,l) and (d) species with higher levels of sexual dichromatism (Figure 2i,l). Full model results are provided in Tables S1–S3.

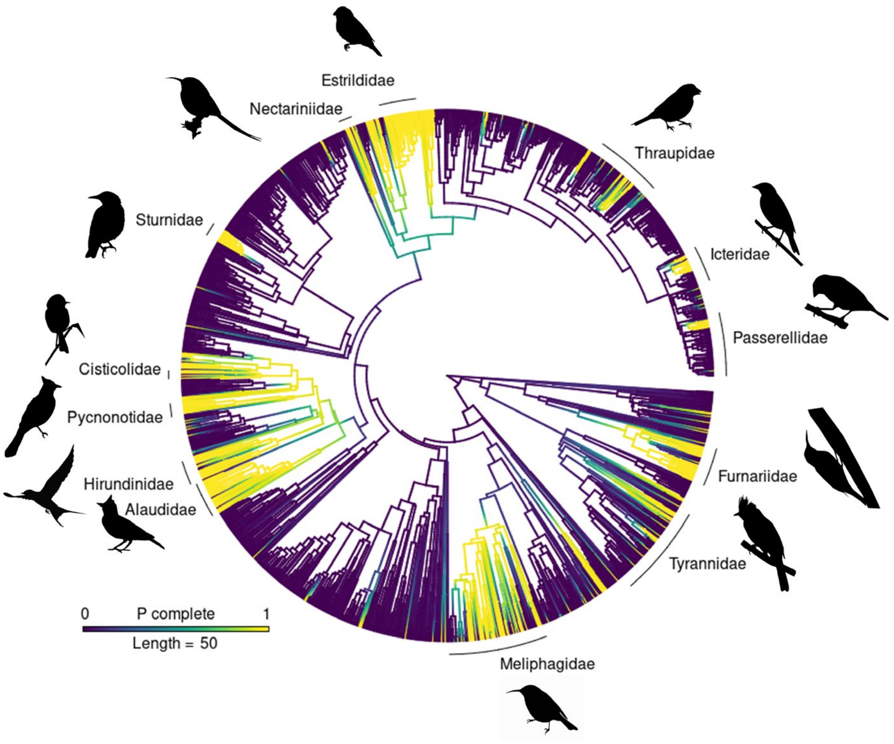


FIGURE 1 Phylogenetic distribution of post-juvenile moult types for 1,315 species of passerine birds. Ancestral state reconstruction based on 100 stochastic mappings on one example phylogeny (for the purpose of illustration), where the colour palette represents ancestral trait reconstruction depicting the probability of having complete post-juvenile moult (yellow = 1). Intermediate colour values represent uncertainty surrounding the location of evolutionary transitions in the phylogeny. Silhouettes (retrieved from www.phylopic.org) represent some selected families with high prevalence of complete post-juvenile moult. The length of the colour palette represents 50 million years on the phylogeny

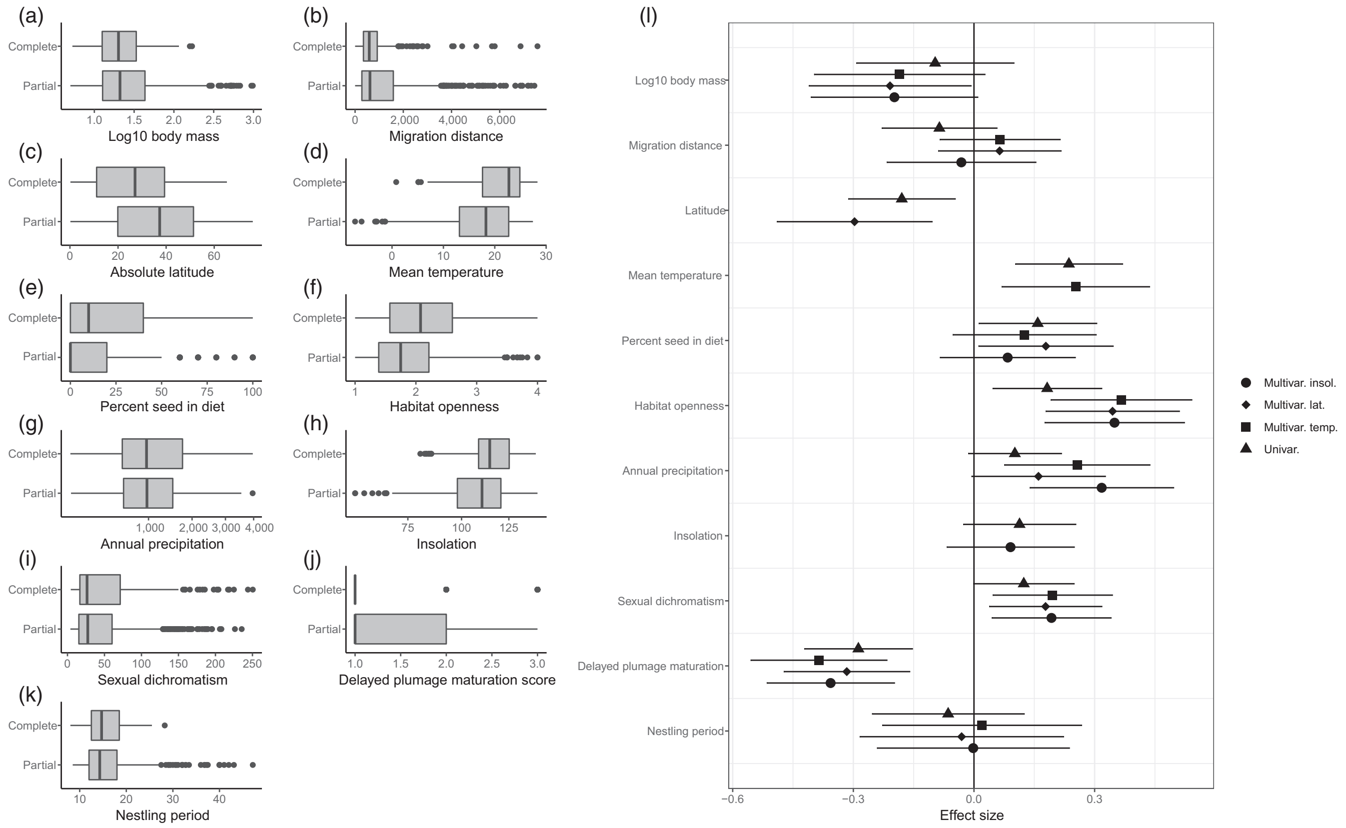


FIGURE 2 Boxplots (a–k) of raw data without phylogenetic correction showing differences between species with partial and complete post-juvenile moult, and a forest plot (l) depicting effects and 95% CIs of explanatory variables included in the phylogenetic logistic regression models. Because there were many missing values in one covariate (nestling period), we carried out the analyses on two datasets: dataset 1 (*N* = 1,266 species), included all covariates except for the duration of the nestling period, and dataset 2 (*N* = 860 species) which also included nestling period. In addition, due to collinearity, latitude, insolation and annual mean temperature could not be included in the same model and were fitted in three separate models. Full model results and output can be found in Tables S1–S7. Boxplots show median and interquartile ranges and outliers (black dots); in the forest plots 95% CIs that do not overlap 0 correspond to statistically significant effects ($p < 0.05$)

Smaller species, and species that feed on seeds were more likely to have complete post-juvenile moult, but these effects were generally not statistically significant (Figure 2l). There were no statistically significant effects of insolation or migration distance (Figure 2l). The phylogenetic signal was strong in all cases, as indicated by the small values of alpha (0.02–0.03, see Tables S1–S14). Multivariate models accounted for ~54% of the variation in post-juvenile moult type (multivariate models with latitude or temperature, $R^2_{\text{conditional}} = 0.54$), but most of this is due to shared phylogenetic history. The explanatory variables together explained 12%–14% of the variation in moult pattern. Out of the three multivariate models tested, the one with latitude had the lowest AICc value (860, Table S1), followed by the model with temperature (AICc = 864, Table S2) and the insolation model (AICc = 873, Table S3). Fitting explanatory variables as single predictor variables yielded qualitatively similar effects, but these were not always statistically significant (e.g. sexual dichromatism, Figure 2l, Table S4). Restricting the dataset to include species for which there was also information on the length of the nestling period (dataset 2, *N* = 860, of which 213 species with complete post-juvenile moult) revealed that species with fast-growing nestlings were not more likely to have complete post-juvenile moult (Figure 2k,l, full model results are shown in Tables S5–S7).

We assessed the robustness of our results through three additional analyses: (a) using an alternative moult classification, (b) excluding species where moult data are more limited and (c) excluding long-distance migratory species to assess whether potential inaccuracies in the computation of their climatic variables is driving climatic effects in the analyses. (a) We used an alternative classification of moult by scoring whether there is complete moult before first breeding regardless of moult type. This analysis shows similar results (Tables S8–S10), except for the migration distance effect, which becomes statistically significant, suggesting that a complete moult before the first breeding season is more likely in species with longer migration distances. (b) We eliminated species for which moult information was based on limited information (*N* = 1,021 species, 245 species excluded). The results were similar (Tables S11–S13), except for the sexual dichromatism effect, which became statistically non-significant. (c) We excluded long-distance migratory species to assess the effect of potential inaccuracies in the climatic variables. However, the effects of temperature and rainfall did not change (Table S14), suggesting that our conclusions are robust.

4 | DISCUSSION

Our survey across >1,300 species, which includes members of most families of passerines, revealed that nearly 25% of the species have at least some individuals or populations that carry out a complete post-juvenile moult. Ancestral trait reconstructions indicate that complete post-juvenile moult has been gained and lost multiple times and is highly phylogenetically conserved (Figure 1a). Our comparative analyses identified several ecological, environmental and life-history predictors that together account for >10% of the variation in the extent of the post-juvenile moult (considered as a binary trait: partial vs. complete; Figure 2). Our results show an increased prevalence of complete moult in warm, favourable environmental conditions with low-resource seasonality, confirming earlier work (Kiat & Izhaki, 2016), and indicating the importance of constraints. However, our study also indicates the important roles of plumage degradation and visual signalling, highlighting the selective pressures that favour complete post-juvenile moult (Figure 3).

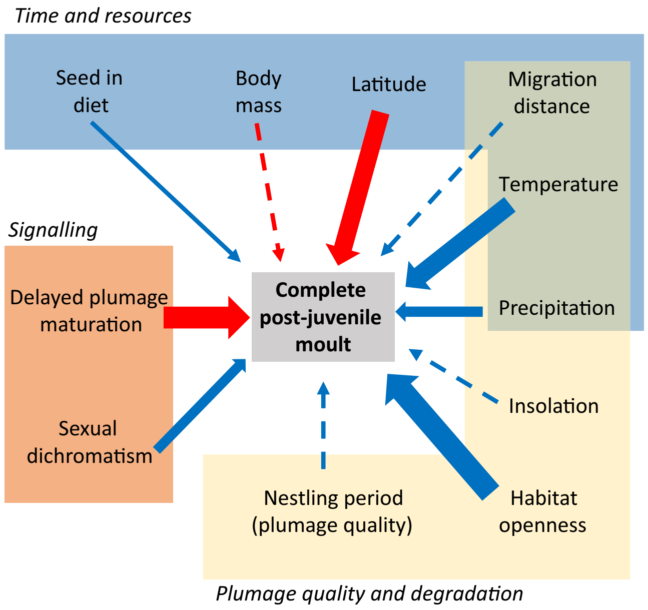


FIGURE 3 Summary of effects associated with complete post-juvenile moult in passerine birds. Arrow thickness represents the strength of the effect (blue positive effects and red negative effects) and dashed lines represent non-significant effects based on Figure 2l. Effects have been grouped into three broad categories: constraints imposed by available time and food resources (light blue), selective forces associated with plumage quality and degradation (light yellow) and selective forces associated with the ornamental signalling functions of plumage (orange)

We hypothesized that lower-quality juvenile plumage and conditions that foster rapid plumage degradation should constitute strong selective factors favouring a complete post-juvenile moult. The quality of plumage in young birds varies greatly and is positively correlated with the time they spend in the nest (Callan et al., 2019). However, our data clearly show that species with shorter nestling periods are not more likely to have a complete post-juvenile moult (Figure 2), despite their presumed poorer quality plumage. This is surprising given that previous work detected clear associations between feather quality and post-juvenile moult (Kiat & Izhaki, 2016; Kiat & Sapir, 2018). By necessity, due to data availability, we used a proxy of feather quality (nestling period) rather than feather quality itself and this could have weakened our inference. Moreover, it is possible that the direction of causation is reversed, meaning that increased quality of nest-grown plumage is an evolutionary response to partial post-juvenile moult (Kiat & Sapir, 2018). Rigorous tests of these ideas, which allow general conclusions beyond Western

Palearctic species (Kiat & Izhaki, 2016; Kiat & Sapir, 2018), will require more data on feather quality.

Plumage degradation is continuous and starts already in the nest, in part through the action of feather-degrading bacteria (Azcárate-García et al., 2020), which are more active and prevalent in warm and humid environments (Burtt & Ichida, 2004). Accordingly, we found that both temperature and, to a lesser extent, precipitation correlated positively with the likelihood of complete post-juvenile moult (Figure 2). Our study thus suggests that increased risk of feather degradation may favour the evolution of complete post-juvenile moult. Feathers also degrade through exposure to sunlight (Bergman, 1982; Surmacki et al., 2011; Test, 1940), and our analyses revealed that species living in open environments, which are more exposed to sunlight, are more likely to have a complete post-juvenile moult (Figure 2k). Following this logic, we also expected that species living in regions with higher levels of solar radiation would be more likely to undergo a complete post-juvenile moult. However, this was not the case: the effect of insolation was positive but clearly not statistically significant (Figure 2). Because the effect of insolation may apply mainly to species living in open habitats, we further tested for a positive interaction between insolation and habitat openness, but the interaction was negative and not statistically significant ($t = -1.045$, $p = 0.29$). Alternatively, the association between complete post-juvenile moult and habitat openness may not only be caused by faster feather degradation in open habitats but also because birds inhabiting such environments rely more on their flying abilities to escape predators, display (Menezes & Santos, 2020) or forage, than species living in closed environments (Guallar et al., 2009). A complete post-juvenile moult would ensure a less worn plumage ready to cope with these challenges during their first year.

The lack of an insolation effect was unexpected, in particular, because insolation strongly correlated with temperature and latitude (see Section 2), two covariates that are linked to complete post-juvenile moult in previous (Kiat & Izhaki, 2016) and in our analyses (Figure 2). Latitudinal gradients in the prevalence of complete post-juvenile moult have been interpreted as evidence that warmer, tropical climates with lower seasonality impose less stringent temporal constraints on post-juvenile moult because environmental conditions do not deteriorate as rapidly as in temperate regions after the summer (Kiat & Izhaki, 2016). Our results are consistent with this interpretation, as are studies of intraspecific variation in moult extent, which reveal that individuals from populations living at lower latitudes and in warmer regions often show more extensive post-juvenile moults (Chabot et al., 2018; Christmas et al., 1989; Ginn & Melville, 1983; Jenni & Winkler, 1994; Rockey, 2016). Furthermore, Kiat et al. (2019) showed that the extent of post-juvenile increased over time in several species of passerines, most likely as a result of climate warming. Warmer or milder climatic conditions allow for earlier breeding (one of the best-documented effects of climate change; Scheffers et al., 2016), resulting in earlier fledging which leads to an earlier start of the post-juvenile moult. Both correlational and experimental data show that birds that start moulting earlier in the year moult slower and achieve more extensive post-juvenile moults (Rymkevich & Bojarinova, 1996; Ryzhanovskiy, 2017; Serra et al., 2007).

Our results provide macro-evolutionary support for the hypothesis that time constraints constitute an important factor explaining variation in the completeness of post-juvenile moult. We also predicted that species that eat mostly seeds—a resource that should decline less rapidly in late summer than insects or fruit—should be more likely to evolve complete post-juvenile moult (Kiat & Izhaki, 2016). While the effect was in the predicted direction, it was not statistically significant in all models (Figure 2). Two other factors associated with time constraints, namely body size (large species moult slower; Rohwer et al., 2009) and migration distance (long-distant migrants are under stronger time constraints; Kiat & Izhaki, 2016; Kiat & Sapir, 2017) did not show statistically significant effects (Figure 2). While the body mass effect was in the expected direction (negative), the effect of migration distance tended to be positive in the multivariate models (Figure 2l). Thus, rather than acting as a constraint, longer migration distances tend to favour the evolution of complete post-juvenile moult. One possibility is that species that migrate farther require plumage in top condition to complete their journeys, and this should apply to flight feathers in particular. Hence, we further tested this idea by focusing on whether species moult all primaries during their post-juvenile moult (obviously, all species with complete post-juvenile moult all primaries, but 97 species with partial post-juvenile moult do so as well). Repeating the analyses in Figure 2 using complete primary moult (no/yes) as response variable revealed that the effect of migration distance was clearly not statistically significant. However, the effect of migration distance became statistically significant when we used an alternative moult classification that indicated whether or not a species carries out a complete moult before their first breeding season (either a complete post-juvenile moult or a complete nuptial moult; Tables S8–S10). We note that the main difference between the two moult classifications stems from the fact that many long-distance migratory species that carry out only a partial post-juvenile moult, perform a complete nuptial moult in their tropical wintering grounds. A complete moult in these species might be more likely because of favourable conditions (reduced constraints; Kiat & Sapir, 2018) while new plumage may be advantageous to successfully complete the spring migration (selective advantage). Thus, although the effect is not clear in all analyses, our results suggest that migration distance may play a role in shaping moult strategies during the first year.

Beyond the constraints imposed by the available resources (food and time) and the feather-degradation potential of the environment, our results also suggest that the signalling functions of the plumage may have played a role in the evolution of complete post-juvenile moult. One of the strongest predictors of complete post-juvenile moult was the occurrence of delayed plumage maturation (DPM), whereby species with DPM were less likely to have a complete post-juvenile moult (Figure 2). In species with DPM, first-cycle males differ markedly in colouration from older males, and these young males usually have lower mating success or forego reproduction entirely, but benefit from reduced aggressive interactions with older males (Greene et al., 2000; Hawkins et al., 2012; Senar et al., 1998). If there is less pressure to look attractive in the first breeding season, replacing all juvenile feathers (often differently coloured from the adult plumage) during the post-juvenile moult may not be beneficial, and hence sexual selection on the extent of post-juvenile moult would be relaxed. In some species, a partial post-juvenile moult may also provide a flexible mechanism for individuals to signal lower status in the same way as DPM, but allowing other—presumably higher-quality individuals—to achieve a more extensive moult and more adult-like plumage, possibly at the expense of increased aggression by older males (López et al., 2005; Senar et al., 1998).

In species without DPM, on the other hand, first-year males may benefit from erasing any subtle cues of age (e.g. moult limits, the differences between old and newly moulted feathers), associated with partial post-juvenile moult. Resembling adults may be more important if the potential rewards are high, for instance, when sexual selection on males is stronger. Indeed, we found that sexual dichromatism—a proxy for the intensity of sexual selection on male birds (Dale et al., 2015; Dunn et al., 2001)—correlates positively with the likelihood of a complete post-juvenile moult (Figure 2). Because the effects of sexual selection intensity should be more marked in species without DPM, one could also predict a negative interaction between DPM and sexual dichromatism. However, our analyses do not support this idea: the interaction term was positive and not statistically significant ($t = 1.16$, $p = 0.24$). Thus, the effects of DPM and of sexual dichromatism seem largely independent of each other, although the sexual dichromatism effect is only statistically significant after accounting for the effects of DPM and other covariates (Figure 2l).

Consistent with the hypothesis that sexual selection affects moult, males moult more extensively than females in many (Bojarinova et al., 1999; Crates et al., 2015; Illera & Atienza, 2002; Jenni & Winkler, 1994; Kiat et al., 2019; Senar et al., 1998) but not all (Jenni & Winkler, 1994; Kiat et al., 2019; Pérez-Granados, 2020) species with partial post-juvenile moult. This suggests that stronger sexual selection on males may have led to sexual dimorphism in moult extent. Thus, we could envision a scenario where strong sexual selection favours more extensive post-juvenile moult, possibly because moulting more feathers signals higher quality (Gosler, 1991; Minias & Iciek, 2013; Minias et al., 2015; Pagani-Núñez & Hernández-Gómez, 2013; Vagasi et al., 2012, but see Crates et al., 2015). Within species, individuals that moult earlier in the season usually moult more slowly and more extensively (Rymkevich & Bojarinova, 1996; Ryzhanovskiy, 2017; Serra et al., 2007), which, in turn, may produce both higher-quality plumage (Dawson et al., 2000) and more colourful feathers (Ferns & Hinsley, 2008; Griggio et al., 2009; Serra et al., 2007). As a consequence, strong directional selection on ornamental plumage may result in complete post-juvenile moult in males, and also in females, either due to genetic correlation or through sexual or social selection acting directly on females (Tobias et al., 2012). Puzzlingly, the extent of post-juvenile moult increased more in females than in males in response to historical climate warming trends, at least in a few sexually dichromatic species (Kiat et al., 2019), suggesting that moult in females may be more sensitive to environmental variation. Finally, while many species develop their first-year plumage colours during the post-juvenile moult, some species do so in a different moulting event, referred to as the nuptial or pre-breeding moult. Interestingly, species that change into breeding colours by means of a nuptial moult show remarkable parallels with those that undergo a complete post-juvenile moult: nuptial moult is also more prevalent in species with more marked sexual dichromatism (Mcqueen et al., 2019).

In sum, our analyses show that a combination of multiple, fundamentally different mechanisms, explain sizeable amounts of variation (>10%) in the extent of post-juvenile moult between species (Figure 3). Our results clearly highlight that constraints faced by young birds during their first independent moult (time and food) are important, but are not the only factors that determine whether a species undergoes a complete post-juvenile moult. Variation between species in the strength of natural and sexual selection acting on functional or ornamental roles of plumage has important effects as well, and suggests that the extent of post-juvenile moult is not simply the outcome of a best-of-a-bad-job situation. In particular, we provide evidence for the surprisingly strong effects of delayed plumage maturation and sexual selection, which seem to have pervasive effects shaping the evolution of different types of moult in birds (Figuerola & Jovani, 2002; Mcqueen et al., 2019; Peters et al., 2013).

ACKNOWLEDGEMENTS

We are indebted to the following colleagues that assisted with securing information on post-juvenile moult: Hyun-Young Nam (Migratory Bird Centre, Korea National park Research Institute, Wonju, Korea), Chang-Yong Choi (College of Agriculture and Life Sciences, Seoul National University Seoul, Korea), Noboru Nakamura (Bird Migration Research Centre, Yamashina Institute for Ornithology Japan) and Marc Herremans (Natuurpunt, Mechelen, Belgium). We thank the Associate Editor, two anonymous reviewers and Y. Kiat for constructive comments. The authors declare no conflicts of interest. Open access funding enabled and organized by Projekt DEAL.

AUTHORS' CONTRIBUTIONS

B.K. and K.D. conceived the study; K.D., S.G., R.R.-H., M.V. and D.W. collected the data; K.D. and M.V. analysed the data; K.D. and B.K. wrote the manuscript with input from all co-authors.

DATA AVAILABILITY STATEMENT

The data are available at https://doi.org/10.6084/m9.figshare.12925895.v1 (Delhey et al., 2020).

ORCID

Kaspar Delhey https://orcid.org/0000-0001-5190-5406
Santiago Guallar https://orcid.org/0000-0002-1121-1968

Mihai Valcu https://orcid.org/0000-0002-6907-7802
Daiping Wang https://orcid.org/0000-0002-9045-051X
Bart Kempenaers https://orcid.org/0000-0002-7505-5458

REFERENCES

Azcárate-García, M., González-Braojos, S., Díaz-Lora, S., Ruiz-Rodríguez, M., Martín-Vivaldi, M., Martínez-Bueno, M., Moreno, J., & Soler, J. J. (2020). Interspecific variation in deterioration and degradability of avian feathers: The evolutionary role of microorganisms. *Journal of Avian Biology*, *2020*, e02320. https://doi.org/10.1111/jav.02320

Barta, Z., Houston, A. I., McNamara, J. M., Welham, R. K., Hedenström, A., Weber, T. P., & Feró, O. (2006). Annual routines of non-migratory birds: Optimal moult strategies. *Oikos*, *112*, 580–593. https://doi.org/10.1111/j.0030-1299.2006.14240.x

Baston, D. (2020). *exactextractr: Fast extraction from raster datasets using Polygons*. R package version 0.2.1.

Beauchamp, G. (2003). Delayed maturation in birds in relation to social foraging and breeding competition. *Evolutionary Ecology Research*, *5*, 589–596.

Bergman, G. (1982). Why are the wings *Larus f. fuscus* so dark? *Ornis Fenn*, *59*, 77–83.

Bojarinova, J. G., Lehikoinen, E., & Eeva, T. (1999). Dependence of postjuvenile moult on hatching date, condition and sex in the great tit. *Journal of Avian Biology*, *30*, 437–446. https://doi.org/10.2307/3677016

Brooks, R., & Kemp, D. J. (2001). Can older males deliver the good genes? *Trends in Ecology & Evolution*, *16*, 308–313. https://doi.org/10.1016/S0169-5347(01)02147-4

Burtt, E. H., & Ichida, J. M. (2004). Gloger's Rule, feather-degrading bacteria, and color variation among song sparrows. *The Condor*, *106*, 681–686. https://doi.org/10.1650/7383

Callan, L. M., La, S. F. A., Martin, T. E., & Rohwer, V. G. (2019). Higher nest predation favors rapid fledging at the cost of plumage quality in nestling birds. *The American Naturalist*, *193*(5), 717–724. https://doi.org/10.1086/702856

Chabot, A. M. Y. A., Hobson, K. A., Craig, S., & Lougheed, S. C. (2018). Moult in the Loggerhead Shrike *Lanius ludovicianus* is influenced by sex, latitude and migration. *Ibis*, *160*, 301–312. https://doi.org/10.1111/ibi.12551

Christmas, S. E., Christmas, T. J., & Parr, A. J. (1989). Geographical variation in greater covert moult in first winter Coal Tits *Parus ater*. *Bird Study*, *36*, 88–90. https://doi.org/10.1080/00063658909477009

Cleasby, I. R., & Nakagawa, S. (2012). The influence of male age on within-pair and extra-pair paternity in passerines. *Ibis*, *154*(2), 318–324. https://doi.org/10.1111/j.1474-919X.2011.01209.x

Cooney, C. R., Sheard, C., Clark, A. D., Healy, S. D., Liker, A., Street, S. E., Troisi, C. A., Thomas, G. H., Székely, T., Hemmings, N., & Wright, A. E. (2020). Ecology and allometry predict the evolution of avian developmental durations. *Nature Communications*, *11*, 2383. https://doi.org/10.1038/s41467-020-16257-x

Cramp, S., & Simmons, K. E. L. (1977). *Handbook of the birds of Europe, the Middle East and North Africa: The birds of the Western Palearctic*. Oxford University Press.

Crates, R. A., Sheldon, B. E. N. C., & Garroway, C. J. (2015). Causes and consequences of individual variation in the extent of post-juvenile moult in the blue tit *Cyanistes caeruleus* (Passeriformes: Paridae). *Biological Journal of the Linnean Society*, *116*, 341–351.

Dale, J., Dey, C., Delhey, K., Kempenaers, B., & Valcu, M. (2015). The effects of life-history and social selection on male and female plumage coloration. *Nature*, *527*, 367–370. https://doi.org/10.1038/nature15509

Dawson, A., Hinsley, S. A., Ferns, P. N., Bonser, R. H. C., & Eccleston, L. (2000). Rate of moult affects feather quality: A mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society B: Biological Sciences*, *267*, 2093–2098. https://doi.org/10.1098/rspb.2000.1254

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., & de Juana, E. (Eds.). (2018). *Handbook of the birds of the world alive*. Lynx Edicions.

Delhey, K., Dale, J., Valcu, M., & Kempenaers, B. (2019). Reconciling ecogeographical rules: Rainfall and temperature predict global colour variation in the largest bird radiation. *Ecology Letters*, *22*, 726–736. https://doi.org/10.1111/ele.13233

Delhey, K., Guallar, S., Rueda-Hernández, R., Valcu, M., Wang, D., & Kempenaers, B. (2020). Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. *figshare*, https://doi.org/10.6084/m9.figshare.12925895.v1

Dufour, P., Descamps, S., Chantepie, S., Renaud, J., Guéguen, M., Schiffers, K., Thuiller, W., & Lavergne, S. (2020). Reconstructing the geographic and climatic origins of long – Distance bird migrations. *Journal of Biogeography*, *47*(1), 155–166. https://doi.org/10.1111/jbi.13700

Dunn, P. O., Whittingham, L. A., & Pitcher, T. E. (2001). Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*, *55*, 161–175. https://doi.org/10.1554/0014-3820(2001)055[0161:MSSCAT]2.0.CO;2

Dunning, J. B. J. (2008). *CRC handbook of avian body masses* (2nd ed.). CRC Press Taylor & Francis Group.

Faccio, M. S. (2018). Tropical frugivorous birds molt and breed in relation to the availability of food resources. *Ornitol Neotrop*, *29*, S11–S18.

Ferns, P. N., & Hinsley, S. A. (2008). Carotenoid plumage hue and chroma signal different aspects of individual and habitat quality in tits. *Ibis*, *150*, 152–159.

Figuerola, J., & Jovani, R. (2002). Ecological correlates in the evolution of moult strategies in Western Palearctic passerines. *Evolutionary Ecology*, *15*, 183–192.

Fogden, M. P. L. (1972). The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis*, *14*, 307–343.

Fritz, S. A., & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, *24*, 1042–1051. https://doi.org/10.1111/j.1523-1739.2010.01455.x

Ginn, H. B., & Melville, D. S. (1983). *Moult in birds*. British Trust for Ornithology.

Gosler, A. G. (1991). On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the Great Tit *Parus major*. *Bird Study*, *38*(1), 9. https://doi.org/10.1080/00063659109477061

Greene, E., Lyon, B. E., Muehter, V. R., Ratcliffe, L., Oliver, S. J., & Boag, P. T. (2000). Disruptive sexual selection for plumage coloration in a passerine bird. *Nature*, *407*, 1000–1003. https://doi.org/10.1038/35039500

Griffin, R. H. (2018). *btw: Run BayesTraitsV3 from R*. R package version 2.0.

Griggio, M., Serra, L., Licheri, D., Campomori, C., & Pilastro, A. (2009). Moult speed affects structural feather ornaments in the blue tit. *Journal of Evolutionary Biology*, *22*, 782–792. https://doi.org/10.1111/j.1420-9101.2009.01700.x

Guallar, S., Santana, E., Sierra, B., Verdugo, H., & Gallés, A. (2009). *Paseriformes del Occidente de México: Morfometría, datación y sexado*.

Hawkins, G. L., Hill, G. E., & Mercadante, A. (2012). Delayed plumage maturation and delayed reproductive investment. *Biological Reviews*, *87*, 257–274.

Heise, C. D., & Moore, F. R. (2003). Age-related differences in foraging efficiency, molt, and fat deposition of gray catbirds prior to autumn migration. *Condor*, *105*, 496–504. https://doi.org/10.1093/condor/105.3.496

Howell, S. N. G., Corben, C., Pyle, P., & Rogers, D. I. (2003). The first basic problem: A review of molt and plumage homologies. *Condor*, *105*, 635–653. https://doi.org/10.1650/7225

Hoy, S. R., Petty, S. J., Millon, A., Whitfield, D. P., Marquiss, M., Davison, M., & Lambin, X. (2015). Age and sex-selective predation moderate the overall impact of predators. *Journal of Animal Ecology*, *84*, 692–701. https://doi.org/10.1111/1365-2656.12310

Illera, J. C., & Atienza, J. C. (2002). Determinacion del sexo y la edad en la Tarabilla Canaria Saxicola dacotiae mediante el estudio de la muda. *Ardeola*, *49*, 273–281.

Ives, A. R., & Garland, T. (2010). Phylogenetic logistic regression for binary dependent variables. *Systematic Biology*, *59*, 9–26. https://doi.org/10.1093/sysbio/syp074

Ives, A. R., & Li, D. (2018). rr2: An R package to calculate R^2s for regression models. *Journal of Open Source Software*, *3*, 1028. https://doi.org/10.21105/joss.01028

Jenni, L., & Winkler, R. (1994). *Moult and ageing of European passerines*. Academic Press.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*, 444–448. https://doi.org/10.1038/nature11631

Johnson, E. I., & Wolfe, J. D. (2017). *Molt in neotropical birds: Life-history and aging criteria*. Taylor & Francis.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 1–20. https://doi.org/10.1038/sdata.2017.122

Kiat, Y. (2018). Divergent rectrix moult: The implications and conditions of moult sequence. *Journal of Avian Biology*, *2018*, e01609. https://doi.org/10.1111/jav.01609

Kiat, Y., & Izhaki, I. (2016). Why renew fresh feathers? Advantages and conditions for the evolution of complete post-juvenile moult. *Journal of Avian Biology*, *47*, 47–56. https://doi.org/10.1111/jav.00717

Kiat, Y., & Sapir, N. (2017). Age-dependent modulation of songbird summer feather molt by temporal and functional constraints. *The American Naturalist*, *189*, 184–195. https://doi.org/10.1086/690031

Kiat, Y., & Sapir, N. I. R. (2018). Life-history trade-offs result in evolutionary optimization of feather quality. *Biological Journal of the Linnean Society*, *125*, 613–624. https://doi.org/10.1093/biolinnean/bly135

Kiat, Y., Vortman, Y., & Sapir, N. (2019). Feather moult and bird appearance are correlated with global warming over the last 200 years. *Nature Communications*, *10*, 2540. https://doi.org/10.1038/s41467-019-10452-1

López, G., Figuerola, J., Varo, N., & Soriguer, R. (2005). White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed. *Ardea*, *93*, 237–244.

Marchant, S., & Higgins, P. J. (1990). *Handbook of Australian, New Zealand and Antarctic Birds* (Vol. 5–7). Oxford University Press.

Mcqueen, A., Kempenaers, B., Dale, J., Valcu, M., Emery, Z. T., Dey, C. J., Peters, A., Delhey, K. (2019). Evolutionary drivers of seasonal plumage colours: Colour change by moult correlates with sexual selection, predation risk and seasonality across passerines. *Ecology Letters*, *22*(11), 1838–1849. https://doi.org/10.1111/ele.13375

Menezes, J. C. T., & Santos, E. S. A. (2020). Habitat structure drives the evolution of aerial displays in birds. *Journal of Animal Ecology*, *89*, 482–493. https://doi.org/10.1111/1365-2656.13132

Minias, P., & Iciek, T. (2013). Extent and symmetry of post-juvenile moult as predictors of future performance in Greenfinch *Carduelis chloris*. *Journal of Ornithology*, *154*, 465–468. https://doi.org/10.1007/s10336-012-0911-6

Minias, P., Włodarczyk, R., Surmacki, A., & Iciek, T. (2015). Silver spoon effects on plumage quality in a passerine bird. *Royal Society Open Science*, *2*, 140459. https://doi.org/10.1098/rsos.140459

Naef-Daenzer, B., & Gruebler, M. U. (2016). Post-fledging survival of altricial birds: Ecological determinants and adaptation. *Journal of Field Ornithology*, *87*, 227–250. https://doi.org/10.1111/jofo.12157

Nakagawa, S., & de Villemereuil, P. (2019). A general method for simultaneously accounting for phylogenetic and species sampling uncertainty via Rubin's rules in comparative analysis. *Systematic Biology*, *68*, 632–641. https://doi.org/10.1093/sysbio/syy089

Newton, I. (2009). Moult and plumage. *Ringing & Migration*, *24*(3), 220–226. https://doi.org/10.1080/03078698.2009.9674395

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018). *caper: Comparative analyses of phylogenetics and evolution in R*. R package version 1.0.1.

Pagani-Núñez, E., & Hernández-Gómez, S. (2013). Extent of post-juvenile moult in wintering Common Chiffchaffs *Phylloscopus collybita* is related to indices of individual quality. *Revista Catalana d'Ornitologia*, *29*, 35–42.

Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *The R Journal*, *10*(1), 439. https://doi.org/10.32614/RJ-2018-009

Pérez-Granados, C. (2020). Post-juvenile and post-breeding moult of the Black Wheatear *Oenanthe leucura* in south-eastern Spain: Slowed down due to climatic aridity? *Ardea*, *108*, 21. https://doi.org/10.5253/arde.v108i1.a6

Peters, A., Kingma, S. A., & Delhey, K. (2013). Seasonal male plumage as a multi-component sexual signal: Insights and opportunities. *Emu*, *113*, 232–247. https://doi.org/10.1071/MU12083

Poole, A. (Ed.). (2005). *The birds of North American online*. Cornell Laboratory of Ornithology. Retrieved from http://bna.birds.cornell.edu/BNA/

Pyle, P. (1997). *Identification guide to North American birds. Part I*. Slate Creek Press.

R Development Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rabosky, D. L. (2015). No substitute for real data: A cautionary note on the use of phylogenies from birth – Death polytomy resolvers for downstream comparative analyses. *Evolution*, *69*, 3207–3216. https://doi.org/10.1111/evo.12817

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Rockey, W. L. (2016). Preformative molt adjustment in phenologically divergent populations of the Lesser Goldfinch (*Spinus psaltria*). *The Wilson Journal of Ornithology*, *128*, 70–74.

Rohwer, S., Ricklefs, R. E., Rohwer, V. G., & Copple, M. M. (2009). Allometry of the duration of flight feather molt in birds. *PLoS Biology*, *7*(6), e1000132. https://doi.org/10.1371/journal.pbio.1000132

Rymkevich, T. A., & Bojarinova, J. G. (1996). Variation in the extent of postjuvenile moult in the Great Tit near Lake Ladoga (Russia). *Bird Study*, *43*, 47–59. https://doi.org/10.1080/00063659609460995

Ryzhanovskiy, V. N. (2017). Completeness of seasonal molting in passerine birds (Aves, Passeriformes) in Northwestern Siberia. *Contemporary Problems of Ecology*, *10*, 502–510. https://doi.org/10.1134/S1995425517050122

Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., & Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, *354*(6313), aaf7671. https://doi.org/10.1126/science.aaf7671

Senar, J. C., Copete, J. L., & Martin, A. J. (1998). Behavioural and morphological correlates of variation in the extent of postjuvenile moult in the Siskin *Carduelis spinus*. *Ibis*, *140*, 661–669. https://doi.org/10.1111/j.1474-919X.1998.tb04712.x

Serra, L., Griggio, M., Licheri, D., & Pilastro, A. (2007). Moult speed constrains the expression of a carotenoid-based sexual ornament. *Journal of Evolutionary Biology*, *20*(5), 2028–2034. https://doi.org/10.1111/j.1420-9101.2007.01360.x

Surmacki, A., Siefferman, L., & Yuan, H.-W. (2011). Effects of sunlight exposure on carotenoid-based and structural coloration of the blue-tailed bee-eater. *The Condor*, *113*(3), 590–596. https://doi.org/10.1525/cond.2011.100167

Test, H. (1940). Effects of natural abrasion and oxidation on the coloration of flickers. *Condor*, *42*, 76–80. https://doi.org/10.2307/1364322

Tobias, J. A., Montgomerie, R., & Lyon, B. E. (2012). The evolution of female ornaments and weaponry: Social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 2274–2293. https://doi.org/10.1098/rstb.2011.0280

Tung Ho, L. S., & Ané, C. (2014). A linear-time algorithm for gaussian and non-gaussian trait evolution models. *Systematic Biology*, *63*, 397–408. https://doi.org/10.1093/sysbio/syu005

Vagasi, C. I., Pap, P. L., Vincze, O., Benkő, Z., Marton, A., & Barta, Z. (2012). Haste makes waste but condition matters: Molt rate – Feather quality trade-off in a sedentary songbird. *PLoS ONE*, *7*, e40651. https://doi.org/10.1371/journal.pone.0040651

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, *95*, 2027. https://doi.org/10.1890/13-1917.1

DATA SOURCES

Alström, P., & Mild, K. (2003). *Pipits and wagtails of Europe, Asia and North America. Identification and systematics*. Christopher Helm.

Barshep, Y., & Manu, S. A. (2013). Breeding phenology and moult of the endemic Bannerman's Weaver *Ploceus bannermani*. *Ostrich*, *84*, 231–233.

Botero-Delgadillo, E., Bayly, N., & Gómez-Montes, C. (2012). Ciclos de muda en Diglossa albilatera (Thraupidae) y evidencia de un patrón en la adquisición del dicromatismo sexual en el género Diglossa. *Bol SAO*, *22*, 10–16.

Craig, A. (1996). The annual cycle of wing-moult and breeding in the Wattled Starling *Creatophora cinerea*. *Ibis*, *138*, 448–454. https://doi.org/10.1111/j.1474-919X.1996.tb08063.x

Diaz, A., & Hernández, F. (2018). Muda preformativa excentrica en un especimen de coleccion de la Tangara azul y amarilla (*Pipraeidaea bonariensis darwinii*, Bonaparte 1983) (AVES: Thraupidae). *The Biologist*, *16*, 273–279.

Dickey, D. R., & Van Rossem, A. J. (1938). *The birds of El Salvador*. Field Museum of Natural History.

DuVal, E. H. (2005). Age-based plumage changes in the lance-tailed manakin: A two-year delay in plumage maturation. *Condor*, *107*, 915–920. https://doi.org/10.1093/condor/107.4.915

Eyckerman, R., & Cuvelier, D. (1982). The moult of some bird species on Mount Cameroon. *Malimbus*, *4*, 1–4.

Ganpule, P. (2019). Field identification of Sand Lark Alaudala raytal and Lesser/Asian Short-toed Lark Alaudala rufescens/cheleensis: An unacknowledged pitfall. *Indian Birds*, *15*, 97–111.

Gauci, C., & Sultana, J. (1979). Moult of the Sardinian warbler. *Il-Meril*, *20*, 1–14.

Gómez, C., Botero-Delgadillo, E., Bayly, N. J., Moreno, M. I., Páez, C. A. (2012). Documentando estrategias de muda en aves Neotropicales: Ejemplos de la Sierra Nevada de Santa Marta, Colombia. *Ornitología Neotropical*, *23*, 129–138.

Guallar, S. X., Rueda-Hernández, R., & Pyle, P. (2021). Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. *Ornithology*, *138*, in press.

Guallar, S., Ruiz-Sánchez, A., Rueda-Hernández, R., & Pyle, P. (2014). Moult topography and its application to the study of partial wing-moult in two neotropical wrens. *Ibis*, *156*, 311–320. https://doi.org/10.1111/ibi.12138

Guallar, S. X., Ruiz-Sánchez, A., Rueda-Hernández, R., & Pyle, P. (2016). Molt strategies of ten neotropical forest passerine species. *The Wilson Journal of Ornithology*, *128*, 543–555. https://doi.org/10.1676/1559-4491-128.3.543

Guallar, S. X., Ruiz-Sánchez, A., Rueda-Hernández, R., & Pyle, P. (2018). Preformative wing molt in 23 Neotropical resident passerine species. *Ornitologia Neotropical*, *29*, 3–10.

Guallar, S., Santana, E., Sierra, B., Contreras, S., Verdugo, H., Gallés, A. (2009). *Paseriformes del Occidente de México: morfometría, datación y sexado*.

Hartley, I., & McGowan, P. (1991). Moult and biometrics in five birds endemic to Palawan, Philippines. *Forktail*, *6*, 74–77.

Hernández, A. (2012). Molt patterns and sex and age criteria for selected landbirds of southwest Colombia. *Ornitologia Neotropical*, *23*, 215–223.

Herremans, M. (1999). Biannual complete moult in the Blacklchested Prinia *Prinia flavicans*. *Ibis*, *141*, 115–124.

Howell, S. N. G., Lewington, I., & Russell, W. (2014). *Rare birds of North America*. Princeton University Press.

Howell, S. N. G., & Webb, S. (1995). *A guide to the birds of Mexico and northern Central America*. Oxford University Press.

Johnson, E. I., & Wolfe, J. D. (2017). *Molt in neotropical birds: Life-history and aging criteria*. Taylor & Francis.

Kamtaeja, S., Suwannapoom, C., Sitasuwan, N., & Chomdej, S. (2015). Moult in the stripe-throated Bulbul, *Pycnonotus finlaysoni*: Sexual differences and timing. *Chiang Mai Journal of Science*, *42*, 339–348.

Kawaji, N., & Hirokawa, J. (1998). Complete post-juvenile moult of the Asian Stubtail *Urosphena squameiceps*. *Bulletin of the Japanese Bird Banding Association*, *13*, 1–7.

Kennedy, J. J., Heavyside, J., Jankowski, J. E., & Scholer, M. N. (2018). Molt patterns and sexing and aging criteria for ten species of high elevation landbirds from southeastern Peru. *Ornitologia Neotropical*, *29*, 63–73.

Kiat, Y., & Izhaki, I. (2015). Post-juvenile moult in Graceful Prinia *Prinia gracilis*. *Ringing & Migration*, *30*, 7–11.

King, J. (1972). Postnuptial and postjuvenal molt in Rufous-collared Sparrows in northwestern Argentina. *Condor*, *74*, 5–16. https://doi.org/10.2307/1366444

Mallet-Rodrigues, F., Castiglioni, G. D. A., & Gonzaga, L. P. (1995). Muda e seqüência de plumagens em Ramphocelus bresilius na restinga de Barra de Maricá, estado do Rio de Janeiro (Passeriformes: Emberizidae). *Ararajuba*, *3*, 88–93.

Nakamura, H. (1979). Summer concentration and moult in the Oriental Greenfinch *Garcluelis sinica*. *Japanese Journal of Ornithology*, *28*, 1–27. https://doi.org/10.3838/jjo1915.28.1

Okahisa, Y., Morimoto, G., Takagi, K., & Ueda, K. (2013). Effect of pre-breeding moult on arrival condition of yearling male Narcissus Flycatchers *Ficedula narcissina*. *Bird Study*, *60*, 140–144.

Park, S.-Y., Seo, S.-G., Nam, H.-Y., Cho, S.-Y., & Jin, K.-S.-S.-J.-Y. (2019). *Moult and ageing of passerines*. Korea National Park Research Institute.

Paxton, E. H., McLaughlin, R., Levins, S., Vanderwerf, E., & Lancaster, N. (2016). *Aging and sexing guide to the forest birds of Hawai 'i Island*. Hilo.

Pinilla, J. (2001). How does the extent of a partial moult vary? Some data for melodious warblers *Hippolais polyglotta* in central Iberia. *Ardeola*, *48*, 81–84.

Prys-Jones, R. P. (1982). Molt and weight of some land-birds on Dominica, West Indies. *Journal of Field Ornithology*, *53*, 352–362.

Pyle, P. (1997). *Identification guide to North American birds. Part I*. Slate Creek Press.

Pyle, P., Engilis, A., Kelt, D. A., & Pyle, P. (2015). *Manual for ageing and sexing birds of Bosque Fray Jorge National Park and Northcentral Chile, with notes on range and breeding seasonality*. Special Publication of the Occasional Papers of the Museum of Natural Science.

Pyle, P., Kayano, K., Tranquillo, K., Murphy, K., Wilcox, B. & Arcilla, N. (2017). *Manual for ageing and sexing landbirds of American Samoa, with notes on molt and breeding seasonality*. The Institute for Bird Populations, Point Reyes Station, California.

Pyle, P., Mcandrews, A., Veléz, P., Wilkerson, R. L., Siegel, R. B., & DeSante, D. F. (2004). Molt patterns and age and sex determination of selected southeastern Cuban landbirds. *Journal of Field Ornithology*, *75*, 136–145.

Radley, P., Crary, A. L., Bradley, J., Carter, C., & Pyle, P. (2011). Molt patterns, biometrics, and age and gender classification of landbirds on Saipan, Northern Mariana Islands. *Wilson Journal of Ornithology*, *123*, 588–594. https://doi.org/10.1676/10-154.1

Round, P. D., Nimnuan, S., Phothieng, D., & Chunkao, K. (2014). Moult in the Asian Pied Starling Sturnus contra floweri population of Thailand. *Forktail*, *30*, 28–33.

Round, P. D., & Rumsey, S. J. (2003). Habitat use, moult and biometrics in the Manchurian Reed Warbler *Acrocephalus tangorum* wintering in Thailand. *Ringing & Migration*, *21*, 215–221.

Ryder, T. B., & Durães, R. (2005). It's not easy being green: Using molt and morphological criteria to age and sex green-plumage manakins (Aves: Pipridae). *Ornitologia Neotropical*, *16*, 481–491.

Salewski, V., Altwegg, R., Erni, B., Falk, K. H., Bairlein, F., & Leisler, B. (2004). Moult of three Palaearctic migrants in their West African winter quarters. *Journal of Ornithology*, *145*, 109–116. https://doi.org/10.1007/s10336-004-0020-2

Smith, C., Walker, L. K., & Ewen, J. G. (2015). Age and sex criteria for the hihi (*Notiomystis cincta*) with additional details on moult patterns. *Notornis*, *62*, 135–142.

Svensson, L. (1992). *Identification guide to European passerines*. L. Svensson.

Tórrez, M. A., & Arendt, W. J. (2016). *La muda en especies de aves de Nicaragua*. UCA Publicaciones.

Ursino, C., Facchinetti, C., & Reboreda, J. C. (2012). Preformative molt in brood parasitic screaming (*Molothrus rufoaxillaris*) and shiny (*M. bonariensis*) cowbirds. *Ornitologia Neotropical*, *23*, 163–171.

Vega-Cortés, N. A. (2017). *Identificación de los eventos de muda y reproducción en aves passeriformes y su relación con las épocas climáticas, en el bosque seco tropical del norte del Tolima*. University of Tolima.

Vellenga, R. E. (1980). Moults of the satin bowerbird *Ptilonorhynchus violaceus*. *Emu*, *80*, 49–54.

Ward, P. (1969). The annual cycle of the Yellow-vented bulbul *Pycnonotus goiavier* in a humid equatorial environment. *Journal of Zoology*, *157*, 25–45. https://doi.org/10.1111/j.1469-7998.1969.tb01687.x

Willoughby, E. J. (1971). Biology of larks (Aves: Alaudidae) in the central Namib Desert. *Zoologica Africana*, *6*, 133–176. https://doi.org/10.1080/00445096.1971.11447408

Wolfe, J. D., Chandler, R. B., & King, D. I. (2009). Molt patterns, age, and sex criteria for selected highland Costa Rican resident landbirds. *Ornitologia Neotropical*, *20*, 451–459.

Wolfe, J. D., Pyle, P., & Ralph, C. J. (2009). Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican resident landbirds. *The Wilson Journal of Ornithology*, *121*(3), 556–567. https://doi.org/10.1676/08-111.1

Yamagishi, S. (1982). Age determination in the Bull-headed Shrike *Lanius bucephalus* based on buff-tips of greater primary coverts. *Journal of the Yamashina Institute for Ornithology*, *14*, 96–102. https://doi.org/10.3312/jyio1952.14.96

Yamashina, Y. (1980). *A natural history of Japanese birds*. Shuppan Kagaku.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Delhey K, Guallar S, Rueda-Hernández R, Valcu M, Wang D, Kempenaers B. Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. *J Anim Ecol.* 2020;89:2896–2908. https://doi.org/10.1111/1365-2656.13354