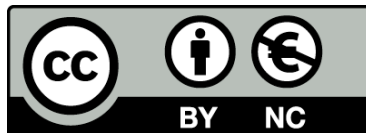




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Individual specialization in foraging and migration strategies in long-lived seabirds

Laura Zango Palau



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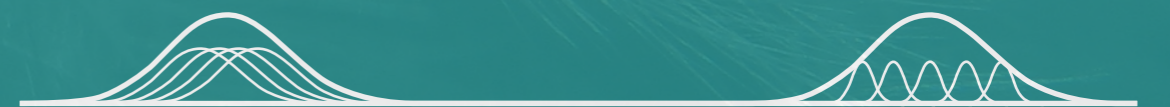
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INDIVIDUAL SPECIALIZATION IN FORAGING AND MIGRATION STRATEGIES IN LONG-LIVED SEABIRDS

2020

LAURA ZANGO PALAU



INDIVIDUAL SPECIALIZATION IN FORAGING AND MIGRATION STRATEGIES IN LONG-LIVED SEABIRDS

Laura Zango Palau

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Ecologia i Ciències Ambientals
Programa de Doctorat en Biodiversitat (HDK04)

INDIVIDUAL SPECIALIZATION IN FORAGING AND MIGRATION STRATEGIES IN LONG-LIVED SEABIRDS

Memòria presentada per

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per optar al grau de Doctora per la Universitat de Barcelona

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Agraïments

Fer una tesi doctoral és com un d'aquests llargs viatges de caminar i motxilla, que són reptes en si mateixos, amb moments d'alegria i fins i tot d'eufòria, i altres moments en els que creus que no hauries de ser allà i que arribes a maleir haver començat. Tot i els moments durs, al final d'aquests viatges sempre t'emportes un bon record, perquè al cap i a la fi has descobert un nou lloc al món, en aquest cas la ciència.

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Hem viscut tants moments que ens hem oblidat que els importants són els que van passant al teu costat.
Moltes gràcies a tots!

Abstract

Individual specialization refers to individuals using different portions of the total ecological niche of the population. The fact that individuals segregate into different strategies has important implications on ecology, evolution and conservation, which can be even greater than the implications associated to differences among species. Therefore, it is important to know the degree of individual specialization in wild populations and in what dimensions of individuals' ecological niche it occurs. Similarly, to understand the processes underlying individual specialization, it is key to study intrinsic drivers and environmental conditions that lead individuals to segregate into different portions of the ecological niche. In this thesis, we aimed to delve into the extent of individual specialization in foraging and migration strategies, as well as to provide insights on the intrinsic and extrinsic drivers that shape it. We used two long-lived seabird species, Cory's (*Calonectris borealis*) and Scopoli's (*C. diomedea*) shearwaters, to study individual specialization in feeding and migratory traits by using stable isotope analyses, global location sensing (GLS) and global positioning system (GPS) loggers. In this thesis, we showed that individuals specialize in several aspects of the ecological niche, namely diet, foraging and wintering grounds, habitat use, daily habits and foraging movements. However, in none of these traits individuals showed high levels of specialization, thus suggesting a stabilizing selection in specialization levels. Regarding intrinsic drivers, our results elucidate that males and females can differ in their degree of individual specialization in diet and foraging movements. These differences were probably driven by a higher use of males on fishery discards. We also showed that the same individual can develop different strategies under different habitats, indicating individual foraging strategies are likely learned with experience when individuals are young and not driven by intrinsic constraints, such as physiological or morphological constraints. Regarding the extrinsic drivers, we provide evidences that resource scarcity is more relevant in driving among-individual variability in foraging movements than resource predictability. Overall, in this thesis we demonstrate that the extent of individual specialization within populations can depend on several intrinsic and extrinsic factors, and that individual specialization is a complex phenomenon that can vary across species and ecological traits. The fact that individuals can develop different strategies independently in different areas indicates a remarkable plasticity that may help them to cope with future natural or anthropogenic changes in the environment.

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General introduction



General introduction

1. Ecological niche and individual specialization

The ecological niche describes a multidimensional space integrated by all ecological requirements that enable a species to persist (Hutchinson, 1957). These factors can be abiotic, such as the range of temperatures that a species can live in, or biotic, such as prey availability or the presence of predatory species. The ecological niche is a key concept to understand the functional role of species within ecosystems, as it describes how a population interacts with the environment and how it, in turn, influences the local community. The ecological niche of a species or population has been traditionally assessed under the assumption that all individuals of the same species are ecologically equivalent. However, individuals can differ in their strategies, consistently exploiting subsets of the total ecological niche of the population (Van Valen, 1965). That is, a generalist population or species can be composed by specialist individuals. Individual specialization refers to this phenomenon, where each individual consistently exploits an ecological niche substantially narrower than that of its population for reasons unrelated to sex, age, breeding status or morphotypes (Bolnick et al., 2003).

Although initially defined regarding diet (Van Valen, 1965), indeed individual specialization can occur in all axis of the ecological niche (Bolnick et al., 2003). That is, individuals can have preferences regarding diet, but also show preferences in habitat, geographical areas (Piper, 2011), foraging or migration behaviour (Phillips et al., 2017), etc. (Table 1).

Table 1

Examples of individual specialization in several traits of the ecological niche along with the method and the timescale used. This is not a detailed review of all aspects of individual specialization and all examples of them, but showing some of the traits that have been more studied.

Trait	Species	Method	Timescale	References	
Diet	Bottlenose dolphin (<i>Tursiops truncatus</i>)	Stable isotopes (teeth)	15 years	Rosman et al., 2015	
	Asiatic black bear (<i>Ursus thibetanus</i>)	Scat sample collection	1 year	Mori et al., 2019	
	Green turtle (<i>Chelonia mydas</i>)	Stable isotopes (skin and scute)	Months (skin) to years (scute)	Thomson et al., 2018	
	Canarian Egyptian vulture (<i>Neophron percnopterus majorensis</i>)	GPS tracking	1 year	van Overveld et al., 2018	
	Burbot (<i>Lota lota</i>)	Stable isotopes (several tissues)	> 1 year	Harrison et al., 2017	
	Clouded Apollo butterfly (<i>Parnassius mnemosyne</i>)	Observational	< 1 month	Szigeti et al., 2018	
	Southern elephant seal (<i>Mirounga leonina</i>)	Satellite tracking	>= 2 years	McIntyre et al., 2017	
	Brown anole (<i>Anolis sagrei</i>)	Observational	2 months	Kamath & Losos, 2017	
	Loggerhead turtle (<i>Caretta caretta</i>)	Stable isotopes (scute)	Years	Cardona et al., 2017	
	Grey-headed albatross (<i>Thalassarche chrysostoma</i>)	PTT tracking	2 months	Bonnet-Lebrun et al., 2018	
Habitat	Rhinoceros auklet (<i>Cerorhinca monocerata</i>)	GPS tracking	< 2 months	Cunningham et al., 2018	
	Bank vole (<i>Myodes glareolus</i>)	Radiotracking	4 days	Schirmer et al., 2020	
	Yellow-shouldered bat (<i>Sturmira lilium</i>)	Radiotracking	1 week	Kerches-Rogeri et al., 2020	
	Striped field mouse (<i>Apodemus agrarius</i>)	Radiotracking	4 days	Schirmer et al., 2020	
	Northern gannet (<i>Morus bassanus</i>)	GPS tracking	Within and between years	Wakefield et al., 2015	
	Bearded seal (<i>Erignathus barbatus</i>)	GPS tracking	1-8 months	Hamilton et al., 2018	
	Black-legged kittiwake (<i>Rissa tridactyla</i>)	GPS tracking	Weeks	S. M. Harris et al., 2020	
	Northern gannet (<i>Morus bassanus</i>)	GPS tracking	Within and between years	Votier et al., 2017	
	Geographical areas (site fidelity)¹				
Foraging behaviour²					

Table 1
Continuation.

Trait	Species	Method	Timescale	References
	Elk (<i>Cervus canadensis</i>)	Radiotracking	3 years	Found & St. Clair, 2016
	Southern elephant seal (<i>Mirounga leonina</i>)	Satellite tracking	>= 2 years	McIntyre et al., 2017
Migration behaviour	Brünnich's guillemot (<i>Uria lomvia</i>)	GLS tracking	>= 3 years	McFarlane Tranquilla et al., 2014
	Common guillemot (<i>Uria aalge</i>)	GLS tracking	>= 3 years	McFarlane Tranquilla et al., 2014
	Brown skua (<i>Catharacta antarctica</i>)	GLS tracking	3 years	Krietsch et al., 2017
Activity habits³	Cory's shearwater (<i>Calonectris borealis</i>)	GLS tracking	2-6 years	Zango et al., 2019
	European shag (<i>Phalacrocorax aristotelis</i>)	GLS tracking	1-6 years	Daunt et al., 2014
	Common cuckoo (<i>Cuculus canorus</i>)	Observational	Within a breeding season	Marchetti et al., 1998
Host	Cuckoo bee (<i>Sphécodes ephippius</i>)	Observational	3 days	Bogusch et al., 2006
	Cuckoo bee (<i>Sphécodes monilicornis</i>)	Observational	3 days	Bogusch et al., 2006
	Slug (<i>Elysia viridis</i>)	Observational (laboratory)	40h	Baumgartner et al., 2014

¹ Site fidelity can occur to both breeding and non-breeding areas.

² Foraging behaviour includes diving and foraging movements (bearing, trip duration, trip distance, etc.).

³ Activity habits refers to when animals are active along the day.

Individual specialization is widespread in the animal kingdom, occurring in a broad array of invertebrate and vertebrate taxa (Bolnick et al., 2003; Piper, 2011). It has been documented in plants, gastropods, crustaceans, arachnids, insects, fishes, amphibians, reptiles, birds and mammals (Fig. 1; Araújo et al. 2011). It occurs in species with different trophic levels across the food web, from primary producers (e.g. seagrass *Zostera marina*; Hughes et al., 2009) to first order consumers (e.g. green turtles *Chelonia mydas*; Thomson et al., 2018) or top predators (e.g. bull sharks *Carcharhinus leucas*; Matich et al., 2011). Individual specialization can also occur in extremely generalist species, such as Asiatic black bears *Ursus thibetanus* (Mori et al., 2019), as well as in less generalist species, such as sea otters *Enhydra lutris* (Newsome et al., 2015) or leopards *Panthera pardus* (Balme et al., 2020). This phenomenon has also been observed in a vast range of ecosystems on both marine and terrestrial environments, from tropical (e.g. thin-toed frogs *Leptodactylus spp.*; Costa-Pereira et al., 2018) to deserts (e.g. Desert tortoise *Gopherus agassizii*; Murray & Wolf, 2013) or arctic habitats (e.g. Arctic charr *Salvelinus alpinus*; Kristjánsson & Leblanc, 2018).

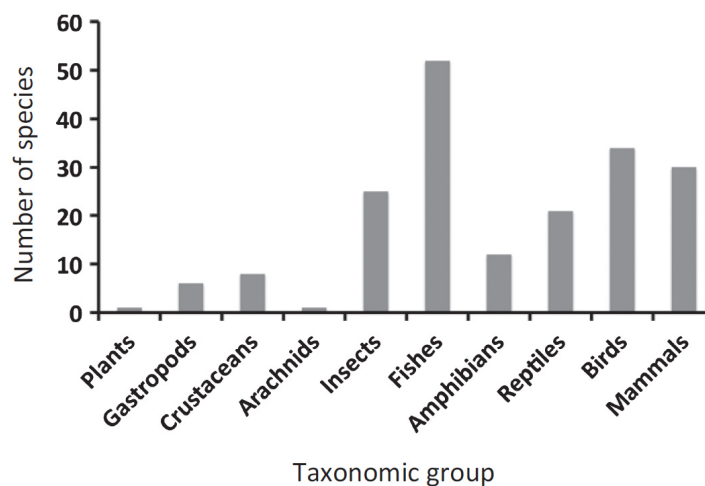


Figure 1

Number of species, classified by major taxonomic group, in which individual specialisation in diet, foraging behaviour, habitat or other niche axis has been documented. Total number of species is 189. From Araújo et al., 2011 (license number 600027806 provided by John Wiley & Sons - Books).

2. Methods to quantify individual specialization and terminology

The procedure to quantify individual specialization is measuring individual traits in more than one occasion and calculating the fraction of variability in that trait that is due to differences between individuals and the variability that is due to differences within individuals. The more similar are the trait values within individuals compared to between individuals, then higher is the individual specialization within the population (Fig. 2). This can be done using several methodologies, although the most used ones are the Bolnick's metric (Bolnick et al., 2003) and the repeatability estimation (Nakagawa & Schielzeth, 2010).

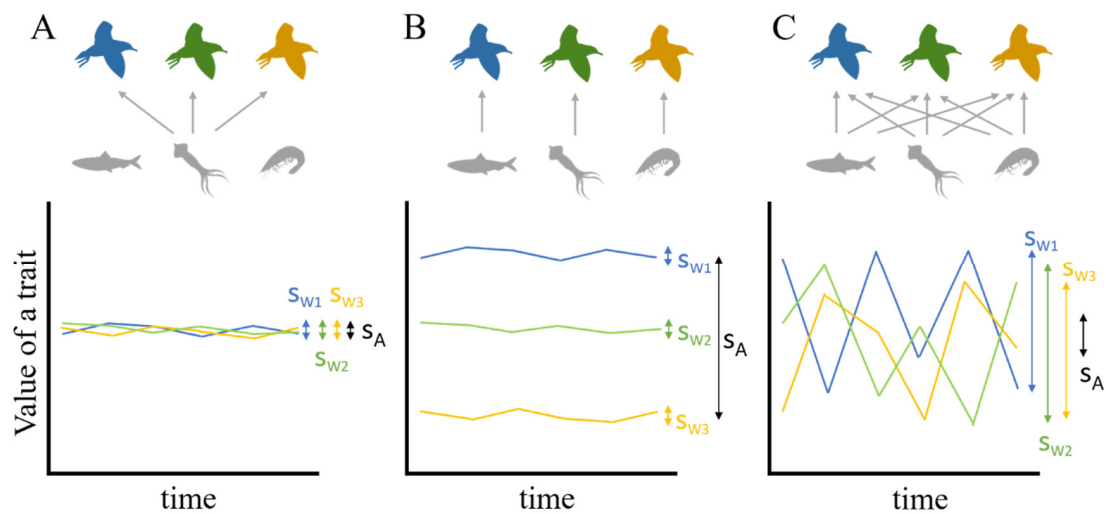


Figure 2

Variability of a trait (for instance diet) across time in three hypothetical populations of three individuals (one of each colour). A) specialist population where all individuals of the population are highly consistent in the trait across time (s_w are small), but their strategies are very similar (s_A is also small), and therefore there is no individual specialization. B) generalist population where individuals show high individual consistency (s_w are small) and differ in their strategies (s_A is large), therefore showing individual specialization. C) generalist population where most of the variability is explained by differences within individuals, i.e. individuals are not consistent in the trait across time (s_w are large), therefore not depicting individual specialization.

The metric established by Bolnick *et al.* to calculate individual specialization is based on the quantitative framework proposed by Roughgarden (1972, 1974) about intrapopulation niche variation. It uses the following formula:

$$\text{WIC/TNW}$$

Where TNW is the total niche width of the population, which is the sum of the within-individual component (WIC) and the between-individual component (BIC). The ratio of WIC and TNW gives therefore an estimation on the importance of the within-individual component in the total niche. The index varies from 0 to 1, being 0 that the individual specialization is maximum and 1 that there is no individual specialization within the population (Bolnick *et al.*, 2003).

Repeatability is one of the most common metrics used to infer individual specialization (Nakagawa & Schielzeth, 2010). This metric is based on the following formula:

$$r = \frac{s_A^2}{s_W^2 + s_A^2}$$

Where r is repeatability, s_A^2 is the variance among individuals and s_W^2 is the variance within individuals, being therefore $s_W^2 + s_A^2$ the total variation in the population or species. The value of r ranges from 0 to 1, where 0 means the trait has no repeatability and 1 that is totally repeatable. Note that individual specialization will only be evident in repeatability if there is among individual variation in the population (i.e. $s_A > 0$). In other words,

in order to be repeatable, a trait must be consistent within individuals but different among individuals (Fig. 2). Note that repeatability metric is basically the same than the methodology proposed by Bolnick, except that in Bolnick's metric the numerator represents the within-individual variance and in repeatability represents the between-individual variation (Carneiro et al., 2017). Therefore, high Bolnick's metrics indicate low individual specialization, whereas high repeatability values indicate high individual specialization within the population.

The aforementioned methodologies define how important is individual specialization within the population, being therefore population metrics. However, these metrics (and others) can also be used to understand how individual specialization differs among groups within the population, such as sex or age classes, when calculated separately for each group (Fig. 3). These groups within the population can be discrete, such as males and females or breeders and non-breeders, or can come from a categorization of a continuous variable, such as boldness or age. For instance, Bolnick's metric was used to understand differences in individual specialization between males and females in South America fur seals (*Arctocephalus australis*) (de Lima et al., 2019). Similarly, in black-legged kittiwakes (*Rissa tridactyla*), repeatability was used to compare individual specialization between bold and shy individuals, categorized based on the mean boldness score of each individual (Harris et al., 2019). Differences in individual specialization among groups should not be confused with niche partitioning among these groups (Fig. 3). For instance, males and females can differ in the resources exploited due to specific nutrition or energetic requirements, competitive avoidance or differential reproductive roles (Wearmouth & Sims, 2008). Similarly, breeding and non-breeding animals can use different resources or habitats as a result of different dietary requirements and specific parental duties, such as central place foraging or territoriality (e.g. Borghello et al., 2019; Mayer et al., 2017). In such cases, there is specialization in these demographic units, but not necessarily at the individual level (Fig. 3).

Apart from at population or group level, Bolnick's and repeatability estimations, as well as other individual specialization metrics, can also be calculated at the individual level to understand how specialist or generalist is each individual of the population (Fig. 4, Ramos et al., 2020). This is done by estimating the within-individual variability per each individual and then calculating either WIC/TNW or repeatability per each individual (e.g. Potier et al., 2015, Rita et al., 2017). This individual-level metric allows understanding if specialist and generalist individuals coexist within populations and how individual specialization correlates with other factors, such as fitness estimations or personality (Fig. 4). For instance, the population of southern elephant seals (*Mirounga leonina*) from Sea Lion Island (Falkland Islands) was composed by 51% extreme specialist, 46% specialist and only 3% generalist individuals (Rita et al., 2017). An individual level metric was also used in African penguins (*Spheniscus demersus*), where individual repeatability in trip duration of parents was positively correlated to chick growth rate in poor-condition years (Traisnel & Pichegru, 2019). Similarly, individual specialization in foraging areas (individual site fidelity) was positively correlated to boldness score of individuals during incubation in black-legged kittiwakes (Harris et al., 2020).

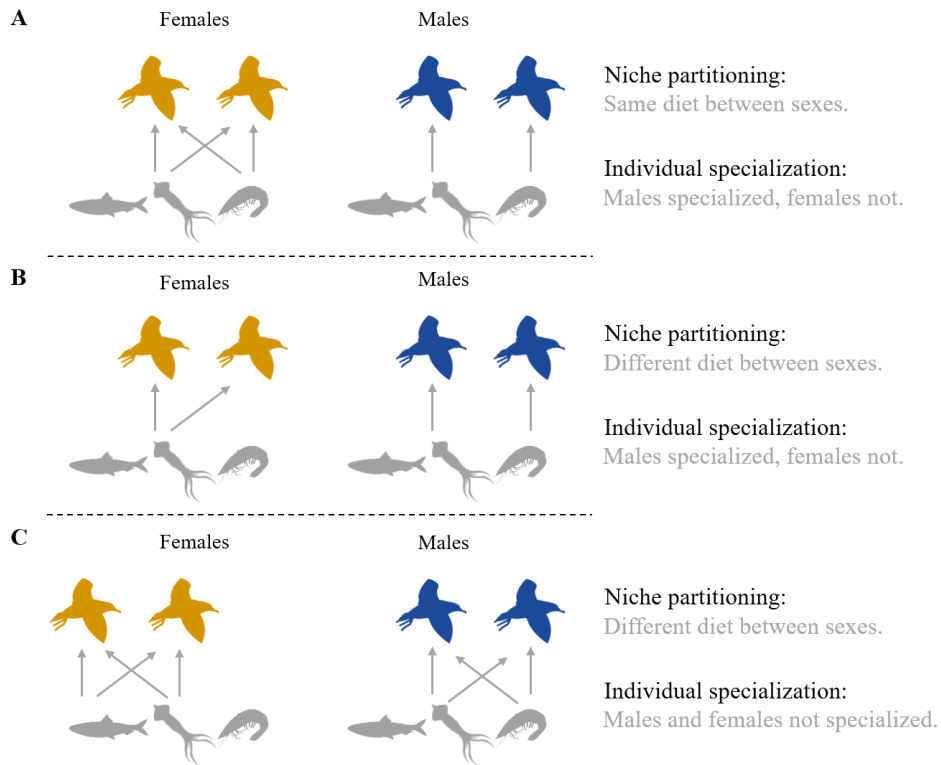


Figure 3

Conceptual diagram about niche partitioning and individual specialization with two population groups, females (yellow) and males (blue) and three potential resources (fishes, cephalopods and crustaceans) in three hypothetical examples (A, B, C). In A) there is no niche partitioning between females and males, as both groups exploit the same prey. However, there are differences in individual specialization, as all females feed on the same types of prey whereas different males have different prey. In B) there is niche partitioning, as females depend only on cephalopods, whereas males feed on cephalopods and crustaceans. There is also individual specialization in males, as they have different strategies, but there is no specialization in females, as all of them have the same strategy, i.e. feeding on cephalopods. Finally, in C) there is niche partitioning, as females depend on fish and cephalopods and males on cephalopods and crustaceans, but there is no individual specialization within each group, as there are no individual strategies.

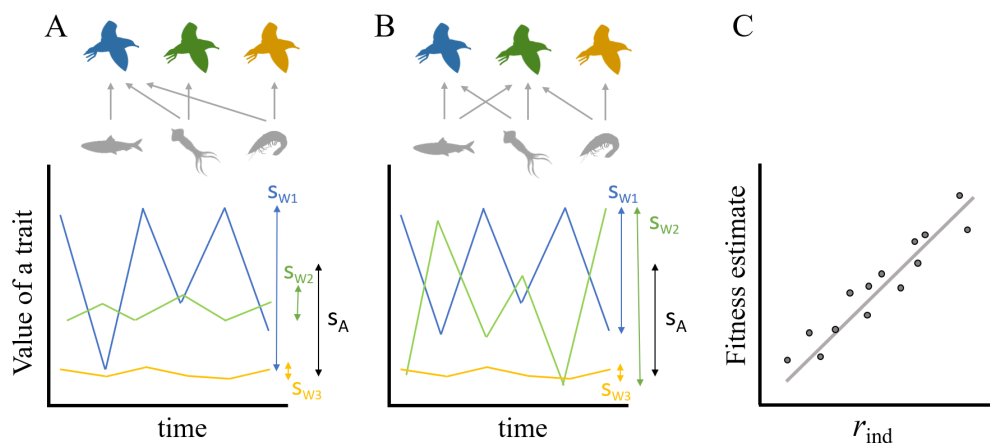


Figure 4

Conceptual diagram about different specialist and generalist individuals within a population (A, B) and hypothetical correlation of repeatability at individual level with a fitness estimate (C). A) generalist population composed by more specialist than generalist individuals, as one individual is generalist (the blue one, feeding on different prey across time, with s_w large) and two are specialist (green and yellow ones, feeding on the same prey across time, with s_w small). B) generalist population composed for more generalist (blue and green) than specialist (yellow) individuals. Note that both blue and green are generalists, but green is more generalist as it feeds on the three possible prey whereas blue only feeds on two. C) correlation indicating that the higher the specialization of the individual (r_{ind}), the higher its fitness (for instance offspring survival).

Terminology associated to individual specialization can be confusing. Individual consistency is sometimes used in a similar manner, but it is more appropriate to differentiate it from individual specialization. The term individual consistency usually refers to individuals maintaining their ecological strategies across time, that is, when there is low within individual variability in the individuals that compose a population. However, individual consistency does not necessarily indicate individual specialization, as it does not imply that individuals of the same population differ in their strategies (Fig. 2). That is, in a specialist species, individuals show consistency, but they do not show specialization (Fig. 2A), whereas in a generalist species, individuals can show both consistency and specialization (Fig. 2B). Individual consistency has been sometimes used in lieu of individual specialization to refer to the same phenomenon (e.g. Hasselquist et al., 2017; Spiegel et al., 2017; Vardanis et al., 2016). Similarly, other terms such as between-individual niche variability, within-population niche variability, consistent individual differences, individual preferences, etc. have been used in lieu of individual specialization. There is no clear consensus on which term should be used, although the most common and used term referring to specialist individuals across time within a generalist population is individual specialization.

3. Links between individual specialization and personality

Behavioural traits are typically categorized into five major behavioural axis, namely activity or the extent of movement in a familiar environment; boldness or the reaction to a risky but known situation; exploration or the reaction to a novel situation; sociability or the reaction to conspecifics; and aggressiveness or the agonistic reaction towards conspecifics (Réale et al., 2007). Personality is defined as the expression of one of these behavioural traits for an individual that is persistent in time and across contexts and that is different from the behaviour of other individuals of the same population (Careau & Garland, 2012; Réale et al., 2010). Like individual specialization, personality is independent of age, sex or discrete polymorphism (Dingemanse et al., 2002). Therefore, whereas individual specialization is the consistent individual differences in the use of resources (food, habitat, geographical areas, etc.), personality refers to consistent individual differences in traits related to the behaviour of the individuals (Toscano et al., 2016).

In the last decade, researches have started to consider causality between personality and individual specialization (Toscano et al., 2016; Vonk et al., 2017). Personality has been suggested to promote individual specialization. That is, individuals with a particular personality trait, for instance shy individuals, may prefer particular food resources or habitats, whereas bold individuals prefer others, thus leading to niche variation between individuals within the population. This relationship has been reviewed in terms of dietary specialization (Toscano et al., 2016), where authors propose that personality can drive differences in foraging

activity, risk-dependent foraging, physiology, social roles or spatial aspects of foraging, which in turn can influence dietary individual specialization (Fig. 5 and Toscano et al. 2016 for details on these patterns). For instance, more active jumping spiders (*Phidippus clarus*) predated on lower active prey, whereas less active spiders predated on more active prey (locomotor crossover hypothesis; Sweeney et al., 2013). Similarly, bold and shy mud crabs (*Panopeus herbstii*) probably have different diets because bold crabs foraged in subtidal parts of reefs, where there are higher foraging opportunities, whereas shy individuals exploited intertidal parts of reefs, where predator exposure is low (Griffen et al., 2012). Although reviewed in terms of dietary individual specialization (Toscano et al., 2016), this causal relationship can be extended to other aspects of the ecology of individuals, such as habitat preference or migration strategies. For instance, bolder individuals of bank voles (*Myodes glareolus*) preferred microhabitats with higher ground cover than shyer individuals (Schirmer et al., 2019). Likewise, shy and bold roe deer (*Capreolus capreolus*) differed in the habitat used: shy individuals exploited safer woodlands, whereas bolder deer occupied rich open habitats (Bonnot et al., 2018). Similarly, bold and more explorative great tits (*Parus major*) exploited urban habitats, whereas shyer and less explorative inhabited forests (Riyahi et al., 2017). Finally, shyer individuals of elk (*Cervus canadensis*) were less likely to migrate than those bolder and more habituated to humans (Found & St. Clair, 2016).

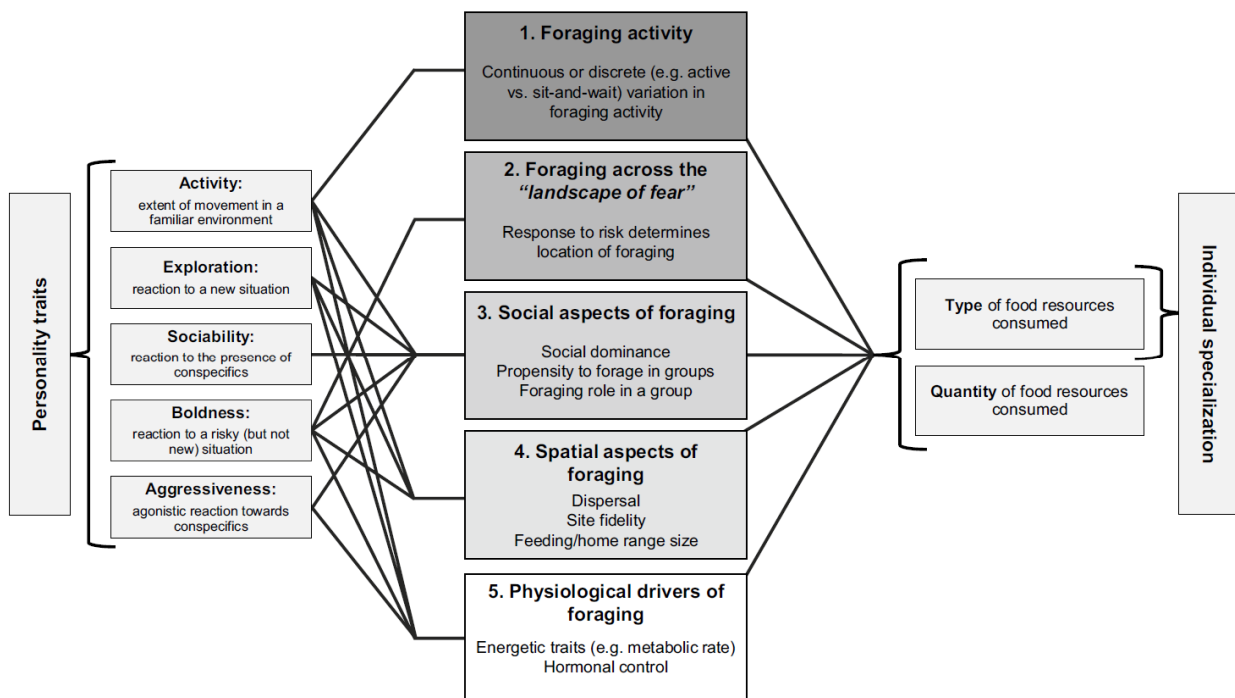


Figure 5

Diagram about how personality traits can explain the existence of individual specialization in diet by driving different aspects of foraging behaviour. For instance, more shy individuals (personality trait) may prefer to forage in a safer to predation environment (foraging across landscape of fear), thus having access to different resources than bolder individuals and promoting between individual variation in diet (dietary individual specialization). Extracted from Toscano et al. 2016 (license number 600027807 provided by Springer Nature BV).

Despite personality driving specialization is the most accepted framework nowadays, it can also be the other way around. Individual specialization can promote the emerge of animal personalities by altering the metabolic engine of individuals (Biro & Stamps, 2010). The use of particular resources can directly modify physiological and energetic traits (Britt et al., 2006), and these in turn may drive consistent individual differences in behaviour (Biro & Stamps, 2010; Yuan et al., 2018). For instance, male Southern field crickets (*Gryllus bimaculatus*) raised on a high protein diet were more aggressive, more active during mating, and less stable in their behaviour than conspecifics that were fed on a high-carbohydrate diet (Han & Dingemanse, 2017). Similarly, crickets raised under higher temperatures were more explorative than those raised at lower temperatures, probably because low temperatures are associated with a reduced expression of activity-related behaviour (Niemelä et al., 2019). Although the fixation of the personality traits in these examples occurred during ontogeny, it is possible that resource use may have driven differences in individual personality later in life.

Alternatively, individual specialization and personality may covary without causation as a result of another variable. However, the causality and the origin of covariation of these relationships is difficult to measure (Toscano et al., 2016). Demonstrating causality implies modifying either an ecological trait or a behavioural trait of an individual to understand how this leads to changes in individual trait variability. Modification of an ecological trait would be, for instance, force captive individuals to feed on a specific diet or to be in a specific environment to latter see if this condition leads to changes in the behaviour of the individuals. Modification of a behavioural trait would be through acclimation or hormone addition (e.g. Farwell et al., 2014). These experiments, however, are challenging since manipulating personality or individual specialization can directly affect other traits and obscure the direction of the causal relationship (Toscano et al., 2016).

4. Implications of individual specialization

The fact that individuals within the same species or population differ in their realized niches has important implications in ecology, evolution and conservation (Bolnick et al., 2011; Raffard et al., 2018). Indeed, recent meta-analyses show that variation among individuals within a species can have even greater ecological effects in communities and ecosystems than the differences exhibited among species (Des Roches et al., 2018; Raffard et al., 2018).

Ecologically, differences in resource exploitation among individuals may reduce intraspecific competition and promote ecological segregation (Lichstein et al., 2007). Variation among individuals in their strategies can also influence species coexistence (Hart et al., 2016; Schirmer et al., 2020) and have profound effects on community structure and ecosystem functioning (Des Roches et al., 2018). Furthermore, individual or parental foraging strategies may be a key component of breeding fitness and these strategies should be considered relevant life-history traits (Pagani-Núñez et al., 2015; Zabala & Zuberogoitia, 2014). Moreover,

in ecological modelling, acknowledging individual-level variation in resource use can result in substantial changes in population dynamics, since individuals using different habitats or resources may encounter different levels of predation risk (Pettorelli et al., 2015), parasitism (Bolnick et al., 2011) or contamination exposure (Santos et al., 2017). For instance, individual temperature preferences affects susceptibility to chytridiomycosis in amphibians (Sauer et al., 2018). Similarly, individual specialization of parents in certain food resources increased offspring Hg levels in lesser black-backed gulls (*Larus fuscus*) (Santos et al., 2017).

From an evolutionary point of view, intrapopulation niche variation provides the base for natural selection to operate. Individuals choosing different resources can be subjected to different selective pressures (Bolnick et al., 2003, 2011). This variation can occur in terms of individuals specialized in different resources or individuals showing different degrees of specialization, i.e. generalist vs specialist. For instance, habitat specialist Herring Gulls (*Larus argentatus*) showed lower foraging effort and increased offspring growth than generalist individuals (Van den Bosch et al., 2019). Similarly, chicks of parents that were specialist in foraging behaviour showed higher growth rates than those from generalist parents in African penguins (Traisnel & Pichegru, 2019). Moreover, individual specialization may theoretically play a role in sympatric speciation, when strong between-individual niche variation generates disruptive selection through assortative mating (Bolnick et al., 2003; Knudsen et al., 2010). However, the extent to which individual specialization can have an evolutionary implication depends on the heritability of the traits (Forsman, 2015). While foraging behaviours have been reported to be slightly heritable in average, migration behaviours are the most heritable traits studied so far (Fig. 6; Dochtermann et al., 2019).

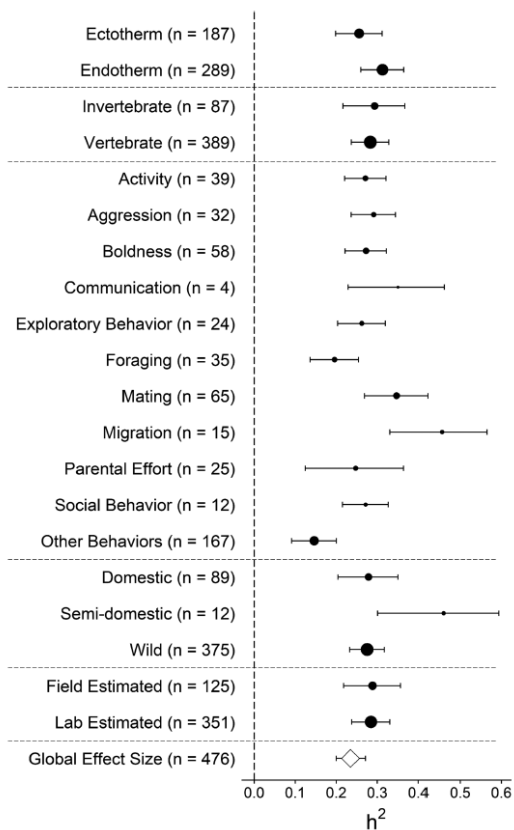


Figure 6

Forest plot of estimated heritability ($\pm 95\%$ confidence intervals) for each moderator. Point size is proportional to the sample size for a particular moderator. Extracted from Dochtermann et al., 2019 (license number 1076008-1).

In conservation, the acknowledgement of individual specialization can help protecting trait variation within populations, which is a keystone for the adaptation of the species to environmental changes. That is, different individual strategies may help the population to cope the loss of specific habitats or resources (Durell, 2000). Moreover, theoretical modelling suggest that populations composed of specialist individuals can be more stable and prone to evolutionary diversification (Bolnick et al., 2003). However, long-term individual specialization may limit behavioural flexibility, thus limiting possible responses of individuals to rapidly changing or novel environments (McIntyre et al., 2017; Snell-Rood, 2013). That is, animals' responses to a changing environment may occur within a generation if individuals are plastic or flexible in their strategies, whereas in populations composed by highly specialized individuals, adaptation will only occur via natural selection, provided that these traits are heritable.

5. Factors modulating individual specialization

Why individuals sharing a common environment would develop differences in their ecological niches? Following the optimal foraging theory, when there is a range of available resources, an individual is expected to choose the set of resources that are less costly and at the same time maximize benefits such as energy income or reproductive performance (Schoener, 1971). These choices may vary among individuals depending on several intrinsic factors, such as personality or physiology. Therefore, phenotypic differences among individuals are proximate causes of individual specialization, which can be (or not) genetically determined (Bolnick et al., 2003). Although individuals can differ in their resource preferences, there are several extrinsic factors that can also alter the degree of individual specialisation (Araújo et al., 2011). That is, individual specialization can be promoted or limited under different environmental conditions (ultimate drivers of individual specialization), for instance differences in prey abundance or the presence of competitor species or predators. Intrinsic (proximate) and extrinsic (ultimate) factors are therefore combined to determine the extent of individual specialization within populations (Table 2; e.g. Auer et al., 2020).

5.1. Intrinsic

Individuals within a population can differ in their physiology, morphology, cognitive abilities, experience and personality, which in turn can lead to differences in their use of resources. Variation in physiology among individuals can make them differ in their digestion capabilities of specific prey items, thus probably leading to differential prey preferences (Afik & Karasov, 1995; Maldonado et al., 2019). The physiology of an individual can also limit its spatial distribution or habitat exploitation due to different tolerances to environmental conditions, such as tolerance to specific salinity or temperature (Eliason et al., 2011). Morphology variation among individuals can also drive between-individual differences in resource use, as it can affect prey catching and handling capabilities of the individuals. For instance, individuals can differ in jaw or beak morphology that make easier or more difficult to capture and handle certain prey (Bolnick & Paull, 2009).

Table 2

Summary of intrinsic (proximate) and extrinsic (ultimate) factors that influence individual specialization. Regarding extrinsic factors, the general influence on individual specialization is presented, although the reverse patterns have also been found in literature, thus suggesting their influence is more context and species dependent (Costa-Pereira et al., 2018). More examples and extensive explanation on the mechanisms can be found in the main text.

Factor	Mechanism	Example
Different physiology	Favours individual specialization through individual differences in e.g. digestion capabilities or tolerances	Maldonado et al., 2019
Different morphology	Favours individual specialization through individual differences in e.g. catching/handling prey	Bolnick & Paull, 2009
Different experience (age)	Favours individual specialization through individual differences in proficiency in certain resource exploitation	Grecian et al. 2018
Sex	Males and females can differ in their degree of individual specialization due to competition avoidance, different food requirements or roles during breeding	de Lima et al., 2019
Different personality	Favours individual specialization because differential boldness, exploration, etc. cause differential resource exploitation among individuals	Griffen et al., 2012
Resource scarcity	Favours individual specialization through segregation of ecological niche to minimize competition	Mori et al., 2019
Resource predictability	Favours individual specialization as individuals can define their strategies	Dermond et al., 2018
Resource diversity	Favours individual specialization as it provides the diversity over which individuals can specialize	Rosenblatt et al., 2015
Occurrence of competing species	Reduces individual specialization as it constrains the population niche by competitive exclusion	Knudsen et al., 2007
Conspecific abundance	Favours individual specialization as individuals segregate into different strategies to avoid competition	Sheppard et al., 2018
Presence of predators	Reduces among-individual variability because all individuals exploit the same safer resources	Eklöv & Svanbäck, 2006

Individual specialization can also emerge as a result of learning and be developed with age. In some animals, like some primates or bottlenose dolphins *Tursiops ssp.*, there's a clear social influence where young individuals learn from their peers and elders by watching and copying their behaviour (Rapaport & Brown, 2008; Wild et al., 2020). Foraging behaviour can also be transmitted from progenitors to their off-spring, as it occurs in polar bears *Ursus maritimus* (Lillie et al., 2018), sea otters (Estes et al., 2003) or orangutans *Pongo pygmaeus* (Jaeggi et al., 2010). Similarly, individuals can also define their strategies through their own experience in a “self-learning” process, called exploration-refinement hypothesis (Campioni et al., 2019; Fayet, 2020; Guilford et al., 2011). For instance, immature northern gannets showed less defined strategies and less proficient foraging than adults (Grecian et al., 2018). Either from social or self-learning, these processes make an individual to improve proficiency in exploiting specific prey or habitats, thus leading to a preference for these resources.

The sex of the individual can also play a role in individual specialization due to competition avoidance, different food requirements or roles during breeding between sexes (Phillips et al., 2017). For instance, male wandering albatrosses (*Diomedea exulans*) show individual specialization in specific water masses, whereas female individuals combine different water masses presumably to avoid competition with males (Ceia et al., 2012). Female Campbell albatross (*Thalassarche impavida*) showed a higher degree of route fidelity compared with males, differences that can be related to the higher competition experienced by females as they remained close to the colony in their foraging trips (Sztukowski et al., 2018). Male South American fur seals showed higher individual specialization than females as they had access to different habitats and resources that allowed them to segregate their strategies, whereas all females showed similar strategies as they remained close to breeding sites for pup nursing (de Lima et al., 2019).

Personality can also be an important driver of variation in resource use among individuals of the same population, although direction of the causal relationship remains unclear (Toscano et al., 2016), as explained above. For instance, bolder individuals may exploit more profitable habitats with higher predation risk, whereas shy individuals prefer to forage in less productive but safer environments (e.g. Griffen et al., 2012). Personality can also drive differences in social dominance, which can in turn result in differences in the exploited resources as dominant individuals can exclude subordinates from more profitable resources (e.g. David et al., 2011; Favati et al., 2014).

5.2. Extrinsic

Although individual's phenotype can lead to differences in resource use among individuals, the conditions of the surrounding environment may promote or limit the expression of individual preferences. There are several environmental conditions that can influence individual specialization, namely resource scarcity, predictability of the environment and diversity of resources. When resources are scarce, intraspecific

competition increases and individuals add alternative resources to their diets, thus segregating their niches (Araújo et al., 2011; Sheppard et al., 2018). For instance, lower resource abundance favoured microhabitat individual specialization in pikes (*Esox Lucius*) (Kobler et al., 2009). Likewise, resource scarcity in summer promoted higher dietary individual specialization in black bear compared to in spring and autumn when resources are abundant (Mori et al., 2019). Predictability of the environment is expected to favour individual specialization, as when resources are predictable, individuals know where and when they can find the food and they can define individual strategies. On the contrary, in unpredictable environments, it is hard for individuals to specialize since difficulty in finding resources limits consistency in individual behaviour (Oppel et al., 2017). Accordingly, brown trout (*Salmo trutta*) showed higher individual specialization in stable and predictable environments than in unstable ones (Dermond et al., 2018). Finally, a high diversity of resources (or ecological opportunity) is expected to promote individual specialization as it provides the diversity over which to specialize (Araújo et al., 2011). For instance, American alligators (*Alligator mississippiensis*) inhabiting areas with high prey and habitat diversity showed higher individual specialization than those from low prey diversity and homogeneous areas (Rosenblatt et al., 2015).

The abundance of individuals from other species and conspecific abundance can also influence individual specialization in different ways (Araújo et al., 2011). On the one hand, when released from competitors, the niche of the species is no longer constrained by competitive exclusion, promoting a population niche expansion and the diversification of niches at individual level (Pianka, 2000; Van Valen, 1965). Accordingly, empirical studies found increased individual specialization in communities with lower species richness, where interspecific competition is expected to be smaller. For instance, Arctic charrs from a lake with few other fish species showed a broader population niche and higher individual specialization than those from a lake with more competitors (Knudsen et al., 2007). Similarly, Antarctic and subantarctic fur seals (*Arctocephalus gazella* and *Arctocephalus tropicalis*) showed niche expansion and higher interindividual niche variation when breeding in allopatry than in sympatry (Kernaléguen et al., 2015). On the other hand, intraspecific competition is generally expected to promote individual specialization, as when competition increases, individuals add alternative sources of food to their diets thereby increasing the total population niche (Araújo et al., 2011; Pianka, 2000). For instance, banded mongooses (*Mungos mungo*) show higher individual foraging specialization when the group size increases (Sheppard et al., 2018).

Predation risk is considered to decrease individual specialization, as individuals may be restricted to use habitats or resources where the predator is absent, thereby reducing habitat heterogeneity and increasing converge in resource use, thus reducing inter-individual variation (Araújo et al., 2011). For instance, individuals of Eurasian perch (*Perca fluviatilis*) were restricted into either littoral or pelagic habitat when the predator was present, but showed strong individual specialization in one of these two habitats when the predator was removed (Eklöv & Svanbäck, 2006).

Despite the aforementioned theoretical framework, other studies found contrasting results regarding the influence of intrinsic and extrinsic factors on individual specialization. For instance, the diversity of available resources decreased individual specialization in Antarctic seals (Kernaléguen et al., 2015) and did not affect individual specialization in four frog species (Costa-Pereira et al., 2018). Similarly, intraspecific competition decreased individual specialization in rufous frog (*Leptodactylus fuscus*) (Costa-Pereira et al., 2018) or seemed unrelated to individual specialization in several species of frogs and toads (Cloyed & Eason, 2016), the alewife (*Alosa pseudoharengus*) (Jones & Post, 2013) or the isopod (*Saduria entomon*) (Svanbäck et al., 2011). Therefore, the influence of these factors on individual specialization seems more dependent on the context and the species than previously thought and general patterns across environments and taxa should not be assumed (Costa-Pereira et al., 2018; Jones & Post, 2016).

6. Anthropogenic influence on individual specialization

Human activities can modify the environment in a way that can either increase or decrease individual specialization within populations (Layman et al., 2015). Individual specialization may be higher when anthropogenic modifications increase habitat heterogeneity or resource diversity. Human activities can alter natural resource availability or even supply new resources previously inaccessible (Newsome et al., 2015), such as landfills on land or fishery discards at sea, thus increasing the range of available resources on which individuals can specialize. Anthropogenic food resources are often more predictable in space and time than natural resources, which makes them an easy resource on which to specialize (Patrick et al., 2015). For instance, herring gull, a generalist species that frequently forage at landfills and in other urban environments, showed higher individual foraging site fidelity when breeding in a highly urbanized environment than in less urbanized ones (Fuirst et al., 2018).

Anthropogenic influence can also decrease individual specialization. Human activities can make habitats more homogeneous, such as in extensive crops of the same type. In these conditions, resource diversity is dropped, and this would result in all individuals showing a similar diet, thus reducing individual specialization. Also, agricultural intensification, wildlife trade, overexploitation, introduction of invasive species or urbanization can lead to local extinction of species (Harris et al., 2015; Kehoe et al., 2017; Spatz et al., 2017). This results in a reduction of prey diversity and possibly individual specialization of the species that feed on them.

Moreover, effects of these alterations can differ among groups, such as age classes or sexes. More experienced individuals or the larger sex may dominate the access to predictable anthropogenic food resources (van Overveld et al., 2018) or to less altered and more productive habitats. Alternatively, younger and less experienced individuals may depend more on predictable resources when they do not have proficient

foraging strategies (Navarro et al., 2010). Therefore, the interplay between human activities and individual specialization can be complex and should be studied carefully.

7. Seabirds as models to study individual specialization

Seabirds are an ideal model to understand the processes that drive individual specialization and the consequences that result from it, and indeed individual specialization has been reported in many seabird species (recently reviewed by Ceia & Ramos, 2015; Phillips et al., 2017). Most seabirds are faithful to the area and even the nest-site where they breed (Schreiber & Burger, 2002), making particularly easy to capture them multiple times. This allows understanding if birds maintain ecological traits in repeated occasions across time. Moreover, most of them breed in large numbers in colonies and have synchronously timed breeding cycles within colonies, thus allowing the possibility to have statistically meaningful sample sizes in field studies. In these colonies, both males and females can be easily monitored, as breeding duties are mostly shared and both can be captured at the nest throughout the breeding season, which allows to assess sexual differences in individual specialization (e.g. Camprasse et al., 2017). Seabird colonies are attended not only by breeding adults but also by a wide range of floaters, such as adults that do not breed (sabbatical birds), failed breeders or immature birds. Therefore, in the same field site, we can concurrently compare the degree of individual specializations among these demographic units (e.g. Votier et al., 2017).

Most seabird species generally breed across large geographical regions, with colonies placed in contrasting environments, allowing the assessment of how oceanographic conditions modulate individual specialization. For instance, some seabird species breed both in highly productive upwelling systems and in oligotrophic oceanic environments (Schreiber & Burger, 2002). Moreover, seabirds generally explore extensive foraging areas (Oppel et al., 2018; Thaxter et al., 2012), thus often encountering variable oceanographic conditions within the same breeding colony. Furthermore, many seabird species are long-distance migrants and perform migrations to areas with potentially different conditions and resources than those encountered in breeding grounds (Schreiber & Burger, 2002). This allows to explore if individual specialization is maintained year-round and therefore probably constrained by individuals' phenotype or if individual specialization is not maintained year-round and therefore reflects temporal adaptive responses to that particular period or environment.

Finally, most seabirds are large enough to be monitored with global positioning system devices (GPS, ~10m accuracy; Forin-Wiart et al., 2015) or global location sensor loggers (GLS, ~200km accuracy; Phillips et al., 2004), which allow the study of movements and habitat use during breeding and non-breeding seasons, respectively (Wakefield et al., 2009). These loggers can be combined with stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of different tissues to study the diet of individuals. For instance, plasma blood samples integrate the

diet of a few days (Barquete et al., 2013) and therefore can be combined with GPS loggers to understand the diet consumed in a particular foraging trip. Similarly, feathers are inert tissues that integrate the diet consumed when these were grown, thus making them useful to understand the diet of individuals during the non-breeding period when seabirds are far from breeding colonies and therefore inaccessible (Ramos & González-Solís, 2012).

Aims

The main aim of this dissertation is to provide insights on the ecological contexts that promote individual specialization within populations and the consequences and implications that derive from it by using seabirds as study model. Within this general aim, we pursued three specific aims:

1. Assess if individual strategies are maintained in the long-term and across ecological contexts, as well as its implications in fitness.
2. Address how individual specialization is shaped among the demographic units of a population, namely sex, age and breeding status classes.
3. Understand the environmental conditions that promote individual specialization in the marine ecosystem.

In the first chapter, we studied year-round individual specialization combining information of both breeding and non-breeding grounds to understand if individual strategies are maintained in the long term within these areas and also between them. We also assessed the consequences of specialist or generalist strategies on breeding performance. We combined the use of GLS devices and stable isotopes to assess wintering areas, foraging strategies and diet in both breeding and non-breeding grounds in Cory's shearwaters (*Calonectris borealis*). In this chapter we showed that some traits are maintained in both areas, and therefore probably constrained by the individual's phenotype, whereas others are not maintained, and therefore probably learned through experience independently in each area. We also showed that intermediate levels of specialization seem to provide fitness benefits.

In the second chapter of this thesis, we studied niche partitioning and individual specialization, among sex, age and breeding status classes and we discuss its possible causes and implications. We combined the use of GPS tracking and stable isotopes in plasma of immature, non-breeding adult and breeding adult Scopoli's shearwaters (*Calonectris diomedea*). In this chapter we provide evidences for different levels of individual specialization between sexes in a slightly dimorphic species, which may come from a different use of human subsidies.

In the third chapter, we assessed the importance of resource scarcity and resource predictability in shaping individual specialization. We used GPS tracking in several colonies of Cory's shearwaters that are placed in different conditions of resource limitation and predictability. In this chapter we provided evidence that resource scarcity is a more important driver than predictability of the resources in promoting individual specialization of foraging movements, whereas individual specialization on habitat can be developed regardless of the environmental conditions.

Supervisor's report



Supervisor's report

As a supervisor of the doctoral thesis entitled “Individual specialization in foraging and migration strategies in long-lived seabirds”, carried out by Laura Zango Palau, I present this report detailing the contribution of the doctoral Student on the following publications.

Chapter 1: Zango, L., Reyes-González, J. M., Militão, T., Zajková, Z., Álvarez-Alonso, E., Ramos, R., & González-Solís, J. (2019). Year-round individual specialization in the feeding ecology of a long-lived seabird. *Scientific reports*, 9(1), 1-12.

- Contribution of the doctoral student: L. Zango has contributed to the study design, the sampling collection, the analysis of the data and the scientific writing.
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Year-round individual specialization in the feeding ecology of a long-lived seabird

Chapter 1

Year-round individual specialization in the feeding ecology of a long-lived seabird

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OPEN Year-round individual specialization in the feeding ecology of a long-lived seabird

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Many generalist species are composed of individuals varying in the size of their realized niches within a population. To understand the underlying causes and implications of this phenomenon, repeated samplings on the same individuals subjected to different environmental conditions are needed. Here, we studied individual specialization of feeding strategies in breeding and non-breeding grounds of Cory's shearwaters (*Calonectris borealis*) for 2–8 years, and its relationship with fitness. Individuals were relatively flexible in non-breeding destinations, but specialized in diet, habitat use and daily activity across years. Daily activity was also consistent throughout the year for the same individual, suggesting that it is driven by individual constraints, whereas individual diet and habitat use changed between breeding and non-breeding grounds, indicating that these specializations may be learned at each area. Moreover, individuals that were intermediate specialized in their diet tended to show higher breeding success than those with weakly and highly specialized diets, suggesting stabilizing selection. Overall, this study suggests that the development of individual specialization is more flexible than previously thought, i.e. it emerges under specific environmental conditions and can develop differently when environmental conditions vary. However, once established, individual specialization may compromise the ability of individuals to cope with environmental stochasticity.

In ecology, it has been traditionally assumed that individuals of the same population are ecologically equivalent¹. However, populations of many apparently generalist species are in fact composed of individuals with different degrees of specialization, varying in their realized niches within a population^{2,3}. This means that individuals consistently exploit a subset of resources, although resources are potentially available for all individuals in the population. These differences may not be attributable to specific classes, such as sex, age or morphotypes, but to differences among individuals, known as individual specialization⁴. Although initially referred to as trophic specialization, individuals have been reported to specialize in different habitats⁵, in more nocturnal/diurnal behaviour or in migration and foraging patterns in terms of timing, routes or areas exploited^{6–8}.

The fact that individuals of the same species consistently differ in their biological traits has broad implications in ecology, evolution and conservation^{4,9}. Ecologically, individual differences in biological traits may have broad consequences on individual fitness. Individual differences in habitat use or diet can influence breeding success. For example, neritic foragers showed better reproductive performance than oceanic ones in the loggerhead sea turtle (*Caretta caretta*)¹⁰, whereas western gulls (*Larus occidentalis*) specialized in exploiting human waste showed significantly lower long-term reproductive success than those specialized in fish¹¹. Individual specialization is also key in evolutionary processes, since differences in resource exploitation among individuals may reduce intraspecific competition and promote ecological segregation¹². Moreover, long-term individual specialization may limit behavioural plasticity and thus responses to changes in the environment¹³. That is, responses to a changing environment may occur within a generation if individuals are plastic or flexible in their strategies, whereas in populations composed of a majority of highly specialized individuals, adaptation will occur via natural selection⁴. From a conservation point of view and in the context of anthropogenic changes, behavioural plasticity at both the individual and population levels is therefore key because adaptation via natural selection is normally too slow for responding to rapid and extensive human-induced changes¹⁴.

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Despite its implications, few studies have focussed on understanding the degree of individual specialization in several dimensions of the ecological niche simultaneously, precluding more general conclusions about its population consequences. This may be due to the difficulty of gathering long-term time series of individual longitudinal data¹⁵, which is often complicated for wild species. Although individual specialization has been broadly studied in past decades, many studies on wild-living animals are short-term, only including observations within the same season or for up to 2–4 years^{4,6,7,16–18} (but see some exceptions^{19,20}). Although there is no consensus on the length of the period needed to study individual specialization, short-term studies may not capture the entire individual repertoire of the traits considered²¹, leading to a gross overestimation of individual specialization.

Little is known about the processes underlying individual specialization. Differences among individuals in resource use reflect a complex interaction between an individual's phenotype, i.e. morphological, behavioural, or physiological variability, and external constraints, such as resource abundance and availability or environmental heterogeneity⁴. In this context, long-distance migrants are a good model to explore the processes driving individual specialization. If individual specialization is maintained year-round, this would suggest that intrinsic constraints exist, such as cognitive processes, memory, physiological abilities, etc., which are part of individuals' traits. On the contrary, specialization maintained only during a particular period of time would indicate a temporal adaptive response related to specific constraints or specific environmental conditions of that given period, such as energetic constraints related to breeding duties or disparate environmental predictability in breeding and non-breeding grounds. In this context, seabirds constitute an ideal model for studying the incidence and consequences of individual specialization, since many of these birds perform complex and long-distance migrations, exposing them to different environmental conditions in breeding and non-breeding grounds. Moreover, their long life span allows an exploration of consistency in different dimensions of the ecological niche over extended periods.

We aim to quantify the extent of individual specialization and its fitness implications in a long-distance migrant, the Cory's shearwater (*Calonectris borealis*), using 74 adult individuals tracked for two to eight years both in breeding and non-breeding grounds and sampled in two breeding colonies of the Canary Islands. Specifically, we explore individual specialization in four dimensions of the ecological niche: non-breeding site fidelity, diet, habitat preference and daily activity (diurnal/nocturnal foraging) evaluated in breeding and non-breeding grounds. Non-breeding site fidelity was evaluated using global location sensors (GLS) devices, combined with stable isotope analyses (SIA) on feathers moulted in breeding and non-breeding grounds to infer seabirds' diet. Habitat preference was inferred with sea surface temperature (SST) recorded by GLS devices. This variable can indicate habitat preferences within the upwellings, since many seabirds forage in upwelling systems, where the motion of deep cold waters towards the surface creates a contrasting gradient in temperature values from highly productive colder areas to oligotrophic warmer waters. Finally, daily activity was inferred using conductivity measured by GLS devices. Daily activity is a key component of seabirds' foraging ecology, as the type of prey and its availability may change during the day and night²².

Cory's shearwaters migrate to distinct areas throughout the Atlantic, and are subjected to different environmental conditions, types of prey and prey availability^{20,23}. We thus hypothesize that individuals will show non-breeding site fidelity, as we expect it to be more beneficial to winter in a specific non-breeding area rather than adapting to different conditions every year. Indeed, non-breeding site fidelity has been previously found in Cory's shearwaters from other colonies²⁰. We also hypothesize that individual specialization will not be maintained year-round, as non-breeding areas are distantly located areas with different environmental conditions than those encountered at the breeding ground²³. However, within breeding and non-breeding grounds, we expect individuals to be specialized in their diet, habitat preference and daily activity across years as a strategy to improve efficiency in resource exploitation and to reduce intraspecific competition⁴. We also expect some individual trait preferences to have an impact on the reproductive success of individuals, as any biological trait with variability can potentially promote differences in fitness among individuals. Finally, we hypothesize that intermediate specialized individuals will show higher fitness, as highly specialized individuals will be less adapted to cope with environmental stochasticity and weakly specialized individuals will be less efficient in resource exploitation^{4,24}.

Results

Non-breeding site fidelity. We obtained GLS data of 59 individuals: 32 tracked for two years, 10 for three years, seven for four years, six for five years and four for six years, comprising a total of 176 year-round trips. At a population level, we found that Cory's shearwaters spent the non-breeding period in eight different areas (Fig. 1): Benguela Current (63.1% of migration events), Canary Current (14.2%), Agulhas Current (10.2%), Brazil Current (6.8%), Angola Current (2.3%), confluence of Brazil-Falklands/Malvinas Currents (1.7%), south central Atlantic (1.1%) and Equatorial Guinea Current (0.6%). We found that 21 of 59 individuals changed their areas at least once over the seven years of the study (i.e. 35.6%): 15 animals changed their non-breeding area once, five changed twice and one three times. Overall, we recorded 28 changes of non-breeding area from one year to the next in a total of 176 migration events (i.e. 15.9%). This corresponded to a Krippendorff's alpha coefficient of 0.55 (95% CI: 0.37–0.69).

Repeatability across years and year-round consistency. We found repeatability to some extent in almost all proxies in all dimensions of the ecological niche, both in breeding and non-breeding grounds, namely isotopic diet (proxies $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measured in two specific feathers: thirteenth secondary, hereafter S13, and the first innermost primary feather, hereafter P1), habitat preference (SST as a proxy) and daily activity (night flight index [NFI] as a proxy) (Table 1). Estimates of adjusted population repeatability values were statistically significant and thus trustworthy (95% confidence interval, CI, did not include 0), with the only exception being SST during breeding (Table 1). However, we did not find a correlation between breeding and non-breeding in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and SST values at an individual level, with the exception of SST in resident animals staying in the Canary

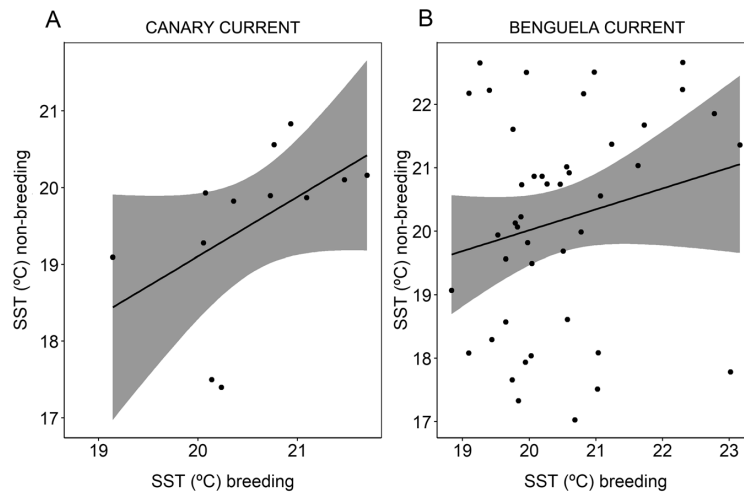


Figure 2. Relationship between sea surface temperature (SST) values during breeding and non-breeding periods of individuals spending the non-breeding period in the Canary Current (**A**; $N = 12$ values from six individuals, $\chi^2_{(1)} = 8.9$; $p = 0.003$, $r^2 = 0.50$) and the Benguela Current (**B**; $N = 44$ values from 20 individuals, $\chi^2_{(1)} = 0.02$; $p = 0.652$, $r^2 = 0.04$). Black lines correspond to the mean of the relationship and the grey shades are the associated 95% CI. Each point represents one individual per year.

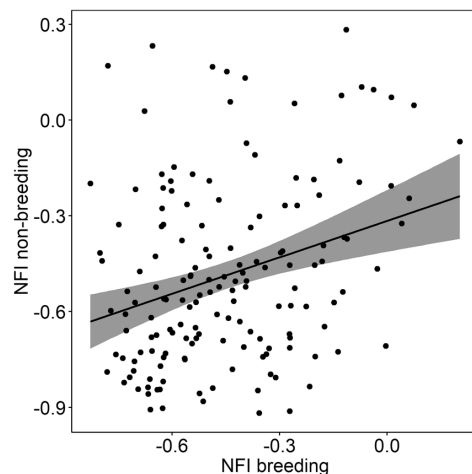


Figure 3. Relationships between night flight index (NFI) values during breeding and non-breeding periods ($N = 158$ from 53 individuals; $\chi^2_{(1)} = 13.00$, $p < 0.001$, $r^2 = 0.15$) only for birds spending the non-breeding period at the Benguela Current. The black line corresponds to the mean of the relationship and the grey shade is the associated 95% CI. Each point represents one individual per year.

two cases: intermediate specialized individuals showed higher fledging success than weakly specialized individuals in $\delta^{13}\text{C}$ values during breeding (Odds Ratio, $\text{OR} = 1.96$, 95% CI 1.02–3.75, $N_{\text{intermediate}} = 22$, $N_{\text{weak}} = 37$, $p = 0.044$, Fig. 4A) and in $\delta^{15}\text{N}$ during non-breeding ($\text{OR} = 4.89$, 95% CI 1.72–13.94, $N_{\text{intermediate}} = 10$, $N_{\text{weak}} = 10$, $p < 0.001$, Fig. 4D). Nevertheless, the mean level of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was not related to fledging success. In regards to NFI, during non-breeding there was a tendency for individuals with higher specialization in NFI to have higher fledging success, although the difference was only significant between weakly and highly specialized individuals ($\text{OR} = 17.93$, 95% CI 2.73–117.95, $N_{\text{intermediate}} = 5$, $N_{\text{high}} = 2$, $p < 0.001$, Fig. 4F). However, we did not find statistical evidence of an influence on the degree of NFI specialization during breeding (Fig. 4E). On the other hand, the more nocturnal that individuals were during breeding (higher NFI values), the higher their fledging success ($\text{OR} = 1.85$, 95% CI 1.06–3.21, $N = 27$, $p = 0.030$, Fig. 5), although we did not find any pattern during non-breeding. Regarding SST, we found that neither trait preferences nor the degree of individual specialization were related to fledging success.

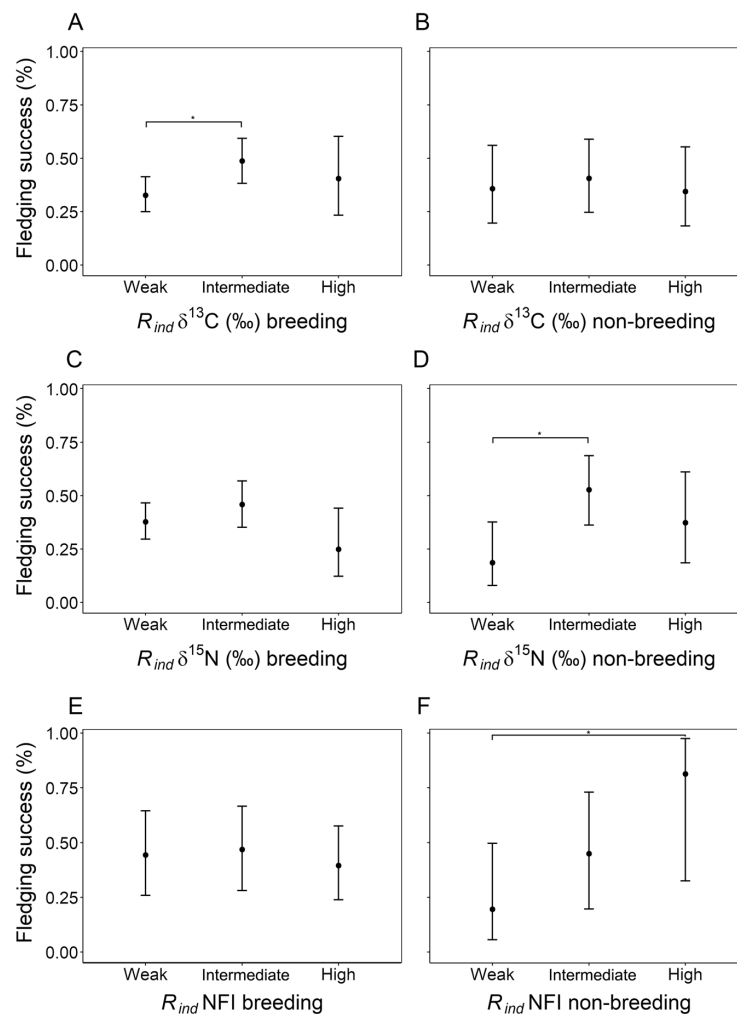


Figure 4. Probability of fledging success \pm 95% CI depending on the degree of individual specialization estimated at the individual level (R_{ind}) in $\delta^{13}\text{C}$ (A,B), $\delta^{15}\text{N}$ (C,D) and night flight index, NFI (E,F), during breeding (A,C,E) and non-breeding periods (B,D,F). Probability of fledging is calculated as the average fledging success (ranging from 0 to 1) for all years of each individual. Significant differences are shown with (*). Note that with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, intermediate specialized individuals tend to have higher mean fledging success than those weakly and highly specialized, although this difference is only significant between intermediate and weakly specialized in $\delta^{13}\text{C}$ during breeding (Odds Ratio, OR = 1.96, 95% CI 1.02–3.75, $N_{intermediate} = 22$, $N_{weak} = 37$, $p = 0.044$) and in $\delta^{15}\text{N}$ during non-breeding (OR = 4.89, 95% CI 1.72–13.94, $N_{intermediate} = 10$, $N_{weak} = 10$, $p < 0.001$). Note that with NFI during non-breeding, the higher the specialization, the higher the fledging success tends to be, although it is only significant between weakly and highly specialized individuals (OR = 17.93, 95% CI 2.73–117.95, $N_{intermediate} = 5$, $N_{high} = 2$, $p < 0.001$).

Discussion

In this study, we addressed inter-annual individual specialization in different aspects of the ecological niche and including the different conditions to which individuals are exposed, by studying several traits of the feeding ecology of Cory's shearwaters in breeding and non-breeding grounds. In general, we found evidence of individual specialization in feeding strategies across years in both breeding and non-breeding grounds, although these individual strategies differed between grounds, suggesting the capacity of individuals to develop disparate strategies when environmental conditions differ. Moreover, the degree of individual dietary specialization seemed to influence fledging success, thus highlighting the importance of individual strategies on fitness.

Individual non-breeding site fidelity has been reported in many seabird species, such as skuas, puffins or albatrosses⁶. The first studies on Cory's shearwaters suggested that individuals are plastic in their non-breeding

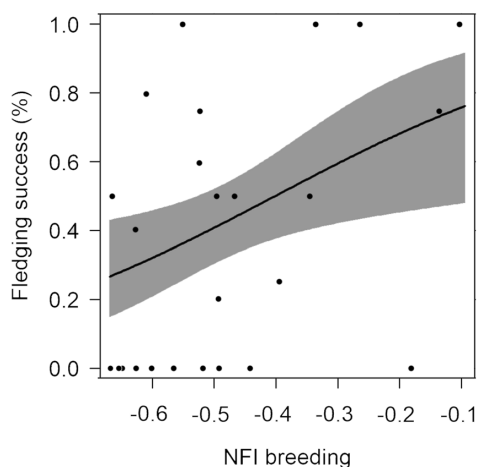


Figure 5. Probability of fledging success \pm 95% CI in relation to individual mean values of night flight index (NFI) during breeding. Probability of fledging is the average fledging success (value ranging from 0 to 1) for all years of each individual. Note that during breeding, the higher the NFI values, the higher the fledging success (OR = 1.85, 95% CI 1.06–3.21, N = 27, $p = 0.030$).

destinations, with 36% of the individuals changing their non-breeding grounds from year to year, although this study was performed on only 13 individuals tracked for two years and one tracked for three years²³. A more recent study with 51 individuals tracked for up to six years suggests that Cory's shearwaters are less plastic than previously shown²⁰. They found that 31% of individuals changed their non-breeding destination at least once during the study period, but that only 16% of individuals changed between consecutive migration events if we take into account all possible changes in all individuals and years²⁰. In our study, we tracked 59 individuals for two to six years and found an overall strikingly similar result, with 36% of individuals changing non-breeding destinations and 16% of changes between consecutive migration events. Previous studies on shearwater species showed substantially higher non-breeding site fidelities than Cory's shearwaters, including the streaked shearwaters (*Calonectris leucomelas*), in which just 2% of the individuals changed their grounds with 39 individuals tracked for two years and seven for three years²⁵, and Scopoli's shearwaters (*Calonectris diomedea*), which showed 0.46 repeatability in the distance travelled to non-breeding destinations with 10 individuals tracked for two years and two for three years²⁶. These differences may emerge from a less complex migration system in these species, with both streaked and Scopoli's shearwaters only having three different non-breeding destinations^{25,27}, but may also be due to small sample sizes and fewer years considered in those studies. Overall, in this study Cory's shearwaters used seven non-breeding areas across the Atlantic and Indian Oceans and some animals remained as residents in the Canary Current year-round, thus making its migration system more complex than the others. However, we should note that one of the non-breeding areas defined for streaked shearwaters was larger (3.4 million km² approximately)²⁵ than those defined in our study (up to 2.3 million km² approximately). If this large non-breeding area of streaked shearwater was divided into smaller areas, as we did in our study, the percentage of change may have been greater.

Despite showing some flexibility in their non-breeding destination, Cory's shearwaters showed specialization across years in the habitat exploited in non-breeding locations, as inferred from the high repeatability values ($R = 0.45$) in SST recorded by GLS. These values implies that individuals specialize in exploiting different foraging grounds within each non-breeding area, ranging from strictly neritic to the shelf slope waters or beyond.

Although shearwaters showed habitat specialization across years in non-breeding grounds, habitat specialization was not maintained all year-round. That is, the SST of the waters used during breeding and non-breeding were unrelated at the individual level, meaning that individuals changed their preferences when moving from breeding to non-breeding grounds. Indeed, there was no individual specialization in SST during breeding. Given that the range of SST was similar within breeding and non-breeding grounds, we can dismiss that these differences in specialization arose from a different range of available habitats in both areas. Ruling out differences in availability, different habitat specializations in breeding and non-breeding grounds could imply that such specializations are not driven by behavioural or physiological constraints, but are likely learned and fixed by experience early in life^{28,29}. This process may occur independently in breeding and non-breeding areas, where environmental conditions are probably different, thus leading to different habitat use in each area. Indeed, only resident animals, spending the breeding and non-breeding periods in the same area (the Canary Current), showed a significant association between the SST used in the two periods, thus indicating changes in specialization between breeding and non-breeding period does not arise from the change in the period but from a change in the area.

Flexible preferences in environmental traits between breeding and non-breeding periods contrast with a year-round maintenance of individual strategies regarding daily activity, as observed by a significant positive correlation between breeding and non-breeding NFI values at an individual level. This implies, for instance, that

birds that are more diurnal during breeding are also more diurnal during the non-breeding period. This suggests that daily behavioural specialization, once it is fixed, may have some returns regardless of the conditions in breeding and non-breeding grounds, such as an increased ability and efficiency in exploiting specific resources. However, this individual specialization maintained year-round may also imply some constraints on the foraging behaviour of individuals that could lead to sub-optimal foraging. Although NFI values showed that shearwaters are mainly diurnal animals, i.e. flight mainly occurs during daylight hours, there may be some individuals that are specialized in taking advantage of crepuscular hours to forage³⁰. Diurnal individuals probably rely on pelagic fish³⁰, whereas crepuscular birds probably depend on prey performing diel vertical migrations, as was previously found in other seabirds^{22,31}. Indeed, the targeted prey of Cory's shearwater includes prey that perform diel vertical migrations, such as Myctophidae species³². Individual specialization in daily activity has also been previously reported in seabirds. Similarly to the studied shearwaters, white-chinned petrel (*Procellaria aequinoctialis*) individuals specialized in their nocturnal activity³³ and European shags (*Phalacrocorax aristotelis*) showed individual consistency in foraging either during morning or afternoon in daylight hours³⁴.

Individual specialization in habitat and daily activity can lead to specialization in diet. Accordingly, we found that Cory's shearwater individuals specialized in diet across years, as inferred by $\delta^{13}\text{C}$ and, especially by $\delta^{15}\text{N}$ values. $\delta^{13}\text{C}$ values of a predator's tissue are widely acknowledged to be good proxies of its food and habitat type³⁵, while $\delta^{15}\text{N}$ values indicate its trophic level³⁵. It is known that Cory's shearwaters mainly feed on epipelagic fish, although some birds can also rely on krill and cephalopods to some extent³². Since these prey show different $\delta^{15}\text{N}$ values according to their trophic level, our results suggest that some individuals specialize on prey at low trophic levels, e.g. incorporating more krill, whereas others mainly feed on prey at mid-trophic levels, such as pelagic fish. Alternatively, higher $\delta^{15}\text{N}$ values may also result from individuals scavenging on demersal fish discarded by trawlers, which typically has greater $\delta^{15}\text{N}$ values than pelagic fish³⁶. This may imply that some individuals specialize in naturally obtained pelagic prey, whereas others specialize on fishery discards to some extent. Indeed, fishery discard specialization has been reported in other seabirds, such as northern gannets (*Morus bassanus*)³⁷, great skuas (*Catharacta skua*)³⁸ or lesser black-backed gulls (*Larus fuscus*)³⁹, although high flexibility regarding fishery waste utilization was also observed in black-browed albatross (*Thalassarche melanophrys*)⁴⁰.

Although shearwaters showed diet specialization across years both, in breeding and non-breeding grounds, we did not find a correlation in the isotopic values between these two periods. This implies, for instance, that individuals with a high trophic level during breeding do not necessarily hold a high trophic level during non-breeding. Similar to the habitat inferred from SST, this result suggests that diet specialization may change between areas. Area-dependent dietary specialization may originate from changes in prey type between breeding and non-breeding areas. Indeed, target species of breeding Cory's shearwaters are not necessarily found in non-breeding grounds. Namely, Atlantic horse mackerel (*Trachurus trachurus*) and European anchovy (*Engraulis encrasicolus*) are only present on the east coast of the Atlantic to northern Namibia, and are thus inaccessible to birds spending the non-breeding period in the west and central Atlantic and southern east African coast. Alternatively, different prey preferences depending on the area may originate from the observed differences in habitat preferences in each area, with neritic and oceanic habitats allocating different prey⁴¹. Accessibility to different prey can also explain the lack of correlation observed between breeding and non-breeding isotopic values of resident animals staying in the Canary Current year-round. Even when staying in the same area and habitat, prey accessibility can change due to seasonal movements, which occurs with sardines and horse mackerels performing seasonally latitudinal migrations in the Canary Current⁴².

The observed individual specialization in the different dimensions of the ecological niche may have consequences on individual fitness. We found some interesting tendencies regarding the implications of individual specialization on fitness, as indicated by fledging success. In the case of the diet, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not relate to fitness, but the degree of individual dietary specialization seems related to fledging success. Low and highly specialized individuals tended to exhibit lower fledging success than those medium specialized, although paired comparisons were only significant between intermediate and weakly specialized in $\delta^{13}\text{C}$ during breeding and in $\delta^{15}\text{N}$ during non-breeding. Higher fitness in intermediate individuals suggests stabilizing selection. This stabilizing selection, which crops the extremes and holds the intermediate phenotypes, is typical in stable environments with little variability⁴³. Upwelling systems could be considered stable environments with high prey availability and spatiotemporal predictability. For instance, Benguela and Canary Current, were most individuals forage in the non-breeding and breeding period respectively⁴⁴, are amongst the most important upwelling systems of the Atlantic⁴⁵. In addition, shearwaters with a weak specialization in diet could be less efficient in resource exploitation than intermediate or highly specialized individuals, which may lead to lower breeding success^{42,44,46}. Indeed, foraging specialization has been shown to increase breeding success in herring Gulls (*Larus argentatus*)⁴⁶. Alternatively, a low breeding success in weakly specialized individuals may be related to the use of fishery discards. This resource is widely used by many seabird species, including shearwaters⁴⁷, and it is also available in both, breeding and non-breeding grounds, of the studied shearwaters⁴⁸. The exploitation of discards could be considered a specialized strategy, but the offered prey is variable in their isotopic values, which may lead to an apparently weakly specialized diet. Individuals exploiting discards may be less experienced and less efficient foragers and may also be those provisioning their chicks with suboptimal prey items from discards⁴⁹. Highly specialized individuals showed similar or slightly lower breeding success than intermediate specialized ones, thus suggesting a limitation to positive effects of specialization, possibly related to a lower capability to cope with environmental stochasticity. Alternatively, the degree of specialization may just respond to different dietary strategies not necessarily related to fitness. Further research with higher sample sizes should ideally be undertaken to actually understand the influence of the degree of individual dietary specialization on the breeding success in long-lived species.

Contrarily, specialization in daily activity during non-breeding seemed to increase subsequent breeding success. However, taking into account the small sample size, with five weakly specialized, five intermediate

specialized and two highly specialized individuals, these results should be interpreted with caution. Individual specialization in other aspects of the foraging strategies has been previously shown to be adaptive in other seabirds. For instance, successful breeders of black-browed albatross showed a substantially lower spatial niche than failed ones⁵⁰, whereas repeatability in diving behaviour was related to foraging efficiency in great cormorants (*Phalacrocorax carbo*)⁵¹. Other studies with larger sample sizes are needed to understand the fitness implications of more nocturnal/diurnal behaviour on shearwaters.

In addition, we found more nocturnal animals during breeding to show higher concurrent breeding success. An increased fitness of more nocturnal animals could be related to the extensive fisheries operating on the Saharan coast of the Canary Current where shearwaters forage during breeding, which is clearly dominated by fisheries targeting epipelagic fish, such as sardines⁵². These type of fisheries are mainly active during crepuscule and night, when high concentrations of epipelagic fish are attracted to the surface by purse seine vessels using powerful lights. In this context, more nocturnal individuals may have large amount of their preferred prey available, thus increasing their body condition and ultimately their breeding performance.

Conclusions

Overall, in this study we found that Cory's shearwaters specialized in diet, daily activity and habitat from year to year. Additionally, daily activity behaviour was individually repeatable across seasons, independently of the areas visited by the individuals. Both results (i.e., repeatability between years and seasons) suggest that these animals may have a limited plasticity in their ecology and behaviour. Global changes, such as the forecasted increase of SST worldwide⁵³, will not only alter the environmental conditions of the habitat itself, but may also alter abundance and distribution of prey⁵⁴. In this scenario, low plasticity of predators could eventually compromise their ability to cope with environmental stochasticity and limit adaptive responses to global changes⁵⁵.

Nevertheless, our study also showed Cory's shearwaters are relatively flexible in their non-breeding destinations and are able to independently develop different habitat and dietary specializations under different environmental conditions. This suggests that individual specialization is not driven by individual constraints but can be acquired independently in different areas, suggesting the specialization process is more plastic than previously thought. Therefore, our study highlights the need to understand the underlying causes of individual specialization, in particular the need to distinguish between the specialization driven by permanent intrinsic traits of the individuals versus that promoted by temporal extrinsic factors, such as the stability or predictability of environmental conditions.

Materials and Methods

Fieldwork. Fieldwork was conducted from 2007 to 2015 in two colonies of Cory's shearwaters (see Supplementary Material for basic information on the species): Veneguera (27°50'39.98"N, 15°47'19"E) and Montaña Clara (29°17'29"N, 13°31'57"E), both located in the Canary Islands. We deployed and re-deployed GLS loggers (global location sensor, models MK4, MK9, MK13, MK18-H and MK19 from British Antarctic Survey and MK3005 from Biotrack) on the same individuals whenever possible. GLS were recovered mainly after one year of deployment (but some of them after up to three years), thus reducing a potential bias of device id on annual measurements. The recovery rate was 93.7% (194 recoveries from 207 deployments). Of those recovered, 8.8% failed and had no light data during the non-breeding period to infer positions, thus resulting in 176 year-round tracks. GLS devices were attached to the leg of the animal with a PVC ring. We only included in this study birds tracked from two to eight years. At the time of recovering each GLS, we sampled S13 and P1 feathers, known to be moulted at the non-breeding and breeding grounds, respectively^{56,57}. To link the specialization and strategies adopted by individuals to their fitness, we recorded fledging success by evaluating whether the chick from every monitored nest was alive around mid-October every year, when they are close to leaving the nest; this data was available for Veneguera but not for Montaña Clara.

Assessing individual specialization. We analysed different dimensions of the ecological niche: non-breeding site fidelity, isotopic diet, daily activity behaviour and habitat preference. As explained below in detail, every dimension was analysed using a different source of information, which means that sample size and number of individuals will vary among them (see Table 1 for sample sizes).

We used the locations obtained from GLS devices to address non-breeding site fidelity. After processing raw GLS data, it is possible to infer two locations per day with an error of ± 200 km⁵⁸ based on timings of sunrise and sunset. We used TransEdit software to inspect light curves and to define dawn and dusk times daily. To filter erroneous locations, we removed the 30 days around the equinoxes and applied velocity filters by removing speed values higher than the 95th percentile. Since shearwaters normally perform some stopovers and occasionally spend the non-breeding period in more than one area, we selected the main non-breeding area of each individual/year as the area where each animal spent the most days. For each individual and year, we calculated the kernel utilization distribution (UD) using positions within the main non-breeding area. To do so we used the function "kernelUD" from the package "adehabitatHR"⁵⁹ and a smoothing parameter equivalent to $\sim 2^\circ$ to account for the spatial error in geolocation. Each centroid of the 5% kernel UD contour per individual and year was then assigned to one out of ten main non-breeding areas known to be used by the species, following the limits of the areas proposed by Militão *et al.* (2018)⁶⁰.

To examine individual specialization in diet, we analysed stable isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for S13 and P1 feathers (see Supplementary Material for details on these analyses). To link trophic with the spatial information of the non-breeding period, each S13 feather sample was related to a non-breeding area inferred from GLS devices previous to the year of feather sampling, when that feather was moulted. P1 feathers were also linked to the previous year of sampling, as it was also the year of moult. To increase sample size during breeding, we included P1 feathers of animals not necessarily tracked with GLS devices.

Daily activity was assessed using the variation of behaviours (flying, resting) exhibited by individuals throughout the day and that are detected by GLS immersion data. GLS devices equipped with immersion sensor measure conductivity every three seconds and can provide information about two elemental states: wet, which means the animal was in contact with water and thus likely sitting on the sea surface, and dry, meaning the animal was flying and likely foraging. To address consistency in the daily activity, we calculated the NFI²³. This index was calculated as the difference between the proportion of time spent in flight during darkness and during daylight, divided by the highest of these two values. Values of NFI range from -1 , flight exclusively restricted to daylight, to 1 , flight restricted to night. We defined day and night using the time of sunrise and sunset generated during the analysis of the light data from GLS devices. Per each individual and year, we calculated the mean of the daily values of NFI in the breeding and the main non-breeding area. Dry records in conductivity occur when birds are flying but also during nest attendance. To avoid misleading results, we selected a period of ~ 30 consecutive days just preceding the onset of post-nuptial migration to calculate NFI, since in this period animals were still at the breeding area but did not frequently visit the nest. We also selected a period of ~ 30 consecutive days in the middle of the period spent in the main non-breeding area, in order to avoid interferences of moonlight activity, which influence shearwaters at-sea behaviour⁶¹.

To understand habitat specialization, we used as a proxy the SST ($^{\circ}\text{C}$) recorded by GLS devices, which is measured every 20 minutes after a minimum of 20 minutes of continuous contact with salt water. We calculated the mean SST per individual and year in breeding and non-breeding stages using the same 30-day window as with NFI. Cory's shearwater are in contact with salt water when drafting and diving, and maximum diving depth is 6–7 meters⁶². Therefore, GLS-recorded temperatures can be considered as SST.

Statistical analyses. All statistical analyses were carried out using R 3.4.3⁶³. Prior to statistical analyses, we checked for normality of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, NFI and SST values using Kolmogorov-Smirnov tests and Q-Q plots. As no severe deviations from normality were found, we used parametric tests throughout. Significant levels in all analyses were set to 0.05. To disregard the possibility that GLS id inflated repeatability values of GLS measurements (SST and NFI), we first included GLS id in the models and in all cases was not significant.

We used Krippendorff's alpha coefficient to estimate how repeatable individuals were in the selection of a specific non-breeding area, i.e. non-breeding site fidelity. This index can be calculated with several years of data and multiple individuals, allowing missing data for some individuals in some years and also taking into account the number of possible non-breeding areas to which individuals can go. This index ranges from 0, meaning the same individual constantly changes its non-breeding area, to 1, meaning the same individual always selects the same non-breeding area. We calculated it using "krip.alpha" function in the "irr" R package⁶⁴ and performed bootstrapping with 10,000 iterations to obtain the 95% CI of the estimate⁶⁵.

Repeatability is a commonly used statistic in behavioural studies to address individual specialization¹⁶. For the traits $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, NFI and SST, we addressed individual specialization by calculating repeatability (R), Eq. (1):

$$R = \frac{s_A^2}{s_W^2 + s_A^2} \quad (1)$$

where R is repeatability, s_A^2 is the variance among individuals and s_W^2 is the variance within individuals, with $s_W^2 + s_A^2$ being the total variation in the sampled population. The value of R ranges from 0 to 1, 0 meaning the trait has no repeatability and the majority of individuals do not show specialization (i.e. population is mainly composed of generalists) and 1 meaning that trait is highly repeatable and individual specialization is at a maximum in a given population (i.e. most individuals of the population do show specialization). Note that in order to be repeatable, a trait must be consistent within individuals but different among individuals⁶⁶. Among and within individual variances can be directly estimated from residuals of Linear Mixed-Effects Models, LMM^{15,66}. Moreover, LMM allow the control of possible effects of confounding factors by including them as fixed factors or covariates, thus providing an adjusted repeatability^{15,66}. We estimated adjusted repeatability (R hereafter) through LMM using the "rpt" function in the "rptR" package, which returns the mean value of R in the population and its 95% confidence interval (CI) calculated by parametric bootstrapping⁶⁷. A 95% CI that does not include 0 means the value of R is statistically significant. We calculated R for the traits $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, NFI and SST, separately for breeding and non-breeding. Each LMM included "year" (the year of moult in the case of isotopic values from feathers), "sex" and "non-breeding area" (the latter only in non-breeding models) as fixed factors and "individual" as a random factor. The factor "colony" (either Veneguera or Montaña Clara) was also added for all models except $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ during breeding, since we do not have P1 from Montaña Clara. We ran 10,000 iterations for each model to obtain the 95% CI. We included year as a fixed factor to keep the possible effects of annual variability out of the residual variance of the models. Animals were sexed either with molecular sexing (68% of individuals) or using discriminant functions (32%) from fieldwork bill measurements. For those models related to non-breeding, we only considered non-breeding areas with a sample size larger than five individuals/year.

To explore the consistency of traits throughout the annual cycle, we performed LMM with the same structure explained previously but also including as a covariate the parameters calculated during breeding, in order to explain the same trait during the following non-breeding season. As an example, NFI during breeding was used as covariate to explain NFI during non-breeding. We used the "lmer" function in the "lme4" package⁶⁸ to run the models. Significance of the non-breeding covariate was estimated using the "mixed" function in the "afex"⁶⁹ package with the likelihood ratio test.

To address the effect of individual strategies on fitness, we explored the influence of individual trait preferences and degree of specialization on the probability of fledging success. Considering each individual and year for which the nest was monitored at the time of fledging (mid-October), we proceeded as follows. First, we calculated the average fledging success (value ranging from 0 to 1) for all years of each individual. We later calculated the

average value of each trait ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, NFI and SST) for all years of each individual. From the previous LMM performed to calculate R , we extracted the individual repeatability value (R_{ind} hereafter) associated with each trait, following previous approaches⁵¹. We considered individuals to be weakly, intermediate or highly specialized according to their R_{ind} value. To classify them objectively, we used the k-means algorithm for clustering R_{ind} values into three groups (note that mean and size of each group varies depending on the range of R_{ind} values in each trait, see summary in Table 1 of Supplementary Material). Finally, we fitted logistic regression models (Generalised Linear Models, GLM, with logit-link function and binomial error distribution) to model the probability of fledging success, including the number of years fledging was recorded as a weight into the models. We included as predictors the R_{ind} group (fixed factor) and the mean value of its associated trait (covariate). The weakly specialized group was set as a reference level. To ensure model suitability, we tested uniformity of residuals and accounted for overdispersion for every GLM using functions provided by the “DHARMA” package⁷⁰. To evaluate the effect of predictors, both the p-value and 95% CI of coefficient estimates were calculated. Pairwise comparisons among levels were calculated based on estimated marginal means and adjusted using post-hoc Tukey correction⁷¹. Regarding mean values of traits, in the cases of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, we used the fledging success following the year of moult in the case of non-breeding variables and of the year of moult in the case of breeding variables. Similarly, for NFI and SST we used the fledging success following the non-breeding period in the case of non-breeding variables and of the concurrent breeding attempt in the case of breeding variables. Regarding non-breeding, we only performed GLM with individuals spending the non-breeding period in the Benguela system, because it was the only area with $N > 5$.

Ethics. All experiments were performed in accordance with relevant guidelines and regulations and all protocols were approved by Gobierno de Canarias (permits: 84/2007, 2011/0795, 2015/1170).

Data Availability

Data will be available at Universitat de Barcelona archive.

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Author Contributions

L.Z. analysed the data and wrote the paper; J.M.R.-G. led the fieldwork, analysed geolocator data, performed statistical analyses and contributed on writing the manuscript; T.M. analysed S.I.A., led the fieldwork, analysed geolocator data and commented on drafts of the manuscript; Z.Z. led the fieldwork, analysed geolocator data and commented on drafts of the manuscript; E.A. participated in fieldwork and commented on drafts of the manuscript; R.R. obtained funding, participated in fieldwork and commented on drafts of the manuscript; J.G.-S. conceived the study, obtained funding, participated in fieldwork and wrote the paper.

Additional Information

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Supplementary information

Study model

Cory's shearwater is a long lived pelagic seabird from Procellariidae family that breeds in Azores, Madeira, Salvagens and Canary archipelagos, as well as in occidental Mediterranean in Terreros and Chafarinas. It is a long distance migrant spending the non-breeding period in west and south African coast, from Angola to South Africa, as well as in Uruguay and Brazil coast, and with some individuals also wintering in the Guine-Equatorial current and others oceanic waters in the central Atlantic. This species usually keeps well away from land, except during the breeding period (del Hoyo et al. 2014). It is globally classified as Least Concern (IUCN 2017). The species feeds mostly on fish, squid and crustaceans, although there are evidences of interactions with trawlers to feed on fishery discards (Traversi & Vooren, 2010).

Stable isotope analyses

P1 and S13 feathers were washed in a 0.25 M sodium hydroxide solution (NaOH), rinsed twice with distilled water and dried in an oven at 40°C. Whole feathers were powdered in a cryogenic impact grinder (Freezer/mill Spex Certiprep 6750; Spex) operating at liquid nitrogen temperature. We placed 0.25-0.30 mg of each sample in a 3.3x5 mm tin cup and used this subsample to obtain $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in a continuous-flow isotope-ratio mass spectrometry (CF-IRMS) at Serveis Científico-Tècnics of Universitat de Barcelona. Isotope ratios are expressed conventionally as δ values in part per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$$

Where X (‰) is $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ and R are the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ related to the standard values. Standard for $\delta^{13}\text{C}$ is Vienna Pee Dee Belemnite (VPDB) and for $\delta^{15}\text{N}$ is atmospheric nitrogen (air). Internal laboratory standards (Acetanilide, IAEA CH6, USGS 42) indicated average measurement errors of 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Table 1 Supplementary Material

Summary of individual repeatability values (R_{ind}) for each group from k-means algorithm, namely weakly, intermediate and highly specialized. NFI is the night flight index and SST is sea surface temperature in °C.

Trait	Group R_{ind}	Breeding					Non-breeding				
		N	Mean R_{ind}	Min R_{ind}	Max R_{ind}	N	Mean R_{ind}	Min R_{ind}	Max R_{ind}	N	
$\delta^{13}C$	Weak	37	0.15	0.04	0.27	9	0.15	0.08	0.25		
	Intermediate	22	0.43	0.32	0.62	9	0.35	0.30	0.45		
	High	7	0.84	0.79	0.95	7	0.74	0.56	0.95		
$\delta^{15}N$	Weak	36	0.17	0.03	0.29	10	0.16	0.04	0.28		
	Intermediate	21	0.43	0.31	0.54	10	0.44	0.33	0.53		
	High	9	0.70	0.59	0.90	5	0.78	0.62	0.89		
NFI	Weak	7	0.49	0.27	0.55	5	0.36	0.21	0.43		
	Intermediate	9	0.69	0.61	0.77	5	0.58	0.49	0.65		
	High	11	0.88	0.81	0.93	2	0.76	0.70	0.81		
SST	Weak	7	0.19	0.11	0.31	9	0.41	0.28	0.50		
	Intermediate	5	0.47	0.38	0.59	5	0.66	0.65	0.66		
	High	4	0.81	0.67	0.97	2	0.95	0.84	0.99		



2

Niche partitioning and individual specialization among age, breeding status and sex classes in a long-lived seabird

Chapter 2

Niche partitioning and individual specialization among age, breeding status and sex classes in a long-lived seabird

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Niche partitioning and individual specialization among age, breeding status and sex classes in a long-lived seabird

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Niche partitioning among different age, breeding status or sex classes allows resource use to be maximized while reducing intraspecific competition. Individual specialization marks the finest scale of niche partitioning where, within a species, individuals differ in their realized niches. Despite having important implications in ecology, evolution and conservation, studies simultaneously addressing the occurrence of both phenomena are scarce. We studied niche partitioning and individual specialization in foraging behaviour in relation to age, breeding status and sex using breeding, nonbreeding adult and immature Scopoli's shearwaters, *Calonectris diomedea*, in Minorca (Balearic Is.) during chick rearing in 2017 with GPS loggers and stable isotopes. Compared to adults, immature birds seemed to exploit a larger area at the population level, possibly to avoid competition. We found similar levels of individual specialization in immature and adult birds, which suggests the former have well-defined foraging strategies prior to prospecting the colony. For breeding status, we did not find niche partitioning or differences in individual specialization, suggesting nest attachment and pair bonds also lead to central-place foraging in nonbreeding adults. Male breeders showed greater individual specialization than female breeders in trip characteristics. At the same time, individual specialization in isotopic diet was higher in females than in males. These opposite patterns are possibly driven by a greater use of fishery discards by males, which would underlie their individual strategies of following vessels, resulting in a highly variable diet, since discarded prey types vary more than naturally accessible prey. Our results suggest that seabirds acquire individual strategies early in life and, once they are sexually mature, breeding constraints do not result in differences in feeding behaviour between breeders and nonbreeders. Finally, we showed that sexual differences in individual specialization can apparently emerge even in slightly dimorphic species sharing breeding duties.

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Niche partitioning within species allows resource use to be maximized while reducing intraspecific competition. It can occur among demographic units, such as age, breeding status or sex classes, where each group of the population exploits (realizes) a subset of the total (fundamental) ecological niche. For instance, in whale sharks, *Rhincodon typus*, adults exploit oceanic waters whereas juveniles are coastal (Ramírez-Macías et al., 2017) and in brown boobies, *Sula leucogaster*, males and females differ in

foraging behaviour (Miller, Silva, Machovsky-Capuska, & Congdon, 2018). At a finer scale, partitioning of niches can also occur at the individual level, where individuals within a species differ in their realized niches, referred to as individual specialization (Fig. 1). For instance, intragroup competition promotes individual specialization in foraging strategies in banded mongooses, *Mungos mungo* (Sheppard et al., 2018). Both niche partitioning and individual specialization have important implications in ecology, evolution and conservation as they are key to understanding the overall picture of foraging behaviours within populations (Bolnick et al., 2011, 2003; Phillips, Lewis, González-Solís, & Daunt, 2017). However, studies simultaneously addressing the occurrence of niche partitioning in foraging strategies among age, breeding status or

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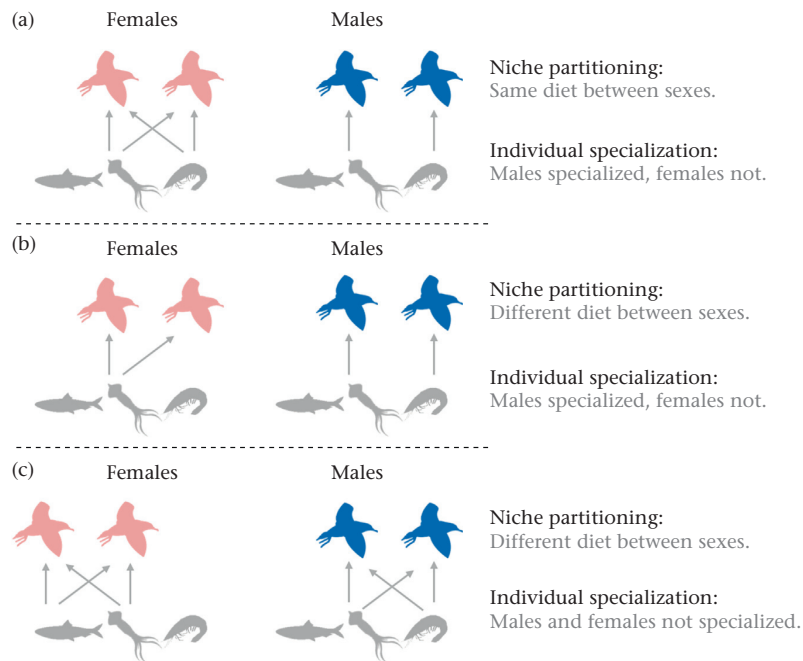


Figure 1. Conceptual diagram about niche partitioning and individual specialization with two population groups, females (light red) and males (dark blue), and three potential resources (fishes, cephalopods and crustaceans) in three hypothetical examples (a, b, c). In (a) there is no niche partitioning between females and males, as both groups exploit the same prey. However, there are differences in individual specialization, as all females feed on the same types of prey whereas different males have different prey. In (b) there is niche partitioning, as females depend only on cephalopods, whereas males feed on cephalopods and crustaceans. There is also individual specialization in males, as they have different strategies, but there is not in females, as all of them have the same strategy, i.e. feeding on cephalopods. Finally, in (c) there is niche partitioning, as females depend on fishes and cephalopods and males on cephalopods and crustaceans, whereas there is no individual specialization as there are no individual strategies within each group.

sex classes and the incidence of individual specialization within these demographic units are still scarce.

Age is an important driver of foraging behaviour, as immatures are normally less proficient foragers or have inferior competitive abilities than adults (Fayet et al., 2015; Grecian, Lane, Michelot, Wade, & Hamer, 2018). In consequence, niche partitioning can occur among age classes and individual specialization may differ between these classes. On the one hand, niche partitioning generally happens when immature animals exploit less productive areas than adults to avoid competition with them, as in Manx shearwaters, *Puffinus puffinus* (Fayet et al., 2015). Immature individuals may also forage in larger areas as a result of dispersive movements and inexperience at foraging, as in northern gannets, *Morus bassanus* (Grecian et al., 2018). On the other hand, individual specialization can develop with age when young individuals acquire a strategy with experience in an exploration–refinement process (Guilford et al., 2011). For instance, experience has been suggested to drive foraging site fidelity in adulthood in northern gannets (Grecian et al., 2018; Votier et al., 2017). Differences in individual specialization between age classes also occur in green turtles, *Chelonia mydas*: juveniles have a generalist diet whereas adults later have a specialized diet at the individual level (Vander Zanden, Bjorndal, & Bolten, 2013).

Once individuals acquire sexual maturity, niche partitioning and differences in individual specialization can occur between breeding and nonbreeding adults, as reproduction poses important time and energetic constraints (Borghello, Torres, Montalti, & Ibañez, 2019), particularly during offspring rearing (Shaffer, Costa, & Weimerskirch, 2003). Niche partitioning can occur when breeding adults are forced to exploit very predictable resources and

are thus exposed to higher intra- and interspecific competition than nonbreeding adults. Breeding constraints may, however, also force breeders to forage in familiar locations rather than exploring extensive unknown areas (Wakefield et al., 2015), resulting in higher individual specialization. Therefore, if adults fail in their reproduction or engage in a sabbatical year, we may expect them to show lower individual specialization. Indeed, in northern gannets failed breeders show higher exploration and less foraging site fidelity than breeding adults (Votier et al., 2017).

Differences in parental investment and sexual size dimorphism can lead to niche partitioning and differences in individual specialization between males and females (Miller et al., 2018; Sztukowski et al., 2018). When breeding duties are shared, as often happens during chick rearing in seabirds (Granadeiro, Nunes, Silva, & Furness, 1998), differences in foraging strategies are expected to be less pronounced (Hedd, Montevicchi, Phillips, & Fifield, 2014; Pinet, Jaquemet, Phillips, & Le Corre, 2012). Sexual size dimorphism can drive niche partitioning, since the larger sex can displace the smaller one from preferred foraging grounds (González-Solís, Croxall, & Wood, 2000; Kazama, et al., 2018). Sex-specific niche partitioning can also lead to differences in individual specialization between males and females. There is, however, no dominant pattern of one sex showing higher individual specialization than the other (Phillips et al., 2017). For instance, female Campbell albatrosses, *Thalassarche impavida*, forage close to the colony, where competition is higher, and have a higher degree of route fidelity than the more pelagic males (Sztukowski et al., 2018). Another example is the Kerguelen shag, *Phalacrocorax verrucosus*: females are more individually specialized than males in their diving behaviour (Camprasse, Cherel, Arnould, Hoskins, & Bost, 2017). In

contrast, male wandering albatrosses, *Diomedea exulans*, individually specialize in specific water masses whereas females forage in different water masses, presumably to avoid competition with males (Ceia et al., 2012).

Seabirds constitute an ideal model to address niche partitioning and individual specialization in feeding strategies among age, breeding status and sex classes. Indeed, both phenomena have been reported for different aspects of trophic ecology in many seabird species (recently reviewed by Ceia & Ramos, 2015 and Phillips et al., 2017). Breeding colonies are attended not only by breeding adults, but also often adults that do not breed or that have failed in their breeding attempts, as well as immature birds. This allows researchers to concurrently compare different foraging behaviours and individual specializations of these demographic units. Seabirds, especially the Procellariiformes, are long lived and have delayed sexual maturity; they therefore have a long period for young individuals to refine their individual strategies. Finally, many species are large enough to be tracked with GPS loggers, allowing researchers to study their foraging movements at a fine spatiotemporal scale. This tracking information can be, additionally and over time, matched with that of stable isotopes of tissues with a high turnover rate, such as blood plasma (Ramos & González-Solis, 2012).

In this study, we aimed to understand niche partitioning and differences in individual specialization in feeding strategies between age, breeding status and sex classes of long-lived seabirds. To do so, we used GPS loggers and stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the plasma of the procellariiform Scopoli's shearwater, *Calonectris diomedea*, in Minorca Is. (Mediterranean Sea) during the chick-rearing period. This species has delayed sexual maturity, with individuals generally not breeding before they are 6–9 years old and immatures attending breeding colonies before recruitment (Jenouvrier, Tavecchia, Thibault, Choquet, & Bretagnolle, 2008). Adults that do not breed or have failed in their breeding attempts also visit the colony during the breeding period. We monitored breeding and nonbreeding adults as well as immatures of both sexes to quantify niche partitioning and individual specialization in foraging movements and diet. Regarding age (1), we hypothesized (1.1) that immature birds would exploit different habitats and larger areas than adults to avoid competition with the latter and as a consequence of dispersive movements and inexperience, and (1.2) that adults would show greater individual specialization than immatures, as a result of learning during early life. Regarding breeding status (2), we expected that nonbreeding adults would (2.1) use larger areas and (2.2) have lower levels of individual specialization than breeding adults as a result of exploring more when released from breeding duties. Finally, regarding sex (3), we hypothesized (3.1) a similar trophic niche and (3.2) no differences in individual specialization among the sexes, as both sexes share breeding duties to a similar extent during chick rearing and the sexual dimorphism of the species is relatively small.

METHODS

Ethical Note

All animals were processed in accordance with relevant guidelines and regulations and all protocols were approved by Conselleria de Medi Ambient, Agricultura i Pesca from Govern de les Illes Balears (permit: ANE02-2017). We adhered to the ASAB/ABS Guidelines for the Use of Animals in Research. All birds were handled for less than 20 min. We alternated GPS deployments between the members of a pair to minimize impact on breeding success. We did not detect any evidence for negative consequences

of the study for the birds, as none were injured and all chicks of tagged pairs fledged successfully.

Fieldwork

Fieldwork was conducted in Cala Morell, Minorca Island (40°3'21"N, 3°52'8"E, Balearic Archipelago, Mediterranean Sea), during the chick-rearing period of shearwaters (July–September) in 2017. We captured breeding adults, nonbreeding adults and immature birds by hand or using a pool-nose tool. We deployed and redeployed GPS loggers on the same individuals whenever possible. We deployed two types of GPS devices: from TechnoSmArt Europe Srl (Rome, Italy; 25 g), and from Perthold Engineering LLC (Dallas, TX, U.S.A.; 18 g). They weighed 3–4% of shearwaters' mass (ca. 610 g), around the recommended limit of 4% (Passos, Navarro, Giudici, & González-Solis, 2010). We put them on the same individual up to three times, each time for 5–15 days, leaving it at least 1 week without the device. GPS devices were attached to the bird's back feathers with Tesa tape and were programmed to take a position every 5 min. In total, we fitted 180 GPS devices on 109 different individuals. Of these, 31 were lost and 21 failed, resulting in a total of 128 files with data. Of the 31 lost birds, some returned without the device and others did not return at all (perhaps because it was late in the season and they were failed breeders or immatures) and we could not retrieve the device. However, devices left on a bird would fall off when the back feathers are moulted and because the tape loses adhesion after some days. When recovering a GPS device, we sampled 2 ml of blood from the tarsal vein with a 2.5 ml syringe. Blood was placed into 2 ml vials with heparin prior to centrifuge (within 6 h after sampling) for plasma analysis. The sex of the birds was determined by molecular sexing.

We considered as nonbreeding adults sabbatical individuals that had bred in previous years and found as floaters in the study year, i.e. not associated with any nest. Nonbreeding adults also included individuals that failed in reproduction before the monitoring. We considered as immatures those birds found as floaters in the colony that had not been ringed previously. From 2012 to 2017, all breeding individuals from all nests in the study area were ringed, thus excluding the possibility of nonringed birds classified as immatures being breeders that immigrated to the colony. Individuals of this species are known to be highly philopatric, not only to the colony but also to the specific area and burrow where they breed. Indeed, from 2012 to 2019 we have not found a single adult moving between the four breeding areas that we are monitoring, which are separated by less than 1 km. During the incubation period, we also checked the brood patch of nonringed immatures to confirm that these were not developed, thus excluding the possibility of immatures being breeders, as the latter have completely developed patches when incubating the egg.

Assessing Niche Partitioning and Individual Specialization

We selected birds with at least two foraging trips or two plasma samples to calculate similarity among trips and isotopic diet, which resulted in 406 foraging trips from 63 individuals and 161 stable isotope values from 60 individuals. We analysed several trip characteristics and isotopic diet to assess niche partitioning and individual specialization for male and female breeding adults, nonbreeding adults and immature birds. We removed erroneous locations from the GPS data by first applying velocity filters (i.e. velocity higher than 120 km/h). We also removed land positions by applying a land mask and removed raft locations within 2 km of the breeding colony.

We defined six trip characteristics for each foraging trip of each individual: percentage of resting behaviour, total trip duration, maximum distance to the colony, daily activity and two habitat use variables. Four behaviours were defined by applying the expectation-maximization binary clustering algorithm EMBC (Garriga, Palmer, Oltra, & Bartumeus, 2016) at the individual level: intensive search, extensive search, resting and relocation. We calculated the percentage of resting behaviour for each foraging trip and used it for the rest of the analyses. Trip duration was defined as the total time spent on a foraging trip (h). Maximum distance to the colony was the distance from the furthest point of the trip to the breeding colony (km).

Foraging behaviour throughout the day (i.e. daily activity) was calculated using the night flight index, NFI (Dias, Granadeiro, & Catry, 2012), which ranges from -1, flight exclusively restricted to daylight, to 1, flight restricted to the night (details in the Appendix). We calculated the NFI per foraging trip of each individual.

Habitat use was estimated by extracting bathymetry and sea surface temperature (SST) for each GPS location of all foraging trips and all individuals using the Movebank platform EnvDat (Somayeh, Gil, & Rolf, 2012) with inverse distance-weighted interpolation. We used daily layers at 4 km resolution and only extracted intensive and extensive search locations. We calculated the mean value of each environmental variable per trip for each individual.

We tested for niche partitioning and individual specialization in diet using stable isotopes of carbon $\delta^{13}\text{C}$ and nitrogen $\delta^{15}\text{N}$ in plasma (details in the Appendix). The $\delta^{13}\text{C}$ values of a predator tissue are widely acknowledged to be good proxies of its food and habitat type, although they also vary in different ecomorphological groups of prey, while its $\delta^{15}\text{N}$ values mainly indicate the trophic level of the species (Bond & Jones, 2009).

To assess foraging site fidelity, we used the utilization distribution area, which is equivalent to the proportion of time spent in an area, of each foraging trip of each individual. We compared the within-individual similarity in utilization distributions with a similarity calculated by assigning the bird identity randomly to foraging trips to see whether there was more foraging site fidelity in individuals than expected by chance (details in the Appendix; Wakefield et al., 2015).

Statistical Analyses

All statistical analyses were carried out with R 3.5.3 (R Core Team, 2019). Before statistical analyses, we checked for normality of all variables using the Kolmogorov–Smirnov test and normal probability plots. When deviations of normality were found, we used the 'bestNormalize' function from the 'bestNormalize' package (Peterson, 2019) to use the best transformation to approximate normality. We used the 'orderNorm' function to transform trip duration, maximum distance to the colony and bathymetry values and the 'sqrt_x' function to transform NFI values (Peterson, 2019). Significance level for all analyses was set to $\alpha=0.05$.

Niche partitioning among groups and sexes

We used linear mixed-effects models (LMM) to test whether breeding adults, nonbreeding adults and immature birds, as well as the two sexes, differed in trip characteristics and isotopes. More specifically, we tested whether the individuals differed in percentage of resting, trip duration, maximum distance to the colony, NFI, bathymetry, SST, $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$. Each model included 'group' as a fixed effect, which was either adult breeder, nonbreeding adult or immature bird, 'sex' as another fixed effect, 'date' as covariate, which was either the day that the foraging trip started or the day of sampling (in stable isotopes) as Julian day, and 'individual' as a random effect. We also included 'moon illumination' for NFI models

as the moon is known to influence the nocturnal activity of seabirds which can forage in moonlight (Yamamoto et al., 2008; Appendix Fig. A1). LMM models were fitted using the 'lmer' function from the 'lme4' package (Bates, Mächler, Bolker, & Walker, 2014) and pairwise comparisons were performed using the 'emmeans' function from the 'emmeans' package with Tukey adjustment for multiple testing (Lenth, Singmann, Love, Buerkner, & Herve, 2019).

We also estimated whether groups (breeding, nonbreeding and immature birds) and sexes differed in the area they exploited at the population level. To do that, we calculated six population level areas, one for each combination of group and sex. We calculated the population area using the 95% kernel density estimation (KDE) of one trip of each individual chosen randomly. We picked one trip of a given individual randomly, combined it with the randomly picked trip of each other individual and we calculated the area for the population. Once a trip was selected in one random process, it was excluded for the following ones. Then, we recorded the number of individuals contributing to each estimation of the population area (since the number of trips per individual differed, our numbers of individuals contributing to each estimation of the population area also differed). With the population level values obtained for each group and sex combination, we used a linear model including 'group' and 'sex' as fixed effects and the number of individuals contributing to that measurement as covariate to correct for their differential contribution. To join the trip KDEs of the different individuals we used the 'st_union' function and we calculated their total area with the 'st_area' function from the 'sf' package (Pebesma, 2018). To perform the linear model, we used the 'lm' function and pairwise comparisons were performed using the 'emmeans' function with Tukey adjustment for multiple testing (Lenth et al., 2019).

Individual specialization among groups and sexes

We modelled differences in foraging site fidelity as a binary dependent variable (either with or without foraging site fidelity) with group and sex as fixed effects, as well as their interaction term. We used a binomial logistic regression using the 'glm' function from the 'stats' package.

We quantified individual specialization by calculating repeatability, which is a commonly used method (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). We calculated repeatability for trip characteristics and stable isotopes, as follows:

$$r = \frac{s_A^2}{s_W^2 + s_A^2}$$

where r is repeatability, s_A^2 is between-individual variance and s_W^2 within-individual variance. The value of r ranges from 0 to 1, where 0 means the trait is not repeatable and therefore the group is composed of generalist individuals, and 1 that it is totally repeatable and therefore the population is composed of specialist individuals. Between- and within-individual variances can be estimated using LMMs by extracting the residuals (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). Moreover, LMMs allow possible confounding effects to be controlled by including them as fixed effects or covariates, thus providing an adjusted repeatability (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). We estimated repeatability using the 'rpt' function from the 'rptR' package (Stoffel, Nakagawa, & Schielzeth, 2017), which also returns the 95% confidence interval performed by parametric bootstrapping (Nakagawa & Schielzeth, 2010) with 1000 iterations. We ran LMMs using as response variables the percentage of resting, trip duration, maximum colony distance, NFI, bathymetry, SST, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, estimated per

foraging trip, or sample for isotopes, of each individual. We fitted different models for each sex and the three groups. Each model included 'date' as covariate, either the day that the foraging trip started or the day of sampling as a fixed effect and 'individual' as a random effect. We also included 'moon illumination' for NFI models as the lunar cycle affects nocturnal activity of seabirds (Yamamoto et al., 2008; Appendix Fig. A1).

To test for differences in individual specialization between groups and sexes, we calculated pairwise differences in Z-transformed repeatability values (Z_r) and estimated the 95% confidence interval (Grecian et al., 2018). If confidence intervals did not overlap with zero, they were considered significantly different.

RESULTS

We obtained a total of 406 foraging trips from 63 individuals and 161 stable isotope values from 60 individuals (Table 1). For each individual, we had between two and 15 foraging trips and between two and six stable isotope values (see Appendix Table A1 for sample sizes). Individuals from all groups foraged mainly in the Minorca channel, the neritic area between Minorca and Majorca islands, and secondarily on the Catalan continental shelf (Fig. 2, Appendix Fig. A2). Shearwaters from this study performed foraging trips from 6 to 365 km from the colony for periods from 4 h to 15 days.

Niche Partitioning Among Groups and Sexes

Regarding age, we did not find differences between immatures and adults, except for the percentage of resting and the SST of foraging positions (Appendix Table A2). Immature birds rested 7.3% more during their foraging trips than breeding adults and 8.7% more than nonbreeding adults (Table 1, Appendix Table A2). Immature birds also foraged in waters 0.5 °C colder than those for both breeding adults and nonbreeding adults (Appendix Table A2). Isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among breeding adults, nonbreeding adults and immature birds did not differ. Regarding breeding status, we did not find significant differences in any of the parameters between breeding and nonbreeding adults. Regarding sex, males and females did not differ in any of the parameters extracted from

GPS devices. Males had higher $\delta^{15}\text{N}$ values than females, although the difference was small with only 0.23‰ (Appendix Table A2). Regarding daily activity, groups and sexes did not differ in nocturnal/diurnal behaviour (NFI, Appendix Table A2) or in the activity pattern throughout the day (Appendix Fig. A3).

Immatures exploited a larger area at the population level than breeders (Fig. 2; $t = 3.8$, $P = 0.001$), but there were no differences between breeding and nonbreeding adults ($t = 1.6$, $P = 0.234$) or between nonbreeding adults and immatures ($t = 2.1$, $P = 0.093$). Males tended to exploit larger areas than females ($t = 1.9$, $P = 0.059$).

Individual Specialization Among Groups and Sexes

Overall, males showed higher foraging site fidelity than females (Fig. 3; $z = 2.0$, $P = 0.041$). However, foraging site fidelity did not differ between breeding adults, nonbreeding adults and immatures; in addition, the interaction between group and sex was not significant.

Overall repeatability values were relatively low, usually lower than $r = 0.5$, with some exceptions (Fig. 4). Male breeders had repeatability values significantly higher than 0 in all foraging trip characteristics, i.e. percentage of resting, trip duration, maximum distance, NFI, bathymetry and SST, but not in stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Fig. 4a). Female breeder repeatability values, however, did not differ from 0 in most foraging trip characteristics, except for the percentage of resting and $\delta^{13}\text{C}$ (Fig. 4a). Regarding nonbreeding adults, males had significant repeatability values in trip duration and SST, whereas in females, repeatability differed significantly from 0 in maximum distance, bathymetry and both isotopes (Fig. 4b). For immature birds, males showed significant repeatability values in trip duration and $\delta^{13}\text{C}$, whereas female repeatability values differed significantly from 0 in the percentage of resting, NFI, SST and $\delta^{13}\text{C}$ (Fig. 4c).

We did not find a pattern of higher repeatability in adults than in immatures or in nonbreeding adults (Fig. 4). However, females from each group showed higher repeatability values than the respective males for the stable isotopes, particularly $\delta^{13}\text{C}$, although differences in repeatability estimates between the sexes were not

Table 1
Mean and range of the variables for male and female breeding adults, nonbreeding adults and immature birds

	Breeding adults				Nonbreeding adults				Immature birds			
	Females		Males		Females		Males		Females		Males	
	N	Mean (range)	N	Mean (range)	N	Mean (range)	N	Mean (range)	N	Mean (range)	N	Mean (range)
% Resting	12 (88)	33 (4.7, 57.5)	14 (94)	35.9 (3.1, 65.5)	5 (38)	33.6 (12.1, 61.2)	9 (57)	29.2 (2.2, 53.4)	11 (57)	34.5 (10.6, 56.7)	12 (72)	39.2 (5.2, 69.4)
Trip duration (h)	12 (88)	33.2 (12, 306.8)	14 (94)	24.9 (4.9, 92.2)	5 (38)	30.7 (15.7, 95.0)	9 (57)	30.4 (4.4, 225.5)	11 (57)	33.6 (7.2, 163.5)	12 (72)	39.3 (4.3, 310.1)
Maximum distance (km)	12 (88)	45.2 (7.8, 204.1)	14 (94)	42.8 (5.9, 337.6)	5 (38)	40.3 (7.8, 200.2)	9 (57)	54.4 (9.3, 203.3)	11 (57)	49.4 (7.8, 251.3)	12 (72)	55.6 (6.7, 365.0)
NFI	11 (57)	-0.3 (-0.6, 0.3)	11 (49)	-0.4 (-0.8, 0.5)	5 (22)	-0.3 (-0.6, 0.1)	5 (23)	-0.4 (-0.6, -0.1)	10 (36)	-0.3 (-0.6, 0)	9 (34)	-0.4 (-0.6, 0.2)
Bathymetry (m)	12 (88)	-116.8 (-1688.0, -38.1)	14 (94)	-172.5 (-1831.9, -32.5)	5 (38)	-149.5 (-1209.1, -31.8)	9 (57)	-292.3 (-1648.1, -27.6)	11 (57)	-297.6 (-1455.2, -24.4)	12 (72)	-304.0 (-2042.5, -36.5)
SST (°C)	12 (87)	26.7 (25.2, 28.7)	13 (87)	26.8 (24.6, 28.3)	5 (38)	26.8 (25.3, 28.2)	9 (57)	26.7 (24.9, 28.5)	11 (57)	26.2 (24.0, 28.0)	12 (72)	26.1 (23.7, 27.5)
$\delta^{13}\text{C}$	13 (41)	-19.3 (-19.8, -18.7)	15 (44)	-19.3 (-20.1, -18.8)	5 (15)	-19.4 (-20.1, -19.0)	8 (17)	-19.3 (-19.8, -19.0)	9 (18)	-19.3 (-20.0, -18.6)	10 (26)	-19.2 (-19.7, -18.8)
$\delta^{15}\text{N}$	13 (41)	9.3 (8.6, 10.8)	15 (44)	9.5 (8.6, 11.6)	5 (15)	9.3 (8.7, 10.2)	8 (17)	9.8 (9.0, 11.4)	9 (18)	9.4 (8.7–10.3)	10 (26)	9.5 (9.0–10.4)

NFI: night flight index; SST: sea surface temperature. Sample sizes (N) include the number of individuals and the number of trips (for GPS variables) or samples (for stable isotopes) in parentheses. Note that sample sizes for NFI and SST are lower than for the other variables (see Methods).

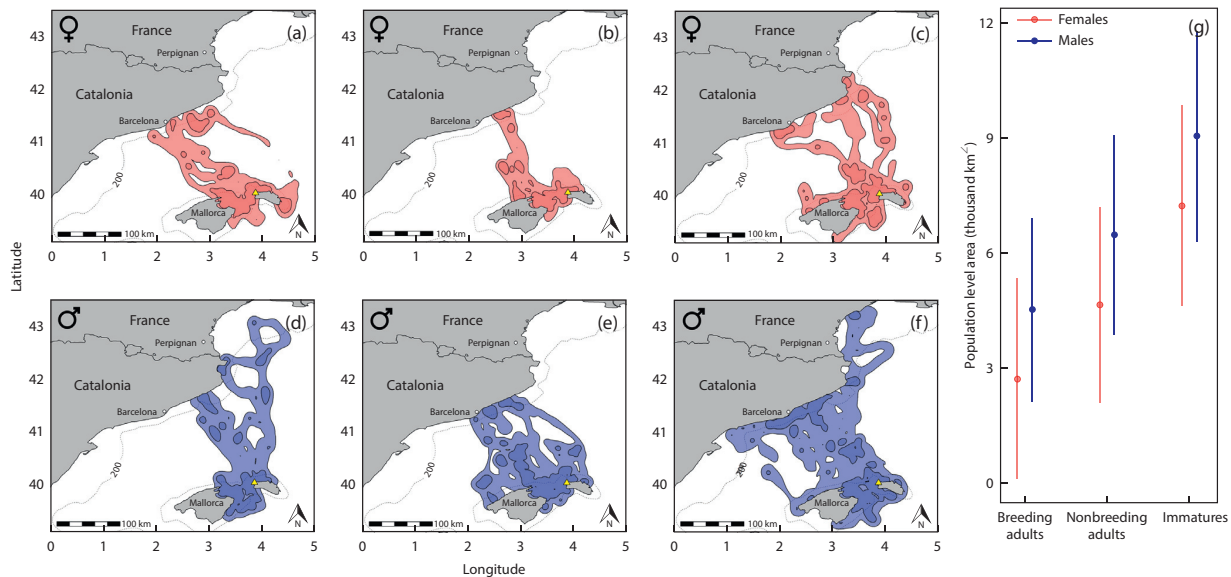


Figure 2. (a–f) Foraging areas of Scopoli's shearwaters at the population level for females (light red) and males (dark blue) from each group from July to September 2019 in Cala Morell, Minorca Is. (a) Breeding adult females ($N = 12$); (b) nonbreeding adult females ($N = 5$); (c) immature females ($N = 11$); (d) breeding adult males ($N = 14$); (e) nonbreeding adult males ($N = 9$); (f) immature males ($N = 12$). Dark and light areas are the 50 and 95% kernel density areas, respectively. The dotted grey line shows the 200 m isobath. The yellow triangle shows the location of the breeding colony. (g) Population level size of the foraging areas of females and males from each group. Error bars represent the 95% confidence interval.

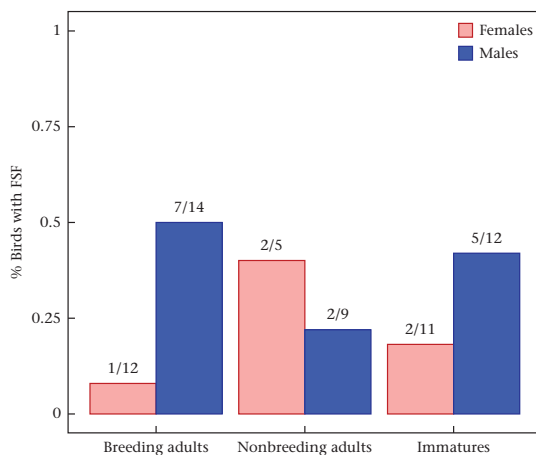


Figure 3. Percentage of birds with a higher foraging site fidelity (FSF) than expected by chance for each group. Ratios above bars are the number of individuals showing foraging site fidelity/total number of individuals for each group and sex.

significant (Figs. 4 and 5). Finally, male breeders showed consistently higher repeatability values than female breeders in foraging trip characteristics, although significantly so only for bathymetry (Figs. 4a and 5).

DISCUSSION

In this study, we addressed niche partitioning among age, breeding status and sex classes and individual specialization within these classes by using male and female breeding adults, nonbreeding adults and immature birds of Scopoli's shearwater. In general, we did not find niche partitioning between immatures and adults, although immature birds used a slightly different

habitat during foraging and tended to disperse more than breeding adults, possibly to avoid competition. Contrary to our expectations, we found similar repeatability values between adult and immature birds, probably because immature birds had already acquired their individual strategies when they started prospecting the breeding colony. Moreover, we found similar repeatability values, and no niche partitioning, between nonbreeding and breeding adults, thus suggesting foraging strategies were generally maintained once individuals acquired sexual maturity. Despite differences in size and breeding duties between males and females being minimal in this species, we unexpectedly found sexual differences in individual specialization whereas females did not, probably because males scavenge on discards of fishing vessels more than females. Male breeders showed specialization in their foraging trip characteristics but had the lowest isotopic specialization of all groups, which can be attributed to male breeders dominating access to fishery discards over immatures and nonbreeders.

Influence of Age on Foraging and Specialization

Immature birds exploited a larger area than breeding adults at the population level (hypothesis 1.1), thus suggesting they disperse more than adults. Differences in dispersion may arise from immature birds using different areas to avoid competition with experienced adults in waters close to the breeding grounds (Pettex, Lambert, Fort, Dorémus, & Ridoux, 2019; Votier, Grecian, Patrick, & Newton, 2011). Indeed, immatures foraged on average in waters slightly colder than both breeding and nonbreeding adults, suggesting that they segregated in slightly different habitats. Alternatively, immature birds may show greater dispersive movements at the population level because some individuals, probably the youngest ones, may have performed more erratic movements as they are less proficient foragers and do not respond to

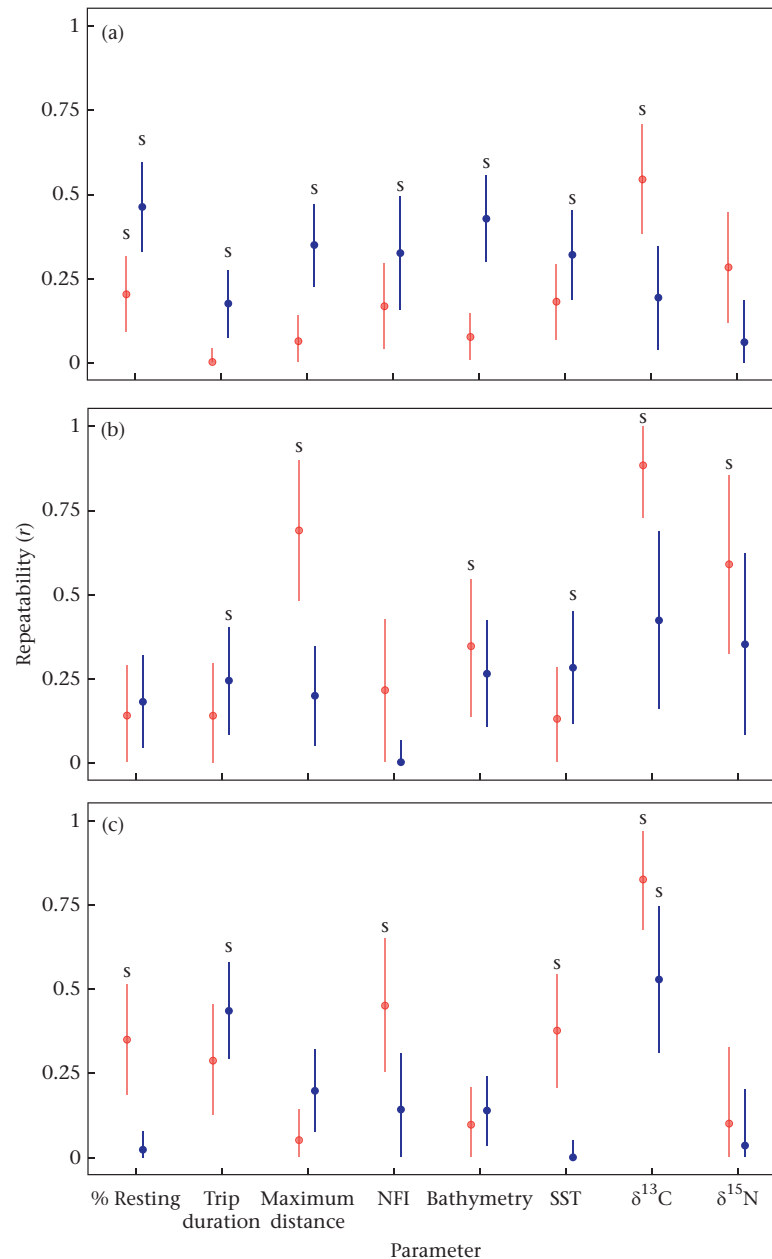


Figure 4. Repeatability values \pm SD for females (light red) and males (dark blue) of each group. (a) Breeding adults; (b) nonbreeding adults; (c) immature birds. 's' indicates significant repeatability estimates. NFI: night flight index; SST: sea surface temperature.

environmental cues as well as breeders (Grecian et al., 2018; Pettex et al., 2019). Less proficient foraging may also imply immatures need more time to rest on the water, which could explain the slightly higher proportion of resting behaviour in foraging trips of immature birds than in adults. However, in general we did not find clear patterns of niche partitioning between immatures and adults; similarly, Péron and Grémillet (2013) also found no clear niche partitioning between immatures and adults in other colonies of this species during the late breeding period.

Individual specialization in foraging strategies can arise from exploration and refinement of young individuals' behaviour. Under

this scenario, immature individuals have variable foraging strategies whereas adults show individual specialization (Grecian et al., 2018; Vander Zanden et al., 2013; Votier et al., 2017). We did not, however, find repeatability values of adults to be higher than those of immature birds (hypothesis 1.2). Immature shearwaters start visiting the colony when they are 3 years old (Jenouvrier et al., 2008), so the immature individuals that we could track were probably 3–6 years old. Therefore, our results indicate that immature long-lived seabirds at 3–6 years of age can be as specialized as adult birds. This may occur because immature Scopoli's shearwaters could rapidly learn the spatiotemporal

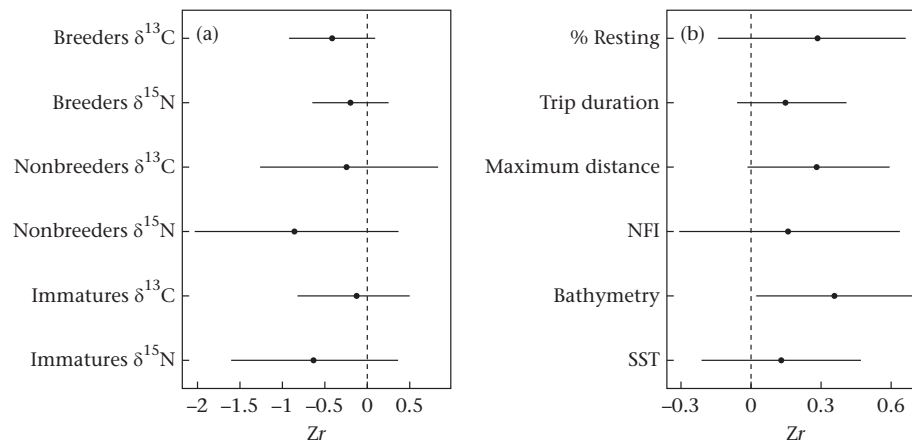


Figure 5. Differences between males and females in the point estimates of repeatability values (Z_r) and 95% confidence intervals for (a) stable isotopes in all groups and (b) foraging trip characteristics of breeding adults. Differences greater than 0 indicate males are more repeatable than females; differences lower than 0 indicate females are more repeatable than males. Those differences whose 95% confidence interval does not cross the dotted line are significant. NFI: night flight index; SST: sea surface temperature.

heterogeneities of the environment and refine their individual strategies before they start visiting the colony.

Influence of Breeding Status on Foraging and Specialization

Niche segregation between breeding and nonbreeding adults is related to the central-place foraging of breeders and to the energetic requirements of reproduction (Borghello et al., 2019; Paiva et al., 2010). In many seabird species such as black-browed albatrosses, *Thalassarche melanophris*, or the sister species Cory's shearwaters, *Calonectris borealis*, breeders and nonbreeding adults are known to have different foraging ecologies as a result of these constraints (Campioni, Granadeiro, & Catry, 2016). However, in our study we found neither niche segregation nor differences in the area exploited between breeding and nonbreeding adults (hypothesis 2.1). This result may be influenced by failed and sabbatical individuals maintaining their attachment to the nest or performing pair bonding that causes nonbreeding birds also to act as central-place foragers. However, as we selected individuals that provided several foraging trips and blood samples, our results might also be biased towards those nonbreeding birds frequently revisiting the colony and missing those individuals performing very long single trips or visiting the colony only sporadically.

In northern gannets, nonbreeding adults show lower individual specialization than breeders as a result of their exploratory movements when released from breeding duties (Votier et al., 2017). However, we did not find differences in individual specialization between breeding and nonbreeding adults and the latter did not perform exploratory movements far from the breeding colony either (hypothesis 2.2). These results may occur because nonbreeding adults may be more efficient at foraging in familiar and closer locations (Wakefield et al., 2015), also avoiding competition with shearwaters from other colonies (Ramos et al., 2013; Wakefield et al., 2013). Alternatively, the differences in the foraging behaviour of breeding and nonbreeding adults may be too small to be picked up with our limited sample size.

Influence of Sex on Foraging and Specialization

In general, we found that foraging patterns of males and females were similar both in trip characteristics and in habitat use (Cecere et al., 2015), although males seemed to exploit larger areas than

females at the population level. This absence of sexual niche partitioning may come from the slight sexual size dimorphism of the species and shared breeding duties during chick rearing (Pinet et al., 2012; hypothesis 3.1).

Contrary to our expectations (hypothesis 3.2), males and females differed in their levels of individual specialization. Females from all groups showed significant repeatability values in $\delta^{13}\text{C}$ and to a lesser extent $\delta^{15}\text{N}$ whereas males generally did not, thus suggesting females were individually specialized in their diet while males had a more variable diet at an individual level. Male breeders were also more individually specialized than female breeders in all parameters related to their foraging trips, whereas this difference was not found in nonbreeding adults and immatures. We hypothesize these patterns are mediated by a complex interplay between fisheries, sex-driven foraging preferences and intra- and interspecific competition.

The Mediterranean Sea suffers from intense pressure by fishery activities (Piroddi et al., 2017). Most of these fisheries return to the sea large amounts of dead or dying biomass that can be used by seabirds, including shearwaters, modifying their feeding ecology in a number of ways (Bartumeus et al., 2010; Real et al., 2018). Fishery discards may come from different vessels and are highly variable in prey type, including both pelagic and benthic demersal fishes, cephalopods and crustaceans in a diverse array of sizes (Tsagarakis, Palialexis, & Vassilopoulou, 2014). Consequently, although association with fisheries may be considered a specialized strategy (Donk et al., 2017; Patrick et al., 2015; Tyson, Shamoun-Baranes, Van Loon, Camphuysen, & Hintzen, 2015), individuals exploiting fishery discards will feed on a highly diverse range of prey. We therefore conclude that males showed less repeatable isotopic values because of scavenging on discards, whereas females showed more repeatable isotopic values because they mainly fed on naturally obtained prey. Indeed, males from this colony are known to interact more than females with fishery vessels (Cortés, García-Barcelona, & González-Solis, 2018). Supporting this hypothesis, males showed slightly higher $\delta^{15}\text{N}$ values than females, probably as a result of including demersal and benthonic prey species in their diet, which are naturally inaccessible to shearwaters and typically have higher $\delta^{15}\text{N}$ values (Votier et al., 2010). In line with their higher fishery interaction, males showed higher foraging site fidelity than females. When resources such as fishery discards are highly spatio-temporally predictable (Bartumeus et al., 2010), individuals are

expected to show higher habitat and site fidelity (Grassel & Rachlow, 2017; Patrick et al., 2015; Weimerskirch, 2007).

Breeding males showed the lowest repeatability values of stable isotopes among all groups, thus suggesting they exploit fishery discards the most. Accordingly, breeding males showed significant repeatability values in all parameters related to the foraging trip, which is expected when individuals have a well-defined individual foraging strategy of following vessels (Patrick et al., 2015). In contrast, nonbreeding males and immatures were not as specialized in trip characteristics. This may be because they are better able to cope with uncertainty, allowing them to forage in less reliable places, thus taking a risk that breeding adults cannot take. Therefore, male breeders would depend on the reliability of fishery discards, whereas nonbreeding and immature birds would act as facultative scavengers. Indeed, breeding Scopoli's shearwaters, especially males, have been caught in long-liners in the Mediterranean more often than nonbreeders, thus supporting a higher interaction of breeding males with fisheries (Cortés et al., 2018). Since January 2019 there has been a ban on discards in the EU which presumably may affect seabirds' feeding strategies, although so far the impact may be more limited than initially thought due to several exceptions and implementation problems.

Conclusions

Overall, our results indicate immature shearwaters from 3 to 6 years of age can be as specialized as adults, suggesting long-lived seabirds with delayed sexual maturity may acquire their individual foraging strategies during their first years of life. In this study, we propose that anthropogenic resources drive the differences in individual specialization. This highlights the need to account for the impacts of alterations in the environment when studying individual level feeding strategies across life stages and sexes. Indeed, a major question in the study of individual specialization is how it is affected by human activities (Layman, Newsome, & Gancos Crawford, 2015).

Author Contributions

L.Z. analysed the data and wrote the paper; LN–H. and M.G.-V. led the fieldwork; K.S. helped in methodology and writing; J.G.-S. conceived the study, obtained funding and wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability

Data are available at the Universitat de Barcelona archive: <http://www.ub.edu/arxiu/en/quisom.html>.

Declaration of Interest

The authors declare that they have no conflict of interest.

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Appendix

Daily activity using night flight index (NFI)

We addressed foraging behaviour throughout the day (i.e. daily activity) by calculating the night flight index (NFI). This index is the difference between the proportions of time spent in flight during darkness and during daylight, divided by the highest of these two values (Dias et al., 2012). It ranges from -1, flight exclusively restricted to daylight, to 1, flight restricted to night. Information on time spent flying during the day or at night was obtained using the EMBC algorithm of behavioural classification, using as flying all behaviours except resting. We defined day and night using the time of sunset and sunrise with the 'sunrise.set' function of the package 'StreamMetabolism' (Sefick, 2009). Since shearwaters make short trips during chick rearing, we used trips that lasted at least 20 h to have representative day and night periods. We calculated the NFI per foraging trip of each individual.

Stable isotope analyses

Plasma samples were dehydrated using a lyophilization process, powdered with a small mortar and homogenized. We placed 0.30 ± 0.03 mg of dehydrated plasma in a 3.3x5 mm tin cup and used this subsample to obtain $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in a continuous-flow isotope ratio mass spectrometer (CF-IRMS) at Serveis Científic-Tècnics of Universitat de Barcelona. Isotope ratios are expressed conventionally as δ values in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1]$$

Where X (‰) is either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ and R the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ related to the standard values. R_{standard} for $\delta^{13}\text{C}$ is Vienna Pee Dee Belemnite (VPDB) and for $\delta^{15}\text{N}$ atmospheric nitrogen (AIR).

Assessing foraging site fidelity

To assess foraging site fidelity, we first estimated the utilization distribution area of each foraging trip of each individual, considering only intensive and extensive search positions defined by the EMbC. To estimate utilization distributions we used the 95% kernel density estimation (KDE), using the same h value for all KDEs ($h = 0.05$), which was the mean of 'href' estimated per foraging trip of each individual. KDEs were estimated using the 'kernelUD' function from the 'adehabitatHR' package (Calenge, 2006). To calculate the similarity between 95% KDE areas we used Bhattacharyya's affinity (Wakefield et al., 2015), which calculates the overlap between pairs of utilization distributions. This index takes values ranging from 0, representing no overlap, to 1, indicating completely overlapping areas. We estimated the within-individual similarity using pairs of utilization distributions from trips of the same individual. However, the within-individual similarity is not particularly informative in terms of individual fidelity, because it reflects both population and individual consistency. To have individual site fidelity, an individual must be faithful to a specific foraging area that is different to that of other individuals. This means that if all individuals exploit the same foraging area, then there is no individual specialization, but there is specialization of the species, the population or the group. Therefore, we compared the within-individual similarity to the within-population similarity to see whether there was more foraging site fidelity in individuals than expected by chance. Within-population similarity was obtained by randomly assigning an individual to a foraging trip and calculating the similarity between pairs of trips of each randomly assigned individual (Wakefield et al., 2015). This randomization procedure was performed 1000 times to obtain a within-population similarity distribution, which was performed for each sex and group. If there is individual foraging site fidelity, then individuals should overlap more when the individual is randomly assigned. The number of trips per individual did not affect the within-individual overlap ($t = 1.2$, $P = 0.245$), so we used all trips from all individuals for this calculation.

NFI: night flight index; SST: sea surface temperature. N_{ind} : number of individuals; N_{trips} : number of trips. Significant differences between groups and sexes are shown in bold. In the differences between groups, t and P values are from post hoc comparisons with Tukey adjustment. P values were corrected for multiple testing with false discovery rate using Holm's sequential Bonferroni procedure (Chen, Feng, & Yi, 2017; Holm, 1979).

Table A1

Number of GPS trips and number of blood samples used in stable isotope analyses per individual from each group (either breeding adult, nonbreeding adult or immature birds) of Scopoli's shearwater

Individual	No. of GPS trips	No. of blood samples	Group	Sex
1	10	4	Breeding	Male
2	8	2	Breeding	Male
3	6	3	Breeding	Male
4	5		Breeding	Male
5		3	Breeding	Male
6	6	5	Breeding	Male
7		4	Breeding	Male
8	4		Breeding	Male
9		2	Breeding	Male
10	4	3	Breeding	Male
11	10	3	Breeding	Male
12	4	2	Breeding	Male
13	6	2	Breeding	Male
14	5	2	Breeding	Male
15	7	2	Breeding	Male
16	4	3	Breeding	Male
17	15	4	Breeding	Male
18	10	4	Breeding	Female
19	9	4	Breeding	Female
20	6	3	Breeding	Female
21	7	3	Breeding	Female
22	4	5	Breeding	Female
23	8	2	Breeding	Female
24	7	3	Breeding	Female
25	7	3	Breeding	Female
26		4	Breeding	Female
27	6	2	Breeding	Female
28	7	3	Breeding	Female
29	10	2	Breeding	Female
30	7	3	Breeding	Female
31	7	2	Immature	Male
32		2	Immature	Male
33	7	2	Immature	Male
34	2	2	Immature	Male
35	7	2	Immature	Male
36	7		Immature	Male
37	6	4	Immature	Male
38	5	2	Immature	Male
39	6	2	Immature	Male
40	5	2	Immature	Male
41	8		Immature	Male
42	3		Immature	Male
43	9	6	Immature	Male
44	5	2	Immature	Female
45	3	2	Immature	Female
46	11	2	Immature	Female
47	2	2	Immature	Female
48	5	2	Immature	Female
49	3		Immature	Female
50	3	2	Immature	Female
51	10		Immature	Female
52	2	2	Immature	Female
53	2	2	Immature	Female
54	11	2	Immature	Female
55		2	Nonbreeding	Male
56	7	2	Nonbreeding	Male
57	6	3	Nonbreeding	Male
58	11		Nonbreeding	Male
59	5	2	Nonbreeding	Male
60	7	2	Nonbreeding	Male
61	5	2	Nonbreeding	Male
62	4	2	Nonbreeding	Male
63	7		Nonbreeding	Male
64	5	2	Nonbreeding	Male
65	8		Nonbreeding	Female
66	6	3	Nonbreeding	Female
67	6	2	Nonbreeding	Female
68	13	6	Nonbreeding	Female
69		2	Nonbreeding	Female
70	5	2	Nonbreeding	Female

Table A2Sample size, R^2 and significance of group (either breeder, nonbreeder or immature birds), sex and date variables on linear mixed-effect models performed for each parameter

	$N_{\text{ind}} (N_{\text{trips}})$	R^2	Group	Sex	Date
% Resting	63 (406)	0.36	$t_{\text{breed-imm}} = -3.4, P = 0.033$ $t_{\text{breed-nonbreed}} = 0.6, P = 1$	$t = -0.6, P = 1$	$t = 5.5, P < 0.001$
Trip duration (h)	63 (406)	0.23	$t_{\text{imm-nonbreed}} = 3.5, P = 0.046$ $t_{\text{breed-imm}} = -1.6, P = 1$ $t_{\text{breed-nonbreed}} = -0.1, P = 1$ $t_{\text{imm-nonbreed}} = 1.3, P = 1$	$t = 1.5, P = 1$	$t = 1.5, P = 0.133$
Maximum distance (km)	63 (406)	0.31	$t_{\text{breed-imm}} = 1.3, P = 1$ $t_{\text{breed-nonbreed}} = 0.4, P = 1$ $t_{\text{imm-nonbreed}} = -0.7, P = 1$	$t = 0.4, P = 1$	$t = -4.8, P < 0.001$
NFI	51 (221)	0.34	$t_{\text{breed-imm}} = 1.5, P = 1$ $t_{\text{breed-nonbreed}} = 0.4, P = 1$ $t_{\text{imm-nonbreed}} = -0.9, P = 1$	$t = 1.9, P = 0.732$	$t = -3.8, P < 0.001$
Bathymetry (m)	63 (406)	0.33	$t_{\text{breed-imm}} = 0.1, P = 1$ $t_{\text{breed-nonbreed}} = 0.3, P = 1$ $t_{\text{imm-nonbreed}} = -0.2, P = 1$	$t = 2.1, P = 0.573$	$t = 2.4, P = 0.018$
SST (°C)	62 (398)	0.32	$t_{\text{breed-imm}} = 3.5, P = 0.035$ $t_{\text{breed-nonbreed}} = -0.4, P = 1$ $t_{\text{imm-nonbreed}} = -3.5, P = 0.035$	$t = 0.8, P = 1$	$t = 2.8, P = 0.006$
$\delta^{13}\text{C}$	60 (161)	0.63	$t_{\text{breed-imm}} = -2.2, P = 0.891$ $t_{\text{breed-nonbreed}} = 0.1, P = 1$ $t_{\text{imm-nonbreed}} = 1.9, P = 1$	$t = -0.1, P = 1$	$t = 9.3, P < 0.001$
$\delta^{15}\text{N}$	60 (161)	0.54	$t_{\text{breed-imm}} = 2.2, P = 0.891$ $t_{\text{imm-nonbreed}} = 1.0, P = 1$ $t_{\text{breed-nonbreed}} = -0.9, P = 1$	$t = -3.3, P = 0.025$	$t = -10.3, P < 0.001$

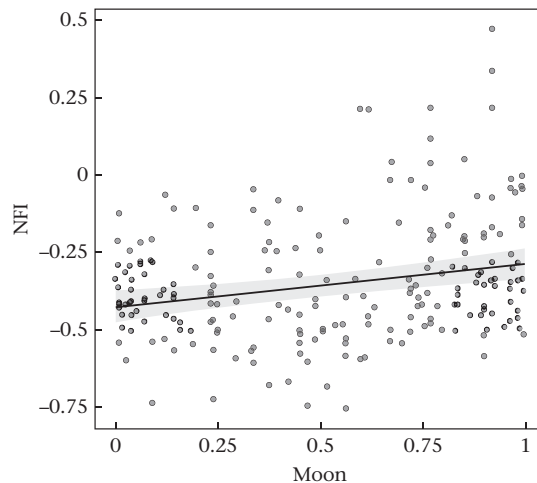


Figure A1. Influence of moon illumination (the fraction of the moon's visible disk that is illuminated) on nocturnal activity of Scopoli's shearwaters. Nocturnal activity was measured as the night flight index (NFI), that is, the difference between the proportions of time spent in flight during darkness and during daylight, divided by the highest of these two values, where -1 is completely diurnal and 1 is completely nocturnal behaviour (Dias et al., 2012). Each point is one individual in one foraging trip, including all groups and sexes, although accounting for their differences. The solid line corresponds to the mean of the relationship and the grey shading is the associated 95% confidence interval. The relationship between moon illumination and nocturnal activity is significant ($t = 3.2, P = 0.001$).

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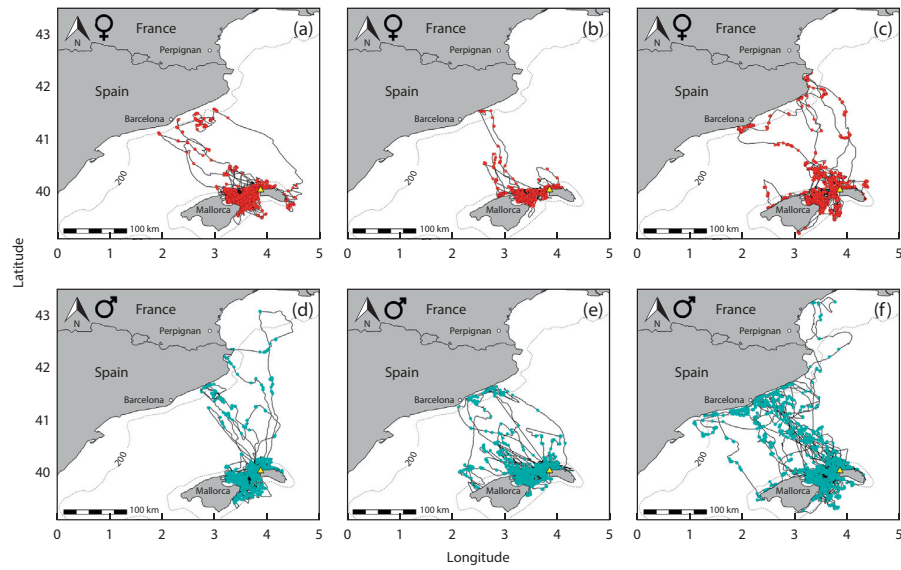


Figure A2. Scopoli's shearwater foraging trips with intensive search locations of females (red) and males (blue) from each group from July to September 2019 in Cala Morell, Minorca Is. (a) Breeding adult females ($N = 12$); (b) nonbreeding adult females ($N = 5$); (c) immature females ($N = 11$); (d) breeding adult males ($N = 14$); (e) nonbreeding adult males ($N = 9$); (f) immature males ($N = 12$). The dotted grey line shows the 200 m isobath. The yellow triangle indicates the location of the breeding colony.

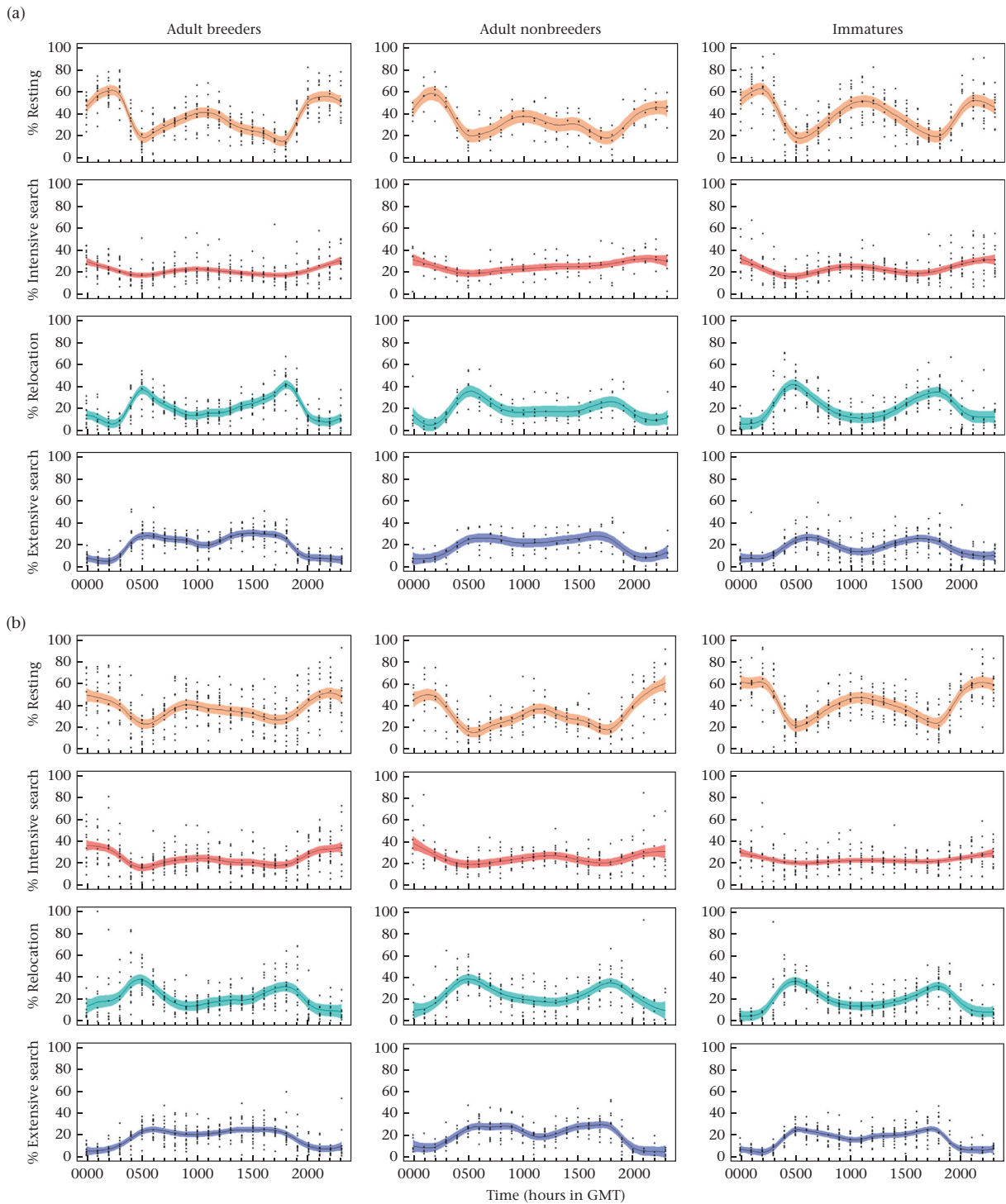


Figure A3. Daily activity patterns in four behavioural modes, as indicated by the EMbC algorithm, for (a) female and (b) male breeding adults, nonbreeding adults and immature Scopoli's shearwaters. Orange: resting behaviour; red: intensive foraging; light blue: relocation; dark blue: extensive search. The solid line corresponds to the mean and the shading is the associated 95% confidence interval.



3

Environmental drivers of individual specialization in foraging strategies in the marine ecosystem

Chapter 3

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Abstract

Individual specialization refers to individuals using different portions of the total ecological niche of the population. Despite having important consequences on ecology and evolution, empirical evidence on what and how environmental conditions promote individual specialization are scarce. On the one hand, resource limitation is expected to promote individual specialization to avoid competition. On the other hand, a high predictability of resources is also expected to promote it, as individuals know where and when they can find their food and can define their own foraging strategies. In the marine ecosystem, neritic environments usually show high abundance and persistence of resources, whereas oceanic environments are less productive, and resources are expected to be more randomly distributed and thus less predictable. Therefore, if resource limitation is driving individual specialization, we would expect it to be higher in animals exploiting oceanic environments, whereas if it is mainly driven by resource predictability, we would expect it to be higher in those exploiting neritic environments. We addressed individual

specialization in foraging movements and in habitat use by GPS-tracking Cory's shearwaters *Calonectris borealis* breeding in six locations spanning a range of environmental variability and accessibility to neritic and oceanic environments. We found that shearwaters foraging in oceanic environments showed higher levels of repeatability in movement characteristics (departure direction, trip duration, distance covered and maximum distance from the colony) than those foraging in neritic environments. This supports the resource limitation hypothesis as the main driver of individual specialization in foraging movements. Repeatability in habitat traits (bathymetry, Chl-a, SST and proximity to seamounts) was relatively high in both, oceanic and neritic environments, indicating that segregation in individual habitat use can occur regardless of the limitation or predictability of resources. To our knowledge, this is the first study in the marine environment to conclude that resource limitation is a more relevant driver of individual specialization in foraging movements than resource predictability.

Key-words

Individual consistency ■ Pelagic seabirds ■ Oceanographic conditions ■ Resource abundance
■ Unpredictable resources

Introduction

Individual specialization refers to individuals consistently using portions of the total ecological niche of the population (Bolnick et al., 2003). When there is individual specialization within a population, individuals have certain foraging strategies maintained across time that are different to the strategies adopted by other individuals, *i.e.* there is low within-individual variation and high among-individual variation in a specific trait. Although initially defined only with dietary specialization (Van Valen, 1965), this phenomenon also occurs in other ecological traits, such as in foraging movements, habitat preferences or spatial fidelity (Bolnick et al., 2003; Phillips, Lewis, González-Solís, & Daunt, 2017; Piper, 2011). Individual specialization is widespread in the animal kingdom, occurring in a broad array of invertebrate and vertebrate taxa (Bolnick et al., 2003; Piper, 2011) and has important implications in ecology, evolution and conservation (Bolnick et al., 2011). Variation among individuals in their foraging strategies reduces intraspecific competition and promotes ecological segregation (Lichstein et al. 2007), as well as can influence species coexistence (Hart, Schreiber, & Levine, 2016; Schirmer, Hoffmann, Eccard, & Dammhahn, 2020) and have profound effects on community structure and ecosystem functioning (Des Roches et al., 2018). Despite its incidence and implications, little is known about the environmental conditions that promote it (Araújo, Bolnick, & Layman, 2011).

Resource limitation is expected to promote individual specialization (Svanbäck & Bolnick, 2005; Tinker, Bentall, & Estes, 2008). When preferred resources are limited, intraspecific competition increases and individuals add alternative resources to their diets, thus segregating their niches (Araújo et al., 2011; Sheppard et al., 2018). Several empirical studies have supported the fact that limitation of resources promotes individual specialization in diet and other aspects of foraging behaviour in several taxa, from invertebrates (Svanbäck, Rydberg, Leonardsson, & Englund, 2011) to vertebrates: fishes (Kobler, Klefoth, Mehner, & Arlinghaus, 2009), birds (Ratcliffe, Adlard, Stowasser, & McGill, 2018) or mammals (Mori, Nakata, & Izumiyama, 2019; Tinker et al., 2008).

Individual specialization can also be promoted by resource predictability or stability (Dermond, Thomas, & Brodersen, 2018; Grassel & Rachlow, 2017). When resources are predictable and stable, individuals know where and when they can find their prey and they can define consistent individual foraging strategies. On the contrary, in unpredictable environments, it is hard for individuals to specialize since difficulty in finding resources limits a consistent individual behaviour (Oppel et al., 2017). Indeed, when resources are randomly distributed, traveling to different areas increases the spatial range covered and may increase the probability of prey encounter (Lerma, Serratosa, Luna-Jorquera, & Garthe, 2020). Accordingly, brown trout showed higher individual specialization in predictable environments than in unpredictable ones (Dermond et al., 2018). Similarly, frigatebirds and several booby species showed low or no individual specialization when foraging in unpredictable environments (Kappes, Weimerskirch, Pinaud, & Le Corre, 2011; Lerma et al., 2020; Oppel et al., 2017; Soanes et al., 2016).

In marine ecosystems, resource abundance and predictability are closely linked. In oceanic environments, waters are usually oligotrophic and therefore with limited resources that tend to be unpredictable (Weimerskirch, 2007). In contrast, in neritic environments, there is high resource abundance and resources are spatiotemporally predictable in the form of persistent oceanic features, such as shelf edges or upwellings (Wakefield, Phillips, & Matthiopoulos, 2009; Weimerskirch, 2007). Therefore, both low resource abundance in oceanic environments and high resource predictability in neritic environments may promote individual specialization depending on the strength of the different factors. Thus, comparing how predators behave in oceanic and neritic environments provide an excellent opportunity to understand what factors have more weight in promoting among-individual differences in ecological traits.

Seabirds constitute an ideal model to address the importance of resource abundance and predictability in promoting individual specialization in the marine environment. They generally breed across large geographical regions, with colonies located under contrasting environmental conditions subjected to different levels of resource abundance and predictability in their surroundings (Schreiber & Burger, 2002). In contrast with most marine animals, seabirds are accessible on land and individuals can

be easily tracked to understand their movements and foraging specialization. Individuals are also highly faithful to specific burrows and act as central-place foragers while breeding (Schreiber & Burger, 2002), thus allowing for repeated tracking and sampling of the same individual over several years. Seabird movements can be easily tracked using Global Positioning System (GPS) devices, obtaining the position of the animal at a fine spatiotemporal scale, *i.e.* every few minutes with an average accuracy of a few meters (Forin-Wiart, Hubert, Sirguy, & Pouille, 2015).

In this study we aimed to disentangle the roles of resource limitation and resource predictability in driving individual specialization in the marine environment. To do so, we addressed foraging individual specialization using GPS devices in the Procellariiform Cory's shearwater (*Calonectris borealis*). We assessed individual specialization in foraging strategies through several characteristics that define foraging movements (departure direction, trip duration, distance covered and maximum distance from the colony), as well as the habitat used during foraging trips (bathymetry, sea surface temperature, chlorophyll-a and distance to seamounts). To understand the influence of resource limitation and predictability, we studied foraging behaviour in six colonies across the Atlantic Ocean: Veneguera, Timanfaya and Montaña Clara in the Canary Islands archipelago; Berlenga in Berlengas archipelago; Corvo in Azores archipelago; and Ilhéu de Cima in Madeira archipelago. Shearwaters from Canary Islands forage in both, oceanic and neritic environments, with individuals combining to a different extent short trips to the oceanic environment close to the archipelago with longer trips to the Canary Current upwelling, which is about 200km apart (Ramos et al., 2013). Berlenga shearwaters mainly forage in the neritic environment of the Portuguese coastal shelf (Alonso et al., 2012), which is the northernmost part of the Canary Current upwelling (Kämpf & Chapman, 2016), whereas those from Corvo and Cima almost exclusively forage in the oceanic environment because neritic areas are >600km apart from the breeding colony (Paiva, Geraldés, Meirinho, Garthe, & Ramos, 2010).

If the 'resource limitation hypothesis' (Tinker et al., 2008) is the main driver of individual foraging specialization, we would expect shearwaters exploiting oligotrophic oceanic environments to show greater levels of individual specialization than those exploiting productive neritic environments. In addition, we would expect to find these trends both at intra-colony and inter-colony levels, with higher individual specialization in oceanic than in neritic trips within the Canary Island colonies and higher individual specialization in the oceanic colonies of Corvo and Cima compared to the neritic Berlenga colony. On the contrary, if the 'predictability hypothesis' (Oppel et al., 2017) is the main driver of individual foraging specialization, we would expect shearwaters exploiting the predictable neritic environments to show greater levels of individual specialization than the unpredictable oceanic environments.

Materials and methods

Fieldwork

Fieldwork was conducted during the chick-rearing period of Cory's shearwaters (July-September) in six breeding colonies: Veneguera (2012, 2015, 2017 and 2019), Timanfaya (2015 and 2016) Montaña Clara (2015-2019) in the Canary Islands archipelago; Berlenga in Berlengas archipelago (2010-2018); Corvo in Azores archipelago (2010, 2015, 2017); and Ilhéu de Cima in Madeira archipelago (2011, 2012, 2014 and 2015). Over the study period, we deployed and re-deployed global positioning system (GPS) loggers on breeding adults. We alternated GPS deployments between members of the pairs to reduce the impact on breeding performance. Models of GPS loggers can be found in supplementary material (Table S1 supplementary material). Total mass of devices was below 3% of the lightest adult mass, as recommended by Phillips, Xavier, & Croxall (2003) and Passos, Navarro, Giudici, & González-Solís (2010). GPS loggers were attached to mantle feathers Tesa® tape and were up to 23 days on individuals.

Data processing

All GPS trips were resampled to have a fix every 15 minutes. We removed erroneous locations by applying a velocity filter (velocity > 120 km/h) and we excluded land and raft positions by applying a land mask and a 2 km buffer from the breeding colony. Most GPS deployments included more than one foraging trip, which were manually cut in the respective foraging trips. We only kept individuals having more than one foraging trip to be able to estimate individual specialization metrics. Foraging trips were defined as either oceanic or neritic depending on where these trips occurred. Therefore, Veneguera, Timanfaya and Montaña Clara colonies included both oceanic and neritic trips, whereas Berlenga only included neritic trips and Corvo and Ilhéu de Cima only oceanic trips. Although Berlenga and Ilhéu de Cima had some oceanic and neritic trips, respectively, we excluded these trips from further analyses because there were less than 10 trips, and these could not properly represent the environment. For each foraging trip, we estimated eight parameters, four of them regarding foraging movements and four of them regarding the habitat used in that foraging trip.

We calculated the following trip characteristics related to foraging movements: departure direction, trip duration, distance covered and maximum distance to the colony. We applied the Expectation-Maximization Binary Clustering algorithm EMbC (Garriga, Palmer, Oltra, & Bartumeus, 2016) at individual level to classify trip locations into four behaviours: resting, travelling, intensive foraging and extensive search. Departure direction was estimated as the circular mean of the first five locations that were 10 km apart from the breeding colony and were classified as travelling positions by the EMbC. Trip duration was defined as the total time spent on a foraging trip (in hours). Distance covered was the cumulative linear distance between consecutive locations (in km). Maximum distance to the colony was the distance from the furthest location of the trip to the breeding colony (in km).

We estimated the following variables of habitat use: bathymetry, sea surface temperature (SST), chlorophyll-a concentration (Chl-a) and proximity to seamounts. We only extracted the environmental variables for locations classified as intensive foraging and extensive search. Intensive foraging represents the active search of prey at small spatial scales, whereas extensive search would be related to search for patches at large spatial scales. See S1 supplementary material for details on the EMbC and examples of trips. Bathymetry, SST and Chl-a were obtained extracting the values for each trip location using the Movebank platform EnvDat (Somayeh, Gil, & Rolf, 2012) with inverse distance weighted interpolation. We used monthly layers at 4km resolution. Proximity to seamounts was obtained using the Seamount Global Database (Kim & Wessel, 2011) and we calculated the Euclidean distance of trip locations to the nearest seamount. We calculated the mean value of each environmental variable per each foraging trip.

Statistical analyses

All statistical analyses were carried out in R 3.6.2 (R Core Team, 2019). Confidence level was set to $\alpha=0.05$.

(1) Productivity and predictability of the environment

We estimated productivity and predictability of the environment using Chl-a layers, as Chl-a is a predictor of seabirds' prey distribution and abundance (Jurado-Ruzafa et al., 2019; McInnes et al., 2017). We used 9km resolution layers from MODIS-Aqua satellite of NASA (NASA Goddard Space Flight Center, 2018). We used monthly layers from July to September between 2010 and 2019, matching shearwaters data, making a total of 30 layers (3 monthly layers per 10 years). We cropped layers by the 95% contour of the Kernel Density Estimation (KDE) for each colony and neritic/oceanic environment. The 95% KDE contour of each colony and environment was estimated at population level, using all trips from all individuals ($h = \text{"href"}$), using "kernelUD" function from "adehabitatHR" package (Calenge, 2011). We used these cropped layers for the calculation of productivity and predictability.

Productivity was calculated as the mean of all cells contained in the 95% KDE from a particular month in a specific year, making therefore a total of 30 layers per each colony and environment.

We analysed resource predictability by addressing how contiguous are patches of relatively high Chl-a values. For each Chl-a layer area, we classified each pixel in high or low Chl-a value, depending on if the value was higher or lower than the mean value of all layers from all colonies (*i.e.* $\text{Chl-a} > 0.23 \text{ mg/mL}^3$). We therefore divided the layer in productive and non-productive patches. Using the productive patches, we calculated the contiguity index to see how contiguous the productive patches are. This index moves between 0 and 1, being 0 that patches are not connected and therefore unpredictable, which is what we would expect in the oceanic environment, and 1 that patches are aggregated and therefore more predictable in space,

which would be expected in the neritic environment. We estimated the contiguity index per each monthly layer of each year, resulting again in 30 layers per colony and environment.

(2) Repeatability and foraging site fidelity

Prior to analyses, we checked for normality of the studied parameters using Kolmogorov-Simonov test and normal probability plots. We used “bestNormalize” function from “bestNormalize” package to use the best transformation (Peterson, 2019). We used “orderNorm” function to transform all variables except for departure direction, which was treated as a circular variable.

We quantified individual specialization in these studied parameters by calculating individual repeatability (Potier, Carpentier, Grémillet, Leroy, & Lescroël, 2015), which is an adaptation from the classic population repeatability (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). We estimated individual repeatability (r) per each individual and their oceanic/neritic trips, following the equation:

$$\text{Eq. 1: } r = \frac{s_A^2}{s_{ind}^2 + s_A^2}$$

Where s_A^2 is the among-individual variance and s_{ind}^2 is the within-individual variance of that specific individual. These variances can be obtained directly from linear mixed models (LMM) by extracting the residuals (Nakagawa & Schielzeth, 2010; Potier et al., 2015). Moreover, LMMs allow the control of possible confounding effects, thus providing an adjusted repeatability (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). We performed LMMs using as response variables the studied variables (except for departure direction): trip duration, distance covered, maximum distance to the colony, bathymetry, SST, Chl-a and proximity to seamounts. We included in the models the starting day of the trip (Julian date) as covariate and breeding season (year) and individual as random effects. We used “lme4” function from “lmer” package (Bates, Mächler, Bolker, & Walker, 2015). We fitted LMMs models per each colony and environment (either oceanic or neritic) and obtained the repeatability of each individual in that environment. We then calculated the 95% confidence interval per each colony and environment. Regarding departure directions, we used circular ANOVAs to calculate repeatability, following previous approaches (Lessells & Boag, 1987; Opper et al., 2017). We used “aov.circular” function from “circular” package to carry out ANOVAs (Lund et al., 2017).

For the colonies that we have both oceanic and neritic environments (*i.e.* Canary Islands colonies), we wanted to understand if specialization in foraging movements and habitat was maintained in individuals regardless of the environment. To do so, we calculated the mean of a variable per each individual and environment. We then correlated the values of both environments at individual level. We performed linear models (“lm” function) using as response variable the mean values of individuals in the neritic environment and as explanatory variables the mean values in the oceanic environment, the colony as fixed factor and the interaction between them.

We assessed individual foraging site fidelity to understand individual specialization in the physical space. We compared the within-individual similarity in foraging areas with a similarity calculated assigning the bird identity randomly to foraging trips in order to know if there was more foraging site fidelity in individuals than expected by chance (details on S2 supplementary material (Wakefield et al., 2015)). In this way we classified if each individual was or not faithful to its foraging area in that environment. To test for differences between neritic and oceanic environments within colonies, we modelled foraging site fidelity as a binary dependent variable (either with or without foraging site fidelity) with colony and environment as fixed effects, as well as their interaction term. To test it among colonies, we modelled equally but only including colony as fixed effect.

(3) Departure directions in colonies and environments

To understand if shearwaters departed directionally in oceanic and neritic environments, we estimated the departure direction of shearwaters for each colony and environment using the package “circular” (Lund et al., 2017). We calculated the circular mean of the departure directions performed per each individual in all its foraging trips. With these values we tested if the distribution of the directions differed from uniformity with a Kuiper’s V test (“kuiper.test” function), since we could not assume unimodal distribution of departure directions (Ruxton, 2017). We performed a Kuiper’s V test per each colony and environment. We also tested if birds from the same colony departed to different directions when performing neritic or oceanic trips with a circular ANOVA, using function “aov.circular”. Then we produced KDE circular plots to understand in which directions seabirds headed more. The KDE for circular data is a non-parametric way to estimate the probability density function of a circular variable (Hall, Watson, & Cabrera, 1987).

Results

(1) Productivity and predictability of the environment

Regarding productivity, we found that neritic areas exploited by Cory’s shearwaters showed higher Chl-a values than oceanic ones (Fig. 1A). This pattern was consistent across years, although we found higher variability in the neritic than in the oceanic environment in Chl-a values (Fig. 1B).

Regarding predictability of the resources, we found in general higher contiguity index in the neritic than in the oceanic environments (Fig. 1C). This pattern was clear when comparing within colonies in Veneguera, Timanfaya and Montaña Clara. This pattern was not maintained among colonies, although we also found a slightly higher mean contiguity index in the Berlenga neritic colony than in the oceanic Corvo and Ilhéu de Cima ones. Contiguity index values varied across years for all colonies, except for Berlenga colony, which was very stable in the studied 10 years (Fig. 1D).

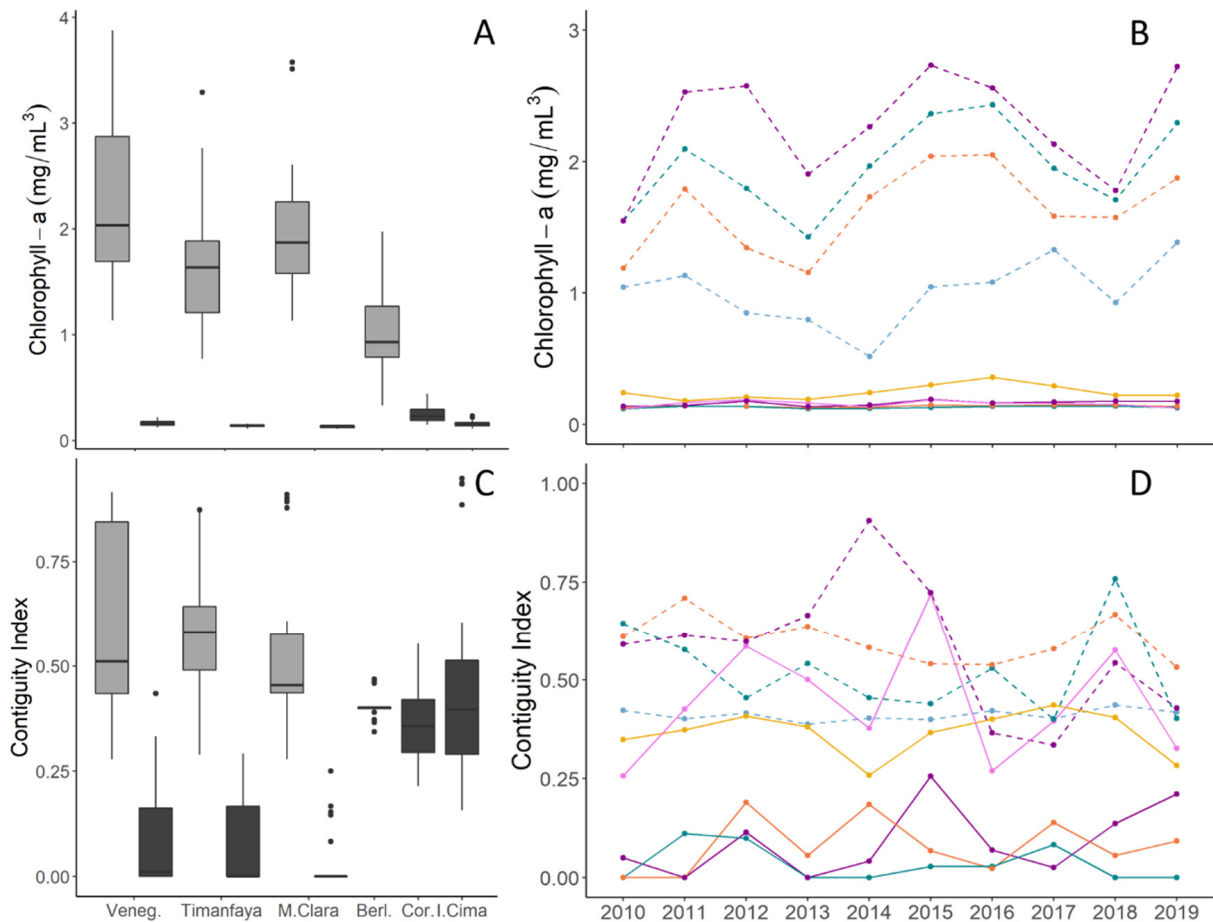


Figure 1

Productivity and contiguity index values (A, C respectively) and across years (B, D) for Veneguera (dark magenta), Timanfaya (orange), Montaña Clara (turquoise), Berlenga (light blue), Ilhéu de Cima (pink) and Corvo (gold) colonies. In boxplots (A, C), neritic is in light grey and oceanic in dark grey. Across years (B, D), dashed lines are for the neritic environment and solid lines for the oceanic environment. Contiguity index was computed classifying each pixel in a layer in high or low Chl-a value and then estimating the index for productive (high Chl-a) patches, which is higher if patches are more connected.

(2) Repeatability and foraging site fidelity

We obtained a total of 2,266 foraging trips of Cory's shearwaters from all colonies, including both neritic and oceanic environments (Fig. 2, Table 1). Overall, birds travelled a maximum distance of 5,159km and were up to 1,840km away from the colony, spending a maximum of 15 days in the foraging trip. The patterns found regarding repeatability values were not affected by the number of trips per individual (S3 supplementary material).

We found a pattern of shearwaters more individually repeatable in movement characteristics when foraging in oceanic environments than when foraging in neritic environments (Fig. 3A-D). Indeed, repeatability values were generally low or not significant for movement characteristics in the neritic environment, *i.e.* the 95% confidence interval included 0. These patterns occurred both within and between colonies. Within colonies, in the colonies that have both neritic and oceanic environments (*i.e.* Veneguera,

Table 1

Mean (range) of the studied trip characteristics and environmental variables of *Cory's* shearwaters *Calonectris borealis* from each colony and environment. N includes the number of individuals and the number of trips in brackets. Environmental variables were extracted from Movebank platform EnvDat and seamounts locations were obtained using the Seamount Global Database (see methods for details).

Colony	Environment	N	Trip characteristics					Environmental variables				
			Departure direction (°)	Trip duration (h)	Distance covered (km)	Maximum distance (km)	Bathymetry (m)	SST (°C)	Chl-a (mg/mL ³)	Seamounts distance (km)		
Veneguera	Neritic	47 (141)	150.4	82.9 (19.5 – 358.2)	1034.5 (498.4 – 3904)	336.8 (205.2 – 852)	-358.7 (-1334 – -27.3)	20.5 (18.3 – 22.8)	2.5 (0.4 – 7.5)	221.1 (99.6 – 393.1)		
	Oceanic	81 (309)	178.9	18.3 (7 – 87.8)	170.5 (50.4 – 773.3)	46 (16.4 – 234.8)	-1518.5 (-3163.2 – -210.7)	23.2 (22.1 – 24.7)	0.2 (0.1 – 0.3)	99.6 (35.2 – 206.6)		
Timanfaya	Neritic	35 (155)	133	71.1 (14.4 – 232.5)	793.9 (240 – 2757.3)	238.9 (99.9 – 831.2)	-177.5 (-1537.3 – -30.4)	20.9 (19 – 23)	4.2 (0.2 – 29.1)	138.2 (62.3 – 319.2)		
	Oceanic	29 (155)	-23.8	17.7 (5.3 – 67.4)	141.2 (26 – 403.1)	36 (10.3 – 138.9)	-867.9 (-2091 – -1740.1)	22.5 (21.4 – 23.8)	0.2 (0.1 – 0.3)	55.9 (14.9 – 85.1)		
Montaña Clara	Neritic	29 (120)	114.5	66.7 (13.8 – 279.6)	806 (241.6 – 2814)	261.1 (118.6 – 856.6)	-157.9 (-676.9 – -19.6)	21 (18.7 – 23.5)	2.7 (0.1 – 19.6)	151.4 (41.4 – 327.5)		
	Oceanic	25 (120)	67.9	19.4 (11.8 – 87.3)	196.7 (48.6 – 825.4)	59.1 (10.3 – 198.2)	-768.8 (-2799.9 – -129.5)	22 (20.2 – 23.9)	0.1 (0.1 – 0.2)	22.2 (6.6 – 87.2)		
Berlenga	Neritic	82 (744)	-142.7	27.9 (4.8 – 159.1)	233 (16 – 2387.8)	60.8 (10.2 – 572.9)	-306.6 (-4302.5 – -8.8)	19.1 (16.6 – 21.5)	1.5 (0.2 – 6.4)	154.2 (52.4 – 268.7)		
Corvo	Oceanic	56 (411)	-21.7	34.6 (12.6 – 353.8)	471.2 (21.3 – 5431.4)	150.9 (10.1 – 1839.8)	-1555 (-4423.5 – -114.9)	23.1 (17.8 – 24.5)	0.1 (0.1 – 0.5)	36.8 (7.6 – 172.7)		
Ilhéu de Cima	Oceanic	24 (111)	26.7	23.6 (5.2 – 282.7)	283.2 (33.3 – 5159.4)	88.7 (10.7 – 1611.9)	-1735.9 (-4304.1 – -172.6)	23.1 (19.9 – 24.7)	0.1 (0.1 – 0.8)	26.3 (7.6 – 147.6)		

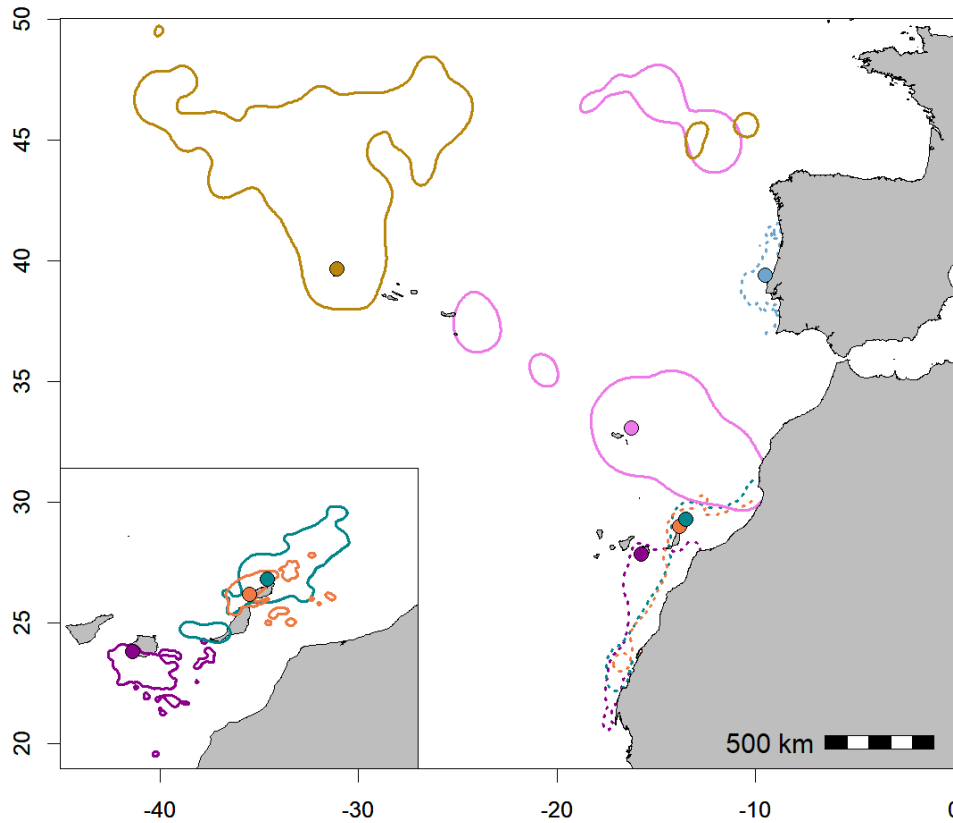


Figure 2

Foraging areas of neritic (dotted lines) and oceanic (solid lines) trips of Cory's shearwaters *Calonectris borealis* from six colonies across the Atlantic Ocean. The location of each colony is shown in a dot with the respective colour: Veneguera (dark magenta), Timanfaya (orange), Montaña Clara (turquoise), Berlenga (light blue), Ilhéu de Cima (pink) and Corvo (gold). Contours represent the 95% Kernel Density Estimation (KDE) at population level. The inset map shows the KDE for the oceanic trips of Veneguera, Timanfaya and Montaña Clara.

Timanfaya and Montaña Clara), we found higher repeatability values in movement characteristics in the oceanic than in the neritic environment. Between colonies, in the colonies where only one type of environment was available, we found the same pattern: the individuals from the oceanic colonies of Corvo and Ilhéu de Cima were more repeatable than those from the neritic colony of Berlenga. Regarding environmental variables, we did not find differences in the level of individual repeatability between oceanic and neritic environments (Fig. 3E-H) and repeatability values of environmental variables were almost always significant.

Individuals from Canary Islands did not maintain their foraging strategies when changing between neritic and oceanic environments. Regarding foraging movements, we did not find significant correlation between neritic and oceanic in any of the parameters: departure direction ($t_{34}=-0.7$, $p=0.477$), trip duration ($t_{63}=-0.6$, $p=0.552$), distance travelled ($t_{63}=0.6$, $p=0.547$) and maximum distance ($t_{63}=1.1$, $p=0.259$). Regarding habitat use variables, we did not find significant correlation between neritic and oceanic environments: bathymetry ($t_{63}=0.6$, $p=0.558$), SST ($t_{59}=1.8$, $p=0.081$), Chl-a ($t_{41}=1.7$, $p=0.099$) and proximity to seamounts ($t_{63}=-0.8$, $p=0.453$).

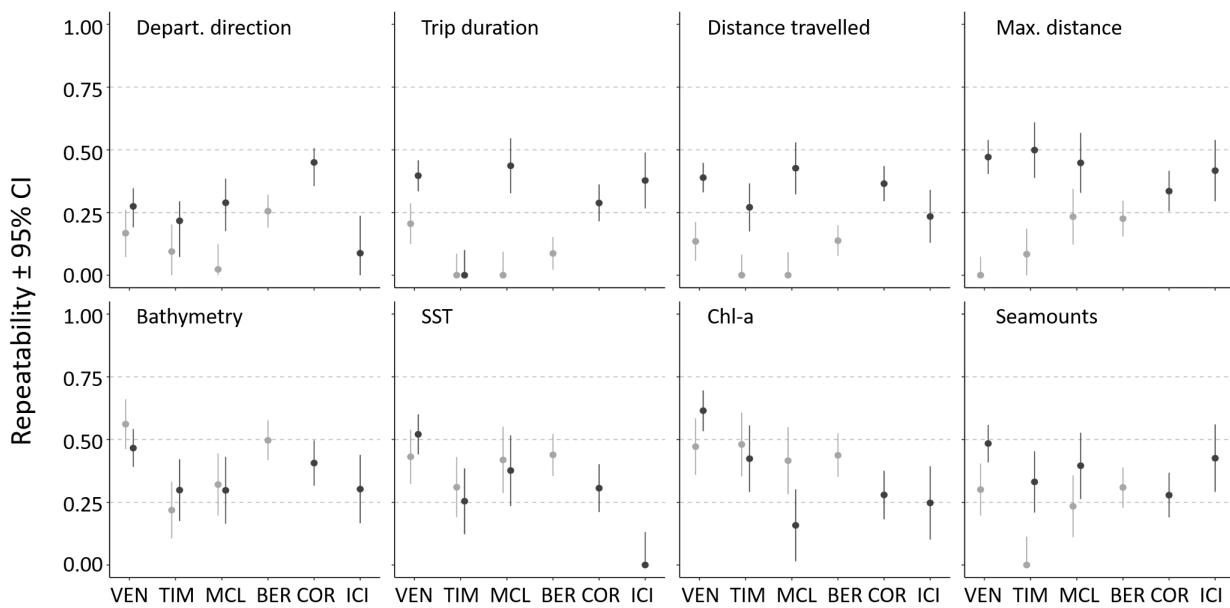


Figure 3

Repeatability values of trip characteristics (A-D) and environmental variables (E-F) for the six studied colonies of Cory's shearwater: Veneguera (VEN), Timanfaya (TIM), Montaña Clara (MCL), Berlenga (BER), Corvo (COR) and Ilhéu de Cima (ICI). Light grey= neritic environment, dark grey= oceanic environment. Repeatability values were estimated using LMMs, except for departure direction that was estimated using circular ANOVAs. Note that Veneguera, Timanfaya and Montaña Clara have both neritic and oceanic environments.

Foraging site fidelity did not differ significantly between neritic and oceanic environments within colonies ($z = 0.951$, $p = 0.342$). Foraging site fidelity did not differ among the neritic colony of Berlenga and the oceanic colonies of Corvo ($z = 1.38$, $p = 0.353$) and Ilhéu de Cima ($z = 1.98$, $p = 0.118$). We found approximately 50% of individuals with more foraging site fidelity than expected by chance regardless of the colony or the environment (Fig. 4).

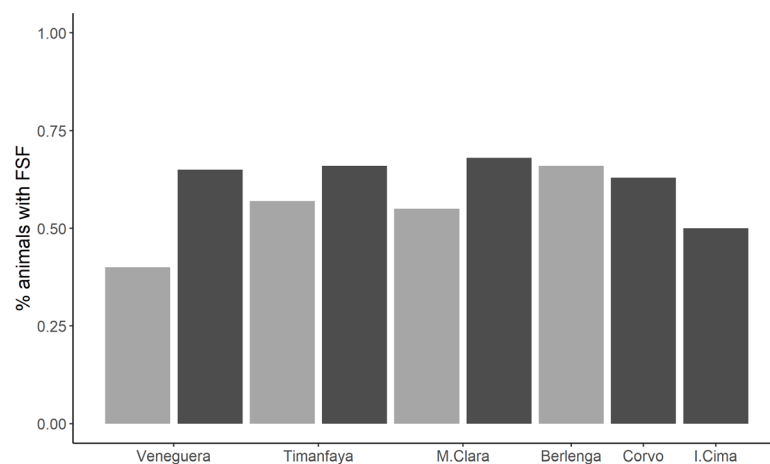


Figure 4

Percentage of animals with more foraging site fidelity (FSF) than expected by chance from each colony and environment. Light grey= neritic, dark grey= oceanic. Note that Veneguera, Timanfaya and Montaña Clara have both neritic and oceanic environments.

(3) Departure directions

We found shearwaters from all colonies departing in non-uniform directions (Fig. 5). This happened in the neritic environment for all colonies: Veneguera ($T_{\text{Kuiper}} = 6$, $p < 0.01$), Timanfaya ($T_{\text{Kuiper}} = 4$, $p < 0.01$), Montaña Clara ($T_{\text{Kuiper}} = 4.7$, $p < 0.01$) and Berlenga ($T_{\text{Kuiper}} = 0.5$, $p < 0.001$). Shearwaters from the Canary Islands colonies headed south east when performing neritic trips (Fig. 5A, C, E), whereas Berlenga birds headed south west (Fig. 5G). Shearwaters departing to an oceanic trip also showed non-uniform directions: Veneguera ($T_{\text{Kuiper}} = 7.2$, $p < 0.01$), Timanfaya ($T_{\text{Kuiper}} = 2.8$, $p < 0.01$), Montaña Clara ($T_{\text{Kuiper}} = 2.7$, $p < 0.01$), Corvo ($T_{\text{Kuiper}} = 0.09$, $p = 0.046$) and Ilhéu de Cima ($T_{\text{Kuiper}} = 0.6$, $p < 0.001$). When doing oceanic trips, birds from the different colonies of Canary Islands headed in different directions: Veneguera ones headed south, Timanfaya north and west, and Montaña Clara east and slightly west (Fig. 5B, D, F). Shearwaters from Corvo headed in all directions, but seemed to avoid south heading (Fig. 5H), whereas Ilhéu de Cima birds headed north and east (Fig. 5I). Birds from the same colony departed to different directions when performing oceanic or neritic trips (Veneguera: $F(1, 134) = 59.1$, $p < 0.001$; Timanfaya: $F(1, 62) = 187.2$, $p < 0.001$; M.Clara: $F(1, 59) = 19$, $p < 0.001$).

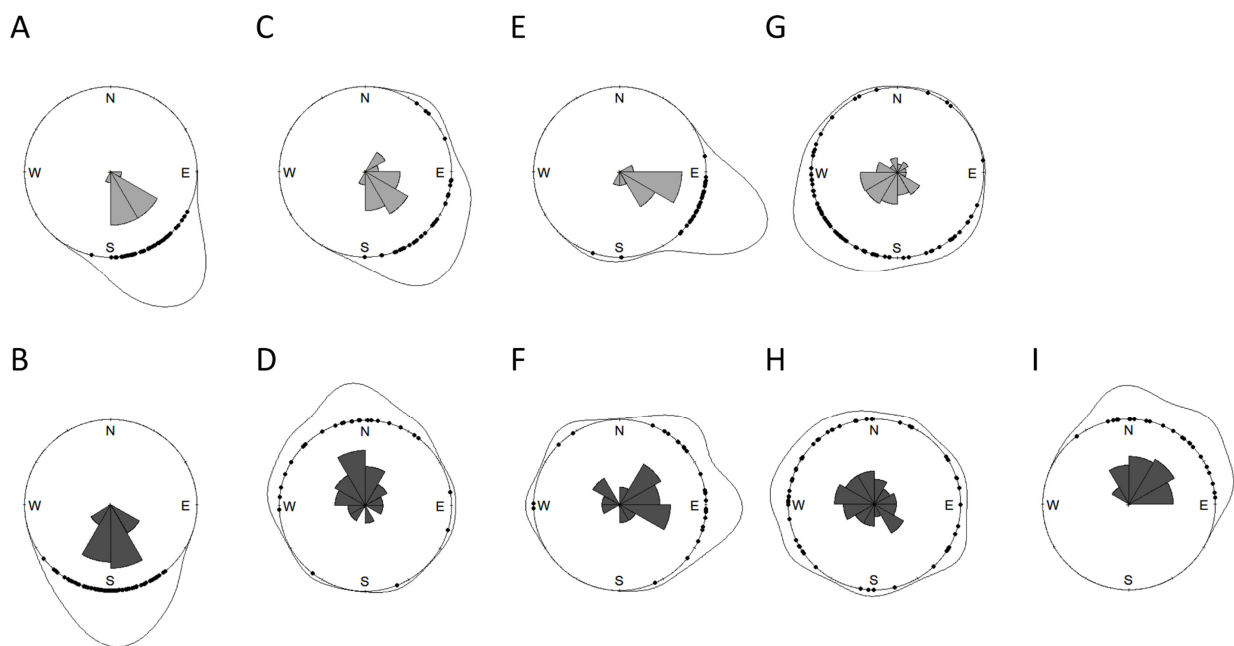


Figure 5

Departure directions of shearwaters from neritic (light grey: A, C, E, G) and oceanic (dark grey: B, D, F, H, I) environments in Veneguera (A, B), Timanfaya (C, D), Montaña Clara (E, F), Corvo (G), Berlenga (H) and Ilhéu de Cima (I) colonies. Outer line indicates the kernel density estimation of departure directions. Points in the circle indicate the raw values of directions of each foraging trip. Inner grey histogram is a rose diagram of departure directions.

Discussion

In this study we addressed whether resource abundance or resource predictability is shaping individual specialization in foraging strategies in the marine environment by comparing repeatability levels of shearwaters feeding in two contrasting environments. That is, we compared shearwaters feeding highly at productive waters in neritic environments with those feeding at oligotrophic waters in oceanic regions across a range of six breeding localities spanning a large geographical area. We used GPS devices on Cory's shearwaters to assess individual specialization in foraging movement characteristics and in habitat features. We found that shearwaters foraging in oceanic environments showed higher levels of repeatability in movement characteristics than those foraging in neritic environments. This result supports the resource limitation hypothesis as one of the main drivers of between-individual variability in foraging strategies. Contrary to foraging movements, repeatability in habitat was relatively high regardless of the environment, indicating segregation in individual habitat use can occur regardless of the abundance and predictability of the resources.

In the marine environment, shelf edges and upwellings are well known for their enhanced productivity (Raymont, 2014). This is the case of the neritic areas exploited by shearwaters breeding in Canary Islands and Berlenga and feeding at the Western African shelf and the Portuguese shelf, respectively. Both areas lay in the Canary Current Upwelling system, which is one of the richest productive marine ecosystems of the world and supports abundant stocks of small pelagic fish (Sambe, Tandstad, Caramelo, & Brown, 2016). On the contrary, oceanic waters are less productive than neritic ones, such as the case of the waters around oceanic islands, for instance those surrounding Canary, Azores and Madeira Islands (Raymont, 2014). Accordingly, we found Chl-a values of oceanic areas lower in an order of magnitude than in the neritic areas, thus matching with higher resource scarcity in the oceanic environment. We also found higher variability in Chl-a values in the neritic environment, which is probably related to the high dynamism of upwelling systems.

Predictability of food resources in the marine ecosystem is highly dependent on oceanographic features such as upwellings or shelf edges where resources are aggregated, which occur in neritic environments (Raymont, 2014). Accordingly, we found a higher contiguity index of productive patches in neritic than in oceanic environments, matching with resources being more aggregated in neritic zones and more randomly distributed in oceanic areas. This was particularly evident when comparing within colonies in the Canary Islands, where the neritic areas exploited by shearwaters clearly showed higher contiguity indices than oceanic areas. When comparing among colonies, we found similar mean contiguity index for the neritic Berlenga colony and the oceanic colonies of Corvo and Ilhéu de Cima. However, Berlenga colony showed very low variability in the contiguity index across years, thus suggesting a stable environment in the spatial distribution of the resources.

Both resource scarcity and predictability can drive individual specialization, as limitation of resources forces individuals to differ in their foraging strategies to avoid competition and resource predictability allows individuals to define their foraging strategies (Araújo et al., 2011; Dermond et al., 2018). In this study, we found that these environmental conditions influenced differently individual strategies in movement and in habitat use, as well as modulated departure directions of birds from the colony.

Regarding movement characteristics, we found higher repeatability values in oceanic than in neritic environments, matching with resource scarcity driving individual specialization in foraging movements. Indeed, repeatability values of movement characteristics in the neritic environment were very low, indicating high individual flexibility in trip characteristics in this habitat. This is probably happening because the Canary Current upwelling is a highly productive area with large amount of available resources, thus there is no pressure for individuals to segregate into different strategies (Araújo et al., 2011). The observed repeatability in movement characteristics could be associated to foraging site fidelity of individuals (Wakefield et al., 2015). However, we did not find differences in foraging site fidelity between oceanic and neritic environment, thus suggesting the repeatability in trip characteristics is mainly behavioural rather than related to visiting the same feeding areas. Within colonies, the higher repeatability values found in oceanic than in neritic trips could be related to the dual foraging strategy. That is, during chick rearing shearwaters combine short trips to feed the chick, which probably occur in the oceanic environment, with long trips for self-provisioning, probably going to the African shelf (Alonso et al., 2012; Magalhães, Santos, & Hamer, 2008). However, the difference between oceanic and neritic environments occurred both within and between colonies, thus excluding the dual foraging strategy as the main driver for differences between environments.

Contrary to trip characteristics, resource limitation does not seem to drive among-individual variability in habitat use, as we did not find differences between neritic and oceanic environments in repeatability values of oceanographic variables. Indeed, repeatability values in both neritic and oceanic areas were relatively high for all oceanographic features. This could occur because individuals seek for certain oceanographic cues regardless of the environment, or due to intrinsic constraints of individuals, such as physiological, morphological or personality-related constraints (Bolnick & Paull, 2009; Krüger, Pereira, Paiva, & Ramos, 2019). However, when studying Canary Islands colonies that have both oceanic and neritic environments, we found that values of oceanographic variables were unrelated at individual level. This means that the same individual changed its foraging strategy when exploiting either the oceanic or the neritic environment. This suggests that the use of oceanographic features is developed independently in each environment, probably learnt and fixed through experience when individuals are young (Votier et al., 2017). However, the fact that the same individual changed its foraging strategy depending on the environment can indeed indicate that individuals are not specialized but plastic. Indeed, the change of strategy occurred at a very short time scale, since individuals perform a dual foraging strategy and constantly combine short trips

to the oceanic environment with long trips to the neritic. Although individuals do show consistent foraging strategies within each environment, they do not maintain them across environments, and we are unsure about using the terminology of individual specialization in this scenario.

The fact that relatively high levels of repeatability in habitat occurred in the oceanic environment may suggest these areas may not be as unpredictable as traditionally thought. Indeed, recent studies show clear associations of seabirds to oceanographic features in oligotrophic and presumably unpredictable environments (McDuie, Weeks, & Congdon, 2018; Paiva et al., 2015).

Departure directions of birds from the studied colonies also supports an association of seabirds to oceanographic features when foraging in the oceanic environment. If there were no associations with oceanographic features, we would expect shearwaters foraging in oceanic environments to spread in any direction from the colony in their foraging trips (Weimerskirch, 2007). However, we found that birds departed to specific directions not only in the neritic but also in the oceanic environment, thus suggesting they knew where to find resources in both environments (McDuie et al., 2018). Regarding neritic areas, shearwaters from the Canary Islands performing neritic trips clearly knew where to find food, as they showed marked heading towards the upwelling system (Navarro & González-Solís, 2009), whereas birds from the neritic Berlenga colony, located in the upwelling itself, departed south west with prevailing tail winds (Paiva, Guilford, et al., 2010). Regarding oceanic environments, seabirds from the oceanic colony of Ilhéu de Cima headed north and east towards the closest seamounts (Biscoito et al., 2017; Paiva, Geraldes, et al., 2010). Shearwaters from the oceanic Corvo colony seemed to depart in all directions, although slightly avoiding southern-heading departure, and they exploited northern waters where a high density of seamounts occur (Morato et al., 2008; Paiva, Geraldes, et al., 2010). Shearwaters from the Canary Islands performing oceanic trips also showed particular directions, as Veneguera birds headed south probably towards eddies that enhance productivity (Sangrà et al., 2009), whereas Timanfaya and Montaña Clara ones headed north and east, respectively, to the Conception Bank seamount (Almón, 2014). This heading towards seamounts may be related to the strong association of the main prey of Cory's shearwater, the chub mackerel *Scomber colias*, with seamounts (Alonso, Granadeiro, Dias, Catry, & Catry, 2018). Alternatively, directionality in departure could be associated to prevailing winds (Berlincourt, Angel, & Arnould, 2015; Paiva, Guilford, et al., 2010). However, winds around the Canary Islands typically head south west (Azorin-Molina et al., 2018), whereas shearwaters from Veneguera, Timanfaya and Montaña Clara departed south, north and east, respectively, thus excluding wind as the main driver of the heading. Alternatively, directionality in departure of oceanic trips can have the purpose of segregating in space to avoid competition with shearwaters from nearby colonies (Bolton, Conolly, Carroll, Wakefield, & Caldow, 2018), but foraging distributions of shearwaters from Timanfaya and Montaña Clara clearly overlapped. In the three colonies of the Canary Islands, we also found that birds from the same colony departed towards different directions depending on if they performed an oceanic or a neritic trip. This suggests shearwaters anticipate

the departure towards a particular foraging area before leaving the colony (Pettex, Bonadonna, Enstipp, Siorat, & Grémillet, 2010). This anticipation may happen because shearwaters perform a dual foraging strategy during the chick-rearing period, and generally perform a long trip after a series of short trips (Magalhães et al., 2008).

In summary, our results suggest that shearwaters know where to find resources in both oceanic and neritic environments, since they departed to specific directions in both environments. Our study also elucidates that segregation in individual habitat use can occur regardless of the abundance and predictability of resources. Individuals did not maintain their foraging strategies when exploiting different environments, showing these strategies are not fixed by the individual's traits but probably learnt when individuals are young. In this study, we provide evidences that resource limitation is a more relevant driver of individual specialization in foraging movements than resource predictability, as repeatability in foraging movement was higher in oceanic than in neritic environments. To our best knowledge, this is the first study to address at the same time the role of resource limitation and predictability in defining individual foraging strategies.

Authors' contributions

LZ analysed the data and wrote the paper; JMP, MCF, VMP, MSS, DVS and JAR led the fieldwork; VHP obtained funding and led the fieldwork. JGS conceived the study, obtained funding and wrote the paper. All authors contributed critically to drafts and gave final approval.

Data Availability Statement

Data will be available at Universitat de Barcelona archive.

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Supplementary information

Table S1

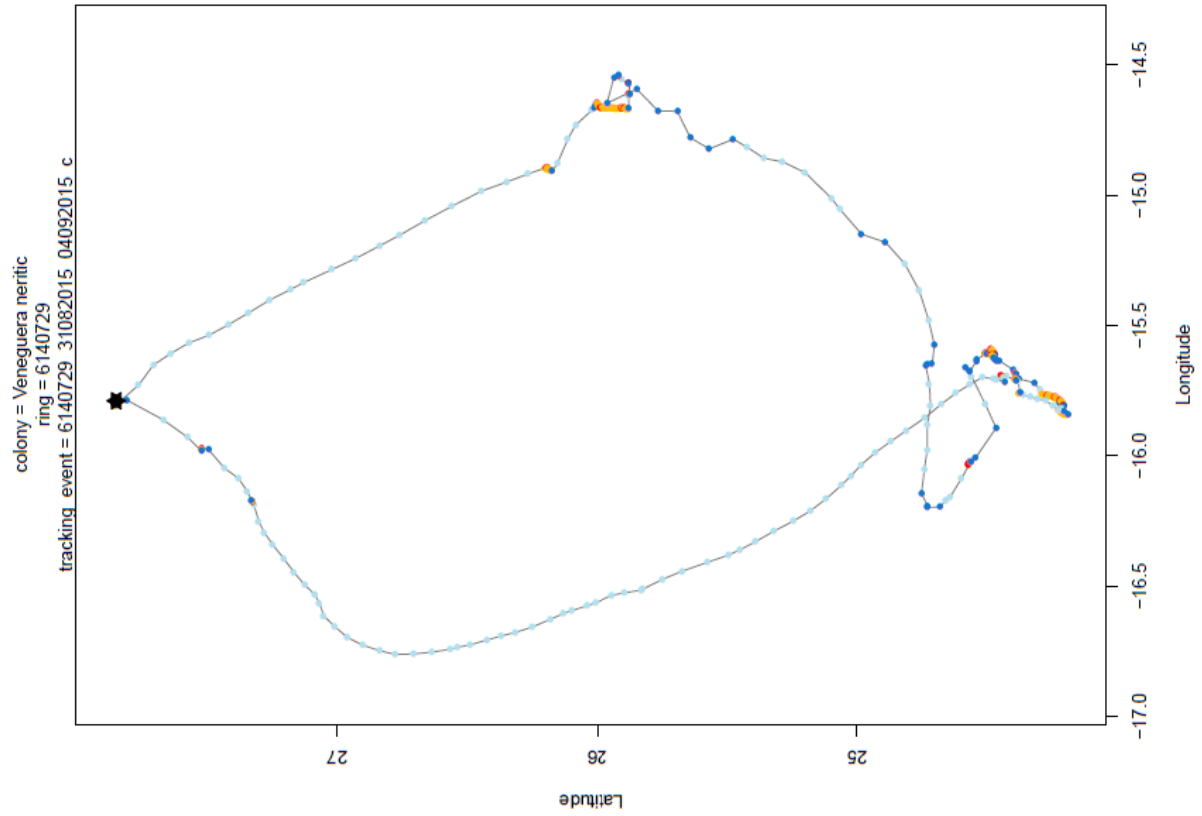
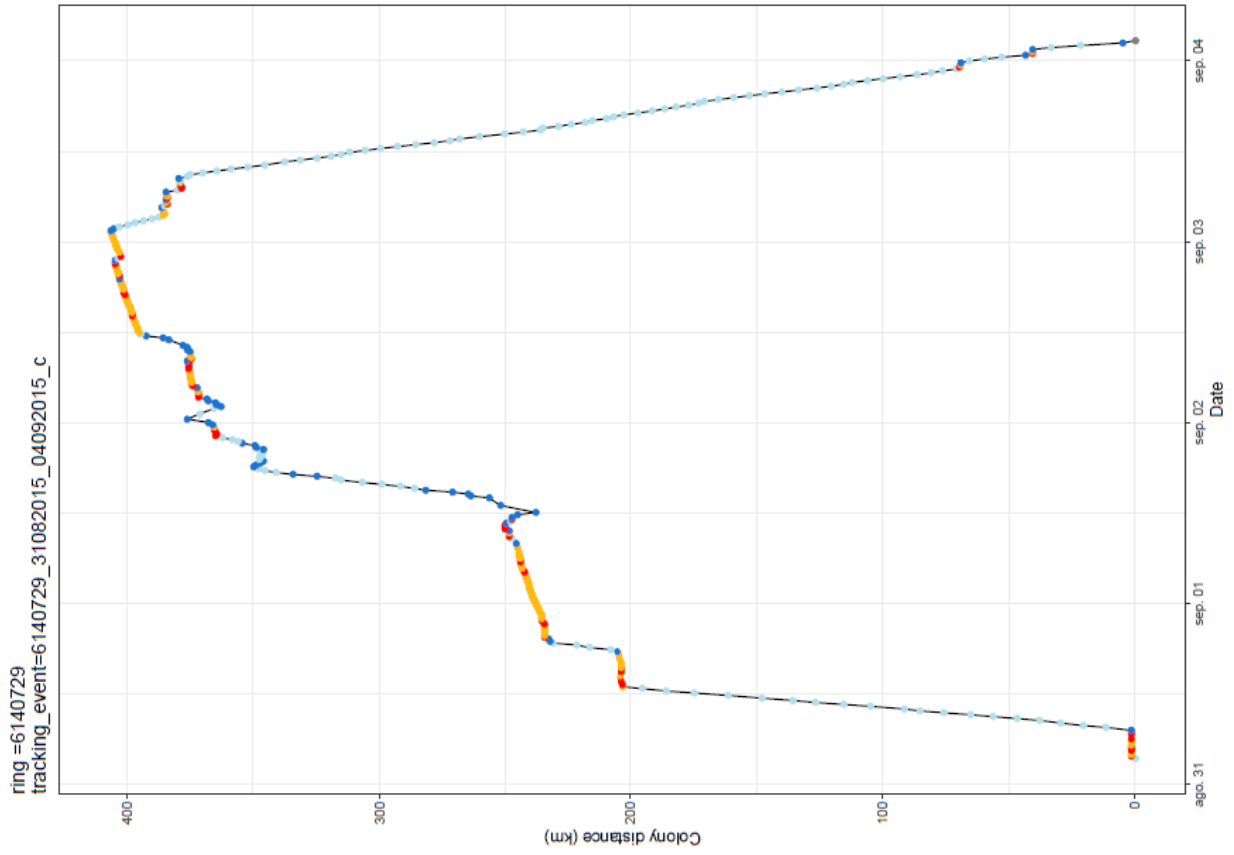
Loggers, their respective weight and suppliers for the six studied colonies.

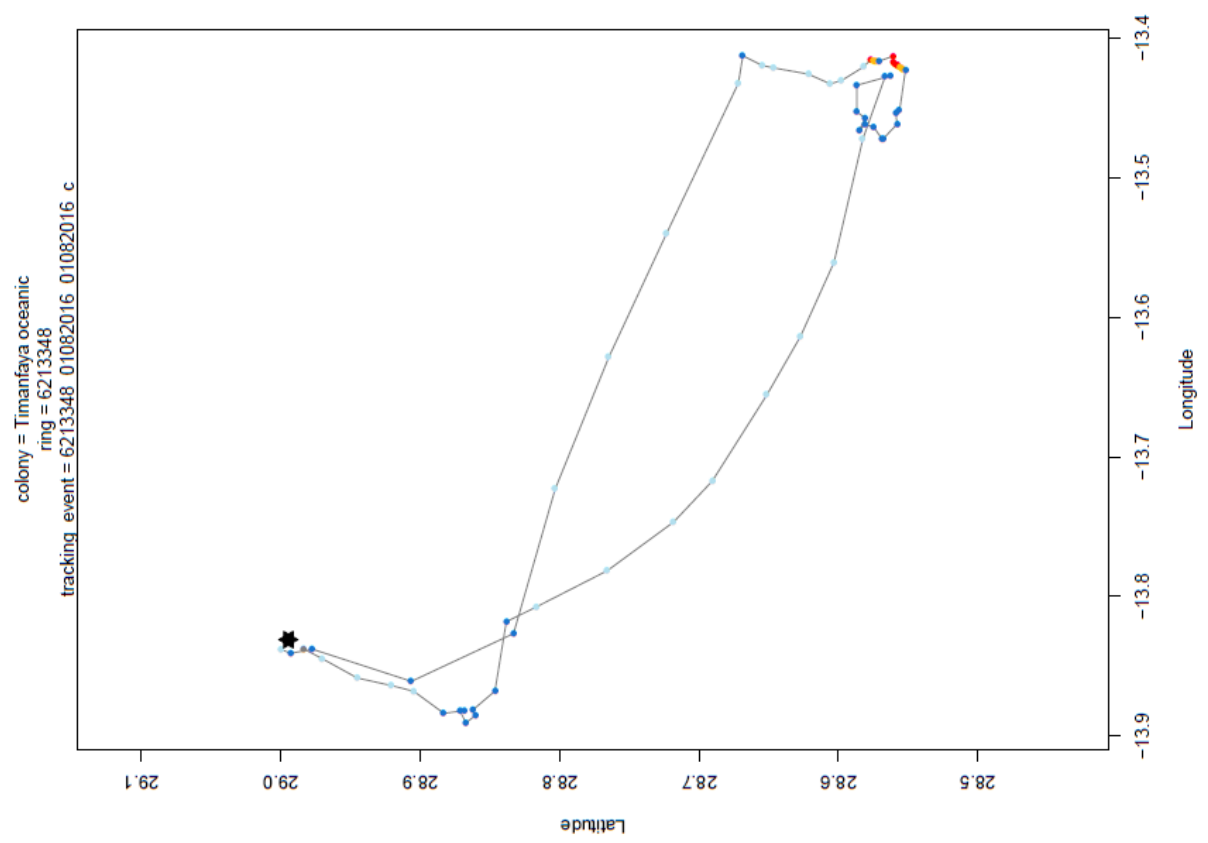
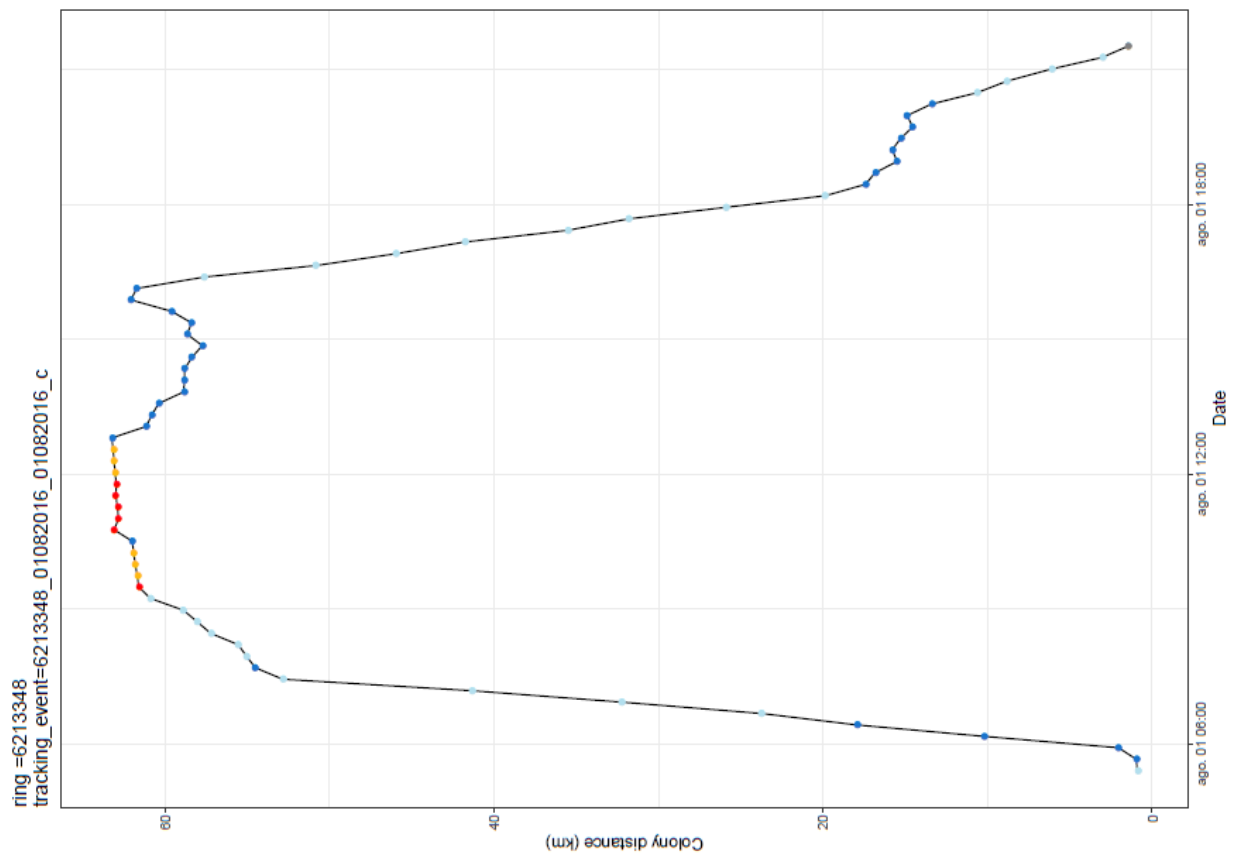
Colony	Loggers	Weight	Supplier
Veneguera	CatTrack I (2012), Timanfaya Catlog-S (2015-2016), Montaña Clara Catlog Gen2 (2017-2019)	25-19g	CatTrack* Technologies / Perthold Industries Ltd.
Berlenga	IgotU GT-120 (2010-2017)	17g	Mobile Action Technology Inc.
Corvo	CatLog2 (2017-2018)	18g	Perthold Engineering; http://www.mr-lee.com/science.htm

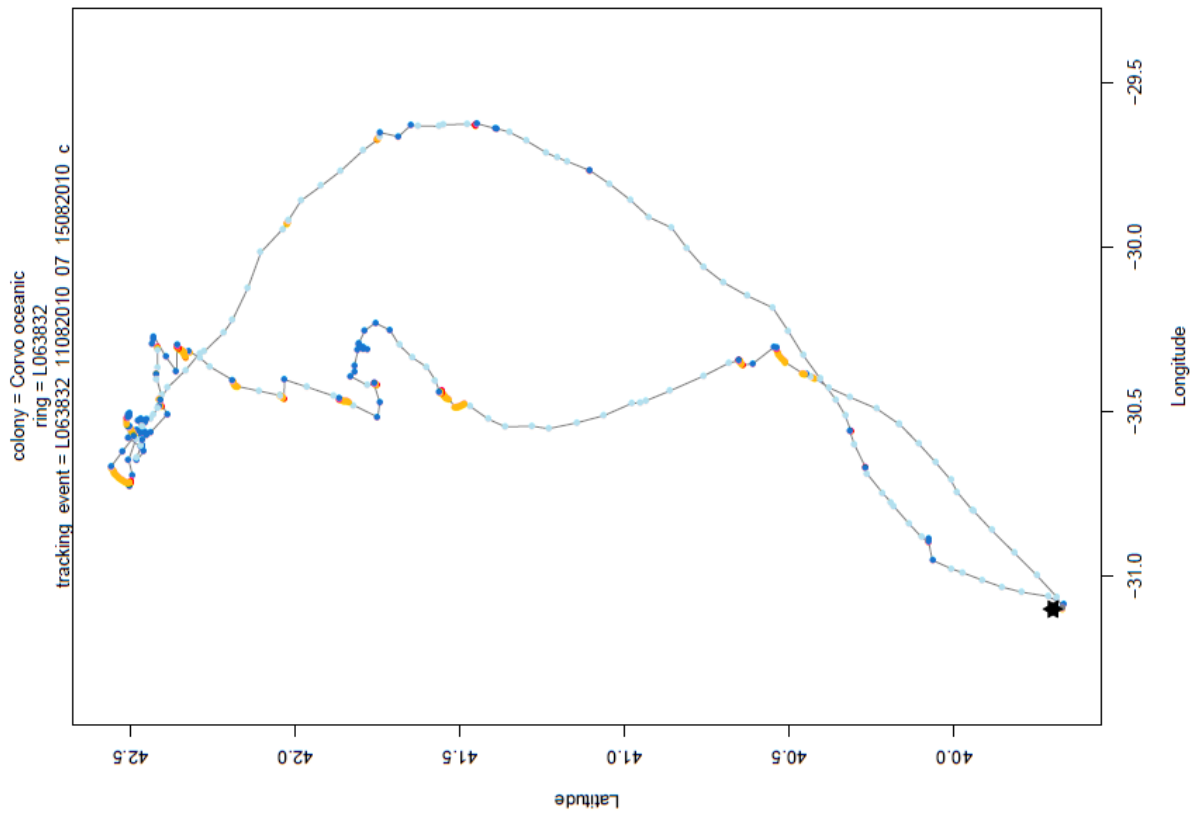
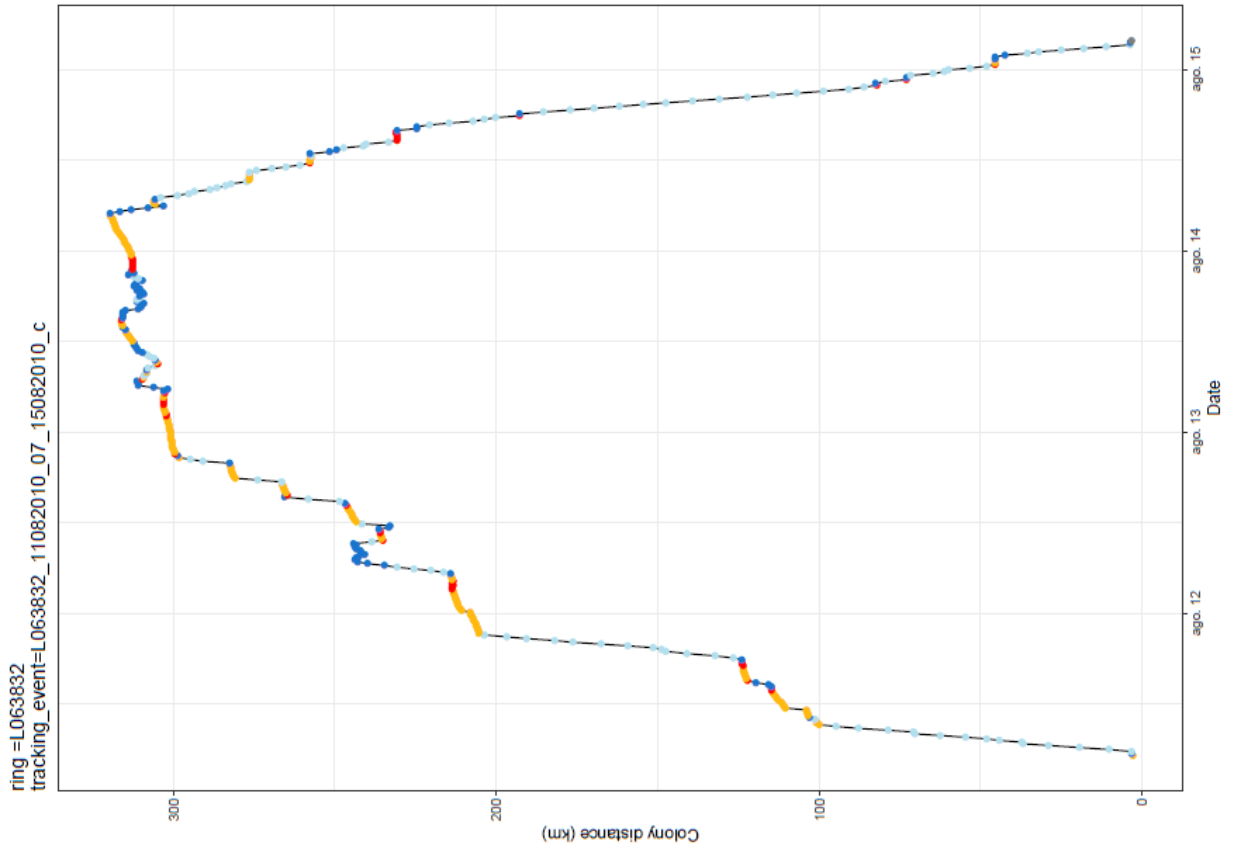
S1. EMbC classification of locations

The Expectation-Maximization binary Clustering (EMbC) is a clustering algorithm for behavioural annotation that is a compromise between statistical power and ease and generality to use (Garriga, Palmer, Oltra, & Bartumeus, 2016). It takes into account the uncertainty of the data and it is suitable for behavioural annotation in animal movement, and indeed it has been broadly used in a wide range of seabird species, including shearwaters (Clay, Opper, Lavers, Phillips, & Brooke, 2019; de Grissac, Bartumeus, Cox, & Weimerskirch, 2017; Ravache et al., 2020; Van Donk, Shamoun-Baranes, Bouten, Van Der Meer, & Camphuysen, 2020). The most common input features for classification are the speed and the turning angle of the locations. In this way, locations are classified as: those having low turning angle and low velocity (resting behaviour); those having low turning angle and high velocity (travelling); those having high turning angle and low velocity (intensive foraging); and those with high turning angle and high speed (extensive search). We used the velocity and turning angle to classify the locations and we also used the smoothing function (smth) to smooth the classification by considering the temporal autocorrelation among labels.

To illustrate the classification in four behaviours of the EMbC, we performed plots of three foraging trips. For each foraging trip we performed two plots: the left one shows the map of the foraging trip in latitude and longitude, with a star indicating the breeding colony; the right one shows in the x axis time and in the y axis distance to the colony in km. In both plots, colour indicates the behavioural classification of the EMbC: orange= resting, cyan= travelling, red= intensive search, dark blue= extensive search, grey= unclassified. As we can see from these figures, positions are classified as resting when birds are showing low velocity and low turning angle, as they are drifting with the sea. Positions are classified as travelling when birds show a directional and straight movement with high speed, as they are relocating to specific areas. Positions are classified as intensive search when birds show low velocity but high turning angles, as they are turning at small spatial scale to locate their prey. Finally, positions are classified as extensive search when birds show high velocity and high turning angles, as they are turning to locate prey patches at large spatial scales.







S2. Foraging site fidelity estimation

We assessed individual foraging site fidelity to understand individual specialization in the physical space. Individual foraging site fidelity was addressed calculating the pairwise overlap of the area used by this specific individual in its foraging trips. We first estimated the utilization distribution area of each foraging trip of each individual. To estimate utilization distributions, we used the 95% Kernel Density Estimation (KDE), using the same smoothing factor value for all KDEs ($h=0.1$), which was the mean of all the individual smoothing factors calculated through the ad hoc (`href`) method provided in the function. KDEs were estimated using “`kernelUD`” function from “`adehabitatHR`” package (Calenge, 2011). To calculate similarity between 95% KDE areas we used Bhattacharyya’s affinity (Wakefield et al., 2015), which calculates the overlap between pairs of utilization distributions. This index takes values between 0 representing no overlap and 0.95 indicating completely overlapping areas. We estimated the within individual similarity using pairs of utilization distributions from trips of the same individual. However, in itself, the within-individual similarity is not particularly informative in terms of individual fidelity, because it reflects both population and individual consistency. To have individual site fidelity, an individual must be faithful to a specific foraging area that is different to that of other individuals. This means that if all individuals exploit the same foraging area, then there is no individual specialization, but specialization of the species or the population. Therefore, the within-individual similarity was compared to the within-population similarity in order to know if there was more foraging site fidelity in individuals than expected by chance. Within-population similarity was obtained randomly assigning a ring to a foraging trip and calculating the similarity between pairs of trips of each randomly assigned ring (Wakefield et al., 2015). This randomization procedure was performed 100 times to obtain a within-population similarity distribution, which was performed for each colony and environment. In this way we classified if each individual was or not faithful to its foraging area in that environment.

S3. Influence of the number of trips per individual on repeatability

Repeatability values can be affected by the number of trips included per each individual (Novak & Tinker, 2015). In this study we considered all individuals having at least two foraging trips, therefore including individuals with only two trips and others with lots of them (up to 40 in a bird from Berlenga tracked for five years). To be sure of our results, we therefore resampled the dataset to have only three trips per individual and we repeated all the analyses to compare them with the whole dataset. Since we mostly found the same results and patterns (Fig. S1), we kept the whole dataset as we considered it more representative of the variation of behaviours within populations

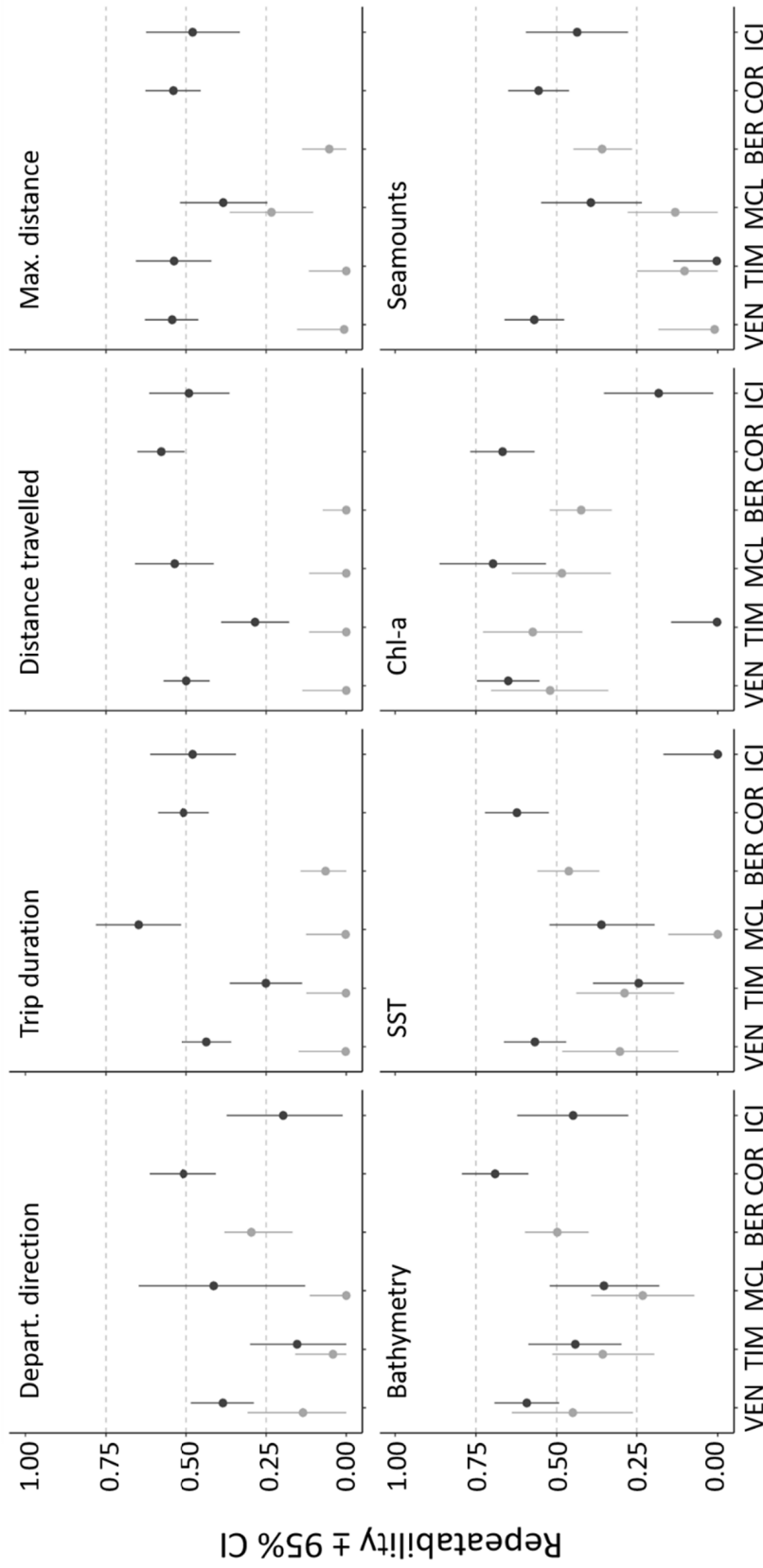


Figure S1

Repeatability values of trip characteristics (A-D) and environmental variables (E-F) for the six studied colonies of Cory's shearwater, using only 3 trips per each individual. Neritic environments are shown in light grey and oceanic environments in dark grey. VEN= Veneguera, TIM= Timanfaya, MCL= Montaña Clara, BER= Berlenga, COR= Corvo and ICI= Ilhéu de Cima. Note that the patterns are the same than in Figure 3, i.e. for trip characteristics, birds are in general more repeatable when foraging in oceanic than in neritic environments.

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General discussion



General discussion

In this thesis, we studied several aspects of individual specialization in long-lived seabirds. In this global discussion, first we are going to briefly summarize and discuss the main findings regarding each of the studied traits related to foraging and migration ecology of Cory's and Scopoli's shearwaters (1): diet, site fidelity, habitat, daily habits and foraging movements. Secondly, we will discuss the intrinsic mechanisms originating individual specialization, specifically if it is acquired through learning or driven by individual intrinsic constraints, as well as the influence of sex (2). Then, we will briefly summarize the results we found regarding the extrinsic environmental conditions that can promote individual specialization (3). Finally, we will discuss the implications of our studies (4) and propose future research that will enable to answer the questions raised in this thesis (5).

1. Individual specialization in different ecological traits

In this thesis we addressed individual specialization in several ecological traits, namely diet, site fidelity, habitat, daily habits and foraging movements. In all the studied traits for both, Cory's and Scopoli's shearwaters, the levels of individual specialization were generally low or moderate, with repeatability values rarely higher than 0.5. These results overall indicate that shearwaters are relatively flexible in their migration and foraging strategies, which could suggest a constraint for higher levels of specialization (Terraube et al., 2011; Van den Bosch et al., 2019). Indeed, previous studies already revealed some degree of flexibility regarding migration and foraging in Cory's (Dias et al., 2011; Ramos et al., 2020) and Scopoli's shearwaters (Courbin et al., 2018). Other seabird species are known to be highly flexible in their foraging and migration strategies at individual level, such as the common guillemot (Gulka & Davoren, 2019) or the yellow-legged gull (*Larus michahellis*) (Lopezosa et al., 2019), as well as other marine animals, such as southern elephant seals (Cotté et al., 2015). Flexibility in foraging and migration strategies has been traditionally linked to the low resource predictability of the

marine environment (Courbin et al., 2018; Opper et al., 2017; Quillfeldt et al., 2010). If individuals are flexible, they can respond to fluctuations in prey availability by adjusting their migration or foraging strategies (Gulka & Davoren, 2019). However, other seabird species showed high levels of individual specialization. For instance, northern gannets (*Morus bassanus*) or Desertas petrels (*Pterodroma deserta*) showed high individual site fidelity in wintering destinations (Grecian et al., 2019; Ramírez et al., 2016), whereas repeatability values of foraging traits during breeding were substantially higher than those found in our studies, i.e. departure direction in great cormorant ($r \sim 0.7$) (Potier et al., 2015). Other marine top predators also showed highly specialized individuals, such as the California sea lions (*Zalophus californianus*), which showed $r > 0.6$ for several spatial and diving characteristics (McHuron et al., 2018). The discrepancy between marine animals suggest a complex scenario where individual specialization can be more species or context dependent (Costa-Pereira et al., 2018).

1.1. Dietary individual specialization

Individual specialization in diet or trophic level is a widespread phenomenon, occurring in many taxa from reptiles (Pajuelo et al., 2016) to mammals (Mori et al., 2019), including several seabird species (Phillips et al., 2017). In the first and second chapters of this thesis we provide two more examples of dietary individual specialization in two species of Procellariiforms, the Cory's and the Scopoli's shearwater, respectively. Dietary individual specialization in Cory's shearwater was only previously reported during breeding in the short-term, within approximately one month (Ceia et al., 2014), whereas here we extended it to year-round, i.e. in breeding and non-breeding seasons, as well as to long-term specialization across years (from 2007 to 2015). To our knowledge, dietary individual specialization in Scopoli's shearwater was not studied so far, although this species was reported to be relatively plastic in resource selection for certain prey species and prey types (Courbin et al., 2018).

The timescale considered is crucial in specialization studies (Carneiro et al., 2017; Ceia & Ramos, 2015). If we compare the repeatability of stable isotopes values between the two studied species during breeding, we can see that repeatabilities of Cory's ($\delta^{13}\text{C}$ 0.14, $\delta^{15}\text{N}$ 0.18) seem slightly lower than those of breeding Scopoli's shearwaters ($\delta^{13}\text{C}$ $r \sim 0.35$, $\delta^{15}\text{N}$ $r \sim 0.2$). This discrepancy may just result from considering different timescales, i.e. repeatability in Cory's shearwaters was studied in the long term (across years), whereas in Scopoli's it was studied just during the same breeding season (within three months). Repeatability in feeding behaviour is expected to decline at longer temporal scales as a result of temporal changes in distribution and availability of resources (Bell et al., 2009; Carneiro et al., 2017; McHuron et al., 2018; Woo et al., 2008). That is, maintaining a certain feeding strategy over a period of three months may benefit the individual because abundance and distribution of resources is unlikely to change. However, maintaining trophic preferences across

years could limit the adaptation of the individual to environmental fluctuations (McHuron et al., 2018; Reed et al., 2010).

In both chapter 1 and 2 we addressed individual specialization using stable isotopes analyses. Stable isotope values of C and N are indeed a broadly used methodology to study trophic specialization in seabirds (Carneiro et al., 2017; Ceia & Ramos, 2015), other birds (Maldonado et al., 2017), mammals (Jacquier et al., 2020) or reptiles (Pajuelo et al., 2016). However, studying dietary individual specialization using stable isotopes may lead to an overestimation of individual specialization. Individuals may differ in their basal metabolism, thus leading to differences in the integration of the different stable isotopes in animals' tissues. These differences in metabolism among individuals have rarely been taken into account when studying individual specialization using stable isotopes. Dietary individual specialization using isotopes is normally addressed calculating repeatability (r), which is the ratio between the among-individuals' variance (s_A) and the within-individuals' variance (s_W) plus the among-individuals' variance (Nakagawa & Schielzeth, 2010). Therefore, consistent differences among individuals in their isotopic metabolism, in particular the diet-tissue fractionation, will lead to an increase of the among-individuals' variance, and the overestimation of repeatability. Individual differences in the isotopic metabolism is not what studies of trophic specialization are aiming to assess, but differences in individuals' behaviour and ecology. Taking into account the increasing number of studies addressing trophic specialization through stable isotopes (Carneiro et al., 2017), understanding the influence of the individual differences in isotopic metabolism on repeatability estimations may be key for further interpretations of individual specialization based on this approach.

One way of exploring the importance of the metabolism in estimating isotopic repeatability may be using captive individuals that have been under the same conditions and fed with the same constant diet (Fig. 1). When controlling the diet, isotopic differences among individuals can only arise by differences in metabolism among individuals (Hobson & Clark, 1992; Klaassen et al., 2004). Indeed, several studies with different bird, mammal, fish and reptile species have found differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among captive individuals fed under a controlled constant diet (Arneson & MacAvoy, 2005; Barquete et al., 2013; Ciancio et al., 2016; DeMots et al., 2010; Kim et al., 2012; Ogden et al., 2004; Seminoff et al., 2006). The example in figure 1 illustrates one of these cases in which penguins fed under the same diet and conditions can reach up to 1‰ consistent differences in nitrogen isotopic values, meaning isotopic specialization would be eventually overestimated due to individual differences in isotopic metabolism.

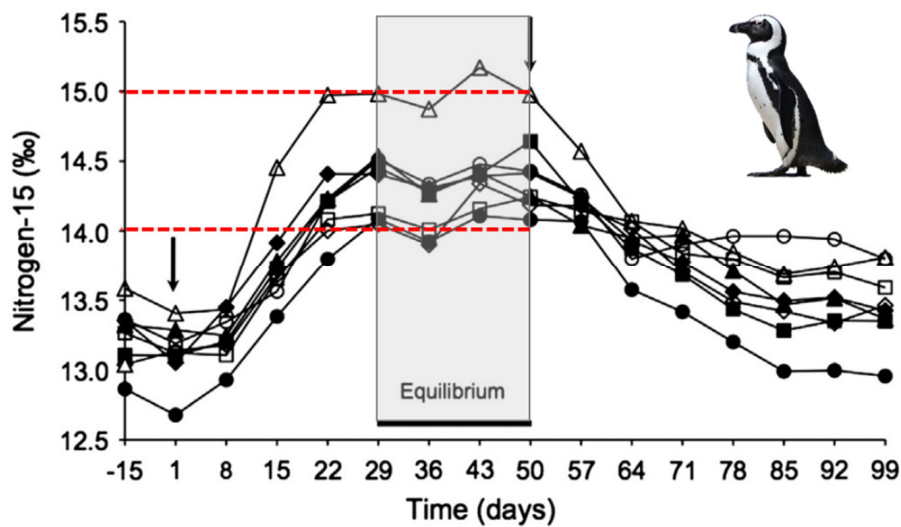


Figure 1

Changes in stable nitrogen isotope values in total blood of eight African Penguins following diet switches to hake (day 1) and back to sardine (day 50 — arrows). Negative numbers mean samples collected two weeks before the beginning of the experiment. Red dashed lines have been added to indicate the range of individual differences at equilibrium. Note that these individuals differ in their nitrogen isotopic values when in the equilibrium in about 1‰. Modified from Barquete et al., 2013 (license number 4944170795589 provided by Elsevier and Copyright Clearance Center).

1.2. Individual specialization in geographical areas

Individual site fidelity is a widespread phenomenon in nature, which confers several advantages to individuals, such as capacity to learn food locations or efficient movement (Piper, 2011). It may happen at different spatial scales as well as both during breeding and during non-breeding periods. In this thesis, we provide evidences of individual foraging site fidelity during breeding in both Cory's and Scopoli's shearwaters in chapters 3 and 2, respectively, as well as non-breeding site fidelity at large scale in Cory's shearwater individuals in chapter 1.

Foraging site fidelity during breeding occurs when individuals become familiar with certain foraging areas during the breeding season. We found approximately 50% of breeding individuals of Cory's shearwater showing individual foraging site fidelity (Fig. 4 chapter 3), whereas around 30% of Scopoli's shearwater breeders (Fig. 3 chapter 2). The higher percentage of foraging site fidelity in Cory's than Scopoli's shearwaters may come from the relatively small areas exploited by Scopoli's shearwaters at population level (Fig. 2 chapter 2). When the population level niche is small, a higher overlap is expected between individuals, thereby decreasing individual specialization (Araújo et al., 2011). However, 50% of individuals showed foraging site fidelity in the relatively small oceanic areas exploited for Canary Islands birds. The high individual site fidelity in oceanic areas may arise as a result of resource scarcity, which increases segregation of strategies among individuals (Kobler et al., 2009; Ratcliffe et al., 2018). Regarding non-breeding site fidelity, in the first chapter we found that 36% of Cory's shearwaters changed their non-breeding destination at least once, whereas we recorded 16% of changes between consecutive migration events (Fig. 2). Non-

breeding site fidelity was very consistent with the existing literature on the species for other colonies (Pérez et al., 2014), which may suggest that the extent of individual flexibility (or specialization) in wintering sites is distinctive of the species.

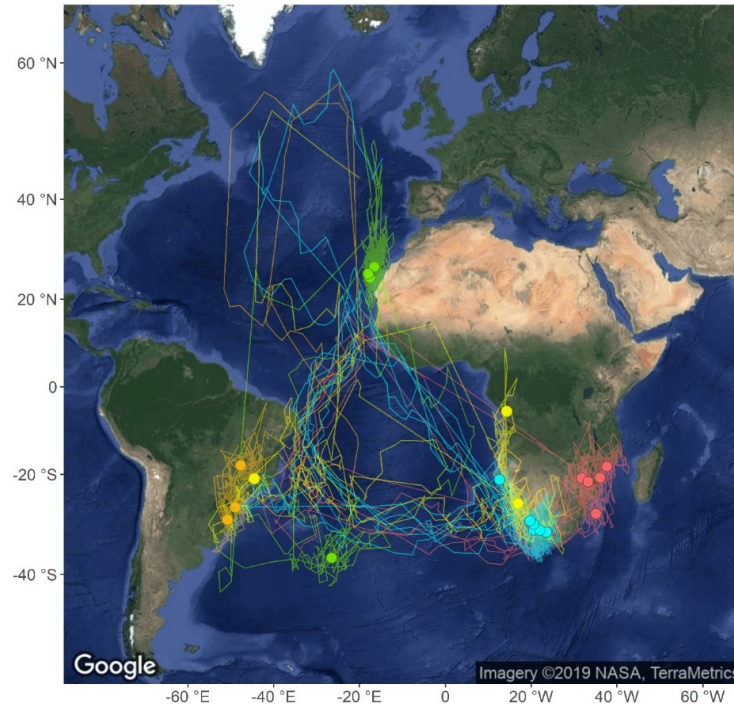


Figure 2

Annual migratory routes of Cory's shearwaters breeding in Veneguera (Canary Is.) and tracked with geolocators. Each dot corresponds to the centroid of the core wintering area. Colours correspond to different individuals. Most birds spent the non-breeding period in a similar area year after year (e.g. red dots), but other change area every few years (e.g. green) or every year (e.g. yellow). All tracks over land result from inaccuracies in the GLS method.

In this thesis, we used different methodologies to address site fidelity during breeding and non-breeding periods. Regarding breeding, the estimation came from calculating the overlap of foraging areas, whereas non-breeding estimation was assessed by defining categorically the main non-breeding area (e.g. Benguela Current) and looking at the changes among areas across years. The overlap estimation is a more direct way of estimating site fidelity, although we believe it can be improved, particularly when studying species with several wintering or foraging destinations that are relatively apart, as it occurs in wintering destinations of Cory's shearwaters (Fig. 1 chapter 1). An overlap estimation is simply overlaying two areas and calculating the percentage of area shared between them, but it is not taking into account neither the distance between the two areas nor their shapes (Fig. 3; Kranstauber et al., 2017). That is, for instance, that Cory's shearwaters wintering in the Benguela Current may have a 0 overlap with those wintering in Angola Current and will have also a 0 overlap with those wintering in the Brazil Current (Fig. 1 chapter 1). However, Benguela and Brazil are far more apart than Benguela and Angola. Instead of an overlap index, we believe the Earth Mover's Distance (EMD) is a more appropriate methodology to estimate similarity of areas in such cases, as it takes into account the distance and shape of these areas (Fig. 3; Kranstauber et al., 2017). In

this thesis, we did not use this approach as it has a high computational cost that requires a super computer to analyse it, particularly when the number of areas to compare is large, as it occurred in our case since we needed comparisons at the individual level. However, we believe further research on spatial similarity should consider the use of EMD, particularly when the areas compared are apart and overlap indices can be frequently 0.

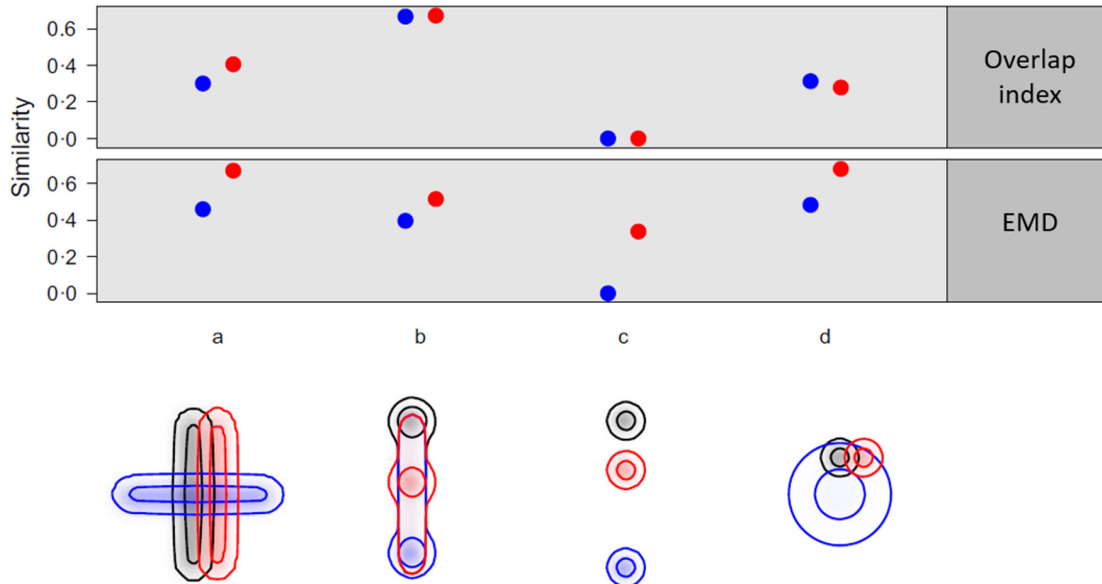


Figure 3

Each column (a, b, c and d) is a comparison of three utilization distributions where the black distribution was compared to the blue and red distribution, respectively. The overlap index is equal for b) and c), even though we would argue that the red distribution is more similar to the black one than the blue is to the black distribution through its spatial proximity; in d), the blue is estimated to be more similar to the black although in terms of shape and proximity the red is more similar to the black. The lines of the visualized utilization distributions indicate the 50% and 95% contours. Extracted from Kranstauber et al. 2017 (license number 600027808 provided by John Wiley & Sons - Books).

1.3. Individual specialization in habitat

Individual specialization in habitat have been reported in many groups (Cardona et al., 2017; Kamath & Losos, 2017; McIntyre et al., 2017), including seabirds (Phillips et al., 2017). In this thesis, we report individual specialization in marine habitat in the two studied shearwaters for the following variables: Bathymetry, SST, Chl-a and proximity to seamounts. Repeatability values were moderate for habitat variables in Cory's shearwaters in all colonies and for both, oceanic and neritic environments, during breeding ($r = \sim 0.25-0.5$, Fig. 3 chapter 3) and non-breeding ($r = 0.45$, Table 1, chapter 1). Similarly, during breeding, male Mediterranean Scopoli's shearwaters showed moderate repeatability values ($r = \sim 0.3-0.4$, Fig. 4 chapter 2), although females showed lower values ($r = \sim 0.1-0.2$). The generally similar values in repeatability indicate individuals from both species specialize in habitat to a similar extent, which could suggest the association with certain oceanographic features provides some advantages regardless of the environment.

During the breeding period in Cory's shearwaters, in the first chapter repeatability values of SST were not significant ($r=0.18$, Table 1 chapter 1), although we did find significant repeatability values ($r \sim 0.5$) in the third chapter for the same Veneguera colony (Fig. 3 chapter 3). As it happened with the dietary specialization, this difference may occur because the first chapter addresses long-term specialization across years, whereas in the third most of the trips of the same individual occurred during the same breeding season (Carneiro et al., 2017). Alternatively, this difference may come from the different methodology used to obtain SST values. In the first chapter we obtained SST values from geolocation, which is directly measured by the geolocators when the bird is on the sea surface, whereas in the third we extracted SST values overlaying the foraging locations from SST layers of 4km resolution. Although the SST from geolocation is more precise, it is measured after 20min in contact with salt water, thereby including resting periods and not only foraging behaviour.

1.4. Link between habitat specialization and foraging site fidelity

Individual specialization in habitat and in geographical space are often linked, although the direction of causality is unclear (Patrick & Weimerskirch, 2017; Wakefield et al., 2015). If individuals are specialized in certain geographical areas and there is spatial autocorrelation of oceanographic features, individuals will also depict repeatability in habitat. The opposite direction may also occur: individuals may seek for certain oceanographic cues, which are likely placed in specific geographical areas (Patrick & Weimerskirch, 2017). Indeed, in this thesis we generally found the same patterns in habitat repeatability than in site fidelity. In chapter 2, we found low foraging site fidelity in female breeders and higher in male breeders of Scopoli's shearwater (Fig. 3 chapter 2), and accordingly we found higher specialization in habitat in male breeders (Fig. 4a chapter 2). In chapter 3, we found moderate values of foraging site fidelity in both oceanic and neritic environments in all colonies (Fig. 4 chapter 3), matching with similar levels of repeatability in habitat among colonies and environments (Fig. 3 chapter 3). Contrasting with our species, other studies found either site fidelity or habitat specialization being dominant in other seabird species. In black-browed albatrosses, individuals were more specialized in the foraging habitat than the geographical area (Patrick & Weimerskirch, 2017), whereas northern gannets showed high foraging site fidelity across years but low habitat specialization, and site fidelity was not correlated to consistency in habitat at individual level (Wakefield et al., 2015). This suggests the relationship between these specializations may be more dependent on the environment and the species.

1.5. Individual specialization in daily habits.

Individual specialization in the daily habits occurs when individuals differ in their activity along the day (Daunt et al., 2014; Mackley et al., 2011). In this thesis, we addressed individual specialization in daily habits (NFI) across years in Cory's shearwaters in both breeding and non-breeding period in chapter 1. We found individuals specialized in a more nocturnal or diurnal behaviour across years in

both periods, as well as a correlation between the daily behaviour of individuals between the two seasons at individual level (Table 1 and Fig. 3 chapter 1). That is, an individual that was more diurnal during breeding, was also more diurnal during non-breeding. These results suggest the daily behaviour is more fixed in individuals, which may limit the adaptation of individuals to changes in the environment (Reed et al., 2010).

1.6. Individual specialization in foraging movements

Individuals can be specialized in certain characteristics of the foraging movements, such as the maximum distance to the colony or the trip duration (Ceia & Ramos, 2015). In this thesis, we studied individual specialization in foraging movements of Cory's (chapter 3) and Scopoli's (chapter 2) shearwaters during breeding by addressing the repeatability of the following variables: % of resting, maximum distance to the colony, trip duration, distance travelled and departure direction. We found similar repeatability values in breeding shearwaters (Cory's Fig. 3 chapter 3; Scopoli's Fig. 4a chapter 2), which were in general low to moderate. However, in Cory's we found higher repeatability values in oceanic than neritic environments, which was related to the resource scarcity of oceanic areas (Araújo et al., 2011), whereas Scopoli's males seemed to be more repeatable than females, difference attributed to a discard use of males (Cortés et al., 2018). Our studies therefore suggest specialization in movement characteristics is more flexible than in other aspects of foraging behaviour, such as daily activity, and individuals can adjust them depending on the environmental conditions or the targeted resource.

2. Intrinsic drivers of individual specialization

Individual specialization can emerge as a result of intrinsic constraints of the individual, such as physiological or morphological constraints (Bolnick & Paull, 2009; Maldonado et al., 2019), or through a learning process during early life (Vander Zanden et al., 2013). In this thesis, we addressed the mechanisms underlying individual specialization using two approaches: by comparing the strategies of individuals under different conditions and by comparing the specialization levels of adults and immature birds. Regarding the first approach, if a certain strategy is fixed in an individual due to intrinsic constraints, we would therefore expect the strategy to be maintained under different contexts, for instance between breeding and non-breeding grounds (chapter 1) or between oceanic and neritic areas (chapter 3). On the contrary, if a strategy is acquired through experience, different strategies can eventually be developed by the same individual in different contexts. Regarding the second approach, if individual specialization is acquired through learning, we would expect immature individuals to be less specialized than adults (Grecian et al., 2018; Votier et al., 2017), whereas if it is fixed due to individual constraints, immatures would show the same levels of specialization than adults (chapter 2).

We used the first approach in chapters 1 and 3 with Cory's shearwaters. In both chapters, we generally found that individuals did not maintain their feeding strategies when conditions changed. This occurred at large spatial scales from breeding to non-breeding grounds, as well as at small spatial scales from neritic to oceanic environments. We found this pattern in diet, habitat and foraging movements, suggesting these traits are not driven by intrinsic constraints of individuals but likely learned independently in each ground or area (Grecian et al., 2018; Votier et al., 2017). Contrarily, daily habits were repeatable across-years in both breeding and non-breeding grounds and maintained year-round in individuals, i.e. correlated at individual level (Table 1 and Fig. 3 chapter 1), thus suggesting daily behaviour is probably driven by intrinsic constraints, such as different optical capabilities to deal with foraging under poor light conditions.

Despite Cory's shearwater studies seemed to show that foraging strategies are generally acquired through learning, we found certain levels of individual specialization in immature Scopoli's shearwaters comparable to those of adults (Fig. 4a,c chapter 2). When individuals are young, their foraging proficiency is still developing, and individuals are not expected to be specialized (Grecian et al., 2018). Our results may therefore suggest certain traits are driven by intrinsic constraints and therefore fixed at all ages. However, since female breeders and non-breeding adults were highly flexible in their foraging strategies (Fig. 4a,b chapter 2), it is not possible that these traits are intrinsically driven. Alternatively, we propose that the significant repeatability values found in immatures may happen because the immatures we tracked were from 3 to 6 years old and they learned their foraging skills earlier in life. Therefore, our results suggest that long-lived seabirds can learn rapidly the spatiotemporal heterogeneities of the environment and define their individual foraging strategies during their first years of life.

Overall, the patterns found in this thesis seem to exclude intrinsic constraints as the proximate driver of individual specialization in foraging strategies (but see Bolnick & Paull, 2009; Maldonado et al., 2019), also suggesting a limited genetic codification of the studied foraging characteristics (Weimerskirch et al., 2015). On the contrary, our studies indicate the process of exploiting a subset of the ecological niche of the species is plastic and the same individual can exploit different subsets of the ecological niche when conditions differ.

The fact that the same individual can change its strategies depending on the context may indicate that indeed individuals are not specialized, because they do not have a fixed strategy, but they are plastic (Fig. 4). Therefore, using the concept of individual specialization when this occurs may be inappropriate. However, the specialization concept has also been used in other species in a similar way we used it when comparing breeding and non-breeding periods (chapter 1), that is, in different moments of time. For instance, Asiatic black bear individuals were dietary specialists in summer, segregating in the proportion of green vegetation, insects, mammals, crop and fruits, but the same individuals changed their diets during spring, where all of them consumed green vegetation and seeds (Mori et al., 2019). Similarly, bold black-legged kittiwakes showed low levels of individual specialization

in trip metrics during incubation ($r=0-0.2$), but high during chick-rearing ($r=0.5-0.6$), suggesting individuals do not have a fixed strategy between the two periods (Harris et al. 2020). However, in the third chapter we found that the same individual changed its foraging strategy depending on the area exploited within the same time period, that is between oceanic and neritic environments during chick-rearing. Indeed, the change of strategy occurred at a very short time scale, since individuals perform a dual foraging strategy and constantly combine short trips to the oceanic environment with long trips to the neritic. This indicates individuals are plastic, as they change from one strategy to the other at a very short time scale (i.e. days or weeks) depending on the area exploited (Fig. 4). Despite within these areas individuals consistently exploited a subset of the ecological niche across time and differed to that exploited by other individuals (Fig. 4 scenario 2), this indicates individuals are indeed plastic, and therefore in this context the terminology of individual specialization may not be appropriate.

The sex of the individual can also influence individual specialization, as males and females can have different food requirements or roles during breeding, as well as one sex may be excluded from some resources due to competition avoidance with the other sex (Phillips et al., 2017). In the second chapter of this thesis we found differences in individual specialization between males and females in Scopoli's shearwaters. Males showed higher repeatability in foraging movements and habitat variables than females, whereas females showed higher repeatability in isotopic diet than males (Fig. 4 chapter 2). We believe these patterns come from a higher use of fishery discards by males, which exclude females from this resource (Cianchetti-Benedetti et al., 2018). Fishery discards are composed by a large array of prey types and sizes (Tsagarakis et al., 2014), thus making individuals that depend on it to show a broad and variable diet, which explains the low repeatability in isotopic diet of males. Discards are highly predictable in space and time (Furst et al., 2018; Patrick et al., 2015; Tyson et al., 2015), which can make individuals to show consistent foraging movements (Patrick et al., 2015), explaining the higher repeatability of breeding males in variables related to the foraging trip. Indeed, males from this colony were very recently found to interact more with fisheries than females, suggesting males outcompete females in the access of discard resources (Reyes-González et al., 2020). Moreover, it is possible that a use of fishery discards also occurs in Cory's shearwater during the non-breeding period, as we found higher repeatability values in $\delta^{15}\text{N}$ than $\delta^{13}\text{C}$ during non-breeding. This may come from some individuals scavenging on discards to some extent and others depending on natural prey, as discards typically depict higher $\delta^{15}\text{N}$ values than naturally obtained pelagic fish (Votier et al., 2010).

Although in our studies we did not directly address discard consumption, it is possible that this predictable human subsidy is shaping individual specialization in these species. Our results also suggest that the use of this resource and its effects on individual specialization may vary among population groups, such as males or females, as well as among areas, such as breeding and non-breeding grounds. Therefore, the interplay between human activities and individual specialization can be complex and depend on both intrinsic and extrinsic factors.

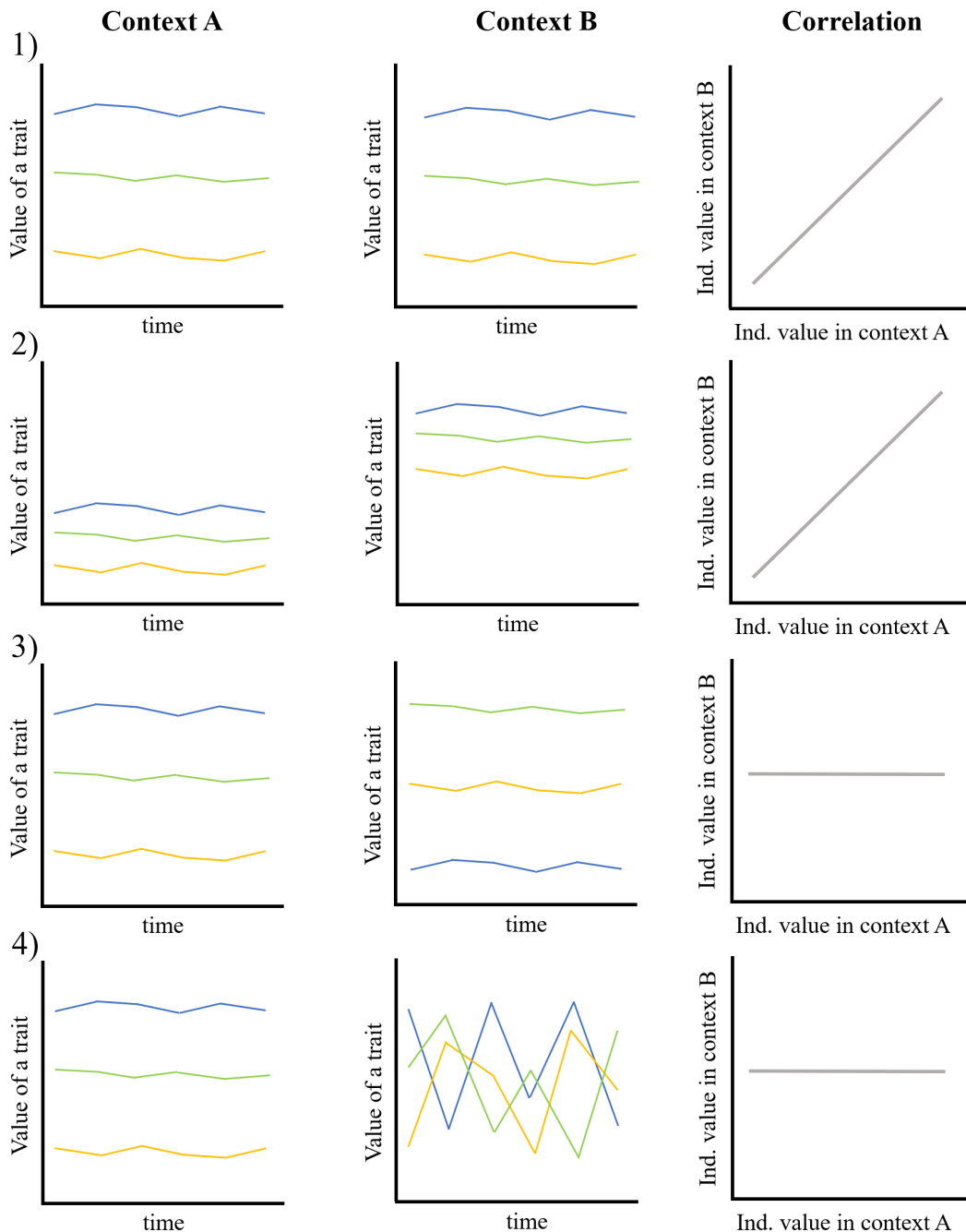


Figure 4

Individual expression of ecological traits for three individuals (blue, green and yellow) under two environmental conditions (context A and context B) in four hypothetical scenarios (1 to 4). Different environmental contexts may be represented by different periods, such as breeding or non-breeding, or different areas, such as oceanic or neritic environments. 1) Individuals are specialized across time in context A and B, that is, each individual consistently exploit a different subset of the ecological niche over time, for instance the blue individual always have a high value of the trait, whereas the yellow always have a low value. 2) Individuals are specialized across time in context A and B and they change the value of their ecological trait in a correlated way, for instance the blue individual has a higher value of the trait in context B than in A, but it is still the individual with the higher value of the trait within the population. 3) Individuals are specialized across time in context A and B, but they change the value of their ecological trait in an uncorrelated way, for instance the blue has high values of the trait in context A, but low values in context B. 4) Individuals are specialized across time in context A, but are generalists in context B, therefore they do not maintain the value of the ecological trait across contexts. In the latter two cases (3 and 4) individual specialization terminology may not be appropriate, although within each context individuals exploit the same subset of the ecological niche across time and differ to that exploited by other individuals. However, most studies on individual specialization are limited to a short time period or area.

3. Extrinsic drivers that promote individual specialization

In this thesis we addressed the environmental conditions that promote individual specialization by comparing environments with contrasting resource abundance and predictability. Resource limitation is expected to increase individual specialization as it promotes that individuals segregate their strategies to avoid competition (Araújo et al., 2011; Mori et al., 2019). A high predictability of resources is also expected to promote individual specialization, as individuals know where and when they can find their food and can define their own foraging strategies (Dermond et al., 2018; Grassel & Rachlow, 2017). In the marine ecosystem, neritic environments usually show high abundance and high predictability of resources, whereas oceanic environments are less productive, and resources are less predictable. Therefore, if resource limitation is the main driver of individual specialization, repeatability should be higher in animals exploiting oceanic environments, whereas if individual specialization is mainly driven by resource predictability, repeatability should be higher in those exploiting neritic environments. We found higher repeatability in foraging movements in oceanic than in neritic environments, supporting resource limitation is a more relevant driver than resource predictability in defining individual specialization in foraging movements (chapter 3). Higher individual specialization with resource scarcity has been found in several vertebrates (Kobler et al., 2009; Mori et al., 2019; Tinker et al., 2008), including one seabird (Ratcliffe et al., 2018). Contrary to foraging movements, individual specialization in habitat was relatively high regardless of the environment, indicating shearwaters can show a consistent habitat use regardless of the abundance and predictability of the resources (but see Courbin et al., 2018).

Although in this thesis we did not directly address other extrinsic drivers, it is possible that some of the results we found could be explained by extrinsic drivers. For instance, we found relatively high repeatability values across years during non-breeding in Cory's shearwaters diet as well as SST habitat contrasting with lower values during breeding (Table 1 chapter 1), respectively indicated by stable isotope values and T recorded by the geolocators. This may happen because of the higher ecological opportunity when birds are released from central place foraging (Araújo et al., 2011; Yurkowski et al., 2016). During non-breeding, birds are not tight to the colony and can explore larger areas, probably encountering different prey or habitats over to which specialize. The same pattern was found in South American fur seals when comparing females, which are tight to the breeding sites for pup-nourishing, with males, which can explore large areas as they do not rear the pups. Males showed high individual specialization as they had access to different habitats and resources, whereas all females showed similar strategies and therefore no individual specialization (de Lima et al., 2019).

4. Implications of this research

Specialization can be adaptive (Patrick & Weimerskirch, 2014), as it can reduce foraging effort and increase the efficiency in prey capture (Terraube et al., 2014; Van den Bosch et al., 2019). Several studies reported higher fitness in specialist than in generalist individuals in seabirds (Patrick & Weimerskirch, 2017; Traisnel & Pichegru, 2019) and other birds (Terraube et al., 2014). Interestingly, in this thesis we found a pattern of intermediate specialized individuals showing higher fledging success than those weekly and highly specialized (Fig. 4 chapter 1), thus suggesting individual specialization is adaptive only to a certain extent. This result matches with repeatability levels found in the three chapters, which were almost never higher than 0.5, suggesting a constraint for higher levels of specialization. Similar results were found with Herring Gulls, where specialist individuals showed higher offspring growth rates, although this positive effect decreased at high levels of specialization (Van den Bosch et al., 2019). Overall, our results suggest specialization is adaptive in individuals as it may increase their efficiency, although upper limited, as specialists may be more vulnerable to fluctuations in the environment (McIntyre et al., 2017; Terraube et al., 2011).

The relative flexibility of individuals in the studied ecological traits and the fact that these traits are not driven by intrinsic constraints of individuals have important implications for conservation (Bolnick et al., 2003). If individuals are relatively flexible and the specialization process is plastic, individuals will probably better cope to alterations of the environment than highly specialized individuals (McIntyre et al., 2017). Human activities are constantly modifying the marine environment either locally or globally and at across variable temporal scales (Avila et al., 2018; Dias et al., 2019; Doney et al., 2012). If these anthropogenic alterations occur at a rapid time scale, adaptation at the individual level may be crucial for the species or population to persist. However, some human alterations may occur extremely fast and affect the individual or its breeding performance. For instance, if fishery discards are banned, this measure may occur at a very short time scale and individuals specialized on it may have their body condition compromised or fail in reproduction (Bicknell et al., 2013). Similarly, our results also evidence that certain traits may be driven by intrinsic constraints, such as the daily activity, and the capability of individuals to modify them may be limited.

Protection of specific foraging or migration strategies, as well as certain areas, may exacerbate the difficulty of the population to cope with environmental changes. For instance, night setting has been suggested as a mitigation measure to reduce seabird by-catch (Belda & Sánchez, 2001; Cortés & González-Solís, 2018). However, we found daily activity specialization in Cory's shearwater, thus implying night setting will only be effective for diurnal animals, leaving more crepuscular or nocturnal animals unprotected. Similarly, setting limits on fishery stocks to protect most preferred prey can be considered a good measure to avoid

seabirds' starvation (Grémillet et al., 2016). However, some individuals may depend on cephalopods or small crustaceans, thus implying a protection of fish stocks will leave these individuals vulnerable to changes in the abundance and distribution of their prey. Likewise, the establishment of protected areas is based on hotspots where most individuals of the population aggregate to forage or to spend the non-breeding period (Krüger et al., 2017; Opper et al., 2018). However, the protection of certain geographical areas or habitats may leave alternative strategies of the population or species unprotected. Although positive at short term, these population-level measures may imply a reduction in phenotypic and potentially genotypic variability in populations, which are keystone for species viability and evolution (Bolnick et al., 2003; Reed et al., 2010). Indeed, intraspecific variability not only has effects on the species itself, but also on the community dynamics and ecosystem functioning, mirroring in magnitude the ecological effects of variability among species (Des Roches et al., 2018; Raffard et al., 2018).

In this thesis we found a broad array of factors that influenced the extent of individual specialization within populations. We provide evidences that individual specialization may differ between breeding and non-breeding grounds, as well as between sexes, colonies and oceanic or neritic environments. Moreover, the extent of individual specialization was also dependent on the time scale considered and differed depending on the ecological trait. Therefore, this thesis evidences that it is key to consider intrinsic and extrinsic factors modulating individual specialization and that the assumption of general patterns regarding individual specialization should be taken with caution (Costa-Pereira et al., 2018).

5. Future research

In this thesis we addressed several aspects of individual specialization that raised new questions or required further attention to demonstrate the patterns we found.

First, we believe it is key to understand the influence of the different methodologies and approaches on individual specialization estimations. More specifically, in this thesis we pointed out the possible influence of the metabolism on individual diet specialization assessed through stable isotopes, as well as the importance of considering the temporal scale used. Future studies using stable isotopes would benefit from a review on the extent of individual differences in stable isotopes. This can be done using individuals raised under the same constant diet and regularly sampled for stable isotopes on the same tissue, such as whole blood, which has been already done for several species of birds (Barquete et al., 2013; Ciancio et al., 2016; Hobson & Bairlein, 2003; Kurlle et al., 2013; Ogden et al., 2004; Pearson et al., 2003), mammals (Arneson & MacAvoy, 2005; Caut et al., 2011; DeMots et al., 2010; Kraefer et al., 2014; Lecomte et al., 2011), fishes (Kim et al., 2012; Madigan et al., 2012) and one reptile (Seminoff et al., 2006). Some studies collaterally addressed the influence of the temporal scale on repeatability estimations (Kernaléguen et al., 2015; McHuron et

al., 2018). However, we believe future research would benefit from an study addressing its implications in several aspects at the same time, such as the different time intervals (Kernaléguen et al., 2015), the number of samples per individual (Ramos et al., 2020) or the inclusion of time-aggregated observations (Novak & Tinker, 2015).

Secondly, in this study we raised the hypothesis that sexual differences in individual specialization in Scopoli's shearwater breeders were related to fishery interaction. To demonstrate this, future research may focus on assessing if the individuals more specialized in foraging movements and habitat variables those highly interacting with fisheries. This could be done by combining GPS data with fishery vessels data (Reyes-González et al., 2020; Soriano-Redondo et al., 2016) or using vessel radar detectors on shearwaters GPS devices (Corbeau et al., 2019; Grémillet et al., 2019; Weimerskirch et al., 2020). Moreover, the role of anthropogenic subsidies on the degree of individual specialization should be further studied to understand if the patterns found for shearwaters also occur in other species and environments (Layman et al., 2015).

Thirdly, the development of individual specialization in foraging strategies of seabirds has been accounted to a learning process during early life (Grecian et al., 2018; Votier et al., 2017). However, in this thesis we found immatures of 3-6 years already specialized in certain foraging traits, thus suggesting the learning process occurs very early in life. Future research should aim to understand this process of defining individual strategies by monitoring individuals from their first years of life onwards (e.g. Campioni et al., 2019). These studies will also disentangle if there are some ecological traits that mirror intrinsic constraints of individuals, such as the daily habits suggested in this thesis.

Fourthly, future research should focus on understanding the role of environmental conditions in shaping individual specialization. Although in this thesis we conclude resource limitation is a more relevant driver than resource predictability, other studies found contrasting results (Courbin et al., 2018; Lerma et al., 2020). Therefore, future studies should aim to disentangle if environmental drivers of individual specialization are common among areas and species in the marine ecosystem. Indeed, drivers of individual specialization can highly dependent on the context and the species (Costa-Pereira et al., 2018; Kernaléguen et al., 2015), thus calling for more research to understand which are the general patterns driving among-individual differences.

Finally, future research should aim to understand the ecological and conservation implications of individual specialization for populations. So far, the implications of individual specialization have been limited to the study of the benefits or drawbacks of a specialist strategy for individuals, which concluded specialist strategies allow individuals to have a better breeding performance or condition (Patrick & Weimerskirch, 2017; Terraube et al., 2014; Traisnel & Pichegru, 2019). However, it is unknown how specialist

strategies would limit the ability of individuals to face changes in the environment, although it will probably reduce them (McIntyre et al., 2017). Similarly, nothing is known about how population-level conservation measures may reduce at the long term the phenotypic and genotypic diversity in populations, which can be key not only for the species but for the community and the ecosystem (Des Roches et al., 2018; Raffard et al., 2018). Although empirical studies on these issues are difficult, we believe future research on this field would benefit from studies modelling the possible conservation implications under different scenarios of changes in the environment.

Conclusions



Conclusions

Regarding individual specialization in several traits:

- Individuals can specialize in several ecological traits related to migration and feeding ecology, namely diet, geographical areas, habitat, daily habits and foraging movements. However, they rarely show high levels of specialization in any of these traits, suggesting levels of specialization are under stabilizing selection.
- In the breeding period, individuals of both species, Cory's and Scopoli's shearwaters, are specialized in foraging sites and oceanographic variables to a similar extent. This foraging site fidelity and habitat specialization may cause one another, although the direction of causality remains unclear.
- When determining individual specialization levels of any trait at different time scales, we generally found lower individual specialization levels across-years than within the same breeding season. This result suggests the timescale considered for assessing specialization levels is crucial, i.e. the longer the time period considered, the lower the specialization level. This effect may be obscuring comparison in specialization levels across studies, and thus further research should be performed to fully understand the influence of different time scales and monitoring methods on individual specialization estimates.

Regarding the intrinsic drivers of individual specialization:

- Under different environmental conditions, the same individual can exploit different uncorrelated portions of the ecological niche of the species, e.g. different diet, habitat and foraging movements. This result indicates the process of exploiting a subset of the ecological niche at individual level can develop independently in different areas or periods. This result opens the question on whether the exploitation of different uncorrelated portions of the ecological niche in different periods or areas should actually be considered individual specialization, thus challenging the most common

approaches to study individual specialization, usually limited to a single period of the lifecycle (e.g. breeding) and a single area (e.g. breeding area).

- The specialization for more diurnal or crepuscular habits is maintained in individuals when they change from breeding to non-breeding grounds, indicating this trait is probably driven by intrinsic constraints of the individual.
- The levels of specialization in immature shearwaters from 3 to 6 years were similarly high to those found in adults (> 6 years), indicating shearwaters are able to develop individual specialization in foraging skills in their first years of life. More generally, this result suggests that, in long-lived species, individuals can rapidly learn the spatiotemporal heterogeneities of the environment and define individual foraging strategies at early stages of their life.
- Although in this thesis we did not directly address discard consumption, our results provide some evidence that this predictable anthropogenic subsidy may be driving differences in individual specialization across sexes. Further research is needed to understand the role of anthropogenic modifications in shaping individual strategies.

Regarding the extrinsic conditions that promote individual specialization:

- Oceanic oligotrophic waters are generally considered less predictable than productive neritic waters. We found higher repeatability values for a number of movement traits in oceanic than neritic areas, indicating resource scarcity is a more relevant driver of individual segregation in foraging movements than resource predictability.
- The moderate repeatability values in marine habitat (oceanographic variables) in both, oceanic and neritic environments, indicate segregation in individual habitat use can be developed regardless of abundance and predictability of the resources.
- A higher ecological opportunity during non-breeding can explain the higher repeatability values in diet and SST habitat during non-breeding compared to breeding, as birds can explore larger areas and encounter different prey and habitats when they are released from the central place foraging imposed by breeding duties.

Regarding the implications of this work:

- In this thesis we showed that the extent of individual specialization within populations may depend on several factors, such as colony, sex or the environmental conditions faced by the same individual at different periods or areas. Overall, these results indicate that general patterns regarding individual specialization should not be assumed and that spatial and time scale chosen to evaluate individual specialization should be carefully considered.

- Most foraging and migration individual strategies are relatively flexible and can be developed independently in different areas, indicating individuals may be able to adapt to anthropogenic alterations of the environment. However, plasticity of certain traits may be limited by intrinsic constraints, such as the daily activity.
- Conservation measures aiming to protect specific hotspots or marine protected areas, will protect most common foraging strategies of the population but this also implies some alternative strategies, occurring in other areas, are left unprotected. This may ultimately reduce the phenotypic variability of the population at the long term, which can increase the difficulty of the population to cope with future environmental changes.

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