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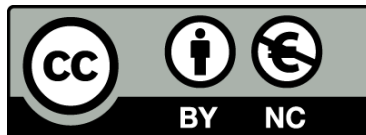
Bird population dynamics in the wintering season: the case of the mediterranean Gull *Larus melanodephalus*

Dinàmiques poblacionals en ocells durant la hivernada: el cas de la Gavina Capnegra *Larus melanocephalus*

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Programa de doctorat en Biodiversitat

Facultat de Biologia

Departament de Biologia Animal

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Memòria presentada per

Carles Carboneras Malet

per optar al grau de Doctor

per la Universitat de Barcelona

Barcelona, Novembre de 2015

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<tr><td>El director de la tesi</td><td>La directora de la tesi</td><td>El tutor de la tesi</td></tr>
<tr><td>Dr. Giacomo Tavecchia</td><td>Dra. Meritxell Genovart Millet</td><td>Dr. Santiago Mañosa Rifé</td></tr>
<tr><td>IMEDEA (CSIC-UIB)</td><td>IMEDEA (CSIC-UIB)</td><td>Universitat de Barcelona</td></tr>
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To my wife Susana

and three children, Rita, Pere and Joan,

who fill my life with multiple colours

ACKNOWLEDGEMENTS

No one can complete a PhD thesis without the help and advice of other people, and I am obviously no exception. Without the generous assistance of many, my initial idea would not have got anywhere. I will try in these few lines to honour the huge debt of gratitude that I owe to all of them. First, and most importantly, to my supervisors Giacomo Tavecchia and Meritxell Genovart, for showing me the ways of good science and for putting me on the right track quite a few times. They played a key role in my wonderful transformation from a naturalist into a scientist, and I will always thank them for that. Even if distance did not make things easy, they were always there. Santi Mañosa was much more than a helpful academic tutor, he also became a good friend; he hosted me at the University of Barcelona and gave me tons of useful advice. Daniel Oro received me into the Population Ecology Group at IMEDEA (CSIC-UIB) and made me feel part of it, whilst contributing with his vision to my work.

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This crossing has not been without its contrary winds, and several dedicated professionals did a fantastic job in making sure I did not drown in the rough seas. I must

Contents

INTRODUCTION

This introduction is arranged in three sections. The first section looks at the wintering season as an important part of the annual cycle of migratory birds, with an insight into some theoretical aspects of migration and wintering, and the demographic consequences of the different strategies. The second section presents the issue of bird conservation through the protection of important areas for wintering populations, and how this applies to seabirds. The third section introduces the study system and the study organism, the Mediterranean Gull, summarising current knowledge on the species and the historical evolution of its spatial distribution, both in the wintering and the breeding season.

Part I – Bird population dynamics in the wintering season

Migration as a strategy to face environmental changes

In temperate regions, the winter period is typically associated with cold temperatures and fewer light hours, and often with reduced food availability. Birds respond to the difficulties of winter in a number of ways, the commonest of which are to avoid costly investments like reproduction and territoriality. As a consequence, it is frequent for birds to increase sociability during the winter, aggregating to search for food and to avoid predators more efficiently (Senar & Borrás 2004). Particularly where weather conditions are harsh, many birds suffer increased mortality during this part of the year (Newton 1998; Barbraud, Barbraud & Barbraud 1999; Daunt *et al.* 2005; Harris, Frederiksen & Wanless 2007).

One strategy to overcome the difficulties associated with the winter period is to migrate to southern regions to find mild weather. By travelling to lower latitudes, birds find more productive environments, and thereby increase their overall chances of survival. This may carry costs, as annual mortality in long-distance migratory species is not concentrated in summer or winter but during the migration periods (Sillett & Holmes

2002; Sanz-Aguilar, De Pablo & Donázar 2015) or is shared between the migration and other parts of the cycle (Buehler & Piersma 2008). The general result must be positive, because migratory strategies have evolved by providing improved survival or fitness to the individuals that engage in long-distance journeys, over those that remain resident (Lack 1954).

Even if the winter does not cause direct mortality, the conditions encountered during those months may have important effects for the individual. For several long-distance migrants, it has been demonstrated that carry-over effects may project onto the following breeding season, influencing breeding performance or even the probability of survival several months after the end of the wintering season. Such effects have been described for White Stork *Ciconia ciconia* (Kanyamibwa *et al.* 1990), Pink-footed Goose *Anser brachyrhynchus* (Kéry, Madsen & Lebreton 2006), Lesser Kestrel *Falco naumanni* (Mihoub *et al.* 2010) and Turtle Dove *Streptopelia turtur* (Eraud *et al.* 2009).

Populations of migratory birds can be limited primarily by events affecting survival during one part of the year differentially more than others (Sherry & Holmes 1995; Newton 1998). Studies covering the whole year are rare, and much of the evidence is deductive, based on the findings on survival during only part of the year, and an extrapolation to the rest (e.g., Blackburn & Cresswell 2015). Populations may be limited by differential mortality in breeding or in wintering areas, or perhaps mortality may be evenly spread throughout the year (Newton 1998, 2008). The distinction has implications for conservation, as the protection of the wintering areas would play a greater role for the long-term viability of the global population, relative to the conservation of the breeding sites, in a winter-limited species.

Nonetheless, despite a potentially crucial role in population dynamics and in species conservation, the wintering period still remains a 'black box' in our understanding of the annual cycle of many bird species. The demographic processes in wintering areas are largely unknown because of the difficulties in monitoring birds of unidentified origin that move freely over large areas and due to the problem of finding discrete populations suitable for monitoring (Robertson & Cooke 1999).

General rules, and exceptions, of birds' migratory strategies

Many birds perform long and complex migrations and in terms of direction, the majority of seabirds tend to travel on a north-south axis, although some species also move on an east-west axis, crossing from one side of an ocean to another, and in the process keep roughly in the same latitude (Berthold 2001). Among gulls, the predominant strategy is a southbound migration to lower latitudes, although some species stay in the general area where they live, even in Arctic waters, throughout the winter. The Mediterranean Gull is another exception to the general latitudinal rule in gull migration. It is the only western Palearctic gull species to migrate across longitudes (Burger, Gochfeld & Bonan 2014) and is in fact one of the very few bird species in the Afro-Palearctic flyway with a migration pattern that is on an east-west axis, instead of the more common north-south, or northeast-southwest, axis (Newton 2008).

In terms of migration length, populations are generally not uniform, as the distance travelled often differs between portions of a population (Cristol, Baker & Carbone 1999). By spending the wintering season in separate areas, different members of a population may face varying degrees of interspecific competition, predation, inclement weather and food scarcity The majority of migratory species show evidence of differential migration, or geographic segregation of age or sex classes of individuals within the same population (Cristol, Baker & Carbone 1999). Adult males generally remain closest to the breeding areas, while juvenile birds travel the farthest (Berthold 2001). Differential migration by age is the dominant strategy also among European seabirds, including gulls, as there is evidence that young birds migrate longer distances than adults in most species (Fig. 1; Siriwardena & Wernham 2002). Specific studies have demonstrated, for example, that Audouin's Gull *Larus audouinii* and Lesser Black-backed Gull *L. fuscus* change individual migratory behaviour as they grow in age (Oro & Martinez 1994; Marques, Sowter & Jorge 2010).
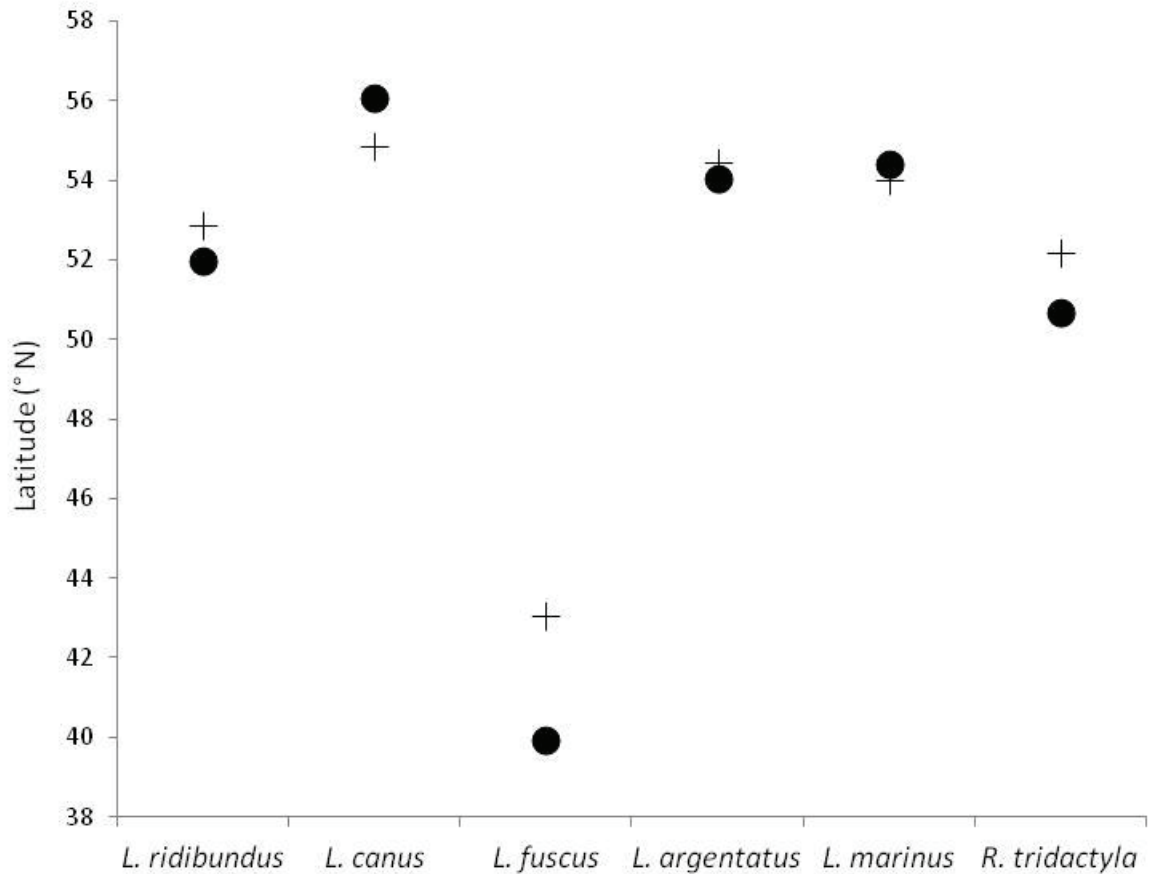
Fig. 1. Differential migration in several species of gulls as shown by the median latitude of the ringing recoveries of adult (crosses; $n = 1160$) and immature (black dots; $n = 2125$) birds from the British Isles. Notice that *Larus argentatus* and *Larus marinus* are non-migratory, and that immature birds are found further north in one species, *Larus canus*. Data from Siriwardena & Wernham (2002).

The absence of differential migration is only found in about one tenth of all migratory species and is thought to evolve under unusual circumstances. So far it remains unexplained why in those few species all sex and age classes migrate the same distance despite differences in body size (males *vs.* females) and in breeding role (adults *vs.* young) (Cristol *et al.* 1999). Non-differential migration is rare and there is little empirical evidence for it, or for the ecological and behavioural reasons behind it, except for those species where parents and offspring travel together. Strong site fidelity and nondifferential migration should logically be associated in a certain manner, because the advantages of site fidelity would be lost if individuals moved to different wintering areas as they age. However, that linkage has not been explored.

Variations on a migratory theme: alloheimy and synheimy

Spatial segregation also occurs between migratory populations of the same species. This phenomenon, known as alloheimy (Fig. 2), is common to most long-distance migrants (Bell 2000). In every species, each distinct breeding population tends to have its own preferred wintering area, which individuals use preferentially every year, although there are variable degrees of mixing with other populations. Studies of tagged water- and seabirds have shown that many individuals spent the winter period in relatively small, well defined winter home ranges (Phillips *et al.* 2003; Leyrer *et al.* 2006; Kubetzki *et al.* 2009), which suggests a specialised use of certain areas. At a population level, González-Solís *et al.* (2007) demonstrated that breeding populations clearly differed in their preference amongst their three major wintering regions; however, they also showed substantial sharing of the same space. In a tracking study of Black-legged Kittiwake *Rissa tridactyla* from multiple colonies, Frederiksen *et al.* (2012) found that birds breeding in various regions across the species' Atlantic range also showed substantial spatial overlap in winter. Hestbeck, Nichols & Malecki (1991) studied movement and site-fidelity of Canada Geese *Branta canadensis* in three distant areas and found that considerable movement occurred among large-scale regions and that, although birds showed strong site fidelity to the wintering areas, geese were also opportunistic in selecting their winter quarters.
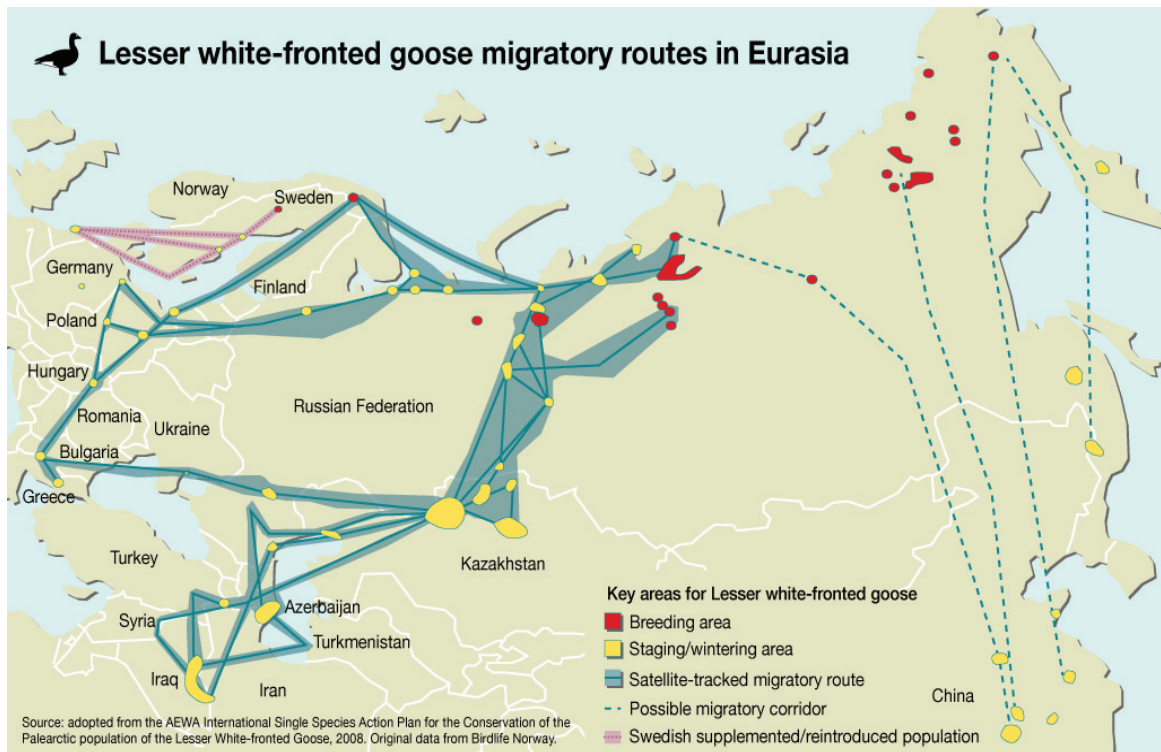
Fig. 2. Distribution of the breeding and wintering areas of the Lesser White-fronted Goose (*Anser erythropus*) in Eurasia, with the migratory routes connecting them. This is a good example of alloheimy, or geographical segregation of populations of the same species. Map layout: Grid-Arendahl, Original data: Norwegian Ornithological Society, WWF Finland, Swedish Association of Hunting and Wildlife Management.

In general, alloheimy is the result of differential survival in each separate wintering area, which leads to the selection of the area with the best winter survival through selective competition in the breeding population. The opposite phenomenon, synheimy, is the co-occurrence in a wintering area of birds from different breeding populations (fig. 3). It is only maintained under special circumstances. As a rule, it occurs transitorily after recent alteration and as birds change their behaviour and shift gradually from synheimy to alloheimy (Newton 2008).
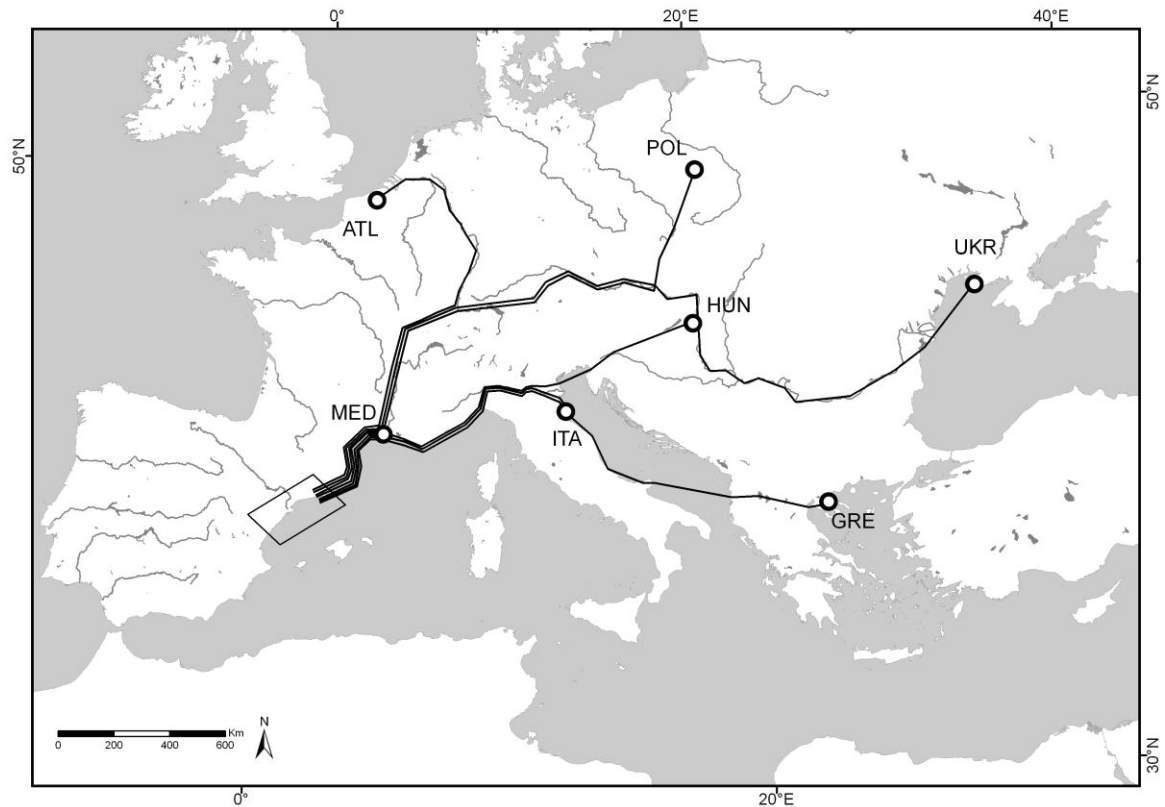
Fig. 3. Breeding areas and migratory routes of Mediterranean Gulls (*Larus melanocephalus*) wintering in the study system. The general wintering area (black box) is used by birds from different breeding populations, spanning over 30° of longitude and represented here by the centroid of their nesting colonies. The lack of geographical segregation may be indicative of synheimy. Map source: Carboneras et al. (2013).

Winter site-fidelity and winter population structure

In the past, seabirds were believed to simply disperse more or less widely over the ocean outside the breeding season (e.g. Lockley 1974; Nelson 1980) with no specific destination. That idea has now been abandoned, as there is growing evidence that several taxa distribute unevenly, and aggregate following heterogeneities of the marine environment. This is the case of albatrosses (Mackley *et al.* 2010), gannets (Kubetzki *et al.* 2009), skuas (Phillips *et al.* 2007) and auks (Harris *et al.* 2009). With individual year-round tagging of animals, it has also become increasingly known that some individuals – but not all – in certain species use the same areas repeatedly over the years (Iverson, Esler & Rizzolo 2004; Phillips *et al.* 2005; Quillfeldt, Voigt & Masello 2010; Meier *et al.* 2015) and that the presence of birds in certain areas may be predictable, given certain conditions, at the appropriate time scale (Robertson & Cooke 1999; Arcos *et al.* 2012).

Site-fidelity measures the individual tendency to return to the same location. Most birds show high levels of site-fidelity to the breeding areas, and return annually to the same territories or colonies, probably in order to find similar conditions and to benefit from their previous knowledge of the area (Greenwood & Harvey 1982). But it is less known whether birds have a similar tendency to return to specific areas for wintering, or the advantages and disadvantages associated with that strategy (Berthold 2001). The question is particularly relevant for seabirds, as habitat discontinuities are less obvious in the marine environment.

Site-faithful individuals have the selective advantage that they can rely on local previously-acquired knowledge, whereas dispersers are continually confronted with novel environments. On the down side, however, individuals that are closely tied to an area may be missing opportunities elsewhere. There is always a trade-off between the benefits and the costs of dispersal, which leads to the existence of different strategies (Clobert, de Fraipont & Danchin 2008). Perhaps the season of the year when it would be more reasonable to expect a nomadic strategy would be the non-breeding season, because it is then that birds are in theory free to travel and their movements are not conditioned by central-place foraging (Iverson & Esler 2006).

Winter site fidelity has been well documented among geese, ducks and waders (Phillips *et al.* 2003; Leyrer *et al.* 2006; Iverson & Esler 2006; Guillemain *et al.* 2009) but it is a less well-known behaviour among seabirds (Harris *et al.* 2009; Grist *et al.* 2014). The reasons for such a difference may lie partly with the difficulties of documenting behaviour in seabirds that distribute potentially over vast extensions, but they may also be intrinsic. Winter site-fidelity would be more likely where resources are stable and predictable, but those conditions are often rare in the marine environment (Hyrenbach, Forney & Dayton 2000). In terms of conservation, site-fidelity may be relevant when a significant fraction of a population of a species of conservation concern shows attachment to an area or a specific site, since the protection of that site can bring positive outcomes on a population level. Moreover, there is a link between site-fidelity and genetic differentiation, so that high levels of site-fidelity would lead to the genetic structure of populations and their relative isolation (Robertson & Cooke 1999).

Populations with strong winter site-fidelity can evolve into a metapopulation structure in situations where the groups of animals occur in isolated groups (subpopulations) that become demographically independent and there is only limited exchange of individuals through dispersal (Esler 2000; box 1). There are important conservation implications of a metapopulation structure, because the probability of extinction is specific to each subpopulation (Gilpin & Hanski 1991) and the probability of rescue is dependent on the rates of dispersal (Reed 2004). Esler (2000) provides several examples of metapopulation structure in wintering populations of migratory birds, including ducks, waders and landbirds (Fig. 4). Further, in a theoretical study of metapopulations among colonially breeding birds and mammals, it has been shown that strong site fidelity actually reduces the connectivity between subpopulations, especially among species with high conspecific attraction. This may delay or even prevent full occupation of potential sites and the colonization of new areas (Matthiopoulos, Harwood & Thomas 2005).

Box 1. Demographic independence and metapopulation structure

Esler (2000) analysed the degree of demographic independence among subpopulations—and thus of the applicability of metapopulation theory—throughout the entire annual cycle of migratory birds. For metapopulation theory to apply, in its classical definition, (1) subpopulations must be sufficiently independent that extinction of a subpopulation can occur irrespective of the demographics of other subpopulations and (2) dispersal among subpopulations must be frequent enough that recolonisation of extinct subpopulations can occur. Subpopulations can be considered to be demographically independent when the above criteria apply; panmixia occurs when subpopulations, in the metapopulation context, do not exist because of a lack of independence of extinction probabilities. The term subpopulation applies to either breeding or wintering areas and may be defined as groupings of birds that are demographically independent. Instances of demographically distinct groups with no probability of exchange of individuals would be appropriately described as isolated and cannot be considered under the metapopulation construct.
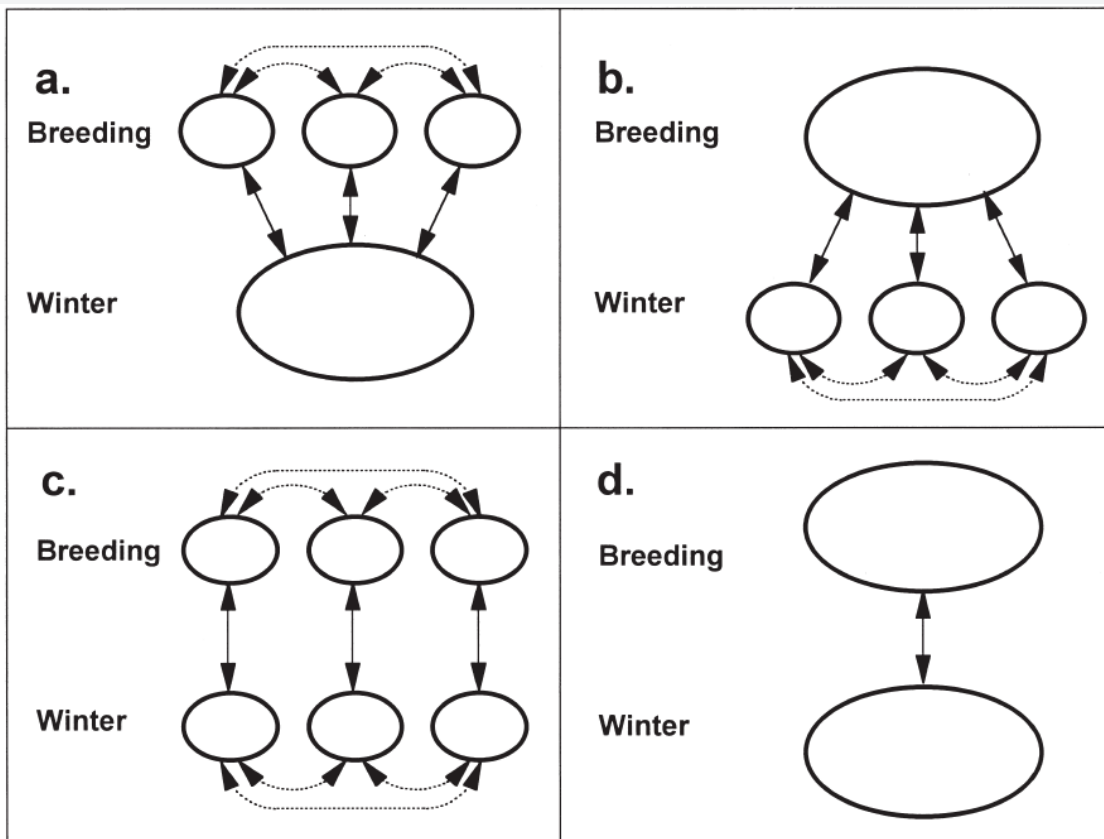
Fig. 4. The four scenarios of spatial and temporal dynamics of migratory birds between breeding and wintering areas described by Esler (2000). Ovals represent geographically distinct groups, solid arrows represent migration, and dashed arrows represent dispersal.

Small-scale movements within the wintering season

A number of species move between different areas within the same winter, normally in response to variation in food supplies, but also after spells of bad weather and in response to disturbance (Newton 2008). Individual mobility and population turnover at the wintering sites have been best studied among geese (Giroux 1991; Phillips *et al.* 2003; Swann *et al.* 2005) and ducks (Caizergues *et al.* 2011; Gourlay-Larour *et al.* 2013) and it is also known to occur in other waterbirds, e.g. storks (Archaux, Henry & Balança 2008).

The level of individual movement through a wintering locality will be given by the total turnover of individuals per fraction of time. This is an important indicator of the importance of that site for the overall population and it can be used as a useful metric to compare the conservation value of sites. The study of population turnover has evolved as methodologies have progressed. The basis has been provided by capture-recapture methods, which allow for the estimation of immigration and emigration probabilities to and from the selected area (Pradel *et al.* 1997; Schaub *et al.* 2000; Frederiksen *et al.* 2001); models have been derived from the empirical evidence that as individual birds move on to continue their voyage, they may be replaced in the same area by conspecifics. Schaub *et al.* (2000) estimated with precision the duration of stopover phases of migratory landbirds using capture-recapture data, e.g., as they cross the Sahara desert. Later, Frederiksen *et al.* (2001) developed proposed a technique to estimate the total number of migratory geese using a staging site, and Hötker & Frederiksen (2001) applied the same methodology to estimate the total number of Avocets *Recurvirostra avosetta* using a moulting site in the Danish Wadden Sea. Until this study, the method has not been used to estimate the conservation value of a wintering area for gulls or other seabirds.

Part II – Conservation: a wintering area perspective

In recent years, following the overexploitation of marine resources and the widespread destruction of coastal habitats, much effort has been devoted to identifying

important areas for the conservation of seabirds, a group of species whose status is deteriorating faster than that of any other group of birds (Butchart *et al.* 2004; Paleczny *et al.* 2015). A lot of effort has been put into describing the defining features, biotic and abiotic, that lead to the identification of key sites and into assessing their adequate size and limits (Boyd *et al.* 2008; Wilson *et al.* 2009; Ronconi *et al.* 2012). Most systems ultimately aim at identifying the location of discrete hotspots of activity that are relevant for a substantial fraction of the population of a single species or a community of species (Lascelles *et al.* 2012). For waterbirds, the Ramsar Convention on Wetlands set an objective threshold of 1% of a biogeographic population for an area to qualify as of international importance for conservation, and the same criterion has been applied to other bird taxa, particularly for the identification of Important Bird Areas or IBAs in the breeding season (BirdLife International 2010). The 1% criterion, and the numerical thresholds established by Wetlands International (2015), have also been used to identify marine IBAs beyond the limits of the breeding colony and, especially, in the non-breeding season (Archaux *et al.* 2008; Lascelles *et al.* 2012).

The Mediterranean Gull is listed in Annex I of the Birds Directive (2009/147/EC) and, consequently, it should be the focus of special conservation measures, including the classification of the most suitable territories as Special Protection Areas (SPAs). The 1% criterion for this species has been set at 770 individuals (Wetlands International 2015); therefore, any site regularly holding at least 770 Mediterranean Gulls should be given protected status. A 'site' is defined as "a discrete area of habitat that can be delineated and, at least potentially, managed for conservation", (BirdLife International 2010).

In the designation of Marine Protected Areas, there has been some debate around the utility of a single-species approach versus an approach that focuses on the identification of multi-species aggregation hotspots (Ronconi *et al.* 2012). The dominant preference is for a multi-species approach based on the overall abundance and/or species diversity; this is currently being used to identify networks of sites across large spatial scales (Lascelles *et al.* 2012). Current methodologies focus on the identification of areas where important activities like feeding, breeding or migration take place, but

they are likely to create a gap when the spatial needs of a population are greater. Ideally, networks of protected areas should be designed to safeguard the long-term viability of the target populations, taking into account the demographic processes (survival, recruitment, dispersal) that ultimately define their viability.

Part III – Study species and study system

The Mediterranean Gull *Larus melanocephalus* Temminck 1820 is a small to medium-sized gull (215 – 350 g) that occurs typically in large monotypic aggregations, or associated to other medium-sized gulls, along the shores of the Mediterranean and Black Seas (Bekhuis, Meininger & Rudenko 1997). It is also found on the Atlantic coasts of Europe and inland, near rivers or wetlands, particularly during the breeding season (Fig. 5). It nests in dense colonies near coastal lagoons, steppe lakes and marshes in open lowland areas, favouring sparse vegetation, often breeding with other species of gulls or terns (Burger, Gochfeld & García 2015). In the non-breeding season, it occurs almost exclusively on coastal habitats, feeding mostly offshore on trawl discards, but also on invertebrates in the intertidal zone and on the hinterland, on invertebrates and olives (Cama *et al.* 2011). Mediterranean Gulls regularly visit fishing harbours in search of discards from fishery but they only rarely scavenges at rubbish tips, in contrast with other gull species (Burger *et al.* 2015). The species shows some degree of sexual dimorphism, males being appreciably larger and longer-legged, and with longer, stubbier bills; however, there is some overlap and individuals cannot be sexed safely in the field. In the wintering season, adult birds have typically all-white body (except for a few dark markings on the head) and wings, a plumage that is acquired in the third year of age (Olsen & Larsson 2004). Juvenile birds show a distinct pattern of grey, brown and black and are easily distinguishable at a distance.

Phylogenetically, the Mediterranean Gull is one of the six species in the "black-headed" clade of gulls, together with Audouin's *Larus audouinii*, Relict *L. relictus*, White-eyed *L. leucophthalmus*, Sooty *L. hemphrichii* and Pallas's *L. ichthyaetus*. This whole group is sometimes separated in the genus *Ichthyaetus* to indicate their differentiation from the other gulls (Pons, Hassanin & Crochet 2005), but other authors prefer to retain

them in the traditional genus *Larus* (Burger *et al.* 2014). The black-headed group of gulls is highly distinct and probably separated from the other gull clades early in evolutionary time. However, all species in this group have relatively restricted distributions and are mainly found in the southern / central areas of the Palearctic region, which is in contrast with the flying ability and the colonisation capacity of gulls. It has been proposed that this lack of success in colonising other areas might be due to the strong natal philopatry typical of all gulls (Crochet, Bonhomme & Lebreton 2000), which may have allowed species to differentiate within flying distance of each other. The Mediterranean Gull is the smallest and perhaps the most social of the *Ichthyaetus*-type gulls. In the western Mediterranean region, it occurs in sympatry with several similar-sized, as well as much larger species, in a complex and competitive system (Fig. 5).
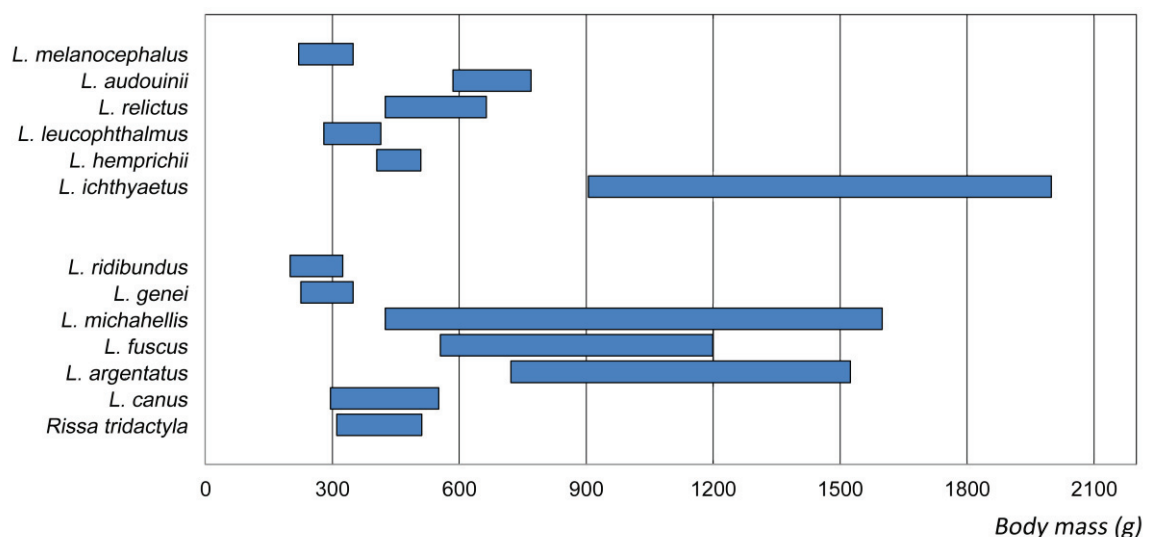
Fig. 5 Comparative size (using body mass as proxy) of the Mediterranean Gull in relation to the other five species in the "black-headed" or *Ichthyaetus* clade (above), and to other seven gull species with which it occurs sympatrically in the western Mediterranean region (below). Data from *Handbook of the Birds of the World Alive* (retrieved from http://www.hbw.com).

Unusually for a mostly European bird species, the biology and ecology of the Mediterranean Gull are still poorly understood. The breeding population has a patchy distribution comprising many coastal regions of Europe and the Central Asia region. The bulk of the breeding numbers are in the Black Sea-eastern Mediterranean area (Bekhuis *et al.* 1997; Burger *et al.* 2015). The species underwent a dramatic large-scale expansion of its breeding range during the 20th century, starting in the Black Sea and quickly

extending mostly in the 1970s–1990s across central Europe to reach the Atlantic coast and the NW Mediterranean. This coincided in time with large increases in the populations of other gull species in various parts of the northern Hemisphere (Harris 1970; Furness & Monaghan 1987) so it was initially interpreted as a population explosion that could be part of the same process (Cramp & Simmons 1982). However, several authors speak more recently of a redistribution of breeding numbers and have linked the species' distribution shift to fluctuations of the population breeding in the Black Sea (e.g., (Bekhuis *et al.* 1997; Sadoul & Raevel 1999). There is still no proof of an overall increase and, despite the consolidation of the breeding population in NW Europe, the species is considered to be stable overall (BirdLife International 2015a).

The bulk of the global population spends the winter in the Mediterranean region, mostly in the central and western basin, on the coasts of mainland Spain, France, Italy and Tunisia, also in Sicily and Malta, with smaller numbers in the Black Sea, eastern Mediterranean and on the Atlantic coast of Iberia and France (Bermejo, Carrera & De Juana 1986; Baccetti & Smart 1999; Poot & Flamant 2006; Cama *et al.* 2011). The winter distribution is also discontinuous and has been historically much more stable than the breeding distribution, with many areas having been occupied since at least the 1950s (cf. Figs. 7 and 8; Mayaud 1954; Shevareva 1955). The species' has remained spatially stable in winter over several decades in the Mediterranean region, where the changes in the coastal landscape and marine ecosystem have been dramatic. Such changes include the elimination of wetlands and littoral habitats, the industrialisation of fishing since the 1970s (Coll *et al.* 2010) and the widespread availability of discards on which the species bases their winter diet, as do some of its competitors (Cramp & Simmons 1982).

The study area for this work is the 350-km long coastal land between the towns of Blanes (41° 41' N) and Borriana (39° 54' N) (Fig. 6). This stretch of Mediterranean coastline is dominated by low-lying shores interspersed with short sections of calcareous cliffs. The hinterland is a typical Mediterranean mosaic landscape with abundant vineyards and olive groves. Human population occurs at high densities, and the coast is dotted with small or medium-sized fishing harbours that provide abundant discards on

weekdays, when trawlers and purse-seine vessels operate all over the continental shelf. The area has been occupied by wintering Mediterranean Gulls for a long time, at least since the 1940s (Fig. 8; Mayaud 1954), and is currently the global winter stronghold for the species, with over 40 000 individuals (Cama *et al.* 2011). On days with fishing activity, birds follow a regular pattern of attending trawlers at sea in the morning, aggregating in pre-roosts on the beach or foraging in fishing harbours in the afternoon, later flying inland to feed on olives or bathing in freshwater (e.g., reservoirs) before finally moving back to the sea for roosting. This general pattern of activity may be broken during the weekend, when trawlers are not allowed to operate and therefore discards are not available. The lack of a predictable food source must cause some disruption, as during the weekend birds often move to nearby wetlands or simply rest at sea. Human visitors are likely to cause disturbance on beaches also during the weekend, making that space less attractive for loafing gulls.
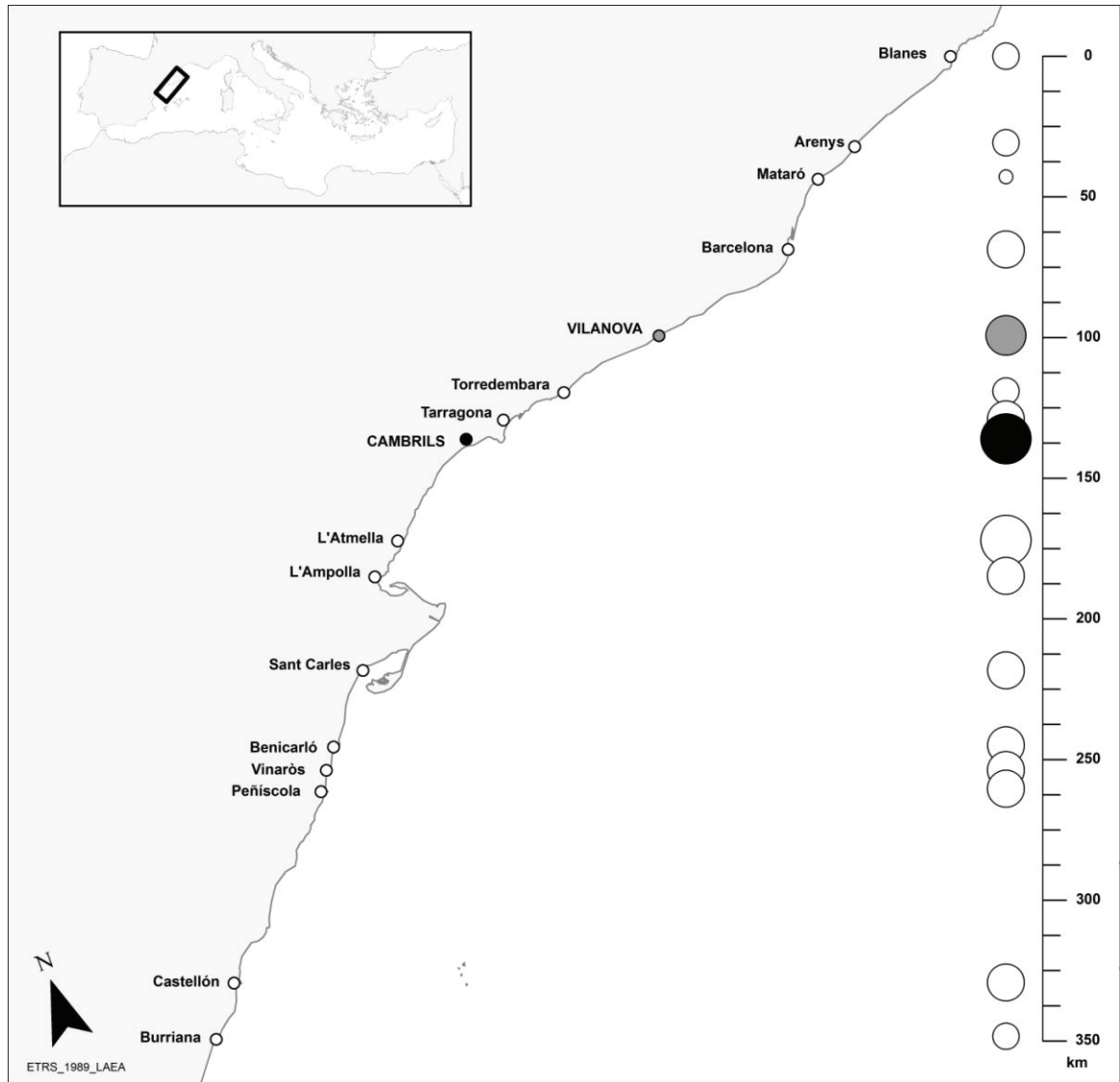
Fig. 6. Location of the study system area showing, right, a schematic representation of the spatial distribution of Mediterranean Gull concentrations associated to the principal fishing harbours. Circle size is proportional to the average Mediterranean Gull numbers on a logarithm scale; there is one order of magnitude difference in the population size between Cambrils (black circle) and Vilanova i la Geltrú (grey circle), the two main localities sampled for marked birds; white circles indicate other sites. Site location is arranged according to the distance (in km) to Blanes (41º41'N, 2º48'E), at the N edge of the wintering area.
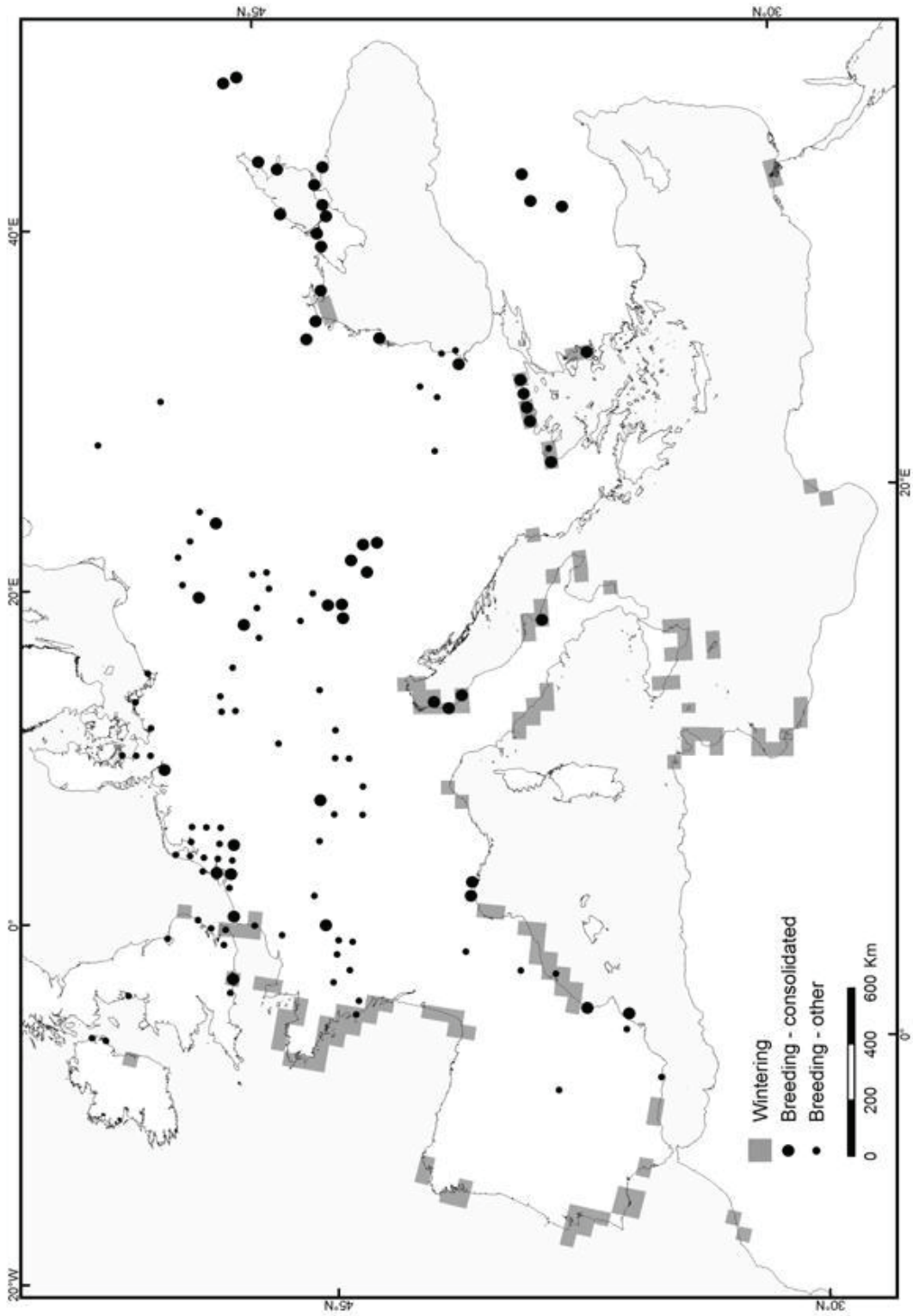
Fig. 7. Current (2015) distribution of the Mediterranean Gull in the breeding (black dots) and wintering (grey squares) seasons, plotted in 50 x 50 km squares. Updated from Bekhuis et al. (1997). The species is present in 127 cells as a breeding bird and in 128 cells in the wintering season.
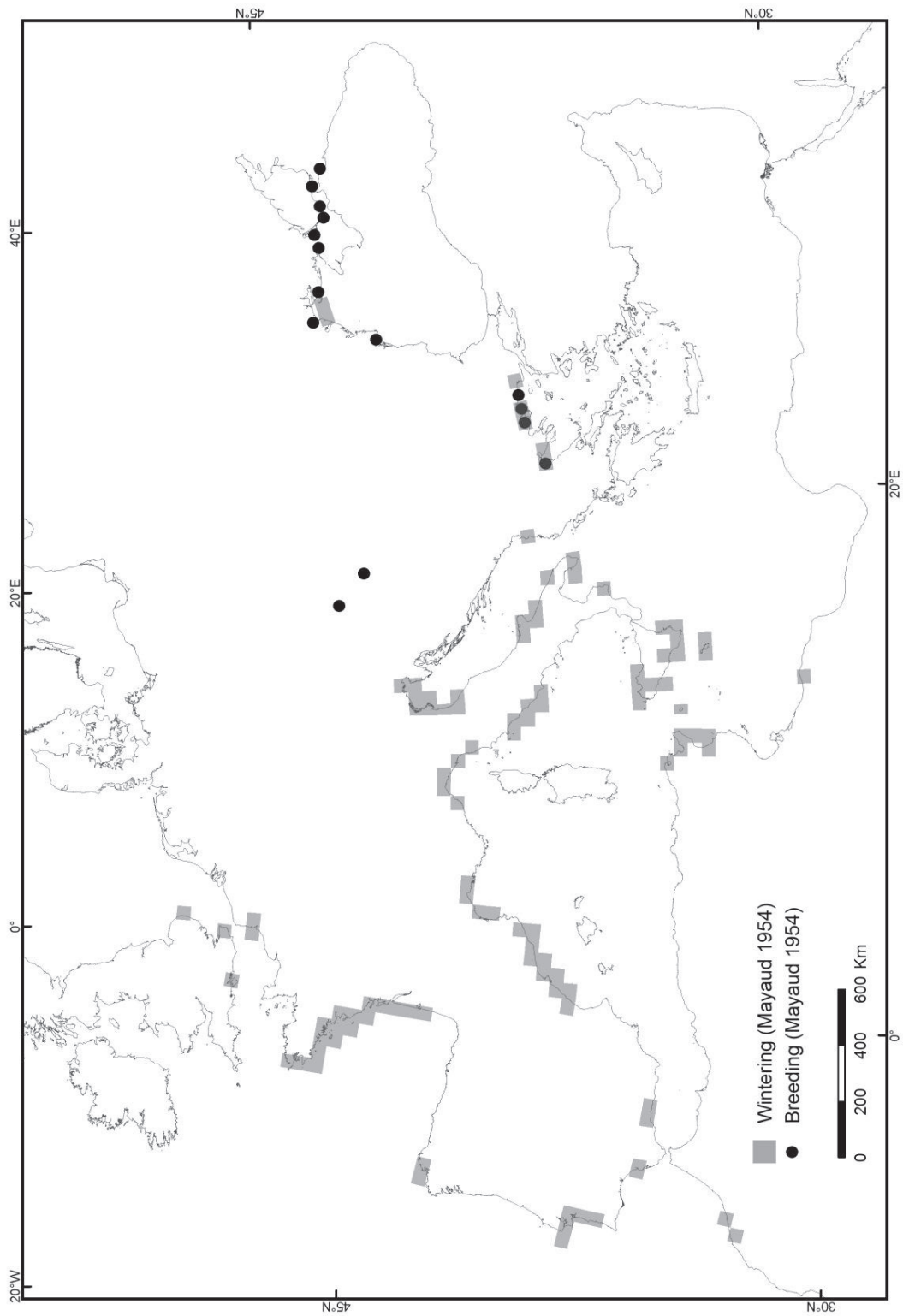
Fig. 8. Pre-1960s distribution of the Mediterranean Gull in the breeding (black dots) and wintering (grey squares) seasons, plotted in 50 x 5 km squares. At the time, the species was present ii 15 cells as a breeding bir and in 102 cells in the wintering season.

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The Mediterranean Gull had been unknown to science until about 200 years ago; therefore, its distribution or habits before that date will probably remain a mystery. However, the first description of the species by Temminck (1820) contains some interesting initial information (Box 2). We know, for example, that the species already frequented coastal habitats around the Mediterranean basin, probably during the winter only, and that it was common on the Croatian coast of Dalmatia, venturing as far north into the Adriatic Sea as Trieste, and in the Gulf of Lyon. The author failed to see the species in the Hungarian lake region, where it now breeds in good numbers; it was reportedly very common in Greece, although no indication of season is given. Of most interest is the record of a juvenile shot dead on the river Rhine in Mainz, Germany, suggestive of certain passage across central and northern Europe, in association with large rivers.

Mayaud (1954) described in detail the migration and wintering of *Larus melanocephalus* up until the 1950s, based on an analysis of the 109 long-distance recoveries available of birds ringed 1947-1953 on the island of Orlov, Tendra Bay, on the coast of Ukraine (46°14′ N, 31°37′ E). At the time of Mayaud's paper, the species was only known to nest on the northern shores of the Black Sea (from Dobroudja, in Bulgaria, to Crimea) and in the Aegean Sea. He described a major east-west migratory route, with the main winter quarters situated in the Adriatic and southern Italy, Sicily and northern Tunisia; also in the western Mediterranean, with a few individuals straggling westwards into the Atlantic, as far west as Cádiz in southern Spain and El Jadida on the Atlantic coast of Morocco. Besides the Mediterranean contingent of migratory and wintering birds, by far the most important, Mayaud described a small migration coming from the Black Sea westwards into central Europe following the Danube, and possibly another in a more northerly direction that reached the Baltic Sea following the Dnieper (Mayaud 1954). He also observed a very small migratory flow along the Atlantic coast, from the Baltic to the Bay of Biscay (July-August) and *vice versa* (March-May).

There is evidence that gulls regularly migrate over land, over water as well as along coasts (Klaassen *et al.* 2012). However, the "river migration" hypothesis

formulated by Mayaud (1954) to explain the migratory routes of *Larus melanocephalus* had so far remained untested.

The westward expansion of its breeding range, of 30° in longitude, across Europe, from the Black Sea to the Atlantic, Baltic and North Sea, has been well documented. The first instance of breeding outside its former Black Sea – Aegean Sea range was in Hungary, where a pure pair nested in Lake Balaton in 1940 (Kovács, Szinai & Hajdu 2015). From there, in its westward expansion towards the Atlantic and north-westwards towards the Baltic Sea, the species probably followed the same inland migratory routes described by Mayaud (1954). The process was notably quick, with the first pure pair breeding in the Netherlands in 1959 (Meininger & Flamant 1998), followed by one in Denmark in 1970 (Fritze 1999). In the western Mediterranean, despite early breeding in the Camargue, France, in 1965 (Sadoul & Raevel 1999), the colonisation by breeding Mediterranean Gulls took place at a later stage (first breeding in Italy in 1978; Angle 1978) and may have occurred as an independent process.

The range expansion of the species' breeding distribution has not been mirrored by its wintering distribution. In the 60 years between 1954 and 2015, Mediterranean Gulls increased their breeding range by 750% but the increase in the wintering range was a much more moderate 25% (Figs. 7 and 8; Table 1 in Appendix). Since the 2000s, the rate of expansion has slowed down considerably and the species has ceased to increase the boundaries of its breeding range; instead, it has entered a phase of apparent spatial redistribution and densification, with new colonies being founded inland, along rivers, and on a few coastal localities in regions where the species was already present. At the same time, other colonies decreased in numbers or even disappeared. Overall, the distribution continues to be patchy, and many tracts of apparently suitable habitat still remain unoccupied.

Uniquely, the Mediterranean Gull has been the focus of a comprehensive international colour-ringing campaign, with ringing taking place at nesting colonies and other areas of concentration throughout its expanded breeding range since 1989 (Table 2 in Appendix). The programme has been in operation for over 20 years and is structured around national managers and an international coordinator. Detailed

information on individual life histories is provided to every observer, promptly and at no cost. A total of 25,066 Mediterranean Gulls were colour-ringed between 1989 and 2009 (Table 2 in Appendix), and the total number of resightings until 2015 was in excess of 250,000. Nevertheless, both ringing and reading effort were unevenly distributed, and were highest for the population that occurs along the Atlantic coast (less than 5% of the global population but 40% of all ringed birds).

In the study system, the proportion of individually-marked birds is on average around 1.5%; therefore, 1 in 70 birds is colour-ringed. Colour-rings are read at a distance with the use of a 20-60x telescope. Typical flock size is 400–1000 individuals, so between 6 and 14 colour-ring readings can normally be expected per monitoring session. The location of the natal or, alternatively, the breeding colony and the year of birth are known for the majority of individuals in the dataset. The total number of different individuals included in this study is 625, which represents 2.5 % of the total number of Mediterranean Gulls ever colour-ringed until the end of the fieldwork in 2010. No birds in this study have been ringed or handled in the wintering area.

Fig. 9. Green 0E9, born on the French Mediterranean coast near Camargue, shown here in the study system in its first-winter plumage. Photo: Carles Carboneras.

OBJECTIVES

The main goal of this work is to study the population ecology of a migratory species from the perspective of the wintering areas, looking at the population composition, structure and dynamics across several spatial scales, and the link between the wintering and breeding areas through connecting migratory routes. I use as a study model a wintering population of the Mediterranean Gull *Larus melanocephalus* made of individuals from multiple origins, a significant proportion of which were individually marked in their natal or breeding colonies. Despite being subject to an extensive colour-ringing programme, many aspects of the biology and ecology of the Mediterranean gull are still only poorly known.

The specific objectives of the thesis are:

- To explore the demographics of a wintering population by estimating the site-fidelity and local inter-annual survival of birds in a wintering area;
- To understand how a given wintering area is chosen initially;
- To establish the pattern of population composition, in terms of the geographical origin of wintering birds, across various spatial scales;
- To analyse the spatial dynamics of the wintering population locally and regionally;
- To find out how the size and distribution of the collective home range relates to the size and distribution of protected areas for the species;
- To explore the relationship between a newly-appeared breeding site and a previously-existing wintering population, and study if the emergence of new opportunities affects individual dynamics.

These objectives are presented as chapters of this thesis in the form of scientific papers (with their corresponding sections, Introduction, Methods, Results, Discussion, and References) to allow for easier comprehension by the reader. However, in order to address the main goal of the thesis, the results of all the chapters are combined and discussed together in a general discussion.

Chapter 1. Using resightings data to study site-fidelity and infer geographic origin, population structure and migration routes of a wintering population of Mediterranean Gulls[1]

Wintering populations are made of birds with potentially different origins, age and life histories. In this study, I use a large database of colour-ringed Mediterranean Gulls from different ringing teams, extending across the entire breeding range and over a 20-year time span, to study local inter-annual survival and population composition in relation to the origin and age of individuals recorded in a wintering population of the species. I tackle the problem of how wintering populations of gulls are formed and maintained, and how they relate spatially to the breeding populations. No studies have so far analysed the relative composition of wintering populations linked to their distance from the birds' natal areas. As colonies are expected to contribute differently in relation to migration costs, and these will depend on the routes followed, I expect to be able to infer the most likely migratory strategy used by this long-lived gull. In addition, I look for any variations in individual attachment to the wintering area as birds grow in age. I use the information on 472 individually-marked Mediterranean gulls of known age and origin, recorded repeatedly at a wintering area to estimate individual interannual survival and winter site fidelity. I also attempt to estimate population composition in the wintering area in relation to the spatial distribution of natal colonies.

[1] *Carboneras C, Tavecchia G, Genovart M, Requena S, Olivé M, Oro D (2013). Inferring geographic origin, population structure and migration routes of a wintering population of Mediterranean gulls from resightings data.* Population Ecology *53.*

Chapter 2. Population structure of Mediterranean Gulls wintering in several areas of Spain and Portugal[2]

Species that breed across different regions and winter over extensive areas are expected to show some degree of spatial structure. To test if this occurs in the Mediterranean Gull, I investigate the connections between the wintering populations in 4 wintering areas distributed around the Iberian Peninsula, in order to determine the

similarities between them and their level of affinity. Using the records of individually-marked Mediterranean Gulls, I study the configuration of the population by looking at the number of individuals shared among the various localities, and formulate several hypotheses of spatial structure for the species. The null hypothesis is that the winter population is not spatially structured. My first alternative hypothesis (metapopulation model hypothesis) is that each subpopulation is discrete and demographically separated, and that subpopulations are only linked through the irregular movements of dispersing individuals. Under this hypothesis, only minimal mixing is to be expected during winter or migration; this will reflect in low levels of affinity among the birds found at the different sites. I consider a second alternative hypothesis that each wintering population is independent and made of different individuals, but birds mix freely during migration, when they visit areas other than their 'own' winter quarters (migratory mixing model). In this situation, differences between the wintering sites would be masked by transient birds travelling to reach their destination, so I would expect to find some population structure but no major differences between the sites. Finally, I look for geographical variation in the population composition of each site, in terms of the origin of birds.

[2] *Carboneras C, Aymí R, Cama A, Duponcheel C, Ferrer J, Flamant R, García S, Garzón J, Gutiérrez A, Olivé M, Poot M. (2010) Mediterranean Gulls* Larus melanocephalus *wintering in Spain and Portugal: one population or several? Airo 20.*

Chapter 3. Local-scale spatial dynamics and within-season movements among wintering Mediterranean Gulls [3]

High site fidelity may be detected in a wintering population, but this parameter is known to be relative to the size of the area being considered and so it is expected to vary according to scale (Robertson & Cooke 1999). We already demonstrated that Mediterranean Gulls show high local survival probability and strong site-fidelity to the general wintering area (Carboneras *et al.* 2013), but observations of individually-coded colour-ringed birds indicate that they may be more mobile on a smaller scale and probably engage in inter-site movements. I use capture-recapture multisite models to

analyse the direction and frequency of individual local-scale movements in order to estimate the probability of residency during the wintering season and to determine the overall spatial needs of the population, taking into account individual dynamics, and the relationship between wintering sites. In addition, I investigate population turnover at a single site to determine the total volume of birds visiting a site at different time scale. This parameter will provide a measure of the overall mobility of individuals within the area. My goal is to compare the spatial dynamics of the wintering population with the size and distribution of the network of protected areas designated to protect it

[3] *Carboneras C, Tavecchia G, Genovart M, Cama A. (2015) Contrasting patterns of site-fidelity across spatial scales in wintering gulls. In prep.*

Chapter 4. Relationship between a spatially-stable wintering population and an emerging breeding population in an expanding species [4]

The emergence of a new breeding colony in the vicinity of a traditional wintering area of the same species provides a rare opportunity to study the relationship between the two populations, both formed exclusively of migratory birds. I first try to determine the rate of annual growth of the new colony and examine whether the observed growth is the result of immigration. I also investigate the geographical origin of the birds that incorporate as (potential) breeders to the new colony. I expect to find some interaction between both populations, such as wintering birds incorporating to the breeding aggregation or some birds in the latter group staying to winter in the area nearby. Therefore, I explore any potential changes in the spatial dynamics or in the migratory habits of birds in both populations as a result of the newly arisen opportunities.

[4] *Carboneras C & Dies JI. (2015) A new breeding population of Mediterranean Gulls Larus melanocephalus in the species' main wintering area maintains independent spatial dynamics. Ibis, in press (doi: 10.1111/ibi.12324).*

SUPERVISORS' REPORT

El doctorand Carles Carboneras Malet presenta en la seva tesi doctoral titulada "Dinàmiques poblacionals en ocells durant la hivernada: el cas de la gavina capnegra *Larus melanocephalus*" una sèrie de treballs científics publicats o pendents de ser sotmesos en revistes científiques internacionals de gran prestigi, majoritàriament incloses en el Science Citation Index. Detallem a continuació la contribució científica que ha realitzat el doctorand en cada un dels articles, així com els seu factor d'impacte (Thomson Institute for Scientific Information):

- Inferring geographic origin, population structure and migration routes of a wintering population of Mediterranean gulls from resightings data.

Carboneras C, Tavecchia G, Genovart M, Requena S, Olivé M, Oro D. (2013)

Revista: *Population Ecology* 53.

Factor d'impacte (2013): 1,70

El doctorand ha contribuït en el disseny del treball, en la recollida i l'anàlisi de dades i en la redacció científica.

- Mediterranean Gulls *Larus melanocephalus* wintering in Spain and Portugal: one population or several?

Carboneras C, Aymí R, Cama A, Duponcheel C, Ferrer J, Flamant R, García S, Garzón J, Gutiérrez A, Olivé M, Poot M. (2010)

Revista*: Airo* 20.

El doctorand ha contribuït en el disseny del treball, en la recollida i l'anàlisi de dades i en la redacció científica.

- Contrasting patterns of site-fidelity across spatial scales in wintering gulls

Carboneras C, Tavecchia G, Genovart M, Cama A. (2015)

Article en preparació, pendent de ser enviat a *Journal of Avian Biology*

Factor d'impacte (2013): 2,235

El doctorand ha contribuït en el disseny del treball, en la recollida i l'anàlisi de dades i en la redacció científica.

- A new breeding population of Mediterranean Gulls *Larus melanocephalus* in the species' main wintering area maintains independent spatial dynamics
Carboneras C & Dies JI. (2015)
Revista: *Ibis*, en prensa (doi: 10.1111/ibi.12324).
Factor d'impacte (2013): 1,861
El doctorand ha contribuït en el disseny del treball, en la recollida i l'anàlisi de dades i en la redacció científica.

Tanmateix, informem que cap dels co-autors participants en els articles que composen aquesta tesi han utilitzat, implícita o explícitament, cap d'aquests treballs per a l'elaboració de la seva pròpia tesi doctoral.

Barcelona, a 17 de Novembre de 2015

Signatura

Vist i plau   Vist i plau
El director de la tesi   La directora de la tesi
Dr. Giacomo Tavecchia   Dra. Meritxell Genovart Millet
IMEDEA (CSIC-UIB)   IMEDEA (CSIC-UIB)

SUMMARY OF RESULTS

In this study, I have developed a novel perspective on the population dynamics of birds from the point of view of wintering areas. My research showed how the detailed study of a species' ecology during one part of the annual cycle can complement the knowledge collected during the rest of the year and it can provide new insight on a species migratory strategy.

The study of demographic parameters such as survival, site-fidelity and dispersal in a wintering population has revealed the strong attachment of individuals to their wintering area, which does not vary with age. This strategy models the winter distribution of individuals, shaping them into a true spatially structured population, with a metapopulation dynamics where each subpopulation has independent demography, determined by area-specific survival and low levels of dispersal.

The focus species was renowned for the large-scale expansion of its breeding range in the 20th century (Cramp & Simmons 1982) but little was known about the relationship of the breeding with the wintering populations. I have developed a model to infer the likely migratory route followed by first-winter birds, and have found that the most likely path is a combination of fluvial and coastal routes in an optimal way, seeking minimal distance along favourable terrain. This strategy, coupled with the individual tendency to return to the same area repeatedly every winter, results in an area-specific composition that varies spatially. Young birds settle in the wintering area in their first year of life according to a probability rule determined by distance, and maintain their choice throughout their lives. Wintering populations of the study species are made of individuals from by different sex and age classes, in one of the few documented cases of nondifferential migration (Cristol *et al.* 1999). Individuals of different age groups and reproductive roles show no apparent differences in the time they spend at the wintering area, with the only exception of first-winter birds.

My research provides a new insight into the spatial scale of the collective home ranges in the wintering season, and its relationship with the network of protected areas. A multi-site capture-recapture analysis on a local scale has revealed a very high turnover

of individuals in the observed localities and a frequent movement, in no particular direction, among localities. This form of dynamic wintering is in strong contrast to the species' strong site-fidelity. The corollary is that the collective home range extends over a large part of the whole wintering area, hundreds of kilometres long, as individuals move frequently among localities instead of staying in one place. Because protected areas are not designated with one species in mind but aim at protecting the spaces where multiple species congregate (Lascelles *et al.* 2012), they offer only partial protection to highly-mobile Mediterranean Gulls on the local scale.

An interesting finding is that the large-scale distribution shift undergone by the species in the 20th century has affected the breeding distribution much more than the wintering distribution. The long-term stability of the latter, combined with the lack of any visible increase in the global population size (Cama *et al.* 2011), suggests that the historical range shift was more properly a redistribution of the once extremely concentrated breeding population across a much wider spatial scale. The expansion, which still continues, is not comparable to that of other species that similarly increased their ranges in the 20th century. This work points at the decisive role of the wintering season in regulating the global population size and provides evidence that the species is likely limited by events taking place in winter, or during the migration periods, perhaps related to increased density-dependence in this species. Additional evidence has shown that birds rely on fish discards to a large extent, and find few alternative food sources, as they occur around fishing harbours in significantly larger numbers immediately after weekends, when no trawling discards are available.

The study of the interactions between the breeding and wintering populations, where they occur in sympatry, has shown that both populations have little interaction and follow independent dynamics. This finding points at a complex system that is probably still unfolding as the breeding population continues to expand and comes closer to the breeding areas. Independent dynamics may also lie behind the observed synheimy, i.e., the co-occurrence of birds from different breeding regions in the wintering population. This is a rare phenomenon and most probably only a transitory situation (Newton 2008);

therefore, it would be interesting to revisit the wintering population after a few decades, to check for any changes.

Finally, through this work I have been able to test hypotheses on the migratory strategy, the winter ecology, the historical distribution shift and the conservation needs of Mediterranean Gulls. The findings reported here provide a baseline and improve current knowledge on this hitherto poorly-known species.

Chapter I

Inferring geographic origin, population structure and migration routes of a wintering population of Mediterranean gulls from resightings data

Carles Carboneras, Giacomo Tavecchia, Meritxell Genovart, Susana Requena, Marc Olivé, Daniel Oro

THE SOCIETY
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ECOLOGY

ORIGINAL ARTICLE

Inferring geographic origin, population structure and migration routes of a wintering population of Mediterranean gulls from resightings data

**Carles Carboneras · Giacomo Tavecchia ·
Meritxell Genovart · Susana Requena ·
Marc Olivé · Daniel Oro**

Abstract Winter congregations of migratory birds are made by individuals of different origins and generally assumed to be variable across space and time, but the demographic characteristics of these temporal populations are poorly known. We used 2,216 observations of 472 colour-ringed individuals to estimate the annual local survival of Mediterranean gulls *Larus melanocephalus* wintering in NE Spain. In addition, by gathering the ringing information on the 19,856 individuals marked as fledglings in 18 countries between 1990 and 2009, we were able to infer the composition of population in relation to the country of origin. We coupled these estimates with geographic information to contrast hypotheses on the migratory pattern most likely used by the gulls in their first migration from their natal colonies to the wintering area. The probability of reaching the study area was negatively associated with the distance from the natal colony. Data were consistent with a migratory strategy that combines fluvial and coastal routes in an optimal way, seeking minimal distance along favourable terrain. We found that, after the first year, annual local survival at the wintering site (0.81 on average) was comparable with the one estimated at the breeding colonies, indicating a high individual fidelity to the areas used in winter. Our work shows that winter groupings may behave as real populations, shaped by breeding output and survival, and that the geographic origin of wintering birds can be explained by a simple model. The study of winter congregations can help understand a species' population structure and movement strategies.

Keywords Capture–recapture · *Larus melanocephalus* · Movement strategy · Site-fidelity · Spatial variation · Survival

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Introduction

A large body of evidence indicates that the winter season is a critical period in the annual life cycle of most birds wintering at high or temperate latitudes (Newton 1998; Fort et al. 2009) and that overwinter mortality is the major determinant of population dynamics, even among those species that migrate to warmer areas in autumn (Barbraud et al. 1999; Tavecchia et al. 2001; Grande et al. 2009; Sergio et al. 2011). The winter period, however, is often regarded as a 'black box' in the life cycle of many birds because demographic processes during this season are largely unknown, particularly for migratory species that are assumed to be distributed over large wintering areas (Frederiksen et al. 2012). This lack of knowledge is reflected into conservation practices, which concentrate

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most of their efforts to protect populations during breeding. Recently, developments of tracking techniques have provided new insights into the migratory and wintering behaviour of medium- and even small-sized birds (Baechler et al. 2010; Egevang et al. 2010; Catry et al. 2011; Stenhouse et al. 2012). Results confirmed that specific areas are often predictable as wintering and stop-over sites (but see Gschweng et al. 2008) although considerable variation exists in individual site tenacity across years (Marques et al. 2010; Dias et al. 2011; Guilford et al. 2011). Age- or sex-related differential migration is the norm among migratory birds (Cristol et al. 1999), and latitudinal segregation by age classes has been found in most species of charadriiform seabirds (Siriwardena and Wernham 2002), including many gull species (Oro and Martinez 1994; Marques et al. 2010). However, some seabirds distribute according to alternative migration patterns, e.g., leap-frog system (Hallgrimsson et al. 2012) and oriented chain migration (Fort et al. 2012).

The heritability of migratory routes (Pulido 2007; Mueller et al. 2011) and the repeatability of large-scale movement patterns (González-Solís et al. 2007; Dias et al. 2011) suggest that winter congregations may be structured according to bird origins. Hence, wintering populations of birds can offer the opportunity to assess survival, population composition and origin of individuals. Population composition and winter site fidelity can be used to estimate annual survival probability and to infer migration routes, an important information to understand population functioning and guide management action (see for example Hestbeck et al. 1991; Gauthier et al. 2001; Tavecchia et al. 2005).

The Mediterranean gull (*Larus melanocephalus*) is a middle-sized, migratory gull whose current breeding population is confined entirely to Europe with the centre of gravity in the Black sea, and significant populations in the Low Countries, the Danube valley and the Mediterranean (Bekhuis et al. 1997). The recent expansion of the species from Eastern Europe towards the Atlantic coast and the NW Mediterranean has been linked to the fluctuations of the Black sea stronghold (e.g., Sadoul 1997). The majority of the population spends the winter around the Mediterranean, mostly in Spain, France, Italy and Tunisia (Cama et al. 2011). Its discontinuous winter distribution has remained fairly constant since at least the 1950s (cf. Mayaud 1954; Shevareva 1955), despite the recent changes in the coastal landscape and marine ecosystem (Coll et al. 2010). Favoured by its aggregative nature, the species has received the attention of multiple colour-ringing programmes along its expanding range, with >25,000 individuals (including 19,856 as chicks in 18 countries) colour-ringed in 20 years, 1990–2009. This extensive database, both spatially and temporally, provides an ideal

framework for studies on survival and population composition in relation to origin and age. Here we tackle the problem of how wintering populations of gulls are formed and maintained, and how they relate spatially to the breeding populations. The mixing up of birds from different origins is common among wintering seabirds (González-Solís et al. 2007; Reynolds et al. 2011; Frederiksen et al. 2012), but no studies have so far analysed the relative composition of wintering populations linked to their distance from the birds' natal areas. As colonies are expected to contribute differently in relation to migration costs, and these will depend on the routes followed, we expect to be able to infer the most likely migratory strategy used by this long-lived gull. We use the information on 472 individually-marked Mediterranean gulls of known age and origin, recorded repeatedly at a wintering area: (1) to estimate interannual survival and winter site fidelity; (2) to estimate population composition on the wintering grounds in relation to the spatial distribution of natal colonies.

Materials and methods

Study area and season

The 350 km of Mediterranean coast of NE Spain, between the towns of Blanes (N41°41′, E2°48′) and Burriana (N39°53′, W0°05′), constitute one of the main wintering areas for the Mediterranean gull (Cama et al. 2011). The area is delimited by two stretches of unoccupied, yet potentially adequate, habitat. In this defined area we conducted observations of individually marked birds for 5 consecutive winters, from 2005 to 2010.

Records of ringed gulls were obtained by watching pre-roost flocks standing on beaches or in fishing harbour premises, from a distance, using a telescope (Table 1).

Table 1 Summary of ringing and reading effort

Country	Ring colour	Total chicks marked	Recorded in study area	Ring readings
ATL	White/ green	6,420	15	81
MED	Green	708	132	809
ITA	Blue	3,435	159	715
HUN	Red	2,729	80	316
POL	Red	246	2	4
GRE	Black	2,002	45	116
UKR	Black	4,316	39	175
Total		19,856	472	2,216

The table shows, for each country ringing programme, the total number of chicks marked in the natal colonies from 1990 to 2009, and the number of individual gulls observed and the total number of rings read in the study area over 5 winter seasons, 2005/06–2009/10

We obtained resightings over nine sites within the study area. Most records (96 %) came from three sites only: Vilanova i la Geltrú, Cambrils and Tarragona. Gulls were present at the study area between late July and late March each year; however, we restricted the analysis to the observations made from 15 September to 15 February. This was done to exclude transient birds that are mainly present from June to mid-September and after mid-February. The goodness of fit test confirmed the absence of transient animals in our dataset (see below). We thus retained 2,216 observations of 472 birds of known age and origin (13 countries). To estimate the proportion of birds from each breeding region that spent the winter in our study area, we obtained information on the annual ringing effort of the 19,856 individuals colour-ringed at fledgling in eighteen different countries from 1990 to 2009. To define the composition of the wintering population, we sorted the data according to 7 main areas of origin by pooling together colonies lying in nearby countries or regions. Birds ringed along the Atlantic coast of France, Belgium, The Netherlands and Germany were considered in a single group (noted "ATL", hereafter). A second group was formed by birds born in Mediterranean France (noted "MED"). The other groups were made by birds born in Italy (noted "ITA"), Hungary, Serbia and Slovakia (noted "HUN"), Poland (noted "POL"), Greece and Turkey (noted "GRE") and Ukraine (noted "UKR"), respectively. Finally, we gathered, as supplementary information, the occasional resightings along the migratory route and in alternative wintering areas of individuals in our data set to help discussions and the interpretation of results.

Modelling survival/site fidelity and recapture probability

Observations of marked birds recorded at the wintering area during the five-year period were coded into individual encounter histories. An encounter history is a series of 0 and 1 s indicating the absence and presence of a given animal, respectively. The frequency of capture histories follows a multinomial distribution whose elementary parameters are the survival and recapture probabilities. These probabilities are estimates from the data using maximum likelihood procedures (see Lebreton et al. 1992 for details of maximum likelihood estimation of parameters and model selection methods). We modelled three sets of parameters: the first-year survival probability, noted φ', the survival probability during subsequent years, noted φ, and the recapture—or detection—probability, noted p. The local survival probability during the first year φ' referred to the joint probability that an individual survived until midwinter and reached the wintering site in NE Spain during its first year of life, an interval shorter (ca. half) than any subsequent ones.

We began the analysis from a general model that assumed all parameters to vary over the years, noted 't' in model notation (model 11 in Table 2). This model, $\varphi'_t \varphi_t p_t$, is an extension of the Cormack–Jolly–Seber model with two age-classes for survival. The fit of this model was assessed using the software U_CARE 2.2 (Choquet et al. 2009; see Appendix in Tavecchia et al. 2008 for more details on the goodness of fit test). In addition to a year-effect in detection probability we considered the effect of the ring colour (noted 'g' in model notation; Table 1) because plastic rings might show differences in their visibility and/or rate of deterioration. We also used a measure of the reading effort (the number of marked birds recorded each winter, noted 'no. readings') as a covariate for the detection probability. Juvenile survival, φ', and adult survival, φ, were set to vary depending on the year (noted 't') and on the area of origin (noted 'c'). To account for the progressive deterioration of plastic rings over time [M. Olivé, unpublished data, Table S1 in Electronic Supplementary Material (ESM)] we added a linear trend in survival, noted 'T' (see "Results"). Finally, we used colony distance to explain the variability in survival parameters (see below).

The resulting 20 models were fitted using program MARK (White and Burnham 1999). We selected the more parsimonious models using Akaike's Information Criterion corrected for sample size (AICc; Burnham and Anderson 1998). Models within 6 points of AICc were considered as equivalent (Burnham and Anderson 1998).

Population composition and migratory routes

In our analysis, survival parameters represent a combination of the true survival, i.e., the probability to survive from one winter to the next, and the probability of reaching the wintering grounds. In this respect, permanent emigration, i.e., the probability of never visiting the area again, would be confounded with mortality. Assuming that juvenile survival is the same regardless of the colony of origin, the variation in the parameter of juvenile survival, φ', should reflect the different proportion of birds reaching the study area. This can be used to test hypotheses on movement patterns (Tavecchia et al. 2005). Indeed, colonies are expected to contribute to the wintering population differently according to their distance; however, the distance between each breeding region and the wintering area varies depending on the migration route. Hence, if migration followed an exclusively coastal route, colonies from the 'GRE' and 'ITA' areas would be expected to contribute similarly because the distances to the wintering area would be similar (2,500 vs. 2,336 km). In contrast, if birds favoured an inland route along the main rivers, ITA-colonies would be expected to contribute many more birds than GRE-colonies, because the distance in the first case is

Table 2 Modelling apparent annual survival and resighting probability of Mediterranean gulls recorded in the wintering area in NE Spain

Model	Juvenile survival (φ')	Adult survival (φ)	Detection probability (p)	AICc	ΔAICc	AICc weight	np	Deviance
1	c	T	t	**5,069.332**	**0.000**	**0.471**	**14**	**866.828**
2	c	c	t	5,071.562	2.230	0.155	19	859.040
3	c	t	t	**5,071.819**	**2.487**	**0.136**	**16**	**865.309**
4	c	t	$g + t$	5,072.419	3.086	0.101	22	853.883
5	c	•	t	**5,074.919**	**5.587**	**0.023**	**13**	**874.418**
6	c	t	$g + no.\ readings$	5,083.852	14.520	0.000	19	871.331
7	c	•	$g + t + g \times t$	5,143.650	74.318	0.000	41	886.987
8	•	•	$g + t$	5,237.592	168.260	0.000	13	1,037.091
9	•	•	$g + no.\ readings$	5,244.820	175.488	0.000	10	1,050.327
10	•	•	$g + t + g \times t$	5,251.083	181.751	0.000	34	1,008.476
11	t	t	t	5,377.167	307.835	0.000	12	1,178.669
12	t	•	t	5,388.623	319.291	0.000	10	1,194.130
13	•	t	t	5,418.612	349.280	0.000	9	1,226.121
14	$\varphi_1;...; \varphi_7$		t	5,424.672	355.340	0.000	12	1,226.174
15	$\varphi_1;...; \varphi_5$		t	5,426.440	357.107	0.000	10	1,231.946
16	•	•	$readings \times occasion^{-1}$	5,440.039	370.707	0.000	4	1,257.555
17	•	•	t	5,666.397	597.065	0.000	6	1,479.911
18	•	•	$g + t + g \times t$	6,103.199	1,033.867	0.000	33	1,862.598
19	•	•	g	6,212.783	1,143.451	0.000	9	2,020.292
20	•	•	•	6,417.110	1,347.778	0.000	2	2,238.628

Parameters: juvenile survival (φ') = survival of gulls in their first year of life; adult survival (φ) = survival of gulls after hatch-year; $\varphi_1;...; \varphi_n$ = survival of gulls variable in n age-classes; p = detection probability. Effects: 'c' = "country" (origin-dependence); 't' = time-dependence; 'T' = linear trend; 'g' = group-dependence (ring colour combination); '$no.\ readings$' = total readings of marked gulls; '$readings \times occasion^{-1}$' = ratio of total ring readings to the number of occasions; '$\times$' = interaction between effects; '$+$' = additive relation between effects; '•' = constant. AICc = Akaike Information Criterion corrected for sample size; ΔAICc = difference with the lowest AICc value; AICc weight = the relative importance of each model; np = number of identifiable parameters in the model; Deviance = model deviance. Models in bold were used to obtain averaged estimates

much shorter (1,071 vs. 2,070 km). To contrast hypothesis on migratory routes, we calculated the weighted centroid, i.e., the centre of the area rather than the geometric centroid, for each of the 7 groups of ringing colonies, by applying the weighted value of the number of individuals in our data set that had been ringed at each site. The distance, d_i, between the weighted centroid of the ringing area i to the study area was measured on the ETRS89 geodetic reference frame (Annoni et al. 2000) using the software ARCGIS 10.0. We considered four possible layouts: under hypothesis A (Euclidean distance) gulls would reach the wintering grounds by flying in a straight line over land and water; under the hypothesis B (coastal routes) gulls would fly to the coast on the shortest possible route and then follow the coastline travelling exclusively over marine waters, so that UKR birds would cross the Bosporus and the Aegean sea, ATL would migrate through the Straits of Gibraltar and ITA birds would fly round the Italian peninsula; inversely, hypothesis C (river routes) favoured inland routes along the main rivers: ATL would follow the Rhine and Rhone to the Mediterranean while HUN, POL,

GRE and UKR would reach the wintering area after following the Danube and Rhone; and hypothesis D (combined routes) predicted that gulls would combine rivers and coastal routes in an optimal way minimising the distance while not crossing inhospitable terrain, thus making UKR, GRE and ITA birds fly chiefly W over land and sea, and ATL birds cross over France, following the main rivers towards the Mediterranean (Fig. 1). The four hypotheses generated a different ranking of the colonies based on their probability to contribute to the population wintering in the study area according to the expected distance calculated under hypotheses, A, B, C and D, i.e., four different vectors of d_i values. We modelled the parameter φ'_i, where i is the ringing area, by the equation of the form:

$$\text{logit}\left(\varphi'_i\right) = \alpha + \beta \ln\left(d_i^H\right)$$

where d_i^H is the vector of distances under hypothesis H (with H = A, B, C or D; see above). The significance of β and the total variance explained by the distance under each hypothesis were assessed using the ANODEV procedure in MARK.

Fig. 1 Hypothetical sketch of the migratory routes of first-winter Mediterranean gulls *Larus melanocephalus* from their colonies of birth (the weighted centroids of the 7 groups of ringing sites: "ATL", Atlantic France, Belgium, The Netherlands and Germany; "MED", Mediterranean France; "ITA", Italy; "HUN", Hungary, Serbia and Slovakia; "POL", Poland; "GRE", Greece and Turkey; "UKR", Ukraine) to the wintering area in NE Spain (inside *box*). Based on demographic model 1 (Table 2), which assumes the spatial variation of juvenile survival φ', and on migratory hypothesis D (Table 3) of a combination of coastal and inland (rivers, lakes) routes in an optimal way, i.e., minimal distance along favourable topography and positive taxis towards water

Results

Modelling annual survival/site fidelity and recapture probability

The goodness of fit test indicated that the general model fitted the data adequately and that the extra-binomial variance was not large ($\chi^2 = 45.13$, $df = 38$, $P = 0.20$). Models with origin-dependent juvenile survival φ' (models 1–7; Table 2) had the lowest AICc values, suggesting that the survival/movement parameter during the first half-year of life varied strongly according to the area of origin. This effect was not present in later years, as the probability of local survival after the first winter was independent of the colony of birth (model 2). Note that the origin of birds is not known after the first year as gulls might have attended a colony other than that of birth. We tried further to refine the probability of detection by incorporating different combinations of reading effort (number of readings, number of occasions) or of ring colour (group) as explanatory variables, but such models failed to improve the accuracy of a time-dependent p, and were not retained (Table 2). Models with an age-dependent survival probability (model 14 for 7 age classes and model 15 for 5 age classes) had little support. In contrast, a model assuming a linear trend—on a logistic scale—in survival to describe the progressive deterioration of the ring (model 1) was preferred (Table 2; Fig. 2). According to this model, apparent survival changed from 0.90 (95 % CI 0.82–0.95) to 0.78 (95 % CI 0.74–0.81) 4 years later (Fig. 2). Assuming that this
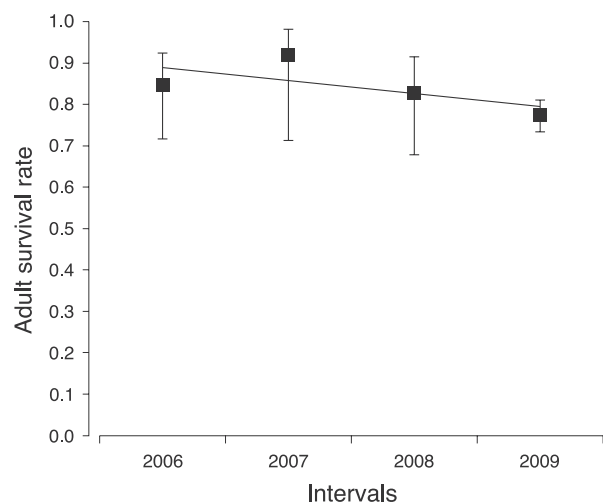
Fig. 2 Inter-annual apparent local survival of Mediterranean gulls after hatch-year as obtained from the time-dependent model (model 3 in Table 2; square symbols with 95 % confidence interval). The *line* shows the linear trend in survival equivalent to 4 % annual tag loss, as estimated by the retained model (model 1)

negative trend in survival was due to the age of the ring and not to the age of the bird, the annual local survival would be 0.90 (95 % CI 0.82–0.95, estimates from model 1), corresponding to the one of a bird carrying a 2-year old ring. In contrast, if the decrease on survival is a real effect of age or a mixture of the two, the average annual survival would be 0.81 (95 % CI 0.79–0.84; estimates from model 5). Although there is evidence of ring loss (supplementary

material, Table 1), we cannot fully differentiate between these two hypotheses. Detection probability fluctuated between years, varying from 0.36 to 0.75, with an average value of 0.49 (95 % CI 0.42–0.55) in the retained model.

Population composition and migration routes

The probability of reaching the study area during the first winter varied largely across the different ringing areas, ranging from 0.13 (area MED) to 0.01 (area ATL) (Fig. 3). As expected, the two nearest regions (MED and ITA), had the highest probability to reach the area and contributed to the population wintering in the study area with nearly two-thirds of the first-winter birds. In the probabilistic framework, the accuracy of the estimates of juvenile survival φ' (length of the 95 % CI bars in Fig. 3) was related to the ringing effort—the total number of juvenile birds ringed in each region (Table 1). The lowest probabilities of reaching the area corresponded to birds from the ATL and the UKR areas. Birds from HUN, GRE and POL showed intermediate probabilities; the wide confidence interval of the POL group was a result of the small number of birds ringed (246 in total) and the small number of individuals present in the study area (2) (Table 1).

The main predictor of population composition was colony distance; indeed, in all hypotheses the slope of the relationship between distance and φ' was negative and

different from 0 (Fig. 3; Table 3). Despite this general trend, the more distant colonies would be expected to contribute differently in relation to the migratory strategy considered. The Euclidean distance (hypothesis A) explained about a third (35.5 %) of the total variance of φ' across colonies but we retained a model assuming a combination of routes (hypothesis D), which had the lowest AICc (Table 3). According to this model, distance explained 48.8 % of the spatial component of φ'. Note that none of these models was preferred when compared to the one assuming a different parameter for each colony of origin (model 1; Table 2). So, despite the general trend, there was an important variation that remained unexplained. This might be due to the presence of multiple strategies occurring simultaneously in a single population (see "Discussion").

Discussion

Consecutive resightings of the same gulls at the wintering area in northern Spain gave us the opportunity to estimate local survival, the product between true survival and site fidelity, of wintering birds. Also, by contrasting these parameters against the total number of animals ringed at different breeding colonies we were able to assess the composition of the population according to bird origin. We additionally inferred the most likely migratory pattern by investigating if the colony-specific probability of reaching the wintering site was consistent with a direct migration route or whether birds deviated to follow rivers or coasts, or optimised their route in a combination of both.

te Marvelde et al. (2009) found that local survival of Mediterranean gulls estimated at medium-sized (approximately 600 pairs; L. te Marvelde, personal communication) breeding colonies was 0.86. We found a similar average estimate (0.81), indicating that fidelity to the wintering area is only ca. 5 % smaller than the propensity to return to the breeding colonies. Our analysis does not take into account a temporal emigration of individuals, which is normally reflected into the probability of recapture. Birds that were not seen in one season might well have visited an alternative wintering area, but the high survival value indicates that they came back to the study site at least once more. The study of individual life histories (obtained from the ringing programme coordinators, listed in the Acknowledgements) provided supplementary information on temporal and permanent emigration that was in agreement with a high site fidelity: only 11 birds of 472 in the data set were recorded alive in other wintering areas (permanent emigration) and only 2 gulls visited alternative areas in subsequent winters and later returned to the study area (temporal emigration). This strong fidelity to the wintering
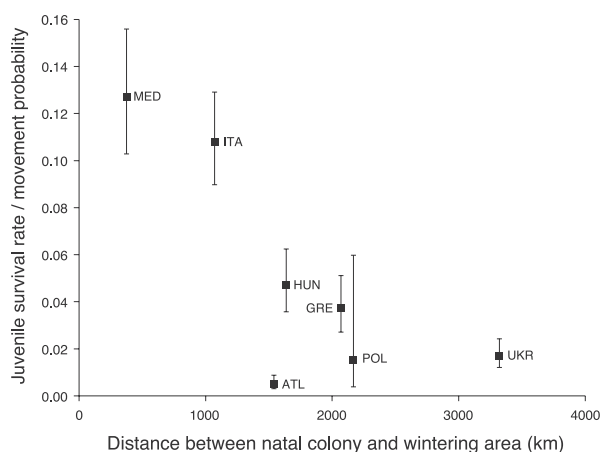

Fig. 3 Plot of juvenile immigration probability against distance. Models with spatial variation in the survival of juvenile birds (first-time immigrants) obtained the lowest AICc values (Table 2). The results for the retained model 1 are plotted here against the distance from the ringing areas, calculated according to the 'optimal' combination of inland and coastal routes of hypothesis D (Table 3). Bars represent 95 % confidence intervals. Notice the low probability of ATL for the estimated distance, which suggests that birds from this group may use alternative routes to reach the wintering area in the Mediterranean, including the 4,000-km route round Gibraltar

Table 3 Proportion of the total variance explained by the distance between the colony of birth and the study area under the different migratory strategies (see also text)

Hypothesis	Expected colony ranking	AICc	Deviance	Percentage deviance explained	Intercept (α; 95 % CI)	Slope (β; 95 % CI)
A Direct flight	MED < ITA < ATL < HUN < POL < GRE < UKR	5,295.40	226.62	35.5	4.1; 2.9/5.3	−1.03; −1.20/−0.86
B Along coastlines	MED < ITA < GRE < HUN < UKR < ATL < POL	5,261.32	192.54	44.8	3.3; 2.4/2.2	−0.84; −0.96/−0.72
C Along rivers	MED < ITA < ATL < HUN < POL < GRE < UKR	5,263.00	194.22	44.3	4.2; 3.2/5.3	−1.01; −1.2/−0.87
D **Along rivers and coastlines**	**MED < ITA < ATL < HUN < GRE < POL < UKR**	**5,248.17**	**179.39**	**48.4**	**4.8; 3.7/5.9**	**−1.1; −1.3/−0.95**

Each hypothesis on movement patterns generated a different ranking of the colonies (2nd column). Differences in the ranking applied particularly to the ATL, GRE, UKR and POL groups. The model for hypothesis D, of a combination of river and coastal routes, had the lowest AICc and was selected (in bold)

areas suggests that wintering individuals form a population, "a set of organisms belonging to the same species and occupying a clearly delimited space at the same time" (Wilson 2000). Also, the strong fidelity to the wintering grounds despite major alterations in landscape in recent decades indicates a complicated spatial structure of wintering populations, where other factors besides the availability of suitable habitat could determine the occurrence of a species.

We assumed that the true (as opposed to local) survival probability during the first 6 months was independent of the colony of origin. This assumption permits to consider the variation in local survival as a consequence of the probability of reaching the wintering area. Thus, the spatial variation of juvenile survival φ' can be used to contrast hypotheses on the selection of migratory routes (Tavecchia et al. 2005). As expected, φ' covaried with colony distance, with the closest colonies contributing the most birds, but the contribution of colonies further away would depend on the migration route followed by the gulls. For example, if birds followed coastlines only (hypothesis B), gulls from north-eastern European colonies (POL group) would be the least represented in the population (Table 3). None of these ultrastructural models was selected indicating that there was not a predominant strategy explaining the movement patterns of all groups. Instead, data suggested that birds adopted a mixed strategy migrating via rivers and coastal routes in an optimal combination of minimal distance along favourable topography with positive taxis towards water. With this simplification we assumed that all birds from a given area migrated in the same way. This assumption is likely to be wrong and is probably the reason why none of the models including the distance as a covariate was preferred. Nevertheless, simple and imperfect as it might be,

our model was able to generate predictions on population composition in other wintering areas. For example, observations of ringed gulls in Portugal (R. Flamant and C. Duponcheel, personal communication), confirmed the model's prediction of a higher probability of ATL birds and a lower probability of MED and ITA birds making up that wintering population, relative to our study area. However, all models suggested a higher than expected contribution of ATL colonies. It is possible that part of the population from some colonies migrated along a 'different-than-optimal' route. Cramp and Simmons (1983) suggested that certain passage might occur through the Straits of Gibraltar, on the basis of some adult birds moving along the western seaboard that returned to Black Sea colonies through the Mediterranean. We cannot exclude this behaviour, but comparative studies in other wintering areas should be done to answer this question.

The spatial variation of juvenile survival φ' seems to reflect the historical route of expansion of the species as reported by Cramp and Simmons (1983). Gulls appear to migrate along a combination of coastal and overland routes on a broad front following a W–SW direction, not unlike the pathway that led to the colonisation of wetlands in central and Western Europe starting in the 1950s, rather than travel directly to the wintering areas. Mayaud (1954) and Shevareva (1955) analysed recoveries of Mediterranean gulls ringed as chicks in Ukraine, at a time when breeding was restricted to the Black and Aegean seas. They reported two findings that are relevant to our study: (a) that our study area was already an important wintering ground for Ukrainian birds in the 1940s and 1950s, and (b) that at the time there was already a small flux of birds that reached the Baltic and North Sea probably by following the main European rivers (Dnieper, Danube, Rhine, Seine, Loire) in

a westward direction. Thus, an incipient migratory pathway developed over inland Europe independently from the large expansion of the breeding range, which took place 3 decades later. Roughly the same migration routes are still maintained today, showing that the species probably has positive taxis towards flying over significant water bodies (rivers, lakes, coast) when on migration. However, the population composition on the wintering grounds today must be different from the 1940s–1950s because the relative distances from and to the breeding areas have changed greatly in the last 70 years. This 'historical' hypothesis cannot be tested because it fails to generate objective predictions on colony ranking.

Our results indicate that wintering aggregations form 'real' populations, and that these are not determined by the turnover of individuals as previously thought, but rather the demographic processes of breeding output and survival. Indeed, winter groups of Mediterranean gulls are formed by the same individuals that visit the same areas across time. Moreover, our results point out a model that may be applied to predict the winter population origin and relative composition along its wintering distribution, and may help to guarantee the long-term preservation of populations throughout the species' range and in all seasons.

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Chapter II

Mediterranean Gulls Larus melanocephalus wintering in Spain and Portugal: one population or several?

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Mediterranean Gulls *Larus melanocephalus* wintering in Spain and Portugal: one population or several?

Gaivotas-de-cabeça-preta *Larus melanocephalus* invernantes em Espanha e Portugal: uma ou várias populações?

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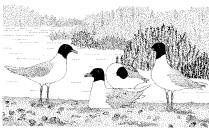
ABSTRACT - Mediterranean Gulls *Larus melanocephalus* originating from several breeding populations (Atlantic, Mediterranean and Black Sea) concur in a few well-known wintering areas in Spain and Portugal. By analysing the records of individuals marked with colour rings, we investigated the connections between the wintering populations occurring in 7 sites distributed around the Iberian peninsula in order to determine the similarities between them. Our observations totalled 1125 individuals in 7 sites (range 44-474) and comprised the whole of the winter season, plus both migration periods. We carried all-time agglomerative hierarchical clustering analysis for the data corresponding to the seasons between 2005-06 and 2008-09 and plotted the results in a dendrogram; additionally, we compared the lists of individuals recorded at each site and calculated a coefficient of similarity between pairs of sites. Our findings reveal the existence of 4 clusters, with relatively high exchange ratios of individuals between contiguous sites inside the two main groups: 0,23-0,24 for NE Spain and 0,06 for SW Portugal. However, inter-group distance was relatively constant at 0,01-0,02, so the relative spacing of sites did not correspond to the physical distances between them. This effect was most pronounced in Málaga, on the Mediterranean coast of Spain, and Ares (Galicia), which appeared as independent lines forming part of the Atlantic coast class. The general picture is consistent with a metapopulation structure, each population being independent and only linked to others through dispersal. This conclusion has implications for the conservation of the species, listed in Annex I of the Birds Directive. Protected areas for this species should be of enough size (to comprise the whole winter range in the Iberian peninsula) and should also be sufficiently representative to be able to afford adequate protection to each independent population.

RESUMO - As Gaivotas-de-cabeça-preta *Larus melanocephalus* originárias de diferentes populações reprodutoras (Atlântico, Mediterrâneo e Mar Negro) confluem para um grupo restrito de áreas de invernada em Espanha e Portugal. Neste trabalho utilizaram-se observações de gaivotas marcadas individualmente (com anilhas de cor) para investigar o grau de permuta de indivíduos entre as populações invernantes que ocorrem em 7 locais distribuídos na costa da Península Ibérica e assim determinar a sua semelhança. Observou-se um total de 1125 indivíduos nos 7 locais (variando entre 44 e 474).

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Foram utilizados algoritmos aglomerativos hierárquicos sobre as observações levadas a cabo entre 2005-06 e 2008-09 e construído um dendrograma. Foi então comparado o elenco de indivíduos observados em cada local, que serviram de base ao cálculo de um coeficiente de semelhança entre cada par de locais. Os resultados sugerem a existência de 4 grupos, sendo de notar uma taxa de permuta relativamente elevada entre grupos contíguos dos dois principais grupos: 0,23-0,24 para o NE de Espanha e 0,06 para o SW de Portugal. Contudo, a distância entre os grupos foi relativamente constante (0,01-0,02), o que sugere uma falta de correspondência entre a semelhança dos locais e a distância real entre os mesmos. Este efeito foi mais pronunciado em Málaga, na costa mediterrânica de Espanha, e Ares (Galiza), que aparecem como grupos distintos incluídos no grupo da costa Atlântica. Estas observações são compatíveis com a hipótese de uma estrutura metapopulacional, envolvendo populações distintas ligadas apenas através de fenómenos de dispersão. Estas conclusões têm implicações para a conservação da espécie, que está listada no Anexo I da Directiva Aves. As áreas que visem a conservação desta espécie devem ser suficientemente abrangentes, de forma a incluir toda a área de invernada na Península Ibérica ao mesmo tempo que asseguram a conservação de cada uma das populações.

The Mediterranean gull (*Larus melanocephalus* Temminck, 1820) is a highly social, middle-sized seabird, long known to occur as a winter visitor in several parts of the Iberian peninsula (e.g., Mayaud 1954, Isenmann 1972), with only one fast-growing colony in Valencia (30~180 breeding pairs; Molina 2008, Dies & Dies 2009). The total winter population in Spain and Portugal has been variously estimated at between 18,000 and 50,000 individuals (Bermejo *et al.* 1986, Díaz *et al.* 1996, Cama 2010) that aggregate in only a few coastal regions. The main wintering areas are in NE Spain (Barcelona-Tarragona-Castellón), Málaga (extending onto nearby Granada) and SW Portugal (Lisbon-Alentejo). Smaller numbers occur in Galicia and Asturias. The species favours low-lying coasts, occurring close to river systems and active fishing harbours and, inland, over a mosaic agricultural landscape which the birds visit for feeding (on e.g., invertebrates and olives). The species' social behaviour is complex, and may also play a role in shaping its occurrence over space. The observed spatial distribution of Mediterranean gulls in winter is not continuous over apparently suitable areas, but tends to occur in clumped localities, leaving large (>500 km) stretches of seemingly suitable habitat empty (Carboneras 2009).

We, therefore, hypothesised that the various local populations might be organised in such a way that each population was discrete and spatially separated, the only links being the irregular movements of dispersing individuals (H_1, metapopulation model). Under this hypothesis, there would be minimal mixing during winter or migration, so we should expect to find significant differences between the list of birds found at each site. We considered a second alternative hypothesis that each wintering population consisted of different birds, but that individuals mixed freely during migration and in this time visited areas other than their 'own' winter quarters (H_2, migratory mixing model). In this way, differences between the sites in winter would be masked by transient birds travelling to reach their destination, so we should expect to find some population structuring but no major differences between the sites. In the same context, our null hypothesis (H_0) was that the species would show no population structuring in winter, so we shouldn't expect to find any significant differences between the sets of birds present at the various sites.

METHODS

Our study was based on comparing the total list of individually marked birds seen at various localities over a given period. We selected all sites ($n = 7$) in the Iberian peninsula for which >40 readings were available for the 4 consecutive nonbreeding seasons 2005/06 till 2008/09. Coincident with the species'

patchy distribution in winter, the sites were not evenly distributed but situated at variable distances from each other (mean of distances between pairs = 1079,87 km ± 155,4 SE; n = 21; range = 17,2 – 2269,95). We assumed that all sites within <500 km were part of the same regional complex. Thus,

3 sites were situated in the NE Spain region, while another 2 were in SW Portugal, plus one locality in Málaga and another in Galicia (fig. 1). Numbers of wintering birds ranged between a few hundred (Galicia) and several thousand (NE Spain, Málaga, SW Portugal), seasonally up to 40 000 in Cambrils.
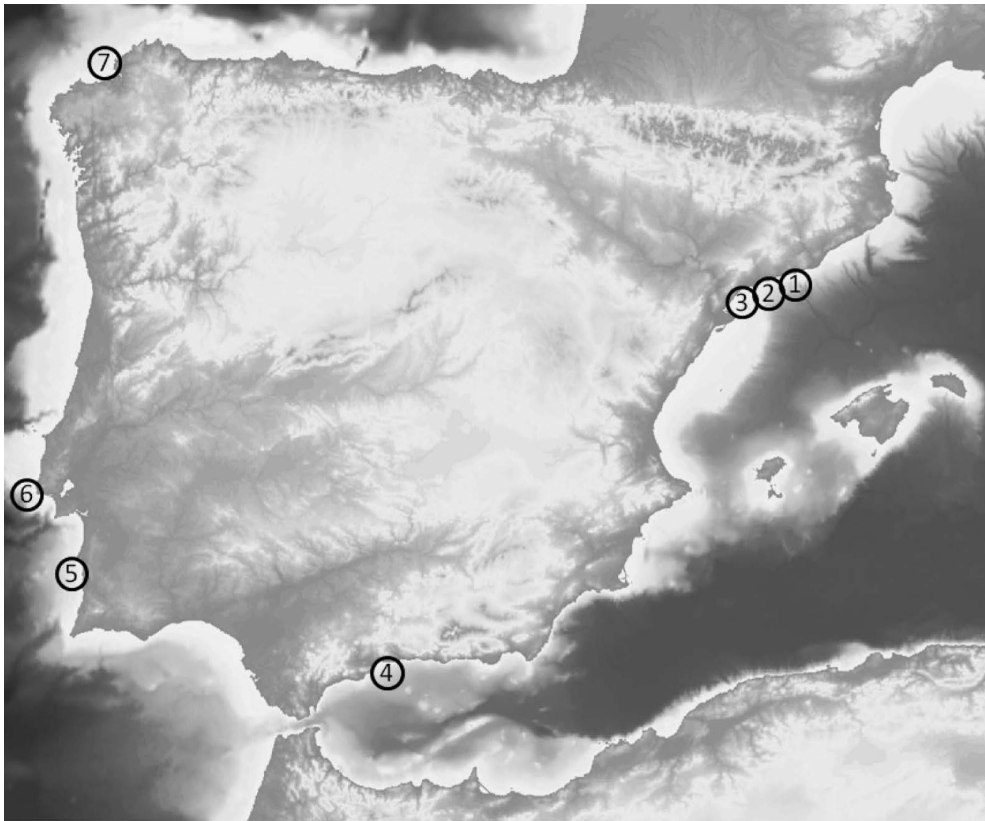
Figure 1. The Iberian peninsula with the location of the 7 sites included in this study: (1) Vilanova i la Geltrú; (2) Tarragona; (3) Cambrils; (4) Málaga coast; (5) Vilanova de Milfontes; (6) Lisbon coast, Cascais & Tagus estuary; (7) Ares, Galicia.

The nonbreeding season comprised the winter proper (15 Sept-15 Feb), plus the two annual migration periods (Jul-Sept and Feb-Apr). The latter were included in order to maximise the probability that a bird might occur at more than one locality in the same time frame (either during winter or on passage, or both), thereby reducing the differences between sites (H_0, H_2). The total number of rings read in this period added to 1612, corresponding to 1125 different individuals. We compared the lists between pairs of sites to build a pairwise comparison matrix, shown as table I, and conducted an agglomerative hierarchical clustering analysis (Ward 1963).

For each pair of sites, we measured the level of affinity or coefficient of similarity (Gower 1971), which we defined as:

$$\text{Coefficient of similarity} = \frac{n_{jk}}{(n_j + n_k) - n_{jk}}$$

with n_j being the number of rings read at site j, n_k being the number of rings read at site k, and n_{jk} being the number of rings read at both sites in the time of our study. Possible values ranged between 1 (complete similarity) and 0 (complete dissimilarity).

Table I. Pairwise similarity matrix between pairs of sites. The left-hand half-matrix contains the coefficient of similarity for each pair of localities (see text for calculation method). The right-hand half-matrix contains the original ratios used to calculate the similarity between pairs of sites and equates to the number of birds recorded at both sites, divided by the sum of all individuals seen at the same sites.

	Vilanova G.	Tarragona	Cambrils	Málaga	Vilanova M.	Lisboa - Tejo	Ares
Vilanova G.		176 / 583	224 / 660	8 / 585	3 / 598	8 / 618	1 / 517
Tarragona	0.3019		132 / 565	6 / 398	4 / 409	4 / 433	0 / 329
Cambrils	0.3394	0.2336		5 / 526	3 / 536	4 / 560	1 / 455
Málaga	0.0137	0.0151	0.0095		4 / 242	4 / 267	0 / 163
Vilanova M.	0.0050	0.0098	0.0056	0.0165		15 / 264	2 / 169
Lisboa - Tejo	0.0129	0.0092	0.0071	0.0150	0.0568		2 / 194
Ares	0.0019	0.0000	0.0022	0.0000	0.0118	0.0103	

We obtained the individual life histories, grouped birds by origin and classified them in two groups, 'Atlantic' and 'Mediterranean', according to the location where they were ringed (as pulli or as breeding adults). 'Atlantic' grouped birds from colonies in Belgium, Netherlands, Britain, Atlantic France, Germany and Poland, while birds from Mediterranean France, Italy, Hungary, Balkan countries, Greece, Turkey and Black Sea (Ukraine) were included in 'Mediterranean'. Colour-ringing of Mediterranean gulls started in 1990 (Meininger 1999) and, according to data obtained from the coordinators of the ringing programmes (listed under Acknowledgements), 9343 birds (40,33%) had been ringed in 'Atlantic' colonies and 13821 birds (59,67%) in 'Mediterranean' colonies until 2009.

Distances were calculated assuming that gulls migrate roughly following the coast, avoiding long crossings over land and flying round Gibraltar to travel between the Atlantic and the Mediterranean.

RESULTS

There were differences in the total number of rings recorded at each site (range 44-474), reflecting local differences both in gull numbers and in reading effort. However, a pairwise comparison matrix (Table I) allowed for direct comparison and an agglomerative hierarchical clustering dendrogram reflected the degree of similarity between the sites (fig. 2). The 7 sites appeared grouped in 4 clusters: Catalonia–NE Spain (Vilanova G., Tarragona and Cambrils), Málaga, SW Portuguese coast (Vilanova M. and Lisbon–Tagus) and Ares. Moreover, Málaga showed closer links with the Portuguese coast than with Catalonia–NE Spain, despite both being on the Mediterranean coast. Ares did not show affinities with any other site and appeared as an independent line.

Inter-site mobility of Mediterranean gulls, expressed in terms of the coefficient of similarity, was much higher for sites that were at distances <500 km (mean = 0,23, n = 4) than for sites that were > 500 km away (mean = 0,009, n = 17). In fig. 3 we plotted the regression of the similarities between pairs of sites against the physical distance between them. Our data did not show a linear correlation of those two parameters. The highest affinity (0,34) corresponded to the pair Vilanova G. – Cambrils (dist. = 61 km), while Tarragona – Cambrils (dist. = 17 km) had 0,23. In Portugal, Vilanova M. – Lisbon (dist. = 123 km) had 0,06. Total reading effort varied between the sites (highest in Vilanova G.), and this may partly account for the differences observed in the results. Affinities between distant (>500 km) sites showed that there was still some degree of interconnection between nearly all pairs of sites (15 of 17).
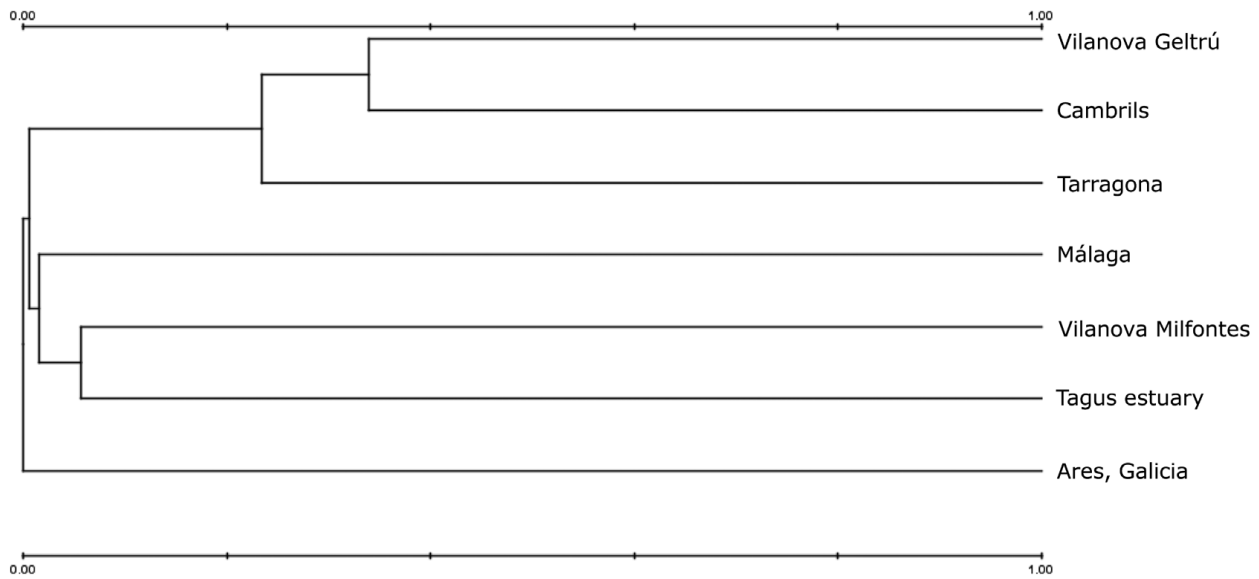
Figure 2. Dendrogram showing the affinity between the 7 sites based on the number of individual Mediterranean gulls *Larus melanocephalus* recorded in common. The coefficient of similarity for each pair of sites and the total number of birds recorded at each site are the same as shown in tables I & II.
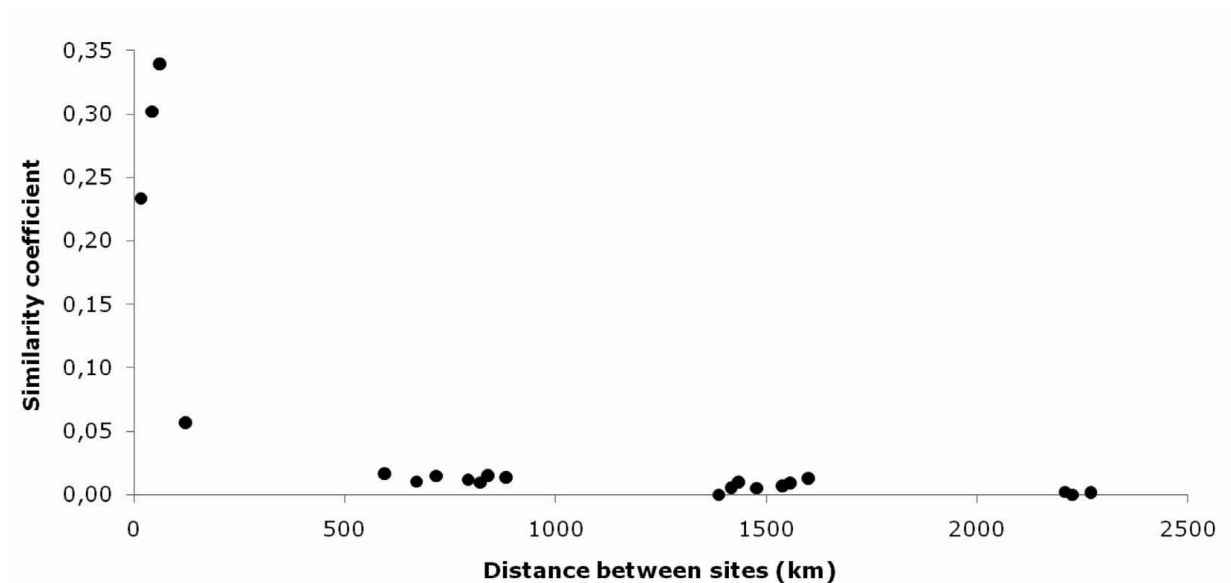
Figure 3. Coefficient of similarity between pairs of sites in relation to the distance between the sites. Distances were calculated assuming a coastal route (see text for details).

The same 4 clusters of sites were shown in the proportions of 'Mediterranean' *vs.* 'Atlantic' birds, according to the location of the colony where they were originally ringed (either as pulli or fully-grown birds), as shown by fig. 4 and table II. Except for Málaga, where the proportion was remarkably similar to what might be expected globally, the ideal proportions were not maintained at any other site. Mediterranean (and Black Sea) birds were disproportionally more numerous in the Catalonia–NE Spain cluster, whereas birds of Atlantic origin were dominant in the Portuguese and Ares sites. The differences were highly significant in all cases, except for Málaga (table II).
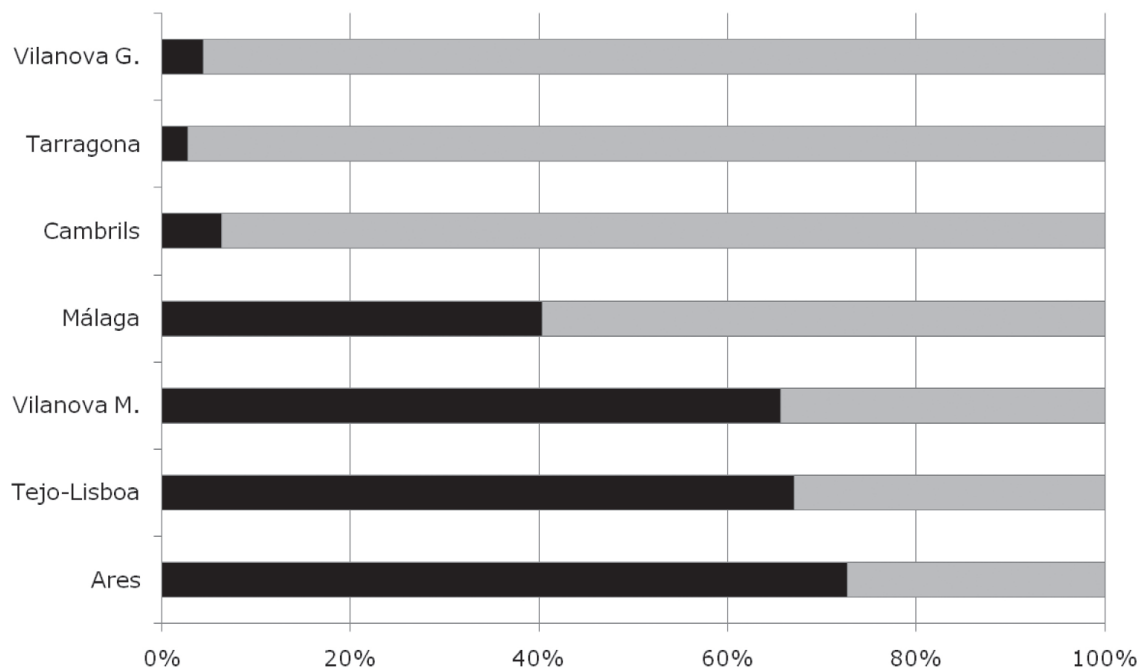
Figure 4. Proportion of Atlantic (in black) vs. Mediterranean (in grey) individuals recorded at each site, according to the localisation of their colony of origin. The division follows the same rules as described for Table II.

Table II. Percentage of individuals recorded at each site, according to the localisation of their colony of origin. Atlantic and Mediterranean mean west or east of the straits of Gibraltar, respectively, the latter category including the Black Sea. Globally, the proportions are 40.33% Atlantic and 59.67% Mediterranean.

site	total n	Atlantic %	Medit. %	chi sq	P
Vilanova G.	473	4.4	95.6	253.791	P < 0.0001
Tarragona	285	2.8	97.2	166.904	P < 0.0001
Cambrils	411	6.3	93.7	197.477	P < 0.0001
Málaga	119	40.3	59.7	0	P = 0.9989
Vilanova-Milfontes	128	65.6	34.4	34.033	P < 0.0001
Tejo-Lisboa	152	67.1	32.9	45.282	P < 0.0001
Ares	44	72.7	27.3	19.19	P < 0.0001

DISCUSSION

Spatial disjunction in the winter distribution of Mediterranean gulls in the Iberian peninsula was already found in first studies on *Larus melanocephalus* (Mayaud 1954, Bernis 1966, Isenmann 1972 & 1976, Carrera *et al.* 1981) and has been described in most subsequent work (Bermejo et al. 1986, Díaz et al. 1996, Paterson 1997, Poot & Flamant 2006). The species seems to be spatially attached to a

number of traditional areas and its distribution has changed little in the last 30 years, despite substantial changes in the seabird community and in the marine ecosystem at regional scale (Carboneras 2009).

Our data in the present study support the prediction that there was some organisation in the species distribution. The existence of 4 clusters, among the 7 sites chosen for this study, appeared

in both the coefficient of similarity (based on the identity of individuals) and the geographical composition of the local subpopulations (based on their origin). Inside the main groups, there were relatively high exchange ratios of individuals between proximate sites (<500 km away). But the similarities between distant groups were quite low and relatively constant (at 0,01-0,02), possibly as might be expected from non-directional dispersal (Newton 2008).

Apart from the distinction between proximate (<500 km) and distant (>500 km) sites, affinities between the sites correlated poorly with distance, so distance alone would not explain the observed frequencies of inter-site or inter-group mobility. The observed frequencies were too low (particularly among distant sites) to estimate the possible attraction effect of intermediate sites lying on the way to more distant localities, although this probably occured. Moreover, the straits of Gibraltar, a natural impediment that increases the costs of dispersal by adding extra distance, does not seem to influence the exchange of birds between the Mediterranean and Atlantic basins.

Among our data, differences in reading effort (highest in Vilanova G.) and in the total number of wintering birds at each location (largest in Cambrils and Málaga) might imply different detection probabilities locally and annually. To overcome this possible bias, we grouped the number of rings read at every site for the 4 seasons (so that every ring present had a higher probability of being detected) and focused on the relationships of similarity between sites. It was the number of birds *in common* at each pair of sites that determined the connection between them.

Of particular interest, in order to test our hypotheses, were the results for Málaga. Lying on the Mediterranean coast and slightly closer to SW Portugal (ca. 600 km, via Gibraltar) than to NE Spain (ca. 800 km), Málaga had a distinct composition "per origin" (60% of 'Mediterranean' birds, as opposed to only 33-34% in SW Portugal), but still had closer affinities to the Portuguese sites. Its low coefficients of similarity with NE Spain (mean = 0,013) and with SW Portugal (mean = 0,016) point to its little sharing of individuals with those two groups. Our results do not support the possibility that the birds that winter in Málaga pass through SW Portugal or

NE Spain while on migration *or at least that they rest there long enough to be recorded.*

In addition, the fact that Ares, in Galicia, revealed as a true outsider provides further arguments against the migration mixing model hypothesis. Apparently, the migratory routes of the birds wintering in SW Portugal and Málaga do not run through Ares. Thus Ares appears also as a distinct site, holding a local population that does not generally mix, in the winter season or during migration, with those of other localities.

The observed distribution and population arrangement are coherent with a metapopulation structure, with high cohesion within regional complexes but very little inter-regional homogeneity. However, identifying a metapopulation structure of wintering birds is more difficult than among more classical examples (nonmigratory organisms living in a patchy environment) and the task must be accomplished with dedicated techniques. Only a handful of studies have succeeded in providing good examples of metapopulation structure among winter populations of migratory birds (e.g., Esler 2000, Williams *et al.* 2008). A key element of such structure is demographic independence of subpopulations. The Mediterranean gull has an ample, patchy breeding distribution that has expanded into western Europe in recent decades (Bekhuis *et al.* 1997). It is not known to what extent the breeding population might be structured, but even in the case of breeding panmixia, distinct wintering subpopulations may function as demographically independent provided that winter area philopatry is high (Esler 2000). Estimating with confidence that important parameter would require more robust data than were available for our study, and is beyond our aim here.

The question of population structure has powerful conservation implications, because under a metapopulation structure subpopulations are subject to differential risks of extinction (Hanski 1999). The Mediterranean gull is a species requiring conservation action at European and Mediterranean level and is listed in Annex I of the Birds Directive. Spain and Portugal hold a large proportion of the global population during the winter months (BirdLife International 2004, Cama 2010). The wintering population of Mediterranean gull in the Iberian peninsula shows some typical characteristics

of a metapopulation structure: (a) spatially disjunct distribution, (b) essentially unrelated mix of individuals in each site, (c) a small but regular exchange of individuals through dispersal. It remains to be tested whether the local populations are demographically independent, e.g. through high winter philopatry. The conservation status of *Larus melanocephalus* requires conservations measures, including the designation of protected areas such as SPAs (Special Protection Areas, part of the EC Natura 2000 network set up by the Birds and Habitats Directives) and SPAMIs (Specially Protected Areas of Mediterranean Importance, established by the UNEP Barcelona Convention and its Protocol on SPA and Biological Diversity) (Arcos *et al.* 2009, Ramírez *et al.* 2009). Therefore, the network of protected areas for this species should be designed taking into account its population structure in order to secure the long-term conservation of population units, as a means of preserving the viability of the population as a whole.

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Chapter III

Contrasting patterns of site-fidelity across spatial scales in wintering gulls.

Carles Carboneras, Giacomo Tavecchia, Meritxell Genovart, Albert Cama

Contrasting patterns of site-fidelity across spatial scales in wintering gulls

Carles Carboneras, Giacomo Tavecchia, Meritxell Genovart and Albert Cama

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Site-fidelity is dependent on the size of the area to which the individual returns, so it is expected to vary according to scale. We examined spatial dynamics in a wintering population of Mediterranean Gulls known to show strong site-fidelity on a regional scale, but resightings of individually-coded colour-ringed birds indicated that they probably engaged in inter-site movements. To study interchange characteristics between localities, we pulled together resightings during 5 seasons from two near localities and used capture-recapture multi-site models to estimate the degree and directionality of movements at a small spatial scale. Results indicated that birds had a low monthly probability of remaining in their current locality (0.56) and that those changing location were equally likely to move to the other observed site (0.22) or to other areas. To estimate the total volume of birds at a single locality, we quantified local population turnover of individuals of all ages for each season independently. On average, 15800 birds visited the locality every season, a large proportion of the regional (43 %) and global (18 %) populations and 16-18 times above the standard midwinter counts. This is the first study of local-scale site-fidelity and within-season movement dynamics in any gull species; it reveals that although populations may be spatially stable and the seasonal presence of individuals may be predictable, they probably visited multiple localities in the course of a single season, including outside the designated protected areas. The high mobility of individuals found here and the high turnover of gulls in a given site has important consequences for the design of protected area networks.

The individual tendency to return to a given area or site-fidelity is a biological trait with important consequences for survival and conservation (Martínez-Abraín et al. 2001). Even if broadly studied during the breeding season, few studies have analysed the individual attachment to an area during the wintering season (but see (Harris et al. 2009, Grist et al. 2014). In the non-breeding season, fidelity to the wintering area is also beneficial as a potential source of valuable local knowledge about food availability and predators'

habits, which may increase individual fitness and overwinter survival (Robertson and Cooke 1999, Péron et al. 2010). Wintering has often been considered a 'black box' in the annual cycle of migratory birds, while movements to and within the wintering area can reveal important individual strategies (Carboneras et al. 2013, Sergio et al. 2014). Migratory species are generally assumed to remain static during the summer and winter stationary periods, yet some bird species show evidence of movements within the non-

breeding season (Newton 2008). The study of population turnover has revealed that some wintering birds, particularly in the family Anatidae (ducks, geese and swans), regularly change site within the same season, normally after the depletion of food sources, extreme weather or disturbance (Newton 2008); this results in the total number of birds using a site being higher than the average number of birds present at any given time (Giroux 1991, Pradel et al. 1997a, Frederiksen et al. 2001, Rees 2006, Gourlay-Larour et al. 2013). From a conservation point of view, this means that more individuals are afforded protection at a given site than initially estimated, but also they are protected only for a short amount of time. Since the assessment of the importance of bird areas is generally based on instantaneous counts and not on the total volume estimated (Heath et al. 2000, Gourlay-Larour et al. 2013), there is a potential mismatch between between the collective home range of a population and the size and location of the protected areas designated for it.

A lot of effort has been put in recent years into defining the features, biotic and abiotic, that lead to the identification of key sites in the terrestrial and marine environments and into assessing their adequate size and limits in order to protect them (Boyd et al. 2008, Wilson et al. 2009, Ronconi et al. 2012). Most systems ultimately aim at identifying the location of discrete areas of activity that are relevant for a substantial fraction of the population of a single species or a community of species, with a preference for multi-species aggregation hotspots (Lascelles et al. 2012). That approach has the potential to leave part of the area occupied by only one species unprotected. It may also be unsuitable for highly mobile species in which individuals shift location frequently and move among neighbouring sites as part of their wintering strategy.

We looked at local-scale site-fidelity and within-season movement dynamics in a wintering population of Mediterranean Gulls *Larus melanocephalus*. The species is known to show high probability of local survival and site-fidelity to the general wintering area (Carboneras et al. 2013) but observations of individually-coded colour-ringed birds indicated that they probably engaged in inter-site movements. We analysed the volume, direction and likelihood of movements between two protected sites designated for the species. This setting was expected to provide information on the spatial scale of individual movements in relation to the network of protected areas.

Material and methods

Study system

We focused our investigation on two localities, hereafter sites, about 50 km apart, Vilanova i la Geltrú ('VNG' hereafter; 41º14'N, 1º42'E) and Cambrils ('CAM'; 41º4'N, 1º3'E; Fig 1), on the north eastern Mediterranean coast of Spain (Fig. 1). Both sites host large numbers of wintering Mediterranean gull *Larus melanocephalus* with average population in VNG of about 800 individuals, (EEA 2014) and in CAM of about 20,000 individuals, (Cama et al. 2011). Both sites are listed in the Natura 2000 network under the EU Birds Directive 2009/147/EC due to their important populations of Mediterranean Gull. At the centre of both sites are large fishing harbours (Fig. 1, VNG: fleet = 83 vessels, average fish daily landings = 3·9t; CAM: fleet = 46 vessels, average fish daily landing = 2·2t), which gulls attend to feed on fish offal and discards. Previous work has shown that the main wintering season of Mediterranean Gulls in this area extends from 15 September to 15 February, and that stopover birds occur outside this period (Carboneras et al. 2013). Sites were thus visited regularly during this period, from 2005 to 2010, in search of individually-marked birds as they concentrated on beaches and around harbour premises before they moved to roost at sea. Sampling effort was more intense in VNG than in CAM, with 116 and 221 resighting days respectively. Observations were made from a distance with the aid of a 20-60x telescope, and there was no handling of any

bird. All gulls had been ringed during the breeding period in other countries over a large area extending from the Black Sea to Belgium and the Netherlands prior to their arrival in the study system.

Fig. 1. Location of the wintering area showing, right, a schematic representation of the spatial distribution of Mediterranean Gull concentrations associated to the principal fishing harbours. Circle size is proportional to the average Mediterranean Gull numbers on a logarithm scale; there is one order of magnitude difference in the population size between Cambrils (black circle) and Vilanova i la Geltrú (grey circle), the two localities sampled for marked birds; white circles indicate other sites. Site location is arranged according to the distance (in km) to Blanes (41º41'N, 2º48'E), at the N edge of the wintering area. The shaded grey area indicates the location of the Marine Protection Areas designated as Natura 2000 sites in the region.

Between-site dispersal

To investigate the direction and frequency of interchange movements within the study area, we built a dataset with the weekly observations of colour-ringed birds made over 5 seasons (30 occasions) at both sites, VNG and CAM. We fitted multi-site capture-recapture models in program MARK (White and Burnham 1999) to estimate site-dependent survival probability at

site r, φ^r, and transition probability, ψ^{rs}, from site r to site s. To maximize the number of individuals, we considered resightings made from the 8th to the 15th of each month (October to February) from 2005 to 2010. Our observations were only made on weekdays, when there was fishing activity. Before conducting the analysis, software U-CARE (Choquet et al. 2009) was used to assess the fit of the general model in which all parameters were site and time dependent. We assumed the presence of a non-observable site, 'NOS' hereafter, with the probability of resighting fixed to 0, to accommodate those individuals that could be alive but not seen neither in VNG nor in CAM (Hénaux et al. 2007). Hence, our computation allowed individuals to move freely among three sites, but only those in VNG and CAM would be visible. In this analysis, we considered four different models (ranked 1-4 in Table A1). Model 1 assumed equal movement probability among the three states, models 2 and 3 assumed a different movement probability associated to each state and model 4 assumed equal probability of reciprocal movement between pairs of states, that is $\psi_{VNGCAM}=\psi_{CAMVNG}$ and $\psi_{CAMNOS}=\psi_{NOSCAM}$ but $\psi_{VNGCAM}\neq\psi_{CAMNOS}$. Model selection followed an information-theoretic approach based on the Akaike Information Criterion adjusted for the small sample size AIC$_c$ (Burnham and Anderson 2002), in which the model with the lowest AICc values should be considered as the best compromise between model fit and the number of estimable parameters. Models with AICc values below 4 points were arbitrarily considered as equivalent (Burnham and Anderson 2002).

Winter population volume and super-population size

We investigated the population volume and the turnover in the smaller of the two localities considered, VNG, for which we had more data, using the encounter histories of birds seen in this site for five consecutive winters (2005/06 to 2009/10). The total number of animals in VNG at any given time was estimated using the POPAN

model (Arnason and Schwarz 2002) available in the software MARK 7.0 (White and Burnham 1999). The POPAN formulation is a particular parameterization of the time-dependent Cormack-Jolly-Seber model (CJS; (Schwarz and Arnason 1996). By assuming a super-population, N, made of the total number of animals ever present in the population, it is possible to estimate at each occasion, i, a recruitment parameter, b_i, which represents the probability of entry in the observed population, i.e., the probability that an animal from this hypothetical super-population would enter the observed population between occasion i and $i+1$ (Schwarz and Arnason 1996). Within each year we identified intervals of 4 weeks (~ one month) and pooled resightings obtained over the first week only, to meet the assumption of no mortality during the resighting period (Lebreton et al. 1992). We considered the 5 wintering seasons independently and constructed one dataset per season with the encounter histories of marked animals. We assumed that ring loss during a single winter was negligible. Not all parameters of the general time-dependent POPAN model are estimable (Cooch and White 2012). We applied the constraint proposed by Williams et al. (Williams et al. 2011) to set $p_1 = p_2$ and $p_k = p_{k1}$, where k is the number of occasions, in order to make all survival and entry parameters estimable in the model. The probability of entry, b, was kept time-dependent because models with constant b have no sensible biological interpretation (Cooch and White 2012). For each winter, we tested a combination of four candidate models: a fully time-dependent model, $\varphi(t)\ p(t)$, a model with constant survival and encounter probability, $\varphi(\cdot)\ p(\cdot)$, and two models in which either encounter probability or survival probability was time-dependent while the other was held constant, $\varphi(t)\ p(\cdot)$ and $\varphi(\cdot)\ p(t)$. The goodness-of-fit, GOF, of the full time dependent model was assessed with program RELEASE. The total chi-square value of the GOF tests, divided by the degrees of freedom, can be taken as a variance inflation factor, $\hat{c}$, and used to correct model deviances (Cooch and White 2012). Following Silva et al. (2010) we corrected the estimates of population size for the proportion of colour-marked individuals relative to the total number available for observation, m. This value was used to estimate the number of birds present on the site (Atkinson et al. 2007) as:

$$\mathrm{N_{gull}} = \frac{N}{m}$$

where $\mathrm{N_{gull}}$ is the estimated number of Mediterranean Gulls (marked and unmarked) using a given site and N is either $\hat{N}$ or $\hat{N}*$, where $\hat{N}$ is the monthly and $\hat{N}*$ is the annual gross super-population size, that includes all individuals that enter and leave the population between consecutive surveys and thus are never available for sampling (Williams et al. 2011). Monthly and seasonal estimates of the number of Mediterranean Gulls visiting VNG were calculated based on the values of $\hat{N}$ in the retained model and the proportion of colour-marked birds calculated on the site ($\bar{x} = 1\cdot397 \cdot 10^2$, SE $= 0\cdot055 \cdot 10^2$).

We collected data on the apparent total number of birds present at the site by means a single-count during each individual sampling occasion ($n = 92$). This value has been used as a comparison with the estimated N. We also used for comparison the data of the local mid-winter International Waterbird Census (IWC) counts carried out in January of each year by an independent observer ($n = 5$) using the same methodology.

Results

Between-site dispersal

The GOF test detected a highly significant presence of transients or permanent emigrants in the general multi-site model (test 3G.SR $\chi^2_{36} = 68\cdot00$, P $= 0\cdot001$). To reduce the effect of an excessive presence of transients in the general model, we suppressed the first capture occasion
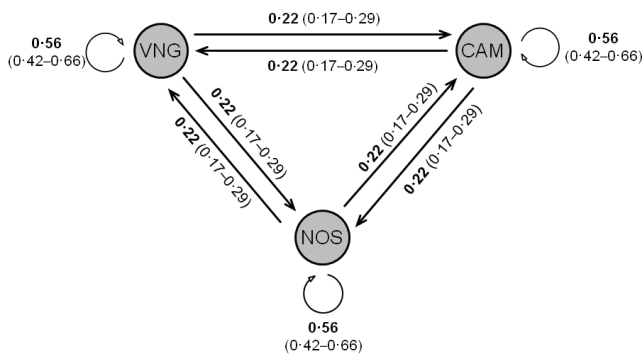
Fig. 2. Transition probabilities ψ (95% CI) among VNG (Vilanova i la Geltrú), CAM (Cambrils) and NOS (non-observable site) estimated by multi-site model 1, based on equal transition probabilities among the three sites that are constant over time (Table A1). The probability of residence is calculated by subtraction $(1 - \psi)$.

(Pradel et al. 1997b), i.e. the first resighting. The reduced data set consisted of 438 encounters of 195 individuals in 30 week-long sampling occasions during the 2005-2010 winters. The second GOF test indicated that the multi-site type fitted the corrected data adequately and that the assumptions of the Jolly-Movement (JMV) model were being met ($\chi^2_{144} = 106 \cdot 71$, P = 0·99). Of the 15 models available in this analysis (Table A1), four (ranked 1–4) had relatively low differences in AICc weight (less than 4 points, or > 0.1%). The main difference between models 1–4 lied in the structure of the transition probabilities, ψ. Model 1 had the highest AIC weight (0.39), more than twice that of similar model 3 (0.17), so it was judged to be the most likely. This model assumes equal movement probability among the three states (but cf. models 2 & 6). Its encounter probabilities were $p_{VNG} = 0 \cdot 40$ (95% CI. 0·34–0·47) for the VNG site, similar to the one found in the single-site approach, and $p_{CAM} = 0 \cdot 10$ (95% CI, 0·08–0·16) for the CAM site. The transition probabilities of this model were $\psi = 0 \cdot 22$ (95% CI, 0·17–0·29) for all transitions among VNG, CAM and 'NOS' (fig. 2). Hence, an individual in VNG or CAM had a 44% monthly probability of

leaving that locality, 22% of moving to the other site and 22% of going somewhere else in the general area. Equally, an individual in state NOS had a 44% probability of moving to VNG or CAM. The monthly probability of remaining on the site, calculated by subtraction, was 0·56 (95% CI, 0·42–0·66) (fig. 4).

Winter population volume and super-population size

In total, we recorded 667 resightings (97-217 per season; average 100) of 501 individuals (76-146 per season; average 133). The goodness-of-fit tests indicated that the POPAN models fitted the data adequately (Table A2). This is in contrast with the results from the first analysis possibly due to the lower observation effort in CAM, with 40 % of occasions with $p = 0$. Nevertheless we used the appropriate $\hat{c}$ for each dataset to adjust model deviance (Table A2). For each seasonal analysis, the model with the highest AIC weight was retained (Table A3).
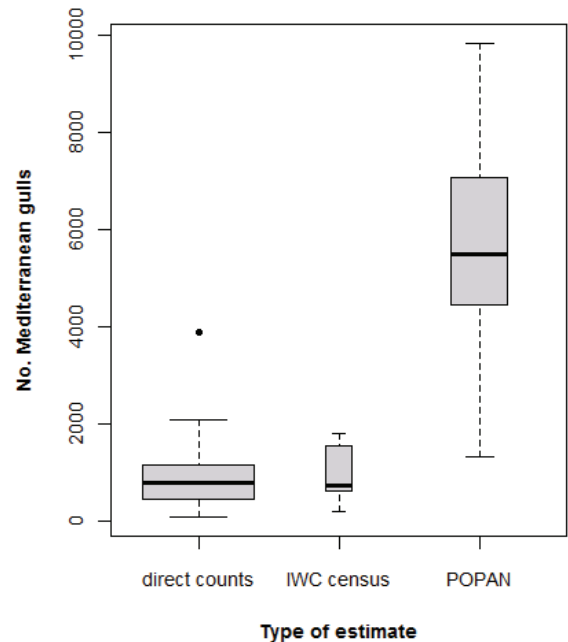
Fig. 3. Boxplot comparison of the results of counting wintering Mediterranean Gulls present in VNG following different methodologies: direct counts, by the same observer, of the number of gulls present at the time of each sampling occasion ($n = 92$); International Waterbird Census (IWC) counts ($n = 5$); and average estimates of the super-population size $\hat{N}$ at the time of each sampling occasion, as derived from the POPAN models ($n = 23$). The width of each box is proportional to the sample size.

The geometric mean of the monthly encounter probabilities p was 0·36 (range, 0·30–0·48) and the geometric mean of the monthly survival probabilities, φ, was 0·86 (range, 0·80–0·92). The models provided monthly estimates of the population size, $\hat{N}_i$ as a derived parameter. Monthly estimates of the number of Mediterranean Gulls visiting VNG each month were consistently high across winters, with peaks between October and January (fig. 2a). Mean estimates of $\hat{N}$ ($\bar{x}$ = 5504, SE = 470, n = 23) were about six times higher than the direct counts of birds present during sampling occasions in the wintering period ($\bar{x}$ = 886, SE = 63, n = 92) and from the International Waterbird Census (IWC) counts, January 2006–2010 ($\bar{x}$ = 990, SE = 298, n = 5) (Fig. 3). Across winters, the average monthly probability of entry between sampling occasions, b, was 0·36 in Oct, 0·24 in Nov, 0·12 in Dec and 0·08 in Jan (fig. 2b). This is the probability that a Mediterranean Gull already present in the super-population entered the VNG site *for the first time* at those points in time.

The volume estimates of the total number of Mediterranean Gulls visiting VNG during a wintering season, $\hat{N}^*$, were: 14 796 (95% CI, 9 579–20 013) in 2005/06, 13 398 (95% CI, 10 135–16 661) in 2006/07, 18 449 (95% CI, 15 411–21 486) in 2007/08, 18 842 (95% CI, 9 934–27 749) in 2008/09

and 14 085 (95% CI, 9 133–19 037) in 2009/10, with a geometric mean of 15 754 (95% CI, 10 630–20 683). This represents 85% of the population wintering in the Catalonia region (Josa et al. 2011), 43% of the total population wintering in the NW Mediterranean and 18% of the global population of the species (Cama et al. 2011, Wetlands International 2015), as based on direct counts and the extrapolation of observed densities.

Discussion

Our study looked into the fine-scale spatial dynamics of a wintering population, and it addresses, for the first time for any gull species, hypotheses on small-scale movements using individual based data. The results revealed that site fidelity appears to be dependent on the spatial scale considered. Individuals were faithful to the wintering area on a regional scale (hundreds of km) but showed little site fidelity on a local scale (tens of km). Despite showing strong site-fidelity both to the breeding grounds (Marvelde et al. 2009) and to the wintering area (Carboneras et al. 2013), individual Mediterranean Gulls in this study were not likely to spend all winter in a single site; their monthly probability of moving away from a site was almost as high as that of staying. When they moved, birds did not follow any preferred direction, and many colour-ringed
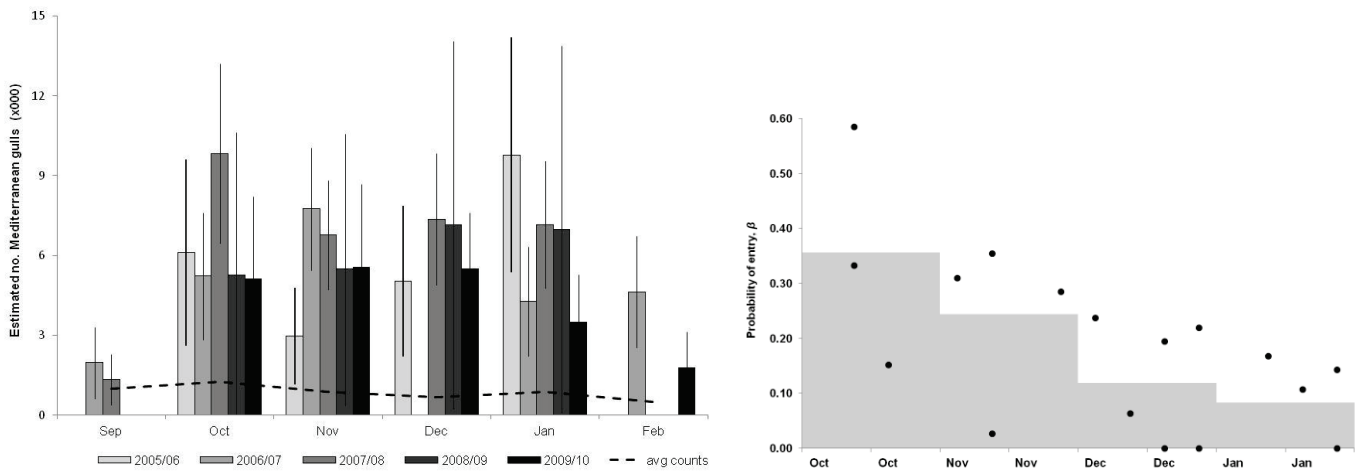
Fig. 4a (left). Estimates of temporal super-population size ($\hat{N}$) at the time of each monthly sampling occasion for the 5 seasons, 2005/06 – 2009/10, as derived from the POPAN models. The wintering period extends between 15 Sep and 15 Feb.
Fig. 4b (right). Estimates of monthly entry probabilities β, as obtained from the selected POPAN models for the 5 seasons. Each point shows the probability that, in a four-week period, an individual present in the super-population N enters the VNG site for the first time in that season. The grey columns show the mean values for each month.

individuals returned to one of the observation localities after having spent time in the other, or vice versa. Being mobile in winter implies spending energy in travelling and perhaps having less detailed local knowledge. Despite the energetic cost, small scale movements increase the chances of optimizing foraging strategies and of adapting to local availability of resources.

Our multi-site model highlighted the equal probability that, once individuals have moved, they travel to one of the well-known wintering localities (shorter distance) or outside the study system (longer distance). Assuming that birds stayed in the same general area all winter (Carboneras et al. 2013), 'elsewhere' would mean any site on a 350-km long coastline. (Carboneras et al. 2010) demonstrated that Mediterranean Gull populations distribute around the Iberian Peninsula following a metapopulation pattern, clumping in wintering units >500 km apart that do not share individuals other than through dispersal. Significant parts of the occupied coastline are protected as MPAs or Natura 2000 sites, on land or at sea (or both), but there are also long stretches of unprotected suitable habitat which the birds may use either as alternative sites, or during their travels. It is clear from our results that wintering in multiple sites on a local scale is a common strategy in this species; we found that birds moved freely within their wintering areas, on a spatial scale much larger than the average coastal MPA or Natura 2000 site.

Mediterranean Gulls follow trawlers offshore during the day, and into the harbours in the evenings, to feed mostly on discards that are available only on weekdays (Cama et al. 2011). Food is less predictable during weekends, so we anticipated that changes of location would be more likely then. To avoid that potential bias, we excluded any weekend observations from our data and, as a consequence, our results reflect changes that occurred, or were detected, only during weekdays. Thus, individuals in our study moved about and travelled >50 km distances

while food was still predictable at the site they were leaving.

In the POPAN model, the distribution of the b values of probability to enter the observed population, reflected the relative probability that a bird, ultimately a visitor to VNG, had been in the general area without visiting the locality. This probability was still high in December (12 %) and into January (8 %), which reflects the dynamism and the size of the wintering population associated to the site. Monthly estimates of the net population size $\hat{N}$ fluctuated seasonally and did not fluctuate greatly between years (Fig. 2a). However, the yearly peaks occurred at different months each year, reflecting that spatiotemporal oscillations in the distribution occurred on a local scale, in the changing proportions of the wintering population that spend time in VNG.

Possibly through a combination of self-acquired and socially-held knowledge, individual gulls might become aware of the existence of foraging opportunities at other sites within the general wintering area. Conspecific density at the destination point might, if known, also play an unknown role in individual decision-making. The total number of birds present at the larger locality (CAM) was on average ten times bigger than in VNG, yet that did not seem to affect the probability of movement in either direction.

The two MPAs designated as Natura 2000 sites in the study area for the conservation of several seabird species, including Mediterranean Gulls, are separated on the coastline by a calcareous massif and comprise two different coastal landscapes. They are sufficiently far apart to justify – to the human eyes – being considered as separate areas for the purpose of conservation, and not as part of the same continuum. However, our study of Mediterranean Gulls revealed that individuals in this species spent the wintering season not in one but in multiple localities, and would travel relatively long distances even in the peak of the wintering season. There was no obvious change in the environmental conditions

in any of the five seasons of our study to explain the individual movements observed. Conversely, the spatial dynamics of waterbirds such as ducks, geese, swans and waders, showed a tendency to change site in the same season following a change of conditions (Tamisier 1978, Hestbeck et al. 1991, Swann et al. 2005, Luís and Goss-Custard 2005). From the high mobility detected, we deduce that most if not all Mediterranean Gulls in the wintering area would eventually spend time in the current network of MPAs designed for its conservation. However, given the discontinuities of the network and the mobility of the species, it is also very likely that most individuals would equally spend time in places without protection. Our study provides direct evidence of within-winter movement and as such it has direct implications for standard management of protected areas, such as MPAs and Natura 2000 sites. Our present results suggest that the population of Mediterranean Gulls wintering along the eastern Spanish coast is occupying sites outside the designed protected areas. On the other hand, it seems unlikely to be able to protect all potential sites visited by the birds. Further research should be done to assess threats on unprotected sites.

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Appendix - Supplementary Material

Table A1. Modelling local survival and transition probabilities among multiple sites. Np = number of parameters, AICc = Akaike Information Criterion corrected for sample size, Δ_i = difference in AICc relative to the best model, w_i = model weight, φ = survival, p = resighting probability, ψ = transition probability of entry. The selected model is shown in bold. Model notation: t = time, $\cdot$ = constant.

Table A2. Results of the goodness of fit (GOF) tests on the datasets used for the POPAN analysis. $\hat{c}$ = variance inflation factor. Each dataset corresponded to a winter season and was analysed separately.

Table A3. Estimating total volume or super-population size ($\hat{N}*$) and entry probabilities β, in VNG site for the 5 seasons, 2005/06 – 2009/10 with POPAN. Np = number of parameters, QAICc = quasi-likelihood in AIC, Δ_i = difference in AIC relative to the best model, w_i = model weight, φ = survival, p = resighting probability, β = probability of entry, $\hat{N}*$ = super-population size. Selected models are shown in bold. Model notation: t = time, $\cdot$ = constant, $\cdot$ = parameter not used.

Table A1.

Rank	Np	AICc	Δ_i	w_i	Deviance	φ	p	ψ
1	**10**	**2137·79**	**0·00**	**0·39**	**1621·72**	**VNG=CAM=NOS (*t*)**	**VNG,CAM,NOS (·)**	**VNG=CAM=NOS (·)**
2	12	2137·90	0·11	0·37	1617·64	VNG=CAM, NOS (*t*)	VNG,CAM,NOS (·)	VNG,CAM,NOS (·)
3	13	2139·49	1·70	0·17	1617·12	VNG=CAM=NOS (*t*)	VNG,CAM,NOS (·)	VNG,CAM,NOS (·)
4	13	2141·29	3·50	0·07	1618·93	VNG=CAM=NOS (*t*)	VNG,CAM,NOS (·)	VNGCAM=CAMVNG, CAMC=CCAM (·)
5	11	2160·22	22·43	0·00	1642·07	VNG,CAM,NOS (*t*)	VNG,CAM,NOS (·)	VNG,CAM,NOS (·)
6	9	2169·11	31·31	0·00	1655·12	VNG=CAM, C (*t*)	VNG,CAM,NOS (·)	VNG=CAM=NOS (·)
7	7	2175·61	37·81	0·00	1665·76	VNG=CAM (·), C (*t*)	VNG,CAM,NOS (·)	VNG,CAM,NOS (·)
8	12	2181·39	43·59	0·00	1661·13	VNG=CAM, C (*t*)	VNG,CAM,NOS (·)	VNGCAM=CAMVNG, CAMC=CCAM (·)
9	4	2191·63	53·84	0·00	1687·93	VNG=CAM=NOS (·)	VNG,CAM,NOS (·)	VNG=CAM=NOS (·)
10	6	2193·08	55·29	0·00	1685·30	VNG=CAM=NOS (·)	VNG,CAM,NOS (·)	VNG,CAM,NOS (·)
11	6	2193·52	55·73	0·00	1685·73	VNG,CAM,NOS (·)	VNG,CAM,NOS (·)	VNG,CAM,NOS (·)
12	9	2208·68	70·89	0·00	1694·69	VNG=CAM=NOS (*t*)	VNG=CAM, C (·)	VNG=CAM=NOS (·)
13	21	2335·54	197·75	0·00	1795·99	VNG=CAM=NOS (·)	VNG,CAM,NOS (·)	VNG,CAM,NOS (*t*)
14	39	79582·10	77444·31	0·00	79001·70	VNG,CAM,NOS (*t*)	VNG,CAM (*t*), C (·)	VNG,CAM,NOS (·)
15	80	79742·10	77604·31	0·00	79055·56	VNG,CAM,NOS (*t*)	VNG,CAM,NOS (*t*)	VNG,CAM,NOS (*t*)

Table A2.

Season	no. occasions	GOF X^2 (test 2 + test 3)	df	P	$\hat{c}$
2005/06	4	0·23	4	0·99	<1
2006/07	5	8·23	7	0·31	1.18
2007/08	5	11·66	6	0·07	1·94
2008/09	4	3·36	1	0.07	3.36
2009/10	5	5·92	4	0·21	1·48

Table A3.

Rank	Np	QAICc	Δ_i	w_i	φ	p	β	$\hat{N}*(\pm SE)$
				2005/06 season				
1	**8**	**145·23**	**0·00**	**0·38**	***t***	**·**	***t***	**207 (±37)**
2	6	145·61	0·38	0·32	·	*t*	*t*	
3	5	146·86	1·62	0·17	·	·	*t*	
4	9	147·40	2·17	0·13	*t*	*t*	*t*	
				2006/07 season				
1	**6**	**184·57**	**0·00**	**0·75**	**·**	**·**	***t***	**187 (±23)**
2	10	187·84	3·27	0·15	*t*	·	*t*	
3	8	189·05	4·48	0·08	·	*t*	*t*	
4	12	191·95	7·38	0·02	*t*	*t*	*t*	
				2007/08 season				
1	**7**	**185·82**	**0·00**	**0·58**	**·**	**·**	***t***	**258 (±22)**
2	8	186·74	0·93	0·36	·	*t*	*t*	
3	11	191·55	5·74	0·03	*t*	*t*	*t*	
4	10	191·94	6·12	0·03	*t*	·	*t*	
				2008/09 season				
1	**6**	**121·30**	**0·00**	**0·62**	**·**	**·**	***t***	**263 (±63)**
2	7	123·02	1·72	0·26	·	*t*	*t*	
3	8	125·31	4·01	0·08	*t*	·	*t*	
4	9	127·64	6·34	0·03	*t*	*t*	*t*	
				2009/10 season				
1	**5**	**114·87**	**0·00**	**0·39**	**·**	**·**	***t***	**197(±35)**
2	6	115·18	0·31	0·33	·	*t*	*t*	
3	8	116·41	1·54	0·18	*t*	·	*t*	
4	10	117·43	2·55	0·11	*t*	*t*	*t*	

Chapter IV

A new breeding population of Mediterranean Gulls Larus melanocephalus *in the species' main wintering area maintains independent spatial dynamics*

Carles Carboneras, J. Ignacio Dies

Short communication

A new breeding population of Mediterranean Gulls *Larus melanocephalus* in the species' main wintering area maintains independent spatial dynamics

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We studied a newly established breeding population of the range-expanding Mediterranean Gull *Larus melanocephalus* in eastern Spain, situated in close proximity to the species' main wintering area. By investigating the origin, population composition and wintering area of the new breeders, we found that recruitment from locally wintering birds was unlikely and that the emerging colonies were probably attracting birds from populations wintering 700–1200 km away in Portugal and southern Spain. Our findings reveal that expanding populations may follow their own dynamics, independently of other populations of the same species, and may consist of different individuals altogether.

Keywords: breeding range, expanding species, migration, population ecology, recruitment, wintering area.

Expanding populations of migratory birds face novel challenges as they establish themselves in new areas. A tendency to return to the traditional wintering grounds should be expected, at least initially, because maintain-

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ing good connectivity with the wintering areas may improve individual fitness during the non-breeding season. In the Mediterranean Gull *Larus melanocephalus*, little is known about the demographics behind the spectacular expansion of its breeding range from SE to NW Europe during the 20th century. Initially confined to the Black Sea coast, in the period 1965–90 it expanded 30° of longitude westwards across Europe to reach the Baltic, Atlantic and North Sea (Cramp & Simmons 1982, Bekhuis *et al.* 1997). Breeding numbers in the Netherlands, Belgium, NW France and UK (hereafter, 'Atlantic' colonies) grew exponentially during the 1990s (to over 2500 pairs in 2002, BirdLife International 2004), and continue to increase. This Atlantic population developed a westerly migration route, wintering mainly in NW Spain, Portugal and in the Mediterranean as far east as Malaga (Fig. 1) (Poot & Flamant 2006, Carboneras *et al.* 2010).

In parallel, new breeding sites were established along the western Mediterranean in France (first breeding 1965, *c.* 3600 breeding pairs in 2010; Cadiou 2011), and Italy (first breeding 1978, 2000–2100 pairs in 2002; Serra & Brichetti 2005). Recently established colonies in the Valencia region of eastern Spain (Dies & Dies 2004), initially assumed to be part of the same process, represented a significant expansion of the breeding range towards the southwest. That population rose from a single pair that attempted breeding in 2001 to 447 breeding pairs in four colonies in 2014.

The Spanish Mediterranean coast has traditionally been the main winter quarters of the species, currently holding over 50% of the global population (Cama *et al.* 2011). Those birds return to breed mostly along the Mediterranean and Black Sea coasts. In this context, the emergence of a new breeding colony provided a rare opportunity to study the relation between a long-standing, spatially stable wintering aggregation, formed exclusively of migratory birds, and a locally breeding population of the same species. To elucidate whether one population or strategy influenced the other, we studied the source population of any new recruits, the wintering area of the new breeders and the degree of mixing between the two populations.

METHODS

We collected and analysed data on the location of Mediterranean Gulls wearing individually coded colour rings on the Mediterranean coast of Spain. Our breeding population dataset consisted of all the birds observed at and around the breeding colony established at the Racó de l'Olla reserve, Parc Natural L'Albufera near Valencia, Spain (39°20′N, 0°19′W). This area, monitored daily since the 1990s, held 275 nesting pairs of Mediterranean Gull in 2012. Forty-two birds of known age and birthplace were recorded visiting, displaying or nesting at the
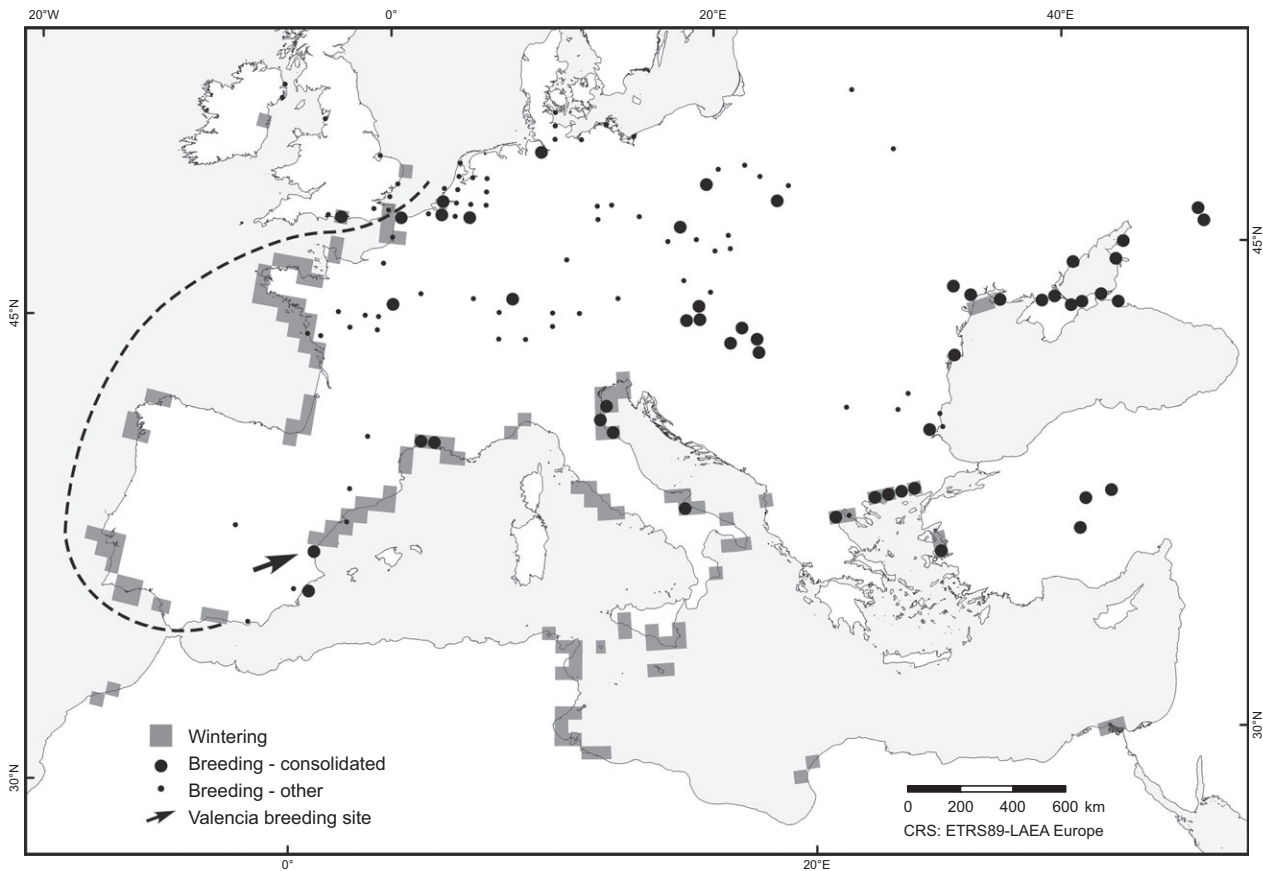
Figure 1. Distribution of breeding and wintering Mediterranean Gulls plotted according to the European Ornithological Atlas 50 × 50 km grid, updated from Bekhuis *et al.* (1997). Consolidated breeding sites held > 25 breeding pairs for > 3 years; shown wintering cells regularly held > 50 individuals. The dotted line indicates the likely migratory route of the western European ('Atlantic') population southwards to Iberia.

colony during the breeding season (April to June) in 2003–2012.

Our wintering season dataset contained observations of colour-ringed Mediterranean Gulls recorded during five winter seasons (15 September to 15 February) in 2005–2010 (625 individuals; 2925 ring-readings), in the 350-km-long stretch of coast between the towns of Blanes (41°41′N) and Burriana (39°54′N) (Fig. 2), the winter stronghold for the species (*c.* 40 000 birds; Cama *et al.* 2011) and known since at least the 1940s (Mayaud 1954). The distance between this area and the Valencia colony site is approximately 65 km.

The species is subject to an international colour-ringing programme comprising all of its known breeding populations. All birds in our dataset had been individually marked in breeding colonies outside Spain prior to their arrival in the study area. Observations were made from a distance with a 20–60× telescope when Gulls concentrated on beaches and around harbour premises

before moving to roost at sea; no birds were handled during our study.

To assess whether the newly established population was growing as a result of its own reproductive output or of immigration, we followed the count-based population viability analysis (PVA) methodology described in Morris and Doak (2002). We fitted a linear regression to the number of pairs counted during the annual census of breeding waterbirds in the Valencia region in 2001–2014 and assumed that the number of nests was equal to the number of females. We used the slope of the regression line as an estimate of the annual growth rate (μ) and the mean squared residual as an estimate of its variance (σ^2) (Morris & Doak 2002).

We inferred the origin of the recruiters to the breeding colony by comparing its population composition (ratio of birds born in colonies west and east of Gibraltar) with the local wintering population, described in detail in Carboneras *et al.* (2013). Furthermore, we
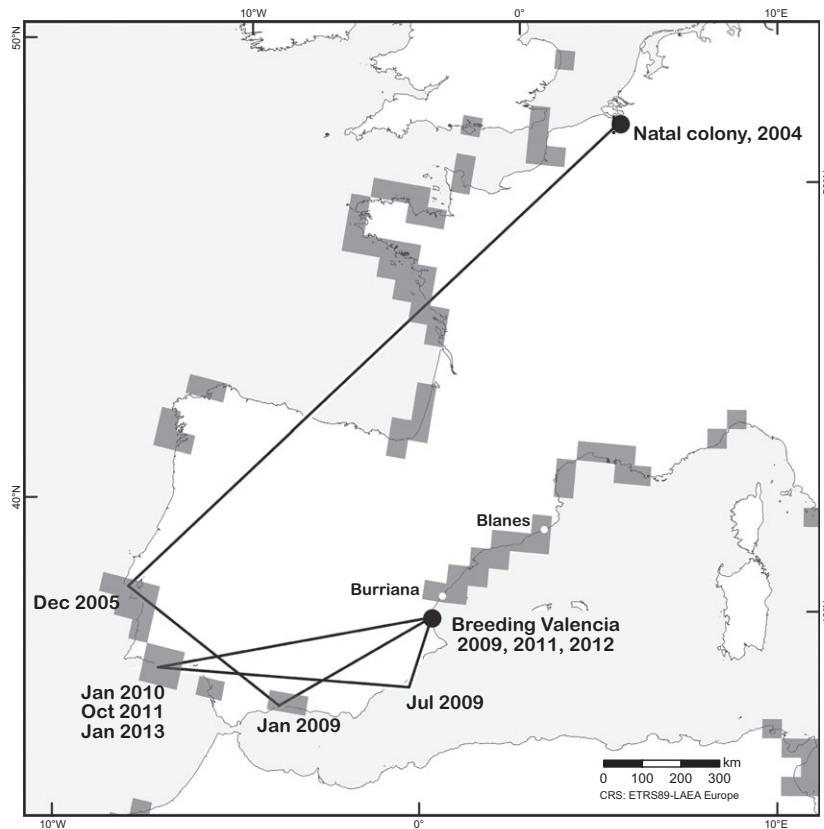
Figure 2. Life history locations of colour-ringed Mediterranean Gull 'Green 30VL' born in Belgium (2004), recorded wintering in Portugal and Spain (2005–2013) and present as a breeding bird in Valencia (2009–2012). Grey cells indicate the species' general wintering areas as in Figure 1.

were able to compare the same ratio with that of other discrete Mediterranean Gull populations wintering in the Iberian Peninsula, as it is known to follow a west to east gradient (Carboneras *et al.* 2010).

RESULTS

The average annual growth rate, μ, estimated by the PVA was 0.47 and its variance, σ^2, 0.22 ($P < 0.01$). This represents an annual increase of 47%.

The two sets of 42 summering and 625 wintering individually marked Mediterranean Gulls contained no individual common to both sets, despite occurring in close proximity. None of the breeding birds was ever recorded in the area during the winter months, and none of the marked wintering birds was ever recorded at the Valencia nesting colonies during the breeding season. Individual encounter histories and field observations showed that the wintering area was vacated completely by late March every year, as birds left for their breeding grounds. A few weeks later, the Valencia breeders were back at the nesting site in mid-April and May.

The natal colonies of the two sets of individuals differed substantially. Although only about 1.5% of the Mediterranean Gulls in the wintering area originated from Atlantic colonies (Carboneras *et al.* 2013), they made up 57% of the breeders and visitors to the Valencia nesting site (Table 1). In contrast, birds born in Mediterranean French and Italian colonies, which form two-thirds of the wintering population, only represented 26% of the summering birds.

The location of the wintering grounds of the Valencia breeding birds remains largely unknown. Only one individual, Belgium-born 'Green 30VL', provided numerous summering and wintering locations in 2004–2013. It moved between the Valencia breeding colony and wintering grounds in SW Portugal and Malaga, southern Spain (Fig. 2).

DISCUSSION

The emergence of a breeding population near a traditional wintering site offered a unique opportunity to study potential changes in the spatial dynamics of those

Table 1. Population assignment of the 42 colour-ringed birds observed ('obs', in bold) at the breeding colony in Valencia, eastern Spain, in 2003–2012 compared with the expected number of individuals if the population followed the same proportions observed in the locally wintering population by Carboneras *et al.* (2013). There is a highly significant overrepresentation of birds from 'Atlantic' colonies (ATL), indicating the probable origin of the summering birds, and an underrepresentation of birds from Italy (ITA), the French Mediterranean (MED), and eastern European colonies in Hungary, Greece, Ukraine and Poland (E Eur).

		MED	ITA	E Eur	ATL	Total	Fisher exact test
Breeders +	exp	3	3	3	0	9	0.02
prospectors	**obs**	**1**	**1**	**1**	**6**		
Visitors	exp	12	10	11	0	33	< 0.001
	obs	**3**	**6**	**6**	**18**		
Total	exp	15	13	14	0	42	
	obs	**4**	**7**	**7**	**24**		

populations as a result of their physical proximity. The new breeding colony of Mediterranean Gulls was able to grow very quickly by attracting immigrants. Unexpectedly, those birds did not come from the spatially stable population wintering in the vicinity. Instead, our data suggest a more distant origin.

Differences in the geographical composition of both populations were considerable. Of all Mediterranean Gulls ringed up to 2009, the proportion of Atlantic vs. Mediterranean birds on a global scale was 40 : 60; among the populations wintering in the Iberian Peninsula, that proportion followed a west to east gradient: 73% of the Mediterranean Gulls in Galicia–NW Spain; 66–67% in W Portugal; 40% in Malaga but only 3–6% in E-NE Spain were of Atlantic origin (Carboneras *et al.* 2010). The proportion of Valencia breeders and visitors born in Atlantic colonies (57%) did not match that of the population wintering in E-NE Spain, pointing to a more likely origin of those birds from either the population wintering in Portugal (over 1200 km away) or from Malaga (over 700 km). Interestingly, all of the wintering records of Green 30VL came from those two regions.

We put considerable effort into ring-reading in winter. A previous study on a subset of our data (Carboneras *et al.* 2013) estimated an average annual resighting probability of 0.49 (95% confidence interval (CI) 0.42–0.55). This is the probability that an individual, being alive and in the area, was recorded at least once during the winter season. The inverse probability (that the bird wintered in the area but was not detected) would be 0.51. Therefore, of our set of 42 summering birds, we would expect to see around 21 at least once every winter. However, none was seen, so we deduce that they were more likely to have wintered somewhere else.

A yearly increase of 47% can only occur through large-scale immigration. Using a Leslie matrix model and demographic data, Sadoul (1997) demonstrated that the 20% annual increase he observed in the Mediterranean Gull colony in Camargue, SE France, was due to immigration. Otherwise, it would have required an unrealistic mean breeding success of at least 1.6, sustained over an extended period. The observed average productivity in France was consistently lower (1.0–1.6 young per breeding pair in predator-free colonies but 0.1–0.5 in disturbed colonies; Isenmann *et al.* 2004). Assuming that the productivity values in Valencia were not different from the French colonies, we infer that only external immigration could explain their increase.

The distribution of Mediterranean Gulls in winter was shown to follow a probability function of distance along the main northeast–southwest route (Carboneras *et al.* 2013); thus, in the main wintering area in E-NE Spain, birds were most likely to come from colonies in nearby France and Italy, and secondly from the eastern Mediterranean. This study reveals, in strong contrast, that the recent colonization has been extending in the opposite direction, from west to east, and that it has consisted mostly of birds born in Atlantic colonies that penetrated and established themselves in the western Mediterranean.

Our findings reveal that the large-scale expansion of a species' range may involve only a fraction of all the individuals available, and that different populations may follow independent spatial dynamics, even where they co-occur. The birds forming part of the spatially stable wintering population did not take advantage of the emergence of new breeding opportunities nearby and consistently migrated to their distant breeding grounds. In parallel, the new breeders continued to behave as if the important wintering area in the vicinity did not exist, and probably returned to their traditional areas. This reveals a strong tendency for populations to maintain their momentum and spatial strategies, and suggests that shifts in distribution (e.g. those expected as a result of a changing environment) may not necessarily be simple, linear processes.

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DISCUSSION

In migratory or dispersive birds breeding in the Palearctic regions, the wintering period has long been considered as a 'black box' in the annual cycle. Whereas breeding populations are regularly monitored and represent the focus of many scientific studies, demographic processes during the winter period are largely unknown. Recently developed techniques such as the use of satellite tracking or geo-locators have shed light on many aspects of migration and of migratory strategies (Berthold 2001; Sergio *et al.* 2014). Those studies are typically confined to a restricted number of animals or to individuals from a given breeding area and do not allow an insight in the demographic processes in the wintering areas. Many authors refer to the winter as a key period in the life cycle of birds especially for the increase mortality that migration or cold winters might induce (Tavecchia *et al.* 2001; Genovart *et al.* 2013), yet few studies have investigated demography in the winter quarters (e.g., Sanz-Aguilar *et al.* 2014; Simmons *et al.* 2015) and whether winter population processes are crucial or not is still to be confirmed. Simmons *et al.* (2015), for example, used state-space models to estimate the demographic trends in wintering population of several waders species in Africa. Their results indicated that the demographic decline observed on the breeding areas was not mirrored by similar trend in winter quarters. Similarly, Pagel *et al.* (2014) used a long-term dataset of surveys of waterbirds wintering along the coast of Eastern Spain and proved that wintering populations of several species have increased over the past decades. The increasing evidence collected on wintering quarters is indicating a possible cost of migration associated with the winter period, rather than the severity of weather conditions as previously suggested (Sergio *et al.* 2014; Sanz-Aguilar *et al.* 2015). The study of winter demographic processes is thus important to i) investigate the mechanisms of winter mortality, ii) to obtain a deeper understanding of population functioning, iii) to have an insight in migratory strategies and finally iv) to guide conservation actions in the wintering quarters.

In my work I have focused on the information collected in wintering areas on birds marked at their breeding colonies and on bird surveys data; I used this information to deepen the knowledge on population functioning, dynamics and migratory strategy of a

migratory seabird, the Mediterranean Gull. I began the current work based on an important, yet simple, hypothesis: winter aggregations of birds constitute true populations (defined as ''a set of organisms belonging to the same species and occupying a clearly delimited space at the same time''; Wilson 2000). This working hypothesis rose naturally from the preliminary observations of the wintering population of Mediterranean Gull along the coast of Catalonia (Eastern Spain) and the multiple resightings over the years and in the same wintering area of previously marked birds. The existence of a 'winter population' has been confirmed by the high levels of winter site-fidelity (see below). I then derived a simple rule to explain the geographic origin of wintering birds (chapter 1), as well as the empiric evidence on the existence of area-specific proportions of birds according to their origin (chapter 2). On a larger, regional scale, the winter distribution of the focus species is organised according to a metapopulation model, with discrete subpopulations separated by >500 km and only linked through dispersal (estimated at 1–2%) (chapter 2). Each subpopulation contributes differently to the global population, as birds are subject to area-specific survival and fitness, and the model is maintained by the tendency of individuals to winter repeatedly in the same areas. The results, which I will discuss in detail below, contribute to a new view of wintering populations, as real demographic entities rather than simple random and homogeneous assemblages, and provide important guidelines for the conservation of the species at their winter quarters. Also, the view 'from the winter quarters' has generated some new important knowledge of the ecology of the Mediterranean Gull and in particular on its migratory strategy.

The use of capture-recapture techniques allows estimating the probability of *local* survival (chapter 1), which is the composite probability of actual survival x site fidelity (Lebreton *et al.* 1992; Esler 2006). In this study, I have found the focus species to show similarly high levels of individual site-fidelity during the winter as those found during the breeding season (Marvelde *et al.* 2009; chapter 1). Site-fidelity is associated with familiarity with the environment and is known to increase individual survival (Greenwood & Harvey 1982; Brown, Brown & Brazeal 2008). It does so through the provision of foraging benefits, such as an efficient match of the foraging strategy to the local resource phenology, and a detailed knowledge of the most productive areas; in addition, it may also increase birds' knowledge of local predators' habits (Péron, Lebreton & Crochet

2010). These potential benefits are probably enhanced in long-lived species that forage, roost and travel communally, because those types of behaviour offer more opportunities to share accumulated knowledge (Ward & Zahavi 1973; Burger 1997).

The combination of local experience and social foraging (Weimerskirch *et al.* 2010) seems particularly well adapted to exploit temporal, superabundant resources distributed irregularly in heterogeneous habitats, as recorded for Mediterranean Gulls (Goutner & Isenmann 1993). However, the advantages of site-fidelity are at the expense of increased intraspecific competition and density-dependent influences, such as interference (Rutten *et al.* 2010). Site-faithful individuals, by definition, have a stronger than average tendency to return to a given area, so a potentially negative consequence is that their populations would be expected to be slower to react to changes in their environment. This delay in responding may carry a reduction in fitness, and site-fidelity may in fact be maladaptive when it is maintained in rapidly degrading habitats (Kokko & Sutherland 2001; Igual *et al.* 2007).

In the case of the Mediterranean Gull, strong site-fidelity to the wintering areas may also be behind its overall spatial stability in the wintering season, maintained at least during six decades, in contrast with its dynamism as a breeding bird (chapter 4). Although breeding and wintering populations are connected by migratory and dispersal events (Clobert et al. 2008), the interrelations between both processes are not fully understood and it is possible that they are not totally independent. It is argued that the Mediterranean Gull is able to adapt more readily than many other species to new habitats (Burger *et al.* 2015) and, in that respect, it has demonstrated the ability to establish a new migratory route connecting the breeding areas around the North Sea and the wintering areas in the Bay of Biscay, north-western Spain and Portugal (Mayaud 1954; Poot & Flamant 2006). Interestingly, the new route is on the more typical north–south axis, common to most gull species, instead of the east–west axis shown by other breeding populations of Mediterranean Gulls (chapter 1). Furthermore, much of the 25% increase in the number of occupied 50 x 50 km grid cells corresponds to the establishment of new wintering areas outside of the Mediterranean (Fig. 5; Poot & Flamant 2006).

One of the consequences of a metapopulation structure in the distribution of birds during winter is the demographic independence of each subpopulation (Esler 2000). The levels of dispersal recorded in the case of Mediterranean Gulls Spain and Portugal would suffice in theory to maintain genetic homogeneity in the population (Bohonak 1999). But, in demographic terms, each subpopulation would be expected to contribute differentially to the breeding population, leading over time to their functioning as relatively independent units. Alloheimy, the geographical segregation of populations that breed and winter in distinct areas, is the expected result from the interaction of breeding and wintering areas in a species showing high site-fidelity to both (Newton 2008).

Contrary to expectations, the population composition of wintering Mediterranean Gulls found in this study is more reminiscent of synheimy as shown by the co-occurrence during winter of individuals from all the breeding populations. The wintering population is made of birds that originate from across the entire breeding range, extending over 30° of longitude between Ukraine and the British Isles (chapters 1 & 2). Synheimy is a rare phenomenon and its finding in a wild population, interesting though it may be, must be interpreted with caution. First, because the population only shows partial synheimy; each wintering population contains a representation of all the breeding populations, but there is spatial variation in that proportion, which can be predicted objectively as a function of distance. There is, therefore, some level of geographical structure in the wintering population. Second, because this is probably only a transitory situation deriving from the Mediterranean Gull's recent large-scale expansion of its breeding range and the species is likely to change from synheimy to alloheimy as breeding populations consolidate and continue to contribute differentially to the wintering populations (Newton 2008).

Mediterranean Gulls are a fully migratory species (Burger *et al.* 2015), and in the study system they completely vacate the wintering area for several months during the length of the breeding season. As explained, information on the historical ringing effort per country, covering the entire period of this study, has allowed estimating the probability that first-winter birds arrived in the wintering area in their first migration as a function of distance (chapter 1). Because the total distance covered must depend on the actual migratory route, information theory was used to estimate the most likely route that

birds would have followed; it showed that that would be a combination of river and coastal routes on a general east–west direction across central Europe. This finding confirms the validity of the river migration hypothesis first put forward by Mayaud (1954), who studied the recoveries of birds ringed in the 1940s and early 1950s at the large, still extant colony of Olrov Island in Tendra Bay, Ukraine (46°16'N 31°44'E). It is noteworthy that the existence of the river migratory route pre-dates the large-scale shift of the species' breeding range across Europe (chapter 1); also remarkably, one of the first individuals ever to be recorded of this species was a young bird shot on 30 September 1822 in Mainz, Germany, on the confluence of the river Main with the Rhein (Mayaud 1954; box 2). This may be evidence that an inland migratory route, possibly followed by only a minority of Mediterranean Gulls (Mayaud 1954), has existed for a very long time.

The occurrence of synheimy has provided a rare opportunity to analyse the composition of the wintering population in the study system, as well as in other wintering areas around the Iberian Peninsula, according to their geographical origin. Chapter 2 confirms the co-occurrence of birds from various breeding regions in the other four wintering areas analysed on a regional scale, as well as the existence of an east–west cline in the proportion of birds born in colonies on the Atlantic *vs.* the Mediterranean coast, in line with the findings of chapter 1. Birds from an Atlantic origin, which make up the majority of the population wintering on the Portuguese coast and a large proportion of those wintering in Málaga (chapter 2), were involved in the range extension that led to setting up a new breeding centre near Valencia (chapter 4). Breeding birds from that population maintained their previous migratory habits and wintering areas in Portugal and/or Málaga and did not mix with the birds wintering in the study system, which was mostly made of birds born in the Mediterranean and Black Sea regions. The finding of independent dynamics in the newly-established breeding population in Valencia, with respect to those of birds in the traditional wintering area nearby (chapter 4), illustrates that those populations are likely be made of different individuals altogether, and function separately from each other.

Many seabirds exhibit markedly different routes on their outward and return journeys, or loop migration (Newton 2008). Those differences tend to relate to the

physics of flying through certain places (e.g., persistent favourable or unfavourable winds) or the availability of feeding opportunities while *en route* (González-Solís *et al.* 2009; Bustnes *et al.* 2013); migratory gulls are known to stop over certain areas for several days or weeks in order to rest and refuel (Klaassen *et al.* 2012). Concrete loop migration has not been documented for any gull species but, in general, it is possible that the routes followed are not exactly the same as in the autumn migration, even in the case of species that travel in groups. In the case of the Mediterranean Gull, there is evidence that birds fan out more widely during the spring migration and an overall increase in the proportion of birds born in Atlantic colonies was observed in the study system at the end of each wintering season. Instead of travelling westwards through the Strait of Gibraltar and round the Iberian Peninsula, a fraction of the birds wintering in e.g., Málaga could follow a northward route through the Mediterranean to return directly to their natal areas in the North Sea area (Fig. 10). This would explain the colonisation of several wetlands in the Valencia region (chapter 4) and the establishment of a handful of breeding pairs in such unlikely places as Estany d'Ivars in central Catalonia (41° 41' N, 0° 59' E) (Estrada 2013) and the river Garonne near Toulouse (43° 36' N, 1° 26' E) (Kergoat *et al.* 2003).
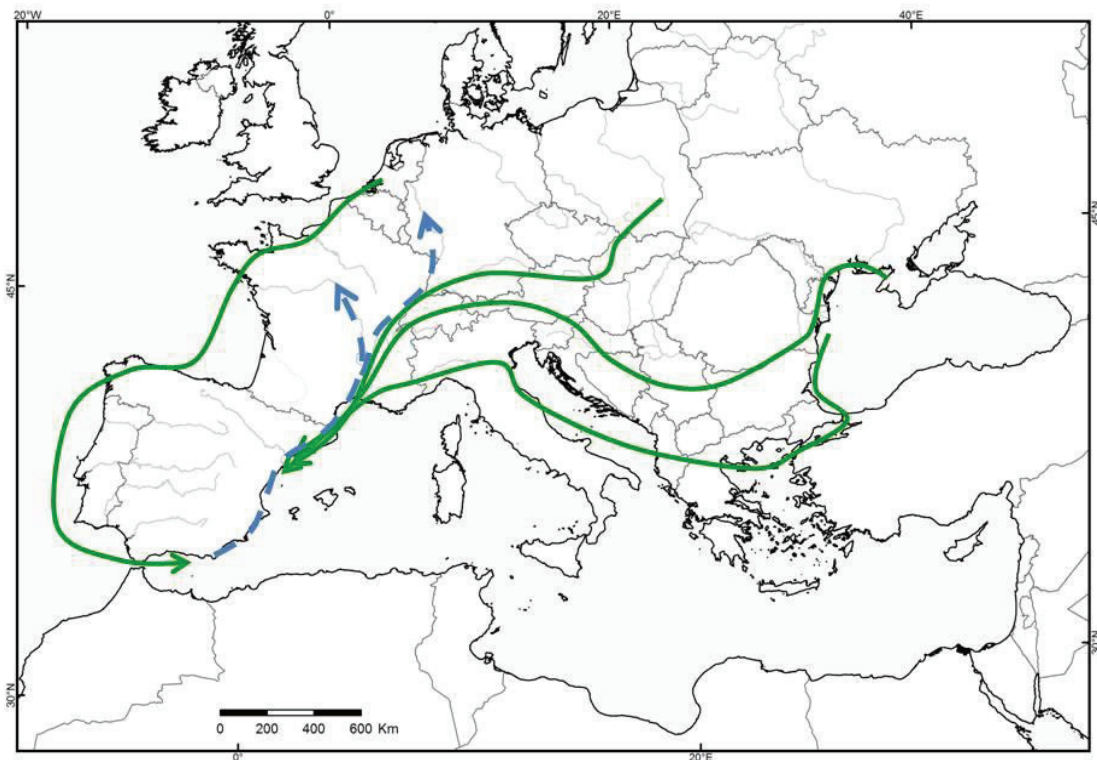
Fig. 10. Schematic representation of the major migratory routes of Mediterranean Gulls from the breeding colonies to the main wintering areas in NE Spain and Málaga, S Spain (green lines). The spring migration is probably along the same routes, except in a minority of cases (dashed blue lines) of birds that likely return from Málaga following a more direct northward route. The current model predicts the future occurrence of resighitngs inland, along the main rivers and sometimes far from seashores (especialy in shouthern Germany, Austria and in other Eastern European countries).

The wintering population of Mediterranean Gulls comprised birds of all age classes between 6 months to 20 years of age and there was no evidence that the probability of wintering in the study area varied with age (chapter 1). An example of site-fidelity maintained through the years is given by Italian blue [A24], born in 1990 and the oldest known individual of the species (Fig. 11). This bird was already seen wintering locally in 1997 and 2000, and then recorded annually in each of the five winters 2005–2010. In the absence of individual tagging, it was not possible to study the level of individual variation in the route, timing or destination of migration. For the whole population, information in the dataset (unpublished data) pointed to non-significant differences in the timing of migration across all age groups, with the possible exception of first-year birds; the latter group seemed to favour a later departure date in spring. The

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group of experienced breeders (between 5 and 11 years of age) spent slightly less time at the wintering area. However, any real differences would be obscured by the co-occurrence in the wintering area of birds that travelled different distances (and therefore required different lengths of time to complete their travel) and the lack of precise information on the exact origin / destination of the migratory journey. The individual colour-ring provided the location of the birds' place of birth or the place of ringing, but it was not possible to know where each bird was travelling from or to in each journey.

Since birds of both sexes (as identified by the external appearance) and all ages are known to be present in the population, the assumption of non-differential migration as would be expected from a species with strong winter site-fidelity must be maintained. This is an uncommon strategy, the consequences of which are not fully understood (Ketterson & Nolan 1983; Cristol *et al.* 1999). The co-occurrence of birds of all sex and age classes over the same, limited space increases competition and density-dependence. This generally reduces individual fitness (Ricklefs 2000) but, on the other hand, in the case of Mediterranean Gulls there is evidence that they tend to be displaced from feeding behind trawlers by larger competing species (Cama 2010), so in those circumstances being in a larger flock could be advantageous. The species' shift in breeding distribution has not seen a parallel increase in overall numbers, suggesting that wintering populations in this non-differential migrant must be much closer to reaching carrying capacity, and this ecological limitation is likely to regulate the overall growth of the population. The global population size of the Mediterranean Gull has been limited most likely by the events happening in the wintering season and, so, it has been demographically 'winter-limited', in the sense of Newton (2008), over the last decades. However, because the mechanisms are not fully understood, it is difficult to be certain if this situation will continue into the future and whether an unprecedented shift in its wintering range could still occur.

Fig. 11. Blue [A24] (right), born in Italy in 1990, was the oldest known individual of the species when it was last recorded in the study system in 2011. It is seen here next to Black [P8K] (left), ringed as a fully-grown adult at a nesting colony in the Black Sea. Notice the partly broken colour-ring of the latter, which it eventually lost completely; since then, it was only identifiable through its metal ring (not visible in this picture). Photo: Carles Carboneras.

Site-fidelity is dependent on the spatial scale (chapter 3; Robertson & Cooke 1999); in the case of the study system, birds show strong site-fidelity to a general area that is 350 km long x 30 km wide (considering that Mediterranean Gulls not only use the actual coastline but extend into the hinterland and offshore), or 10^4 km². On a finer spatial scale, though, the situation is very different; individuals show little attachment to individual sites within the wintering area, and move freely among localities in no particular direction or seasonal trend (chapter 3). Birds maintain their very high mobility throughout the wintering period. The low monthly probability of local, or site, residency (0.56; chapter 3) contrasts with the high probability of annual survival in the general wintering area (0.81; chapter 1) and reveals a contrasting pattern of attachment to the general wintering area *vs.* the individual locality.

It is possible to infer from the above that, in the studied population of Mediterranean Gulls, the size of the individual home range during the wintering season must comprise a substantial part of the whole wintering area. Tamisier (1978) defined a 'functional unit' as a geographical section of the wintering area exploited by a stable and independent group of individual waterbirds, with no mixing with other groups. Each functional unit comprised an area of diurnal concentration for comfort activities and a nocturnal foraging area exploited in exclusivity. The concept has been proven to apply to wintering aggregations of several species of waterfowl (Tamisier & Tamisier 1981) and waders (Luís & Goss-Custard 2005); however, this study demonstrates that it cannot be applied to the spatial dynamics of wintering Mediterranean Gulls.

If individual Mediterranean Gulls move freely and frequently over a very large area, how do they acquire the advantageous familiarity with the environment? Although this aspect has not been investigated in this study, casual observations prove the existence of quite detailed local knowledge among wintering Mediterranean Gulls, like the location of inland reservoirs and olive groves (Cama *et al.* 2011) or the timing of trawlers' return to harbour, which varies locally. The mechanism of knowledge acquisition and transfer may be linked to the species' longevity and its highly gregarious nature, even in comparison to other gulls.

The Mediterranean Gull's substantial shift in breeding distribution (a 750% increase in the number of grid cells occupied between 1954 and 2015, with only a 12% overlap between cells) is quite unprecedented even among the agile-flying gulls; the process has been well documented but so far its causes remain to be explained. The restricted distribution of most species in the group of closely-related "black-headed" gulls indicates that the group has not specialised in a strategy of widespread colonisation (Crochet *et al.* 2000), which adds special interest to the case of Mediterranean Gulls. The first evidence of summering outside of the traditional breeding areas in the Black and Aegean seas dates from the 1930s in the Netherlands (although breeding did not start until much later) and early 1940s (Hungary). The distribution shift did not acquire full force until the 1960s–1970s and was maintained in that stage until the 1990s. The process seemed to have slowed down in the 2000s, but the expansion still continues

(chapter 4). During the expansion, new breeding sites were established linked to the presence of suitable wetlands along or near large rivers, rather than to the existence of important wintering areas, so the expansion was spatially independent from wintering. The pre-existence of a river migratory route across Europe on an east–west axis would have eased the way for the colonisation of new areas.

Two other bird species underwent comparable large-scale expansions of their distribution range in Europe in the 20th century, the Fulmar *Fulmarus glacialis* and the Collared Dove *Streptopelia decaocto*. The increase of the former extended over two centuries and was in a south-eastern direction mostly from the high Arctic; its population explosion is thought to have been related to an important change in food supply (Fisher 1966). In the case of the Collared Dove, which extended north-westwards in record time from the Black Sea – Balkan region across Europe, its explosive range expansion is attributed to a genetic alteration of the peripheral populations (Mayr 1951). The latter possibility cannot be ruled out as an explanation for the 20th century changes in the Mediterranean Gull's distribution range, particularly in view of the separation between sympatric populations that maintain independent dynamics (chapter 4), but that analysis was beyond the scope of this study. However, Collared Doves are non-migratory and their expansion was remarkable in the fact that they settled to breed immediately after arriving in a new area (Fisher 1953). Their population size also increased in line with the increase in occupied area. None of those facts apply to the Mediterranean Gull's range expansion.

Significantly, the distribution shift in the Mediterranean Gull has not been associated to an overall increase in population size (Cama *et al.* 2011) and the global population may in fact be decreasing (BirdLife International 2015a). Sadoul (1997) demonstrated that the population increase of the colonies in Camargue, France, during the period of active colonization, was largely due to immigration and the breeding population in the Valencia region also increased through immigration, probably from distant wintering areas (chapter 4). The Mediterranean Gull's recent spatial dynamics may be more properly defined as a redistribution of numbers over a wider area; in this

aspect, too, it is unlike the population explosion of both the Fulmar and the Collared Dove.

The global winter distribution of Mediterranean Gulls has not changed historically as dramatically as that of the breeding season; 60 years on from Mayaud's analysis, the number of occupied 50 x 50 km grid cells has increased by 25%, 30 times less than the breeding range (Table 1 in Appendix). The winter distribution continues to be patchy, with roughly the same patches occupied as in the 1950s, particularly along the Mediterranean coast. There is a 73% overlap in the number of occupied grid cells between 1954 and 2015, the difference being mostly due to the occupation of new wintering areas on the Atlantic coast (Figs. 3 and 4) following the consolidation of the breeding populations in the North Sea area (Poot & Flamant 2006). The species' consistent use of the same wintering areas continues to leave large extensions (typically, over 500 km) of apparently suitable habitat that remain unoccupied (chapter 2). Matthiopoulos *et al.* (2005) demonstrated the link between site-fidelity and patchy distribution in colonially-breeding populations of birds and mammals. The studies in chapters 1, 2 and 3 show that the same relationship applies to the distribution of Mediterranean Gulls in the non-breeding season.

Mediterranean Gulls breed mostly on wetlands (both coastal and inland) and move to coastal habitats during the wintering season (Cramp & Simmons 1982). In winter they feed mostly on fish items that they capture directly or from trawler discards; Bernis (1967) and Isenmann (1972) already noted that the distribution of Mediterranean Gulls coincided with important fishing harbours, some time before the generalised industrialisation of trawl fishing and the widespread availability of discards, which has taken place since the mid 1970s. The species' association with fishing harbours may not be a determining factor in their choice of habitat, though, as many areas with important harbours still hold no significant populations of Mediterranean Gulls (Carboneras 2009). On a larger spatial scale, wintering areas are also often associated with large river systems, such as the Ebro, Rhône, Po, Evros, etc. (Fig. 3), and it might appear that river systems could be key to the species' distribution, given their role as migratory routes. However, other traditional wintering areas, such as the central Mediterranean (southern

Italy, Sicily, northern Tunisia and Malta) or Málaga in southern Spain, are not associated to major rivers. The mechanism of habitat choice in Mediterranean Gulls is poorly understood; it is possible that social and non-environmental factors (e.g., conspecific attraction, tradition) may be involved as well (Carboneras 2009) but the process still remains to be explained.

The analysis of the spatial needs of a population of wintering Mediterranean Gulls reveals a mismatch between the birds' dynamic strategy, with frequent movement among various localities, and the size and location of the areas designated for the protection of the species (chapter 3). As a consequence, individuals in the study system will be protected only during part of the time that they spend in the wintering area, but not when they move beyond the statutory sites into unprotected territory, or in the spaces between protected sites. With a low monthly probability of local residency (0.56, chapter 3), individuals are likely to move to other localities several times in the course of the wintering season. The high levels of turnover recorded locally show that the total number of individuals that visit any given locality over the entire season is several times the apparent resident population at each individual site, and that the concept of 'local population' cannot be applied on a spatial scale smaller than the entire wintering area. Therefore, the impact of any potential source of mortality, from a pollution incident to an ill-placed wind turbine, would have implications far beyond the local scale.

The requirement to designate Special Protection Areas (SPAs) for Mediterranean Gulls under the EU Birds Directive has not been implemented in its literal terms. The current preferred approach in relation to Marine Protected Areas is to designate areas where several species are found sympatrically in relevant numbers (Lascelles *et al.* 2012), so that the spatial requirements of a species are put in relation to those of the other species. This approach has the potential to leave part of the area occupied by one species – but not shared with others – unprotected. For the highly mobile Mediterranean Gull, those unprotected spaces that form part of the population home range could become a population sink if mortality varies spatially for the reason that the level of protection is not uniform across the entire wintering area. For example, if measures to

protect seabirds from accidents with fisheries are only adopted within the framework of a protected area but not more widely.

Fig. 12. Evidence of actual threats faced by Mediterranean Gulls in the study system: above, adult bird with amputated foot, probably as a consequence of interaction with a fishing vessel; middle, severe instance of oiling in a second-winter bird; below, adult bird with swallowed hook; the line can be seen protruding from its mouth. Photos: Carles Carboneras.

Even if not incorporated into the estimation of interannual survival (chapter 1), there is evidence that mortality does occur during the wintering season. During the fieldwork for this study, Mediterranean Gulls were observed getting involved in various incidents with the potential to cause direct mortality, including bycatch in fishing gear, traumatic accidents with fishing vessels, and oiling and others forms of pollution (Fig. 12). Given the importance of the wintering season for the species and its contribution to the overall demography of Mediterranean Gulls, studying the levels, patterns and causes of mortality within the wintering season must be a research priority for the future. The current global population trend is of a moderate decline (BirdLife International 2015b) and, although that assessment does not specify which part of the mortality is associated with the wintering season, any increase in winter mortality could have grave implications for the species' conservation status.

This study has made extensive use of capture-recapture techniques (chapters 1 – 4) as a tool to study population demography, individual movement, migratory routes, spatial dynamics, and the relationship of between breeding and wintering areas (Oro &

Ruxton 2001; Tavecchia, Serra & Baccetti 2005; González-Solís *et al.* 2007; Oro, Tavecchia & Genovart 2011; Genovart *et al.* 2013). The comprehensive approach developed here has been made possible through the combination of two unique factors: the long (in time) and wide (in area) international colour-ringing programme that has been in place for the species; and the large number of individuals in the study dataset, which represented 2.5% of the global number of Mediterranean Gulls ever to be colour-ringed. The extent of the ringing programme has allowed for the modelisation of the migratory routes of first-winter birds (chapter 1), the discovery of nondifferential migration and synheimy in the population (chapters 1 & 2) and the analysis of population composition in the various wintering areas (chapter 2); it has also indicated the origin of the potential breeders recruiting to a new colony established near the main wintering area (chapter 4). In this respect the current work benefited from and would like to acknowledge the long-term field activities conducted in many of the breeding areas.

Effort in a capture-recapture study can be low for the initial marking but it is high on resighting afterwards. Quite intensive fieldwork, however, allowed for reasonably high resighting probabilities (chapters 1 & 3), which reduced uncertainty in the estimation of values. The fact that no individuals in the dataset had been ringed or were handled in the wintering area, meaning that they all had completed a migratory journey before entering the study system, fulfilled a basic assumption of capture-recapture models: that individuals mix randomly and their fates are independent, so that they will have equal probability of being resighted (Lebreton *et al.* 1992). Even so, there was individual variation in the probability of moving between sites and, therefore, some individuals appeared to be more likely to be encountered, or 'trap happy' (chapter 3). This was corrected statistically, even though given the method it was probably more an artefact of the data than an actual inequality in the reencounter probability.

Through the analysis in chapter 1 it has been also possible to detect and estimate the incidence of tag loss in colour-ringed individuals (ring loss). The occurrence of ring loss has been verified by reading of the metal ring that all colour-ringed birds carried as well (Fig. 11). Ring loss must be widespread phenomenon, particularly among long-lived animals that are marked as chicks, but it is seldom taken into account and only

rarely quantified (Nichols & Hines 1993). Our ability to estimate the level of ring loss allowed increasing precision in the estimation of the demographic parameters. The recommendation follows that any level of ring loss should be verified, and estimated if possible, as best practice of capture-recapture studies where individuals can have their marks on for many years.

As a result of the large sample size, the methods used and the wide geographical origin of the animals available for sampling, the results obtained can be taken as representative of the whole population wintering in the study system. Studies based on the individual tagging of animals offer more precise data on the timing and direction of movements, but they are rarely conducted on a large, sufficiently representative sample of the whole population and over several years. Furthermore, the wide geographical span that characterises this study has been achieved only very rarely in tagging studies (Frederiksen *et al.* 2012).

This work contributes to a better understanding of bird population dynamics in the wintering season and shows how the detailed study of a species' ecology during one part of the annual cycle can help comprehend what happens during the rest of the year. The 'view from the winter quarters' can bring important and complementary information to the study of birds during the breeding period. Moreover, the findings reported here set a baseline on several aspects of Mediterranean Gulls' ecology, winter dynamics, the migratory strategy, the evolution of its spatial distribution, the relationship with the breeding population and its conservation needs.

CONCLUSIONS

(1) The study of demography from the perspective of wintering areas has helped to understand the formation, structure, composition and persistence of wintering populations of a migratory species. Distinct subpopulations, each with independent demography, organise into a metapopulation structure with little sharing of individuals and no common dynamics. Demographic parameters like survival, site-fidelity and dispersal play a key role in shaping a species' spatial distribution and overall strategy during the wintering season.

(2) The Mediterranean Gull, the focus species of this work, shows high local interannual survival at the wintering area, ranging between 0.81 and 0.90, depending on whether an effect of ring loss is taken into account. This value is comparable to what has been observed at a breeding colony in Belgium and The Netherlands. The probability of local apparent survival is not related to the age of the bird, indicating that individuals should be expected to continue to use the same area repeatedly over the years, conditional on being alive.

(3) The spatial scale of the wintering area used by Mediterranean Gulls is much bigger than a single locality. Individuals move freely and frequently among the various localities, with no obvious direction, at any time during the wintering season. This finding is in contrast with the theoretical advantages of site-fidelity (accumulated local knowledge leading to increased fitness); it more likely points to the size of the area effectively used by individual Mediterranean Gulls being on a regional scale (hundreds to thousands of km^2) rather than on a local scale (tens of km^2).

(4) Frequent, regular movements to several localities within the study system take individuals beyond the statutory sites and into unprotected territory. This study documents a mismatch between the spatial needs of wintering Mediterranean Gulls and the size and location of the protected areas designated for the species.

(5)   The findings in this work about the likely migratory route connecting the breeding and the wintering areas validate the hypothesis – first formulated by Mayaud in 1954 – that the species follows the main rivers in its travels across Europe; most relevant to birds wintering in north-east Iberia are the Danube, the Rhine and the Rhône. Mediterranean Gulls also probably cross over stretches of sea, particularly the Aegean, the Adriatic and central Mediterranean. The historical expansion of the species' breeding range has likely occurred along the same migratory routes.

(6)   The development of a new migratory route following a north–south direction broadly along the coastline Atlantic, also predicted by Mayaud (1954), is compatible with the migration models built in this study and the observed variation in the composition of the wintering populations along the Iberian Peninsula. The new route is on the opposite axis to all the previously known routes of the species (east–west); it developed in less than a century and is evidence of dynamic microevolution in the Mediterranean Gull.

(7)   The large-scale expansion of the Mediterranean Gull's breeding range, with a 750% increase in 60 years, is not paralleled in the wintering population, which showed only a 25% increase over the same period. The fact that the global population has apparently not increased despite the expansion must be taken to indicate that it is limited by events happening during the winter or, perhaps, during the migration periods. This places additional value to the conservation of the wintering areas, as their role might be decisive in the long-term viability of the population.

(8)   The discovery of high levels of winter site-fidelity, independent of the age of the bird, and the observation that the wintering population in the study system was made of returning birds of all ages support the idea that the Mediterranean Gull is among the minority of species showing non-differential migration. As with the other species with a similar strategy, it may be difficult to understand the ecological and behavioural reasons behind it, but it sets important strategies for conservation as protected areas are likely to encompass all population strata.

(9) Exceptionally, in the Mediterranean Gull, breeding populations do not winter separately; the population composition of the individual wintering areas is made of a representation of all the breeding populations ("synheimy"), with the proportions varying as a function of the distance to each breeding centre. The finding of synheimy in wintering populations of this species reveals a likely transitional situation associated to the large-scale, rapid expansion of its breeding range, historically not matched by an equivalent expansion of its wintering range.

(10) The population wintering in the study area and the breeding population recently established in its vicinity are formed of different individuals and follow independent spatial strategies. Expanding (breeding) and stable (wintering) populations maintain their dynamics where they co-occur, and it may take some time before birds take advantage of the new opportunities (for breeding / wintering) that are available in the vicinity of the area they occupy.

(11) Capture-recapture statistical methods are a powerful technique to study population dynamics of wintering birds, particularly when the species has been ringed extensively over a large part of its breeding range and the sample size of resighted individuals is large. Compared to studies of tracked individuals, a sample size equivalent to 2.5% of the total number of ringed birds in the species, as in the case of this study, reduces uncertainty in the extrapolation of the observed results to the whole population.

(12) Wintering populations must be regarded as real demographic entities rather than simple random and homogeneous assemblages. The study of demography from a wintering area can help comprehend what happens during the rest of the year. The view 'from the winter quarters' can bring important and complementary information to the study of birds during the breeding period for a full understanding of species' ecology during the whole annual cycle.

RESUM DE LA TESI DOCTORAL EN CATALÀ

Introducció

Les poblacions d'ocells migratoris poden veure's limitades principalment per esdeveniments que afecten la supervivència durant una part de l'any de manera diferencial sobre les altres (Sherry & Holmes 1995; Newton 1998). Son rars els estudis que cobreixin tot l'any, i molta part del coneixement es deductiu, basat en els descobriments sobre supervivència en una part de l'any, i extrapolat a la resta (e.g., Blackburn & Cresswell 2015). Les poblacions poden estar limitades per la mortalitat diferencial a les zones de cria o a les d'hivernada, i també la mortalitat pot estar repartida de manera mes uniforme al llarg de l'any (Newton 1998, 2008). Aquesta distinció es important de cara a la conservació, ja que la protecció de les àrees d'hivernada ha de tenir un paper mes rellevant en la viabilitat a llarg termini de la població total, comparada amb les àrees de cria, en les especies limitades per la demografia hivernal.

Malgrat el seu paper important en les dinàmiques poblacionals i en la conservació de les especies, el període hivernal continua essent una 'capsa tancada' en el nostre coneixement del cicle anual de moltes especies d'ocells. Els processos demogràfics que tenen lloc a les àrees d'hivernada segueixen essent desconeguts per les dificultats que suposa el seguiment d'animals d'origen no identificat que es mouen lliurement sobre grans extensions i degut al problema de trobar poblacions suficientment individualitzades que siguin apropiades per fer-ne el seguiment (Robertson & Cooke 1999).

En el tema de la designació d'àrees marines protegides, hi ha un cert debat sobre la utilitat de centrar-se en una sola espècie o be fixar-se en la identificació d'àrees de diversitat per a agregacions de múltiples especies (Ronconi *et al.* 2012). La preferència dominant es per a l'opció de múltiples especies en base a l'abundància total i/o a la diversitat d'espècies; aquest es l'enfocament que s'està utilitzant actualment per a identificar xarxes d'espais en diverses escales espacials (Lascelles *et al.* 2012). Les metodologies actuals es centren en la identificació de les àrees on tenen lloc activitats

importants, com l'alimentació, la reproducció o la migració, però es probable que generin llacunes en el cas de poblacions amb necessitats d'espai mes grans. Idealment, les xarxes d'espais protegits haurien de cercar garantir la viabilitat a llarg termini de les poblacions objectiu, tenint en compte els processos demogràfics (supervivència, reclutament, dispersió) que defineixin la seva viabilitat en última instancia.

La Gavina Capnegra *Larus melanocephalus* Temminck 1820 es una gavina de mida mitjana (215 – 350 g) que es troba en grans agregacions mono específiques o en associació amb altres gavines, al llarg de la costa mediterrània i del mar Negre (Bekhuis, Meininger & Rudenko 1997). Estranyament, tractant-se d'una espècie majoritàriament europea, es coneix poc de la seva biologia i ecologia. La població reproductora es distribueix en forma de petits focus sobre una gran part de regions costaneres d'Europea i la regió d'Àsia central. La major part dels efectius nidifiquen a la zona del mar Negre i el Mediterrani oriental (Bekhuis *et al.* 1997; Burger *et al.* 2015). L'espècie va experimentar una espectacular expansió de la seva area de cria durant el segle XX, començant pel mar Negre i estenent-se ràpidament sobre tot durant els anys 1970–1990 a traves de l'Europa central fins arribar a la costa atlàntica i al Mediterrani nord-occidental. Aquest desplaçament va coincidir en el temps amb grans augments en les poblacions d'altres especies de gavines en diverses parts de l'hemisferi Nord (Harris 1970; Furness & Monaghan 1987) i per això inicialment es va interpretar com una explosió demogràfica de la població que podia formar part del mateix procés (Cramp & Simmons 1982). No obstant, recentment alguns autors parlen mes aviat d'una redistribució dels efectius reproductors i han lligat el canvi en la distribució de l'espècie a fluctuacions en la població reproductora del mar Negre (p.ex., Bekhuis *et al.* 1997; Sadoul & Raevel 1999). Encara no hi ha cap evidència d'un increment generalitzat i, malgrat la consolidació de la població reproductora al nord-oest europeu, l'espècie es considera estable a nivell mundial (BirdLife International 2015a).

Objectius

El principal objectiu d'aquesta tesi és l'estudi de l'Ecologia de Poblacions en ocells durant l'època de la hivernada, investigant la composició de la població,

l'estructura i la dinàmica a diverses escales espacials, així com el lligam entre les àrees de reproducció i d'hivernada a través de les rutes migratòries que les connecten. Utilitzo de model d'estudi una població hivernant de Gavina Capnegra *Larus melanocephalus* formada per individus amb diversos orígens geogràfics, una alta proporció dels quals havien estat marcats individualment com a polls o adults a les seves colònies de reproducció. Malgrat que es tracta d'una espècie que ha estat objecte d'un ampli programa de marcatge amb anelles de colors, molts aspectes de la seva biologia i ecologia encara són poc coneguts.

Els objectius específics de la tesi són:

- Explorar la demografia d'una població hivernant d'ocells a través de l'estima de la fidelitat al lloc i la supervivència interanual local en una zona d'hivernada
- Comprendre com els individus fan la selecció de les zones d'hivernada en primera instancia;
- Establir quin és el patró de composició de les poblacions, en relació a l'origen geogràfic dels ocells hivernants, a diverses escales espacials;
- Analitzar les dinàmiques espacials, a nivell local i regional, de la població hivernant;
- Esbrinar com la mida i la distribució del domini vital col·lectiu es relaciona amb la mida i la distribució de les àrees protegides designades per a aquesta espècie;
- Explorar la relació entre un nucli reproductor aparegut recentment i la població hivernant preexistent i estudiar com l'aparició de noves oportunitats afecta les dinàmiques individuals.

Aquests objectius es presenten de manera individual o agrupada com a capítols de la tesi en forma d'articles científics (amb les corresponents seccions, Introducció, Mètodes, Resultats, Discussió i Referències bibliogràfiques) per a la millor comprensió del lector. No obstant, per tal d'assolir l'objectiu principal de la tesi, els resultats de tots els capítols es presenten de manera combinada, i es discuteixen conjuntament en una discussió general.

Capítol 1. Ús de dades sobre reavistament per a l'estudi de la fidelitat al lloc i per inferir l'origen geogràfic, l'estructura de la població i les rutes migratòries en una població hivernant de Gavines Capnegres

Les poblacions hivernants estan formades per ocells que potencialment poden tenir diferents orígens geogràfics, edats i historials de vida. En aquest estudi, utilitzo una base de dades de Gavines Capnegres anellades amb marques de colors provinents de tota l'àrea de distribució, sobre un període de dues dècades, per estudiar la supervivència interanual local i la composició de la població en relació a l'origen i l'edat dels individus. Adreço la qüestió de com es formen i es mantenen les poblacions hivernants, i com aquestes es relacionen espacialment amb les poblacions reproductores. No es coneixen estudis que hagin analitzat la composició relativa de les poblacions en relació a llur distància amb les àrees de naixement. Com que es preveu que les colònies contribueixin de manera diferencial en relació als costos de la migració, i aquests depenen de la ruta elegida, espero poder inferir l'estratègia migratòria més probable en aquesta gavina. A més, investigo si hi ha variacions en el lligam individual amb l'àrea d'hivernada a mesura que els animals van adquirint més edat. Utilitzo les dades sobre 472 Gavines Capnegres marcades individualment i d'edat i origen conegut, observades repetides vegades a la zona d'hivernada, per estimar la supervivència interanual individual i la fidelitat al lloc d'hivernada. També cerco d'esbrinar la composició de la població al lloc d'hivernada en relació a la distribució espacial de les colònies de naixement.

[1] *Carboneras C, Tavecchia G, Genovart M, Requena S, Olivé M, Oro D (2013). Inferring geographic origin, population structure and migration routes of a wintering population of Mediterranean gulls from resightings data. Population Ecology 53.*

Capítol 2. Estructura poblacional de les Gavines Capnegres hivernants en diverses àrees d'Espanya i Portugal [2]

És lògic esperar que les espècies amb àmplies àrees de distribució a l'època de cria i que hivernen en àrees també extenses mostrin un cert nivell d'estructura espacial.

Per determinar si aquest és el cas en la Gavina Capnegra, investigo les connexions entre les poblacions hivernants en quatre àrees distribuïdes al llarg de la Península Ibèrica, per tal de determinar les semblances entre les poblacions i el seu nivell d'afinitat. Utilitzo les observacions d'individus marcats per estudiar la configuració poblacional analitzant el nombre d'individus comuns entre diverses localitats i formular hipòtesis sobre l'estructura espacial en l'espècie. La hipòtesi nul·la és que la població hivernant no tingui estructura espacial, perquè els individus tinguin la mateixa probabilitat de ser observats en qualsevol de les localitats d'hivernada. La primera hipòtesi alternativa (hipòtesi de model de metapoblació) és que cada subpoblació estigui aïllada físicament i demogràficament, i que les subpoblacions només estiguin connectades a través dels moviments irregulars dels individus en dispersió. Sota aquesta hipòtesi, només podem esperar nivells mínims de mescla durant la hivernada o la migració; això es reflectirà en nivells baixos d'afinitat entre el conjunt d'ocells observats en cada localitat. La segona hipòtesi alternativa és que cada subpoblació hivernant sigui independent i estigui composta per individus diferents, però que els ocells es barregin lliurement durant la migració, època en la que podrien visitar zones d'hivernada diferents a les 'pròpies' (model de barreja migratòria). En aquest cas, les diferències entre els llocs d'hivernada quedarien ocultes pels ocells en pas camí de llur destí final, per tant esperaria trobar algun tipus d'estructura en la població però no grans diferències entre els llocs. Finalment, cerco variacions geogràfiques en la composició de la població en cada lloc, en quant a l'origen geogràfic dels ocells.

[2] *Carboneras C, Aymí R, Cama A, Duponcheel C, Ferrer J, Flamant R, García S, Garzón J, Gutiérrez A, Olivé M, Poot M. (2010) Mediterranean Gulls* Larus melanocephalus *wintering in Spain and Portugal: one population or several? Airo 20.*

Capítol 3. Dinàmiques espacials a nivell local i moviments durant la temporada hivernal en Gavines Capnegres [3]

Algunes poblacions hivernals mostren als nivells de fidelitat al lloc, però és sabut que aquest paràmetre està en relació a les dimensions de l'àrea considerada i per tant

s'espera que pugui variar en relació a l'escala (Robertson & Cooke 1999). Les Gavines Capnegres mostren altes probabilitats de supervivència local i nivells alts de fidelitat a la zona d'hivernada (Carboneras *et al.* 2013), però les observacions d'individus marcats amb anelles de colors indiquen que podrien ser més mòbils a escala local i que probablement emprenguin moviments entre diferents localitats. Utilitzo models de captura-recaptura sobre múltiples llocs per tal d'analitzar la direcció i la freqüència dels moviments individuals d'escala local i estimar la probabilitat de residència durant l'època hivernal i per determinar les necessitats espacials de la població, tenint en compte les dinàmiques individuals, i la relació entre els llocs d'hivernada. Examino, a més, el gir poblacional total al voltant d'un sol lloc d'hivernada per esbrinar el volum total d'ocells que visiten un lloc a diferents escales temporals. Aquest paràmetre ha de permetre estimar la mobilitat general dels individus a l'interior de la zona. El meu objectiu és determinar les necessitats espacials de la població hivernant, i comparar-les amb les dimensions i la distribució de la xarxa d'àrees protegides per protegir l'espècie.

[3] *Carboneras C, Tavecchia G, Genovart M, Cama A. (2015) Contrasting patterns of site-fidelity across spatial scales in wintering gulls. In prep.*

Capítol 4. Relació entre una població hivernant espacialment estable i una població reproductora emergent d'una espècie en expansió [4]

El sorgiment d'una nova colònia reproductora en la proximitat d'una zona d'hivernada tradicional de la mateixa espècie proporciona una oportunitat única d'estudiar la relació entre ambdós grups, ambdós formats exclusivament per ocells migratoris. En primer lloc, intento determinar la taxa de creixement anual de la nova colònia per tal de saber si el creixement observat és resultat de la immigració. També investigo l'origen geogràfic dels ocells que s'incorporen com a potencials reproductors a la nova colònia. Espero trobar algun tipus d'interacció entre ambdues poblacions, tals com que alguns ocells hivernants s'incorporin al nucli reproductor o que alguns ocells d'aquest darrer grup es quedin a hivernar a la zona propera. Exploro, per tant, els canvis potencials en les dinàmiques espacials o en els hàbits migratoris d'ambdues poblacions com a resultat de les noves oportunitats sorgides.

[4] *Carboneras C & Dies JI. (2015) A new breeding population of Mediterranean Gulls Larus melanocephalus in the species' main wintering area maintains independent spatial dynamics. Ibis, in press (doi: 10.1111/ibi.12324).*

Discussió

Per a les especies migratòries o dispersives de les regions paleàrtiques, sempre s'ha considerat l'època hivernal com una 'capsa tancada' en el coneixement del seu cicle anual. Mentre que les poblacions reproductores tenen un seguiment regular i son el focus d'atenció de molts estudis científics, els processos demogràfics durant el període hivernal son molt poc coneguts. Determinades tècniques desenvolupades recentment com l'ús del seguiment per satèl·lit o els geolocalitzadors han aportat nova llum sobre molts aspectes de la migració i les estratègies migratòries (Berthold 2001; Sergio *et al.* 2014). De manera típica, aquells estudis es circumscriuen a un nombre restringit d'animals o a individus en una determinada area de cria i una permeten tenir una visió mes amplia dels processos demogràfics que tenen lloc a les àrees d'hivernada. Molts autors es refereixen a l'hivern com un període crític en el cicle vital dels ocells especialment per l'augment de mortalitat que poden anar associats a les migracions o als hivern crus (Tavecchia *et al.* 2001; Genovart *et al.* 2013), però pocs estudis han investigat la demografia en els quarters d'hivernada (p.ex., Sanz-Aguilar *et al.* 2014; Simmons *et al.* 2015) i encara esta per confirmar si els processos poblacionals durant l'hivern tenen un paper crucial. Simmons *et al.* (2015), per exemple, fa servir models estat-espacials per estimar les tendències demogràfiques en les poblacions hivernants de diverses especies de limícoles a l'Àfrica. Els seus resultats indiquen que el declivi observat a les zones de cria no es reflectia en una tendència similar a les zones d'hivernada. Igualment, Pagel *et al.* (2014) analitzen una llarga base de dades a escala temporal de censos d'ocells aquàtics hivernants a la costa oriental de la Península Iberica i demostren que les poblacions hivernants de diverses especies han augmentat al llarg de les darreres dècades. Un nombre creixent d'evidències recopilades als quarters d'hivernada indica un possible cost de la migració associada al període d'hivern, mes que el rigor de les condicions hivernals com es suggeria anteriorment

(Sergio *et al.* 2014; Sanz-Aguilar *et al.* 2015). L'estudi dels processos demogràfics durant l'hivern es doncs important: i) per investigar els mecanismes de mortalitat durant l'hivern, ii) per obtenir un coneixement mes aprofundit sobre el funcionament de les poblacions, iii) per tenir una visió de les estratègies migratòries i finalment iv) per orientar les accions de conservació als quarters d'hivernada.

En el meu treball, m'he centrat en la informació obtinguda a les àrees d'hivernada sobre ocells marcats a les àrees de cria i en dades de censos; he utilitzat aquesta informació per aprofundir en el coneixement sobre el funcionament de les poblacions, les dinàmiques i l'estratègia migratòria d'un ocell marí migrador, la Gavina Capnegra. Vaig començar aquest treball basant-me en una hipòtesi simple però important: que les concentracions hivernals d'ocells constitueixen veritables poblacions (definides com "un conjunt d'individus pertanyents a la mateixa espècie que ocupen una area clarament delimitada de manera sincrònica"; Wilson 2000). Aquesta hipòtesi de treball va sorgir de manera natural de les observacions de la població hivernant de Gavina Capnegra al llarg de la costa catalana i els múltiples reavistaments al llarg dels anys i a la mateixa zona d'ocells prèviament marcats. L'existència d'una 'població hivernant' ha estat confirmada pels alts nivells de fidelitat al lloc (veure mes avall). A continuació van derivar una regla simple per explicar l'origen geogràfic dels ocells hivernants, així com l'evidencia empírica de l'existència de proporcions variables en cada zona d'ocells segons el seu origen geogràfic. A una escala regional, la distribució hivernal de l'espècie focus esta organitzada segons un model meta poblacional, amb subpoblacions separades per >500 km i nomes vinculades a traves de la dispersió (estimada en 1–2%). Cada subpoblació contribueix de manera diferencial a la població total, ja que els ocells es veuen exposats a unes condicions d'estat i supervivència que son especifiques de cada area, i el model es mante per la tendència dels individus d'hivernar de manera repetida a les mateixes zones. Aquests resultats aporten una nova visió de les poblacions hivernants, com a veritables entitats demogràfiques més que com a simples conjunts aleatoris i homogenis d'individus, i aporten valuoses orientacions per a la conservació dels ocells a les zones d'hivernada. Tanmateix, la visió 'des dels quarters d'hivernada' ha generat un coneixement important sobre l'ecologia de la Gavina Capnegra i en particular sobre la seva estratègia migratòria.

Aquest treball contribueix a millorar el coneixement sobre les dinàmiques poblacionals dels ocells durant la hivernada i mostra com l'estudi detallat de l'ecologia d'una espècie durant una part del cicle anual pot ajudar a comprendre el que succeeix durant la resta de l'any. La 'visió des dels quarters d'hivernada' pot aportar informació important i complementaria a la de l'estudi dels ocells durant l'època de reproducció. Encara mes, les aportacions fetes aquí marquen una línia de base en el coneixement sobre diversos aspectes de l'ecologia, les dinàmiques hivernals, l'estratègia migratòria, l'evolució de la distribució espacial, la relació amb la població reproductora i les necessitats de conservació de la Gavina Capnegra.

Resum de resultats

En aquest estudi, desenvolupo una nova perspectiva sobre les dinàmiques poblacionals dels ocells des de les zones d'hivernada. La meva recerca demostra com l'estudi detallat de l'ecologia d'una espècie durant una part del cicle anual pot ajudar a comprendre allò que passa durant la resta de l'any.

L'estudi de paràmetres demogràfics tals com la supervivència, la fidelitat al lloc i la dispersió en una població hivernal demostren el fort vincle dels individus amb llur àrea d'hivernada, el qual no varia amb l'edat. Aquest estratègia dóna forma a la distribució hivernal dels individus, i els conforma com a veritable població amb una estructura meta poblacional. Cada subpoblació té una demografia independent, la qual ve determinada per una supervivència específica de cada àrea i nivells baixos de dispersió.

L'espècie objectiu era coneguda per l'àmplia expansió de la seva àrea de cria durant el segle XX (Cramp & Simmons 1982) però fins ara se sabia poc sobre la relació de la població reproductora amb la hivernant. Amb aquest motiu, he desenvolupat un model per inferir la ruta migratòria més probable que segueixin els ocells de primer hivern, i he trobat que la trajectòria més probable és una combinació de rutes fluvials i costaneres de manera òptima, cercant la mínima distància sobre terreny favorable. Aquesta estratègia, combinada amb la tendència individual de tornar repetidament a la mateixa àrea cada hivern, resulta en una composició concreta de la població en cada lloc, amb variacions espacials. Els ocells joves s'estableixen a la zona d'hivernada en el

seu primer any seguint una regla de probabilitat determinada per la distància, i mantenen llur elecció al llarg de la seva vida. Les poblacions hivernants de l'espècie d'estudi estan formades per individus de diferents classes de gènere i edat, en el que és un dels pocs casos documentats de migració no diferencial (Cristol *et al.* 1999). No hi ha diferències aparents, entre individus de diferents grups d'edat i rol reproductiu, respecte del temps que passen a l'àrea d'hivernada, amb l'única excepció dels ocells de primer hivern.

La meva recerca aporta una nova aproximació a l'estudi de l'escala espacial del domini vital col·lectiu durant l'època d'hivernada, així com de la seva relació amb la xarxa d'espais protegits. Una anàlisi de captura-recaptura multi-estat ha permès conèixer l'elevat grau d'intercanvi d'individus a les localitats estudiades, així com un moviment freqüent, i en capa direcció concreta, entre localitats. Aquesta forma d'hivernada dinàmica contrasta amb la fidelitat al lloc mostrada per l'espècie. El corol·lari és que el domini vital col·lectiu comprèn una gran part de la superfície de l'àrea d'hivernada, de centenars de quilòmetres, sobre la qual els individus es mouen amb freqüència entre localitats enlloc de romandre en un sol lloc. Donat que la designació d'espais protegits no es duu a terme amb una espècie al cap sinó que va dirigida als espais sobre els quals es concentren múltiples espècies (Lascelles *et al.* 2012), la protecció que ofereixen a espècies amb alta mobilitat a escala local com la Gavina Capnegra és només parcial.

Una descoberta interessant és que l'expansió a gran escala que ha experimentat l'espècie durant el segle XX ha afectat la distribució com a reproductora molt més que com a hivernant. La llarga estabilitat d'aquesta darrera, combinada amb la manca d'un augment apreciable en la mida de la població mundial de l'espècie (Cama *et al.* 2011) suggereix que el canvi històric de distribució es tractaria més aviat d'una redistribució de la població, que havia estat extremament concentrada, sobre una àrea molt més àmplia. L'expansió, que encara continua, no és comparable a la d'altres espècies que també van incrementar la seva distribució al llarg del segle XX. Aquest treball destaca el paper decisiu de l'època d'hivernada a l'hora de regular la població mundial de l'espècie i demostra que l'espècie ha d'estar limitada per esdeveniments que tenen lloc durant

l'hivern, o durant els períodes migratoris, potser vinculats a l'augment de la denso-dependència. Addicionalment hi ha proves que els ocells depenen en gran parts dels descarts de la pesca i no troben massa fonts d'alimentació alternatives, ja que freqüenten els ports pesquers en major nombre immediatament després dels caps de setmana, dies en els quals no hi ha activitat pesquera.

L'estudi de les interaccions entre les poblacions reproductora i hivernant, allà on conflueixen de manera simpàtrica, ha mostrat que ambdues poblacions tenen poques interaccions i que segueixen dinàmiques independents. Aquesta troballa apunta cap a un sistema complex que probablement encara s'està desenvolupant mentre la població reproductora es continua expandint i s'aproxima a les àrees d'hivernada. La sinhèmia trobada, és a dir la concurrència d'ocells provinents de diferents regions reproductores a la població hivernant. Aquest és un fenomen rar i probablement es tracti d'una situació transitòria (Newton 2008); per tant, resultaria interessant tornar a examinar la població hivernant transcorregudes algunes dècades, per veure com ha evolucionat la situació.

Finalment, a través d'aquest treball he pogut testar hipòtesis sobra l'estratègia migratòria, l'ecologia hivernal, els canvis en la distribució història i les necessitats de conservació de la Gavina Capnegra. Els resultats d'aquest estudi aporten el coneixement de base i milloren el que se sabia fins ara sobre aquesta espècie encara poc coneguda.

Conclusions

(1) L'estudi de la demografia des de la perspectiva de les zones d'hivernada ha permès comprendre la formació, l'estructura, la composició i la persistència de les poblacions hivernants d'una espècie migratòria. Diferents subpoblacions, cada una amb una demografia independent, s'organitzen en una estructura meta poblacional amb poc intercanvi d'individus i sense dinàmiques comunes. Paràmetres demogràfics com la supervivència, la fidelitat al lloc i la dispersió juguen un paper clau a l'hora de determinar la distribució espacial i l'estratègia general durant l'època d'hivernada.

(2) La Gavina Capnegra, l'espècie focus d'aquest treball, ha mostrat nivells alts de supervivència interanual local a l'àrea d'hivernada, que oscil·len entre 0.81 i 0.90, en funció de si es té en compte l'efecte de la pèrdua d'anelles. Aquest valor demostra un lligam molt alt amb la zona d'hivernada, comparable al que s'ha observat en colònies de cria a Bèlgica i Holanda. La probabilitat de supervivència local aparent no està relacionada amb l'edat de l'ocell, de manera que s'espera que els individus continuïn a fer servir la mateixa àrea d'hivernada de marea repetida al llarg dels anys, suposant que segueixin vius.

(3) L'escala espacial de l'àrea d'hivernada que utilitzen les Gavines Capnegres és més gran que la localitat individual. Els individus es mouen lliurement i amb freqüència entre les diverses localitats, sense cap direcció aparent i en qualsevol moment de l'època hivernal. Aquest resultat contrasta amb els avantatges teòrics de la fidelitat al lloc a escala local (el coneixement acumulat comporta un augment de la seva aptitud. Més probablement indicaria que les dimensions de l'àrea d'hivernada que fan servir de manera efectiva els individus de Gavina Capnegra siguin en l'escala regional (centenars a milers de km^2) més que en l'escala local (desenes de km^2).

(4) Moviments freqüents i regulars a localitats dintre del sistema d'estudi porten els individus més enllà de les àrees protegides en territori desconegut. Aquest estudi demostra el desacoblament entre les necessitats d'espai de les Gavines Capnegres hivernants i les dimensions i l'emplaçament de les àrees protegides designades per a l'espècie.

(5) Les descobertes en aquest estudi relatives a la ruta migratòria probable entre les àrees de cria i les d'hivernada validen la hipòtesi ja formulada per Mayaud l'any 1954 que l'espècie segueix els rius principals en els seus desplaçaments a través d'Europa. Els rius més destacables per a les Gavines Capnegres hivernants al NE de la Península Ibèrica són el Danubi, el Rin i el Roine. Les Gavines Capnegres també probablement travessin braços de mar, especialment l'Egeu, l'Adriàtic i el

Mediterrani central. L'expansió recent de l'àrea de distribució reproductora de l'espècie probablement hauria seguit les mateixes rutes migratòries.

(6) L'aparició d'una nova ruta migratòria en direcció Nord–Sud al llarg de la costa atlàntica europea, també sospitada per Mayaud (1954), és compatible amb els models de migració desenvolupats en aquest estudi i la variació observada en la composició de les poblacions hivernants al llarg de la Península Ibèrica. La nova ruta es situa en l'eix oposat a aquells que es coneixien anteriorment per a l'espècie (Est–Oest). S'ha desenvolupat en menys d'un segle i demostra la microevolució tan dinàmica en la Gavina Capnegra.

(7) L'extraordinària expansió de l'àrea de distribució reproductora de la Gavina Capnegra, amb un creixement del 750% en 60 anys, no té paral·lel en la distribució hivernal, que només va créixer un 25% en el mateix període. El fet que la població mundial no hagi augmentat aparentment malgrat l'expansió espacial s'ha d'interpretar com a indicadora que l'espècie està limitada per esdeveniments que tenen lloc durant la hivernada, o potser durant les migracions. Aquest fet afegeix valor de conservació de les àrees d'hivernada, ja que poden jugar un paper decisiu en la viabilitat a llarg termini de la població.

(8) La descoberta d'alts nivells de fidelitat a les àrees d'hivernada, independentment de l'edat de l'ocell, i la constatació que la població hivernant en el sistema d'estudi està formada d'individus repetidors de totes les edats donen validesa a la idea que la Gavina Capnegra es troba entre la minoria d'espècies amb una migració no diferencial. De la mateixa manera que per a les altres espècies amb una estratègia similar, pot resultar difícil comprendre les raons ecològiques i etològiques que la justifiquin, però determina estratègies importants de cara a la conservació ja que resulta probable que les àrees protegides comprenguin tots els estrats de la població.

(9) De manera excepcional, a la Gavina Capnegra, les poblacions reproductores no es hivernen de manera separada; la composició de la població de les diferents

àrees d'hivernada està formada per una representació de totes les poblacions reproductores ("sinhèmia"), en proporcions variables en funció de la distància a cada zona de cria. La troballa de sinhèmia en les poblacions hivernants d'aquesta espècie demostra una situació probablement de transició lligada a l'àmplia i ràpida expansió de la seva distribució com a reproductora, que històricament no ha tingut paral·lel en una expansió equivalent de l'àrea de distribució hivernal.

(10) La població que hiverna al sistema d'estudi i la població reproductora establerta recentment a la rodalia estan formades per individus diferents, i segueixen dinàmiques independents una de l'altra. Les poblacions mostren una gran tendència a mantenir la seva pròpia inèrcia i les seves estratègies espacials, i poden trigar un temps abans que els ocells d'una o altra comencin a aprofitar les noves oportunitats (per reproduir-se o per hivernar) que sorgeixen a prop de les àrees que ocupen. Els canvis importants en la distribució (p.ex., els que es poden esperar com a resultat de canvis ambientals) no tenen per què ser necessariament processos simples o lineals.

(11) Els mètodes estadístics de captura-recaptura són una tècnica eficaç per a l'estudi de les dinàmiques poblacionals d'ocells hivernants, especialment quan les espècies han estat objecte d'amplis programes d'anellament en una gran part de la seva àrea de distribució i la mida de la mostra dels exemplars reavistats és gran. En comparació amb els estudis d'animals marcats amb emissors, una mida de mostra equivalent al 2,5% de la xifra total d'animals marcats de l'espècie, com és el cas d'aquest estudi, redueix la incertesa en l'extrapolació dels resultats observats a tota la població.

(12) Cal considerar les poblacions hivernants com a veritables entitats demogràfiques mes que com a simples conjunts aleatoris i homogenis d'individus. L'estudi de la demografia des de la zona d'hivernada ens pot ajudar a comprendre el que succeeix durant la resta de l'any. La visió 'des dels quarters d'hivernada' pot aportar informació important i complementaria de l'estudi dels ocells durant el

període de cria, per tal d'assolir la plena comprensió de l'ecologia de les especies durant el cicle anual complet.

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Appendix – Tables

	No. of grid cells Mayaud (1954)	No. of grid cells current (2015)	% increase	% overlap
breeding	15	127	750	12
wintering	102	128	25	73

Table 1. Comparison between the number of occupied 50 x 50 km grid cells in Fig. 3 (current distribution, 2015) and Fig. 4 (data from Mayaud 1954) during both the breeding and the wintering season.

	YEAR	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	Total
Belgium	chick	0	0	0	30	0	1	9	71	60	205	67	66	102	684	178	240	162	125	60	147	154	**2361**
	flying	0	0	0	0	1	0	1	45	21	43	95	103	646	324	31	131	249	448	325	71	57	**2591**
Netherlands	chick	0	35	42	27	109	98	78	139	160	208	84	35	19	2	2	0	97	0	1	0	0	**1136**
	flying	0	24	11	11	0	14	3	0	5	21	34	9	20	0	0	0	0	4	56	0	0	**212**
Denmark	chick	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	6	6	1	1	**20**
	flying	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	**5**
Norway	flying	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**
France - ATL	chick	0	0	0	0	0	0	3	5	26	8	22	52	181	23	172	144	72	105	237	230	891	**2171**
	flying	0	0	23	15	66	18	56	30	47	40	26	13	83	59	32	50	7	163	82	32	24	**866**
France-MED	chick	0	0	0	0	0	0	0	0	0	0	0	0	222	0	0	0	233	253	0	0	0	**708**
	flying	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Czech Rep.	chick	0	0	0	0	0	0	0	0	0	12	2	9	8	22	14	9	21	9	7	2	19	**134**
	flying	0	0	0	0	0	0	0	0	0	0	0	3	4	0	2	11	8	1	5	1	6	**41**
Slovakia	chick	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	2	0	0	0	0	0	**17**
	flying	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	10	5	0	5	0	1	**23**
Hungary	chick	0	0	0	0	0	107	180	204	208	263	43	22	80	197	100	139	74	11	236	249	322	**2435**
	flying	0	0	0	0	0	0	0	0	22	6	44	12	14	19	15	0	5	0	7	5	12	**161**
Poland	chick	0	0	0	0	0	0	0	0	0	0	0	3	9	3	12	13	14	35	78	19	31	**217**
	flying	0	0	0	0	0	0	0	0	0	0	0	1	20	12	20	29	42	28	88	17	21	**278**
Serbia-Mont.	chick	0	0	0	0	0	0	3	0	0	0	0	0	8	0	2	20	57	9	8	10	26	**143**
	flying	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	11	6	1	13	**37**
Italy	chick	0	104	167	193	146	66	28	35	165	458	281	264	87	226	281	266	0	40	189	292	147	**3435**
	flying	0	0	0	0	0	1	0	0	1	35	19	49	123	123	53	54	141	104	118	26	7	**854**
Spain	flying	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	3	0	0	**24**
Germany	chick	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38	122	124	95	72	**451**
	flying	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	74	56	47	**203**
UK	chick	0	0	0	0	0	0	0	0	0	4	2	6	30	0	0	0	6	4	0	0	0	**52**
	flying	0	0	0	0	0	0	0	0	14	0	15	0	4	0	31	0	0	0	0	0	0	**64**
Ireland	chick	0	0	0	0	0	0	0	0	0	0	0	1	0	3	6	0	3	1	0	0	0	**14**
	flying	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Ukraine	chick	0	0	0	0	0	292	0	0	0	300	975	566	0	1544	300	0	0	0	300	0	0	**4277**
	flying	0	0	0	0	0	4	0	0	0	0	0	90	0	0	0	0	0	0	0	0	0	**94**
Greece	chick	0	0	0	0	0	0	0	0	145	0	118	148	0	354	0	0	0	140	155	57	50	**1167**
Turkey	chick	0	0	0	0	0	0	0	79	225	107	77	0	137	0	100	80	0	30	0	0	0	**835**
Russia	chick	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	**20**
Romania	chick	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	0	**19**
TOTAL																							**25066**

Table 2. Number of colour-ringed Mediterranean Gulls per country, 1989-2009. 'Pulli' = unfledged chicks; 'fledged' = full-flying birds of any age.