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

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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

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 preroost 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	$\varphi_1;\ldots;\varphi_7$		*t*	5,424.672	355.340	0.000	12	1,226.174
15	$\varphi_1;\ldots;\varphi_5$		*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; $\varphi_1;\ldots;\varphi_n$ = 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; '×' = 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:

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

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.

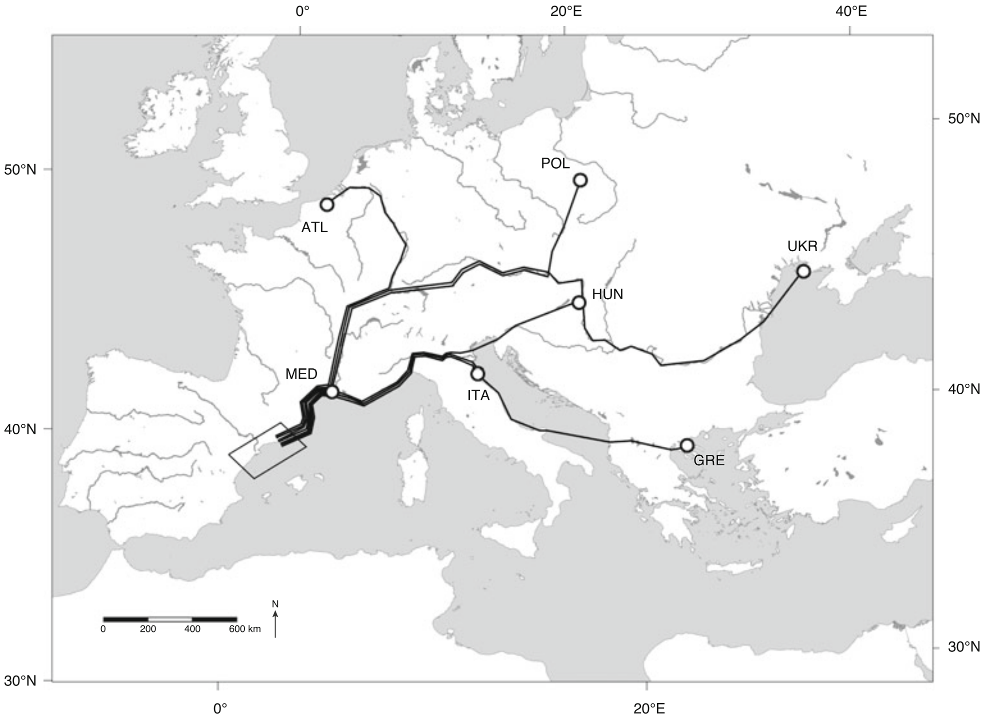

Fig. 1 Hypothetical sketch of the migratory routes of first-winter Mediterranean gulls *Larus melanocephalus* from their colonies of birth (the weighted centroids of the 7 groups of ringing sites: "ATL", Atlantic France, Belgium, The Netherlands and Germany; "MED", Mediterranean France; "ITA", Italy; "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 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

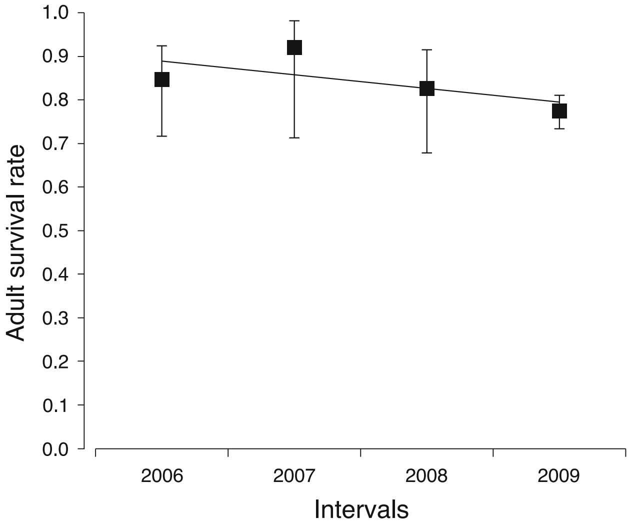

Fig. 2 Inter-annual apparent local survival of Mediterranean gulls after hatch-year as obtained from the time-dependent model (model 3 in Table 2; square symbols with 95 % confidence interval). The *line* shows the linear trend in survival equivalent to 4 % annual tag loss, as estimated by the retained model (model 1)

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”).

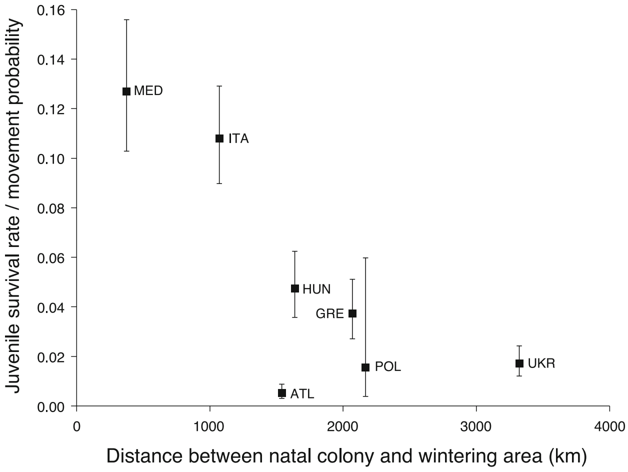

Fig. 3 Plot of juvenile immigration probability against distance. Models with spatial variation in the survival of juvenile birds (first-time immigrants) obtained the lowest AICc values (Table 2). The results for the retained model 1 are plotted here against the distance from the ringing areas, calculated 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

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

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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