

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?

Carles Carboneras^{1*}, Raül Aymí², Albert Cama¹, Camille Duponcheel³, Joan Ferrer¹, Renaud Flamant⁴, Salvador García⁵, Jorge Garzón⁶, Antonio Gutiérrez⁷, Marc Olivé⁸, Martin Poot⁹



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).

¹ Universitat de Barcelona, Dept. Biologia Animal, Facultat de Biologia, Avda. Diagonal 645, 08028 Barcelona, Spain; * - address for correspondence: carles@gavines.org / ² Institut Català d'Ornitologia, Barcelona, Spain / ³ 59181 Steenwerck, France / ⁴ Belgian Ornithological Research Association, BELORA, Belgium / ⁵ Instituto Español de Oceanografía, Málaga, Spain / ⁶ 18179 Víznar, Granada, Spain / ⁷ 15403 Ferrol, A Coruña, Spain / ⁸ 08800 Vilanova i la Geltrú, Barcelona, Spain / ⁹ 4101 KH Culemborg, The Netherlands

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 \pm 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.

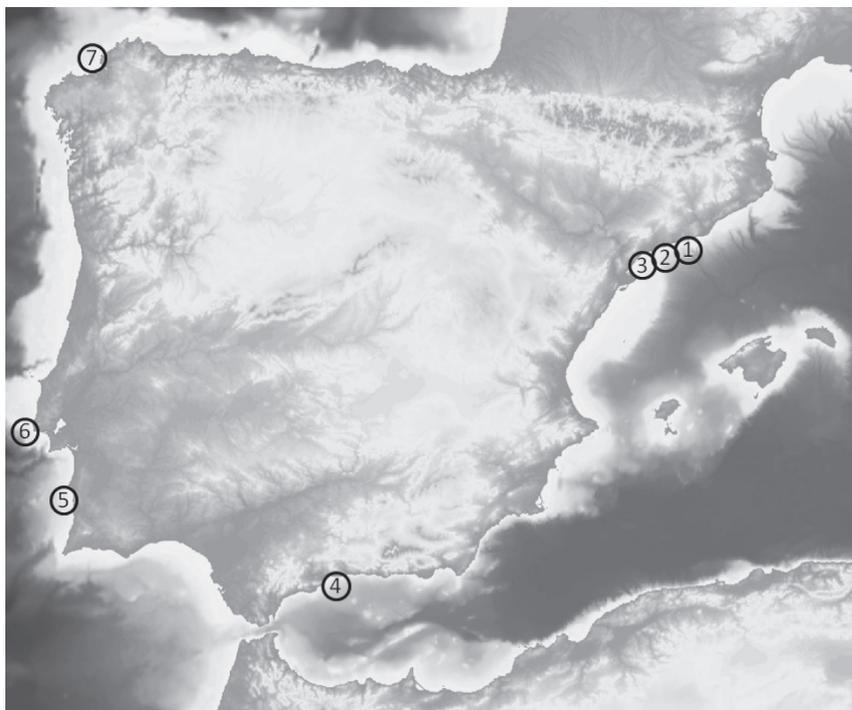


Figure 1. The Iberian peninsula with the location of the 7 sites included in this study: (1) Vilanova i la Geltrú; (2) Tarragona; (3) Cambrils; (4) Málaga coast; (5) Vilanova de Milfontes; (6) Lisbon coast, Cascais & Tagus estuary; (7) Ares, Galicia.

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).

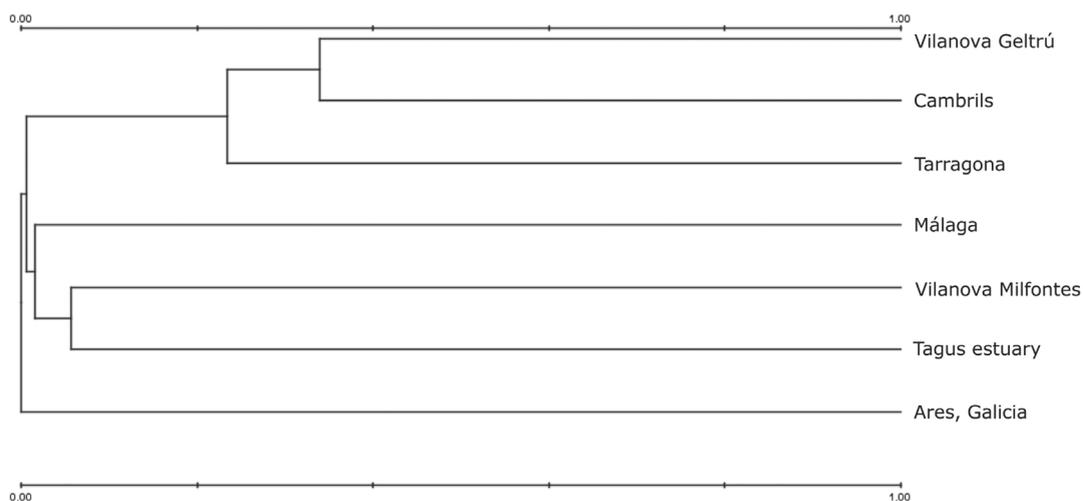


Figure 2. Dendrogram showing the affinity between the 7 sites based on the number of individual Mediterranean gulls *Larus melanocephalus* recorded in common. The coefficient of similarity for each pair of sites and the total number of birds recorded at each site are the same as shown in tables I & II.

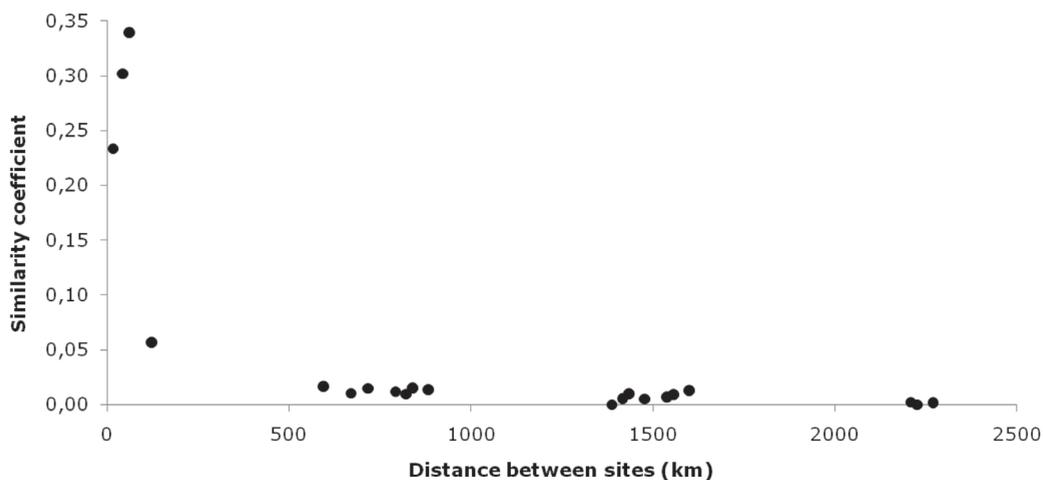


Figure 3. Coefficient of similarity between pairs of sites in relation to the distance between the sites. Distances were calculated assuming a coastal route (see text for details).

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 disproportionately 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).

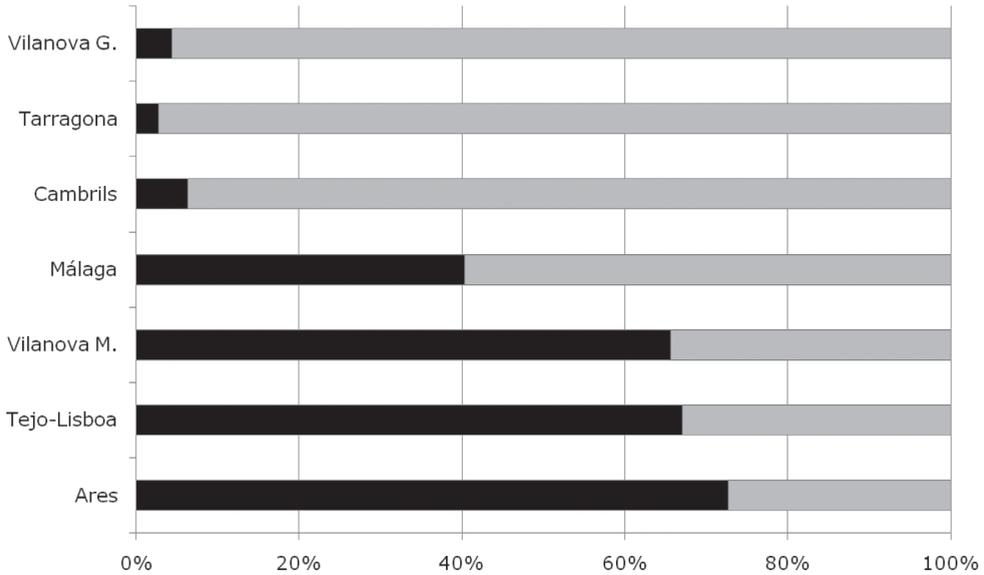


Figure 4. Proportion of Atlantic (in black) vs. Mediterranean (in grey) individuals recorded at each site, according to the localisation of their colony of origin. The division follows the same rules as described for Table II.

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 <i>n</i>	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 occurred. 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 conservation 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.

Acknowledgements: special thanks are due to a large number of people who made possible the present study, in particular the ringers and coordinators of the national ringing programmes: Tatyana Ardamatskaya, Nicola Baccetti, Martin Boschert, Albert Cama, Josef Chytil, Monika Czyzak, Camille Duponcheel, Joan Ferrer, Pete Findley, Renaud Flamant, Vassilis Goutner, Lars Hansen, Sühendan Karauz, Peter Meininger, Antonina Rudenko, Vladimir Slobodnik, Jan Svetlik, Adriano Talamelli, Monika Zielinska, Andreas Zours, Karcza Zsolt and Antun Zuljevic. We also thank the other collaborators who kindly provided additional data, which we used for some of the tests. The following observers contributed >20 readings: Manuel Enrique Carballal, José Luis Greño, Ferrán López, Miguel Tirado. Raül Ramos, José Pedro Granadeiro and an anonymous referee reviewed and improved an earlier draft. Acknowledgements are extended to the organisers of the *VI Congreso de Ornitología da SPEA & IV Congreso Ibérico de Ornitología*, in particular to Vanessa Oliveira and Iván Ramírez, who worked very hard to make the conference a success.

REFERENCES

- Arcos, J.M., J. Bécares, B. Rodríguez & A. Ruiz. 2009. *Áreas Importantes para la Conservación de las Aves marinas en España*. LIFE04NAT/ES/000049-Sociedad Española de Ornitología (SEO/BirdLife). Madrid.
- Bekhuis, J., Meininger, P.L., Rudenko, A.G., 1997. Mediterranean Gull *Larus melanocephalus*. In: Hagemijer, E.J.M., Blair, M.J. (Eds.) *The EBCC Atlas of European Breeding Birds: their distribution and abundance*. T & A.D. Poyser, London, pp. 324-325.
- Bermejo, A., Carrera, E., de Juana, E. & Teixeira, A. M. 1986. Primer censo general de gaviotas y charranes (Laridae) invernantes en la Península Ibérica (enero 1984). *Ardeola*, 33: 47-68.
- Bernis, F. 1966. *Aves migradoras ibéricas: según anillamientos en Europa*. Vol. I. SEO, Madrid.
- Cama, A. 2010. Seabird distribution patterns and ecological factors driving larid presence at the Ebro delta shelf (NW Mediterranean). PhD thesis, Univ. Barcelona.
- Carboneras, C. 2009. Selection of winter habitat in a gregarious long-lived seabird. MSc thesis, Univ. Barcelona.
- Carrera, E.; Ferrer, X. , Martínez-Vilalta, A. & Muntaner, J. 1981. Invernada de láridos en el litoral mediterráneo catalán y levantino. *Ardeola*, 28: 35-50.
- Díaz, M., Asensio, B. & Tellería, J.L. 1996. *Aves Ibéricas. Vol. I. No Paseriformes*. J.M. Reyero Ed., Madrid.
- Dies, B. & Dies, J. I. 2009. *Afianzamiento de la gaviota cabecinegra en l'Albufera de Valencia*. Available at <http://www.birdingalbufera.es>
- Esler, D. 2000. Applying Metapopulation Theory to Conservation of Migratory Birds. *Conserv. Biol.*, 14(2): 366-372.
- Gower, J.C., 1971. A General Coefficient of Similarity and Some of Its Properties. *Biometrics* 27(4), 857-871.
- Hanski, I. 1999. *Metapopulation Ecology*. New York: Oxford University Press.
- Isenmann, P. 1972. Notas sobre algunas especies de aves acuáticas en las costas mediterráneas españolas (Enero 1972). *Ardeola*, 16: 242-245.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity

- for biological control. *Bull. Entomol. Soc. Am.*, **15**: 237–240
- Mayaud, N. 1954. Sur les migrations et l'hivernage de *Larus melanocephalus* Temminck. *Alauda*, **22**: 225-246.
- Meininger, P.L. 1999. The history of colour-ringing Mediterranean Gulls *Larus melanocephalus*. In: Meininger, P.L., Hoogendoorn, W., Flamant, R., Raavel, P. (Eds) Proceedings of the 1st International Mediterranean Gull Meeting, Le Portel, Pas-de-Calais, France, 4-7 September 1998. EcoNum, Bailleul, pp. 61-68.
- Molina, B. 2008. Gaviota cabecinegra. Pp. 10-20 in: A. Bertolero, M. Genovart, A. Martínez-Abraín, B. Molina, J. Mouríño, D. Oro & G. Tavecchia. *Gaviotas cabecinegra, picofina, de Audouin y tridáctila, y gavión atlántico en España. Población en 2007 y método de censo*. 74 pp. SEO/BirdLife. Madrid.
- Newton, I., 2008. *The migration ecology of birds*. Academic Press, London.
- Paterson, A.M. 1997. *Las Aves marinas de España y Portugal = Seabirds of Spain and Portugal*. Lynx Edicions: Barcelona, Spain. ISBN 84-87334-21-0. 444 pp.
- Poot, M. & Flamant, R. 2006. Numbers, behaviour and origin of Mediterranean gulls *Larus melanocephalus* wintering along the west coast of Portugal. *Airo* **16**: 13-22.
- Ramírez, I., P. Geraldés, A. Merinho, P. Amorim & V. Paiva. 2009. *Áreas Marinhas Importantes para as Aves em Portugal*. Projecto LIFE04NAT/PT/000213 – Sociedade Portuguesa Para o Estudo das Aves. Lisboa.
- Ward, J.H., 1963. Hierarchical Grouping to Optimize an Objective Function. *Journal of the American Statistical Association* **58**(301), 236-244.
- Williams, C. K., Samuel, M.D., Baranyuk, V.V., Cooch, E.G. & Kraege, D. 2008. Winter Fidelity and Apparent Survival of Lesser Snow Goose Populations in the Pacific Flyway. *Journal of Wildlife Management*, **72** (1): 159-167.