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SELECTION OF WINTER HABITAT BY A GREGARIOUS LONG-LIVED SEABIRD

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Selection of winter habitat by a gregarious long-lived seabird

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ABSTRACT

Background: The ecology of seabirds in the winter season, when they are free to move between areas of different ecological value, has been little studied. The Mediterranean Gull *Larus melanocephalus* is a migratory species that concentrates (often, in the thousands) in a few traditional areas on the Mediterranean coast, with a diet based primarily on fish discards. Other, perhaps suitable, areas remain unoccupied.

Methodology/Principal Findings: I obtained and analysed data on 45 fishing ports (19 occupied by the species, 26 unoccupied) situated along the NW Mediterranean coast. The variables measured abundance of theoretically positive/negative factors or distance to sources of ecological relevance, so were linear in all cases. An exploratory PCA found 2 principal components and significant correlation of *Larus melanocephalus* numbers with spatial aggregation (2 variables) and primary productivity (Chl-*a*). Further, a linear discriminant analysis (Fisher's LDF) produced a model with 5 variables: spatial aggregation (2 variables), beach length and agricultural hinterland (2 variables). The model allowed for successful discrimination of 93% occupied *vs.* unoccupied ports (42 of 45 matchings). My data support the importance of social factors (aggregation) in shaping the winter distribution of Mediterranean gulls, which tended to occur over areas of productive marine waters close to a countryside with traditional Mediterranean agriculture.

Conclusions/Significance: The role of social factors in the selection of winter habitat in the Mediterranean gull reveals the existence of a two-step process: birds choose to settle where there are already other birds (step 2), but the place of concentration requires a combination of ecological characteristics (step 1). This means that in order to be occupied a site needs to appear suitable both from the ecological and also from the social point of view. Other traits of the species (conspecific attraction, site-fidelity, longevity) presumably contribute to and reinforce this strategy.

[Selección del hábitat invernal en una especie de ave marina gregaria y longeva]

Carles Carboneras

RESUMEN

Antecedentes: El estudio de la ecología de las aves marinas durante la época invernal, cuando pueden moverse libremente entre áreas de distinto valor ecológico, ha recibido poca atención. La Gaviota cabecinegra *Larus melanocephalus* es una especie migratoria que realiza concentraciones (a veces, de varios miles) en algunas zonas tradicionales de la costa mediterránea, y cuya dieta se basa principalmente en los descartes pesqueros. Otras zonas, quizás adecuadas, permanecen sin ocupar.

Métodos/Principales hallazgos: Se obtuvieron y analizaron datos correspondientes a 45 puertos de pesca (19 ocupados por la especie, 26 sin ocupar) situados a lo largo de la costa del Mediterráneo noroccidental. Las variables miden cuantitativamente factores teóricamente positivos/negativos, o bien la distancia a fuentes ecológicamente relevantes, de forma que son lineales en todos los casos. En un análisis de CP realizado de forma exploratoria, se obtuvieron dos componentes principales y una correlación significativa de la abundancia de *Larus melanocephalus* con la agregación espacial (2 variables) y con la productividad primaria (clorofila-*a*). Posteriormente, en un análisis discriminante lineal (Fisher LDF) se obtuvo un modelo con 5 variables: agregación espacial (2 variables), longitud de la playa y área de influencia agrícola (2 variables). El modelo permitió discriminar con éxito el 93% de los puertos ocupados frente a los no ocupados (42 de 45 aciertos). Los datos apoyan la importancia de los factores sociales (agregación) a la hora de moldear la distribución invernal de la Gaviota cabecinegra, que tiende a frecuentar zonas marinas de alta productividad situadas junto a paisajes de agricultura mediterránea tradicional.

Conclusiones/Significación: El papel de los factores sociales en la selección del hábitat invernal en la Gaviota cabecinegra pone de relieve la existencia de un proceso en dos fases: los individuos eligen para asentarse aquellas zonas donde ya se encuentran otras aves (fase 2), pero el lugar de concentración debe reunir una combinación de características ecológicas (fase 1). Esto significa que, para ser ocupado, un lugar debe parecer adecuado tanto desde el punto de vista ecológico como social. Otras características de la especie (atracción conespecífica, fidelidad a los lugares de invernada, longevidad) previsiblemente contribuyen a esta estrategia y la refuerzan.

[Selecció de l'hàbitat hivernal en una espècie d'au marina gregària i longeva]

Carles Carboneras

RESUM

Antecedents: L'estudi de l'ecologia de les aus marines durant l'època hivernal, quan poden moure's lliurement entre àrees de diferent valor ecològic, ha rebut poca atenció. La Gavina capnegra *Larus melanocephalus* es una espècie migratòria que fa concentracions (a vegades, de diversos milers) en algunes zones tradicionals de la costa mediterrània, amb una dieta basada principalment en els descarts pesquers. Altres zones, potser adequades, romanen sense ocupar.

Mètodes/Principals troballes: Es van obtenir i analitzar les dades corresponents a 45 ports de pesca (19 ocupats per l'espècie, 26 sense ocupar) situats al llarg de la costa del Mediterrani nord-occidental. Les variables mesuren quantitativament factors teòricament positius/negatius, o bé la distància a fonts ecològicament rellevants, de manera que són lineals en tots els casos. En una anàlisi exploratòria de CP, es van obtenir dues components principals i una correlació significativa de l'abundància de Larus melanocephalus amb l'agregació espacial (2 variables) i amb la productivitat primària (clorofil·la-*a*). Posteriorment, en una anàlisi discriminant lineal (Fisher LDF) es va obtenir un model amb 5 variables: agregació espacial (2 variables), longitud de la platja i àrea d'influència agrícola (2 variables). El model va permetre discriminar amb èxit el 93% dels ports ocupats (42 de 45 encerts). Les dades recolzen la importància dels factors socials (agregació) a l'hora de modelar la distribució hivernal de la Gavina capnegra, que tendeix a freqüentar zones marines d'alta productivitat situades a prop de paisatges d'agricultura mediterrània tradicional.

Conclusions/Significació: El paper dels factors socials en la selecció de l'hàbitat hivernal per part de la Gavina capnegra posa de relleu l'existència d'un procés en dues fases: els individus trien per assentar-se aquelles zones on ja hi ha altres ocells (fase 2), però el lloc de concentració ha de reunir una combinació de característiques ecològiques (fase 1). Això significa que, per ser ocupat, un lloc ha de ser adequat, tant des del punt de vista ecològic om social. Altres característiques de l'espècie (atracció conespecífica, fidelitat als llocs d'hivernada, longevitat) previsiblement contribueixen a aquesta estratègia i la reforcen.

I. Introduction

THE WINTER SEASON

The study of habitat selection has mostly been focused on the breeding season, as breeding performance may provide an indication, or even a direct measurement, of individual fitness and/or of habitat quality (Newton 1998). Studies of selection of habitat for reproduction have allowed the development of theoretical models, such as the ‘ideal free’ and the ‘ideal despotic’ distributions (Fretwell & Lucas 1970) and the testing of their predictions in many types of organisms, including seabirds (cfr. e.g. Oro 2008).

The distribution of organisms over space outside of the breeding season is more difficult to predict, although this choice may be equally important in terms of individual fitness. Perhaps not surprisingly, the settling of organisms in the winter months and the decision processes implied –what leads an individual to eventually establish in a given area in order to spend the least productive part of the annual cycle– have received little attention. Migratory birds are highly mobile and (in principle) free to settle, so they may constitute an ideal subject to study this process, and how it links to the observed distribution of numbers over a known region.

From an ecological perspective, for birds, the winter season differs significantly from the summer season in at least two aspects: (a) food intake needs are limited to each individual and, although its energetic requirements may be greater in this season because of the lower temperatures, its decisions are not conditioned by the need to feed others, and (b) each bird can vary its location daily to try to be best positioned to exploit the available resources, as there is no central place (such as the nest) to return to.

In the temperate zone, many habitats change in structure and extension through the seasons. Often, they also vary in the resources and opportunities they offer. Migratory birds have evolved to exploit winter habitats as effectively as they exploit their breeding habitat. Therefore, they must make choices as to the areas they inhabit. Basic ecological principles like competition and predation apply also during the winter months.

THE SPECIES

The Mediterranean Gull *Larus melanocephalus* is a small- to medium-sized gull (300 g) of the Mediterranean basin. Philogenetically, it appears to be most closely related to *L. relictus* and *L. ichthyaetus* of Asia, to *L. hemprichii* and *L. leucophthalmus* of the Red Sea and NW Indian Ocean, and to *L. audouinii* of the Mediterranean and E Atlantic, with which it forms a distinct clade, the ‘black-headed’ species group, an early division of the tribe Larini that probably differentiated in the southern/central Palearctic region (Crochet *et al.* 2000).

Larus melanocephalus is strongly gregarious at all times. It feeds on a wide variety of organisms in virtually all trophic levels (see Table I in Annex). Most 'prey' are taken on the ground or on water, generally in open landscapes, but also in cultivated areas of open canopy such as olive groves. The food items chosen by this species include many that form temporarily superabundant concentrations: terrestrial arthropods on Russian steppes (Cramp & Simmons 1983), fallen olives in Spain and Tunisia (Carrera 1987, Baccetti & Smart 1999), *Artemia salina* in Camargue saltpans (Isenmann 1975), fish discards on Spanish coast (Isenmann 1972, Carrera 1987), earthworms, molluscs, etc. (see Table I for details & sources). The concept of social foraging has received much attention (see review in Giraldeau & Caraco 2000) but it is still difficult to delimit what constitutes a 'social forager'; the category most probably encompasses the Mediterranean gull, as it typically congregates for feeding on swarming items and has been observed to gain competitive advantage against larger or more aggressive seabirds by forming dense flocks around food sources (e.g. over trawler discards) (*pers. obs.*).

The species shows great plasticity in its choice of habitats. Goutner & Isenmann (1993) characterise the typical habitat of this species as 'grassy offshore and inshore islands with lagoons for breeding and a steppic cultivated or uncultivated hinterland where the birds collect their diet based on various invertebrates and vertebrates'. In winter, the species mainly chooses offshore waters of the western Mediterranean basin where it fishes and/or follows trawlers, but also uses coastal inland habitats (Goutner & Isenmann *op. cit.*).

DISTRIBUTION

Formerly a near-endemic of the Mediterranean-Black Sea region, in the 1970s-1990s, the Mediterranean gull spread its breeding range to include the Atlantic coast of central Europe (Benelux, France, Great Britain), with a further extension inland towards the central plains of the European continent, almost always linked to lakes and lowland marshes (Burger & Gochfeld 1996). There is still some debate as to whether this significant shift in distribution was the consequence of an earlier population increase at its breeding stronghold on the Black Sea coast (e.g. Cramp & Simmons 1983, Chernichko 1993, Van Impe 2005) or if it was attributable to a redistribution of numbers coincident with population changes in that region (e.g. Rudenko 1996, Bekhuis *et al.* 1997, Ardamatskaya 1999).

Its presence as a winter visitor in the NW Mediterranean has long been documented (Saunders 1871, Chapman & Buck 1893, Mayaud 1954, Isenmann 1976, Carrera *et al*. 1981, Bermejo *et al.* 1986). The former two authors also cite the species as breeding in southern Spain in May 1867-68 and again in 1883; sporadic breeding in Iberia still continues to this day (Molina *in* Martí & del Moral 2003, Dies & Dies 2009) but proper establishment has not occurred.

Winter census data indicate that there may have been an overall increase in the total number of individuals present 1970s-2000s, although it is difficult to confirm this because of the great differences in methodology. It is certain, however, that there have not been major changes in the occupied area over this period. Table II (in Annex) summarises the results of the surveys carried out on the Spanish Mediterranean coast since the 1970s and fig. 1 shows those data on the map.

OBJECTIVES

The overall aim of this study is to find the reasons that best explain the observed distribution of *Larus melanocephalus* in the NW Mediterranean in winter. The hypothesis to be tested is that the observed distribution is not a mere product of chance but, rather, it has a biological and/or an ecological basis. This can be measured as the result of a combination of variables.

To provide a robust answer to the aforementioned question, this study specifically aims to:

(a) synthesize and illustrate the current distribution of *Larus melanocephalus* in the winter months in the NW Mediterranean, and compare it with the data available from previous decades;

(b) find differences between the localities situated along a N – S gradient that might explain the presence/absence of the species;

(c) consider the mechanisms that might be acting and influencing the spatial distribution of the species; find evidence of their possible effect

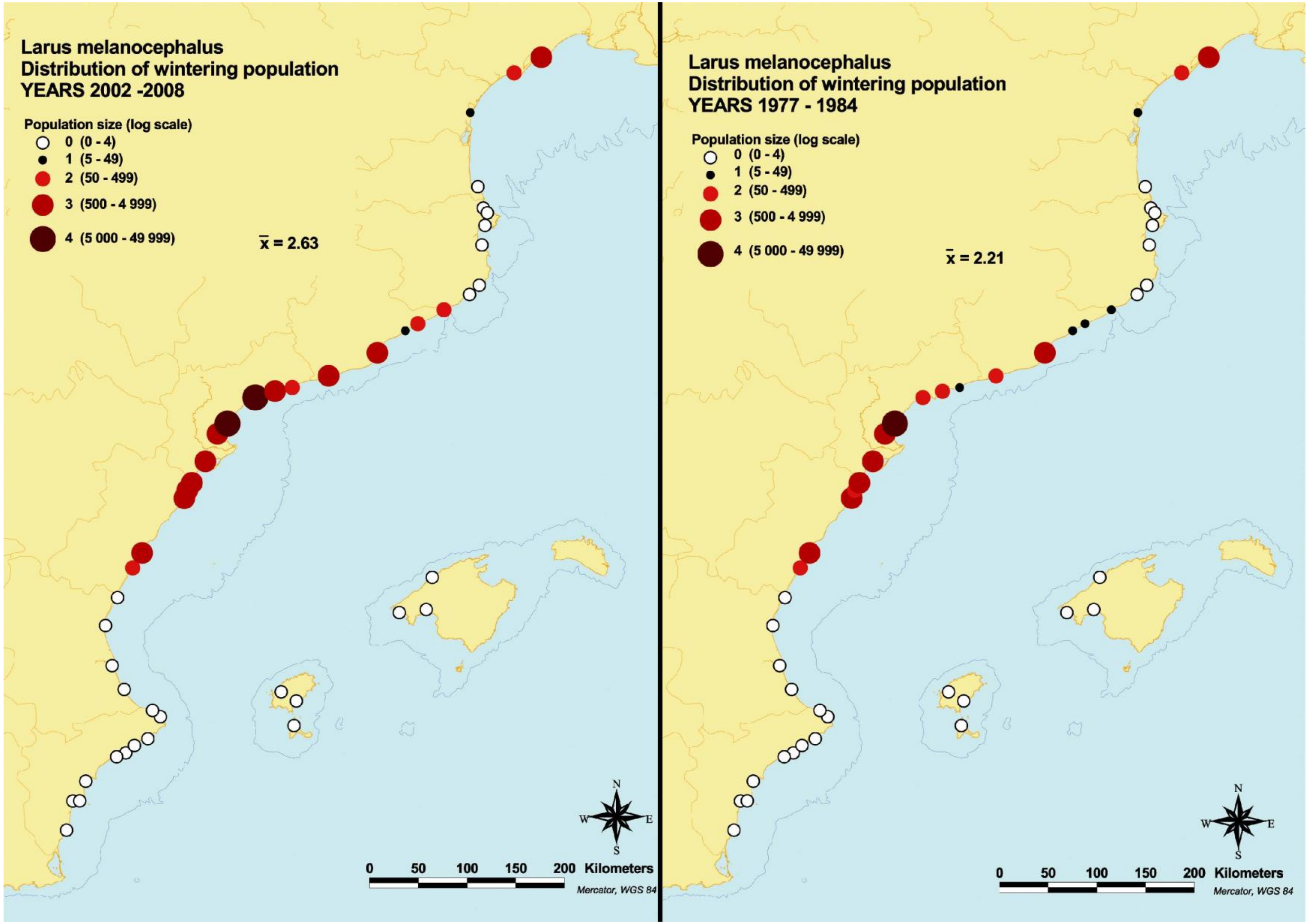

Fig. 1. Location of the 45 sites and Mediterranean gull *Larus melanocephalus* winter distribution and population size in log_{10} scale for the two periods 1977-1984 (right) and 2002-2008 (left) considered in this study. See text and Table II (Annex) for details.

II. Study area and methods

CHOICE OF STUDY AREA

Given the clumped distribution of Mediterranean gulls in the NW Mediterranean in winter (fig. 1), for the purpose of this analysis it was decided that the study area should encompass a good selection of sites where the species was regularly present in the winter season (‘occupied’ sites) and also those areas not inhabited by *Larus melanocephalus* in the winter months (‘empty’ sites). Defining a ‘site’ is difficult for such a mobile species, so fishing ports were chosen as the centroid for each locality. This corresponds well with the species’ dependence on fish discards for food (Isenmann 1972, Carrera 1987) and reduces one degree of freedom.

45 localities (19 ‘occupied’ + 26 ‘empty’) were selected for this study and are listed in Table II (Annex). The sites are contiguous fishing ports situated along a N–S gradient, from Sète (43.40°N, Golf du Lion, France) to Torrevieja (37.97°N, Alicante, Spain). In addition, 6 fishing ports from the westernmost Balearic Is (Ibiza, Formentera, Mallorca) were also included, given their proximity to ‘occupied’ sites on the mainland and, so, their potential for habitat suitable for this species.

DESCRIPTION OF THE DATA

For each locality, data on *Larus melanocephalus* numbers, plus 21 independent variables were obtained. Mediterranean gulls often concentrate in large flocks and the spatial distribution of these may change over small periods of time (subject to, e.g., disturbance). Therefore, data on the number of birds present at each site were obtained from several comprehensive winter surveys done in the periods 1977-1984 and 2002-2008. The censuses were carried out in mid-January by official personnel and experienced volunteers with local knowledge and were specifically designed to provide a picture of the presence and numbers of gulls and other relevant waterbirds. This helped reduce bias, as many counts were done simultaneously in various localities. Further, in order to avoid the effects of interannual variation due to stochastic reasons, data were grouped and transformed into a logarithmic scale by order of magnitude for the analyses. Localities with censuses ≤ 4 individuals were given a value of 0 in the $\log_{10}$ scale, as such small numbers were considered irrelevant for this widely gregarious species and might have brought in confusion. Additionally, I reviewed and compiled all relevant winter observations of Mediterranean gulls published in the regional yearbooks and local literature and added those data to the results summarised in Table I (Annex).

For the independent variables, magnitude values were obtained from official statistics sources, and distances were calculated from satellite images through GoogleEarth™ (under CGS-WGS84, Google Inc. 2009). Presence/absence data (e.g. a reservoir relatively close to the site) were taken as distance to the nearest point with such attribute, so that all data became linear, although only a few showed a normal distribution (fig. 2 in Annex).

The variables measured are described in Table III in Annex. Two variables were designed specifically to measure spatial aggregation: distance to nearest 'occupied' site (DIST_NEAR_OCCU) and distance to nearest 'empty' site (DIST_NEAR_EMPTY). Their expected values would point in opposite directions, i.e.: from the centre of the 'occupied' area, distance to the nearest 'occupied' site would be minimal and distance to the nearest 'empty' site would be maximal, and vice versa.

All distances to points lying on the coast were calculated "as the gull flies" (i.e., avoiding significant crossings over land) as opposed to "as the crow flies" (i.e., in a straight line).

STATISTICAL ANALYSES

Data were treated statistically and tested with GINKGO multivariate analysis software (Bouxin 2005): (a) after standardisation, with principal components analysis (PCA) for initial exploration; (b) for correlation, using Spearman's rank correlation; (c) in order to discern differences between 'occupied' and 'empty' sites, with a Linear Discriminant Function (Fisher's LDF). This option was chosen because it is based on two classes only and seemed most adequate, as the species had shown long-term stability in its distribution (100% matching between 1977-84 and 2002-08 data in 'occupied' and 'empty') although it had gone through a considerable increase in numbers ($\bar{x}$ = 2.21 to 2.63 in the log scale over the same period).

III. Results

The number of Mediterranean gulls present in each of the 45 localities during the winter season are shown in Table II and fig. 1. They reveal a clumped distribution in the N – S gradient of fishing ports that remained unchanged between the two periods.

The analyses carried out on the variable data greatly reduced uncertainty as to the habitat preferences of Mediterranean gulls in the winter months, and the selection process involved. The PCA analysis identified two components that had the highest relative eigenvalues and accounted for 25.2% and 15.8% of the total variance (41% cumulatively) and were retained.

The first principal component (PC-1) pointed to the relevance of the marine environment, with an oceanographic component (primary productivity, extension of continental shelf) and a littoral component (proximity to lagoon / halophytic meadow habitat). Also, outstandingly, it showed the importance of spatial aggregation. In contrast, the two variables that might indicate availability of discards (No. VESSELS, TOTAL_CATCH) obtained the lowest loading values for both PC-1 and PC-2 and, therefore, occupied a central place in the graph. This was taken as an indication that resource availability may not be a limiting factor in order to explain the observed distribution of *Larus melanocephalus*, possibly because food is plentiful or readily available throughout the geographical gradient.

PC-2 pointed to the importance of the hinterland and showed a dry cultivation component (proximity to vineyards, olive groves and arable land) and a less clear water-related component (proximity to sources of fresh water and to salt-pans). Town size, a measure of the potential presence of people (and, therefore, disturbance) on the beach, also showed with a negative loading.

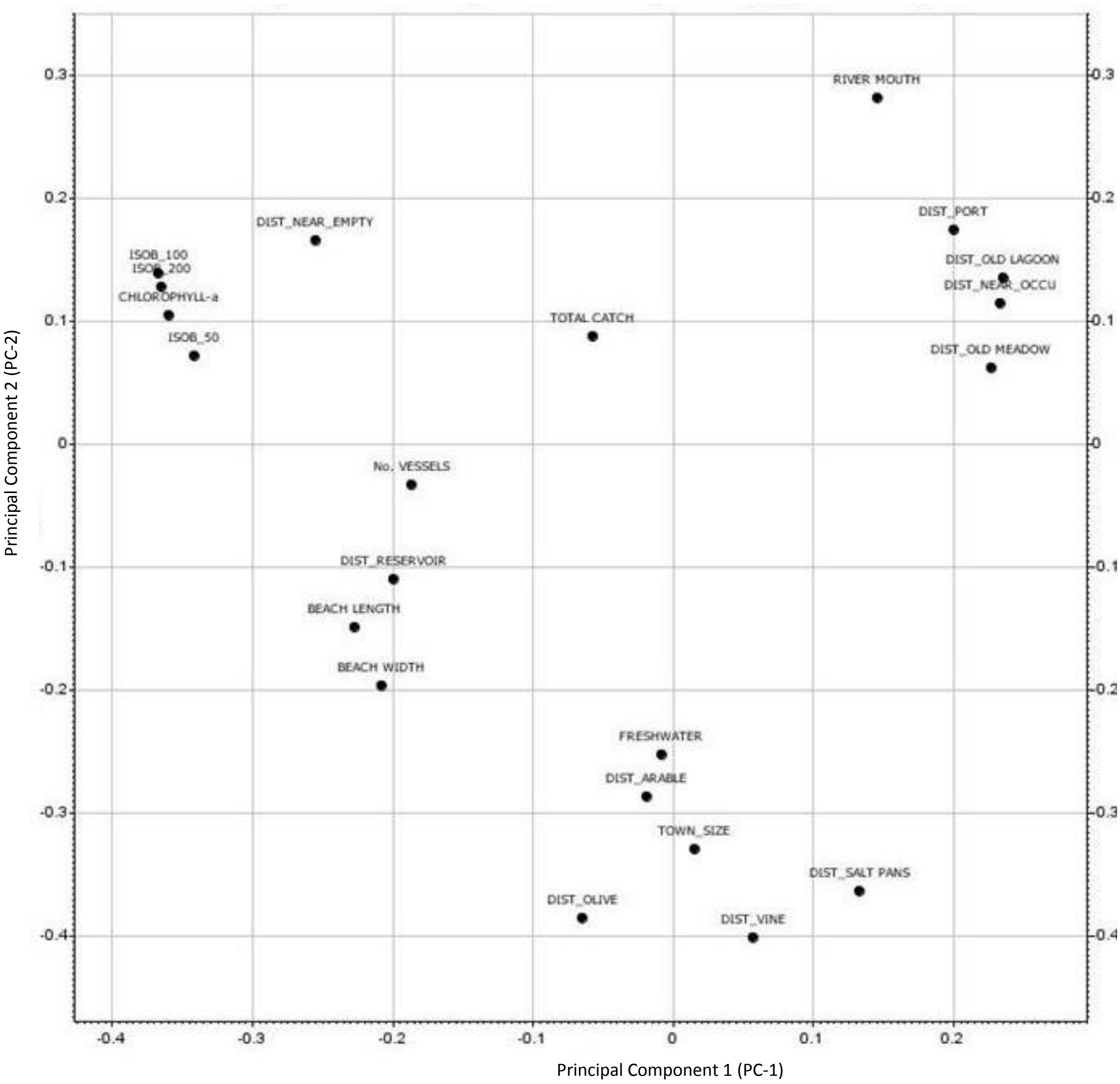

Fig. 4. Results of the exploratory Principal Component Analysis (PCA), with the variables plotted against the two components (PC-1 and PC-2) retained. PC-1 points to the relevance of the marine environment, with an oceanographic and a littoral component. PC-2 points to the relevance of a cultivated hinterland.

Further, the (Spearman's) correlation analysis revealed that there was significant correlation of Mediterranean gull numbers only with three variables: the two indicating spatial aggregation, and primary productivity (CHLOROPHYLL-*a*). Table V (in Annex) shows the Spearman correlation matrix for all variables. Those corresponding to oceanographic features (extension of continental shelf, productivity) and to spatial aggregation showed the highest correlation ranks between them. Vineyards and olive groves were also mutually correlated, as were beach width and beach length. Interestingly, fleet size and total fish catch showed only a slight correlation with each other, as fleet size did with productivity, but they had no significant correlation with any other features or with numbers of *Larus melanocephalus*.

The Linear Discriminant Function (Fisher's LDF), run on the step-wise mode, selected a model that included the following 5 variables:

DIST_NEAR_EMPTY	partial $R^2 = 0.42535$	$\lambda = 0.57465$	F = 28.86769	Pr(f) > F = 0.00000
DIST_NEAR_OCCU	partial $R^2 = 0.41773$	$\lambda = 0.58227$	F = 27.97928	Pr(f) > F = 0.00001
DIST_ARABLE	partial $R^2 = 0.15739$	$\lambda = 0.84261$	F = 7.28499	Pr(f) > F = 0.01023
BEACH LENGTH	partial $R^2 = 0.12231$	$\lambda = 0.87769$	F = 5.43494	Pr(f) > F = 0.02500
DIST_VINE	partial $R^2 = 0.12022$	$\lambda = 0.87978$	F = 5.32944	Pr(f) > F = 0.02636

DIST_NEAR_EMPTY and DIST_NEAR_OCCU, the two variables indicative of spatial aggregation, weighed the most in the model. The other variables included reflect the importance of the dry cultivations in the hinterland and of extensive beaches, generally linked to low-lying coastland.

Port name	LDF 'occupied'	LDF 'empty'
SETE	occupied	
AGDE	occupied	
PORT-L-NOUV	occupied	
PORT-VENDRES		empty
LLANÇA		empty
PORT-SELVA		empty
ROSES (*)	empty	
L'ESCALA		empty
PALAMÓS		empty
St. FELIU G.		empty
BLANES (*)		occupied
ARENYS	occupied	
MATARÓ	occupied	
BARCELONA	occupied	
VILANOVA G.	occupied	
TORREDEMBARRA	occupied	
TARRAGONA	occupied	
CAMBRILS	occupied	
AMETLLA M.	occupied	
L'AMPOLLA	occupied	
St. CARLES R.	occupied	
VINARÒS	occupied	
BENICARLÓ	occupied	
PEÑÍSCOLA	occupied	
CASTELLÓN	occupied	
BURRIANA	occupied	
SAGUNTO (*)	empty	
VALENCIA		empty
CULLERA		empty
GANDÍA		empty
DENIA		empty
JAVEA		empty
CALPE		empty
ALTEA		empty
BENIDORM		empty
VILLAJOIOSA		empty
ALICANTE		empty
SANTA POLA		empty
TORREVELLA		empty
EIVISSA		empty
S ANTONI P		empty
FORMENTERA		empty
PALMA		empty
ANDRATX		empty
SOLLER		empty

Table IV . The result of applying the 5-variable model, obtained through Fisher LDF, to the initial set of 'occupied' and 'empty' ports. The second and third columns correspond to the results obtained after application of Leave-One-Out discriminant to occupied and empty ports according to the model, respectively. The text shows the true condition of each port.
The three mismatches are marked with an asterisk. Notice that Blanes and Sagunto lie on the edges of their respective groups, whilst Roses probably fills all the environmental conditions to hold a population but lies away from the occupied area.

Once obtained through LDF, the 5-variable model was used to reclassify the original set of data (‘occupied’ *vs.* ‘empty’ sites) by leave-one-out evaluation. This exercise resulted in successful matching of 42 out of 45 sites (93 %). Two of the three sites that were not correctly classified by the model, Blanes and Sagunto, lie on the N and S edges of the main area of occupation. The other, Roses, ranks high for the environmental variables but lies far from any occupied sites. All three miss-matches are compatible with the important role of spatial aggregation in shaping the species’ winter distribution.

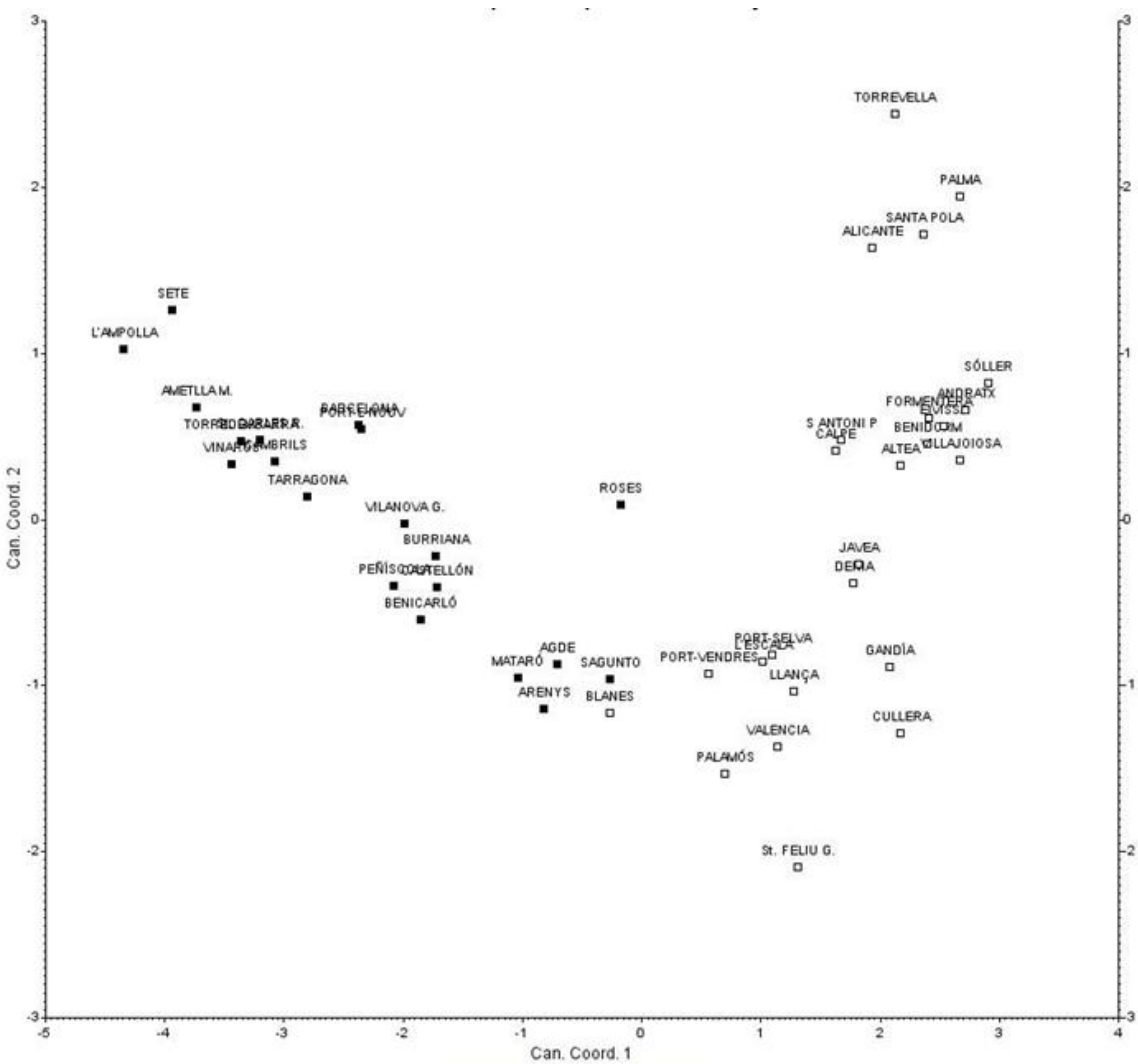

Fig. 5. The Linear Discriminant Function (Fisher LDF) model allowed for successful discrimination of occupied [■] *vs.* empty [□] ports. The best results were obtained using a 2-group discriminant analysis, which gave 93.33% (42 of 45) matchings. Notice that the three mismatches (Roses, Sagunto and Balnes) lie in the area of intersection between the two categories and that their values are close to 0 on canonical coordinate no. 1.
The Fisher LDF was chosen because the species showed long-term stability in its distribution (100% matching between 1977-84 and 2002-08 data in ‘occupied’ and ‘empty’ ports) although it had gone through a significant increase in numbers ($\bar{x}$ = 2.21 to 2.63 in the log scale) over the same period. See fig. 1 and text for further details.

IV. Discussion

CLUSTERED DISTRIBUTION AND THE ROLE OF SPATIAL AGGREGATION

Results show that a combination of spatial aggregation and environmental variables explain the observed distribution of Mediterranean gulls in winter. Or, in other words, the species tends to favour a certain type of environment but its exact distribution is shaped by social factors. The tendency to aggregate with conspecifics is remarkable in this species (Cramp & Simmons 1983), with average flock size of 400 birds in autumn-winter in southern France (Isenmann 1975). Its plumage is one of the whitest of all gulls, and this may be linked to its evolution as a social forager (Beauchamp & Heep 2001).

Aggregation, mostly operating through conspecific attraction, is known to condition the spatial distribution of organisms, including birds (Reed & Dobson 1993, Nocera *et al.* 2009). However, most studies have focused on breeding populations, and little is known of its potential to shape the distribution of birds in winter, when individual energetic requirements and the availability of resources are different to those faced by the species in the breeding season.

Conspecific attraction, as the mechanism of aggregation, operates on individuals by driving them towards the core of the distribution area (Stamps 1988) and away from the unoccupied vicinity. A clear separation is generated at the edges, between the favoured area (where the species may be even abundant) and the rest of space, which remains empty. This is reflected in the spatial distribution, which does not show a coincidence between the resources available and the number of individuals present.

CLUSTERED DISTRIBUTION AND EMPTY SPACES

It is characteristic of clustered distributions that not all potential sites are occupied (Newton 1998) so that there is no total coincidence between suitable habitat and the observed distribution. This is reflected in: (i) the prominent role of aggregation as one of the variables that explain the distribution, and (ii) the existence of empty patches of suitable habitat that are currently not occupied but which have the potential to be occupied in the future. The conservation value of the latter as alternative sites has been emphasised (Oro *et al.* 2009).

In practice, finding empirical evidence of the existence of those empty patches constitutes a real challenge. By definition, empty patches *are* suitable habitat, so there may not be appreciable differences between them and occupied patches, save for the presence of the species in question. It is necessary to resort to indirect evidence, and this may come when the species is temporarily present in the same physical space (e.g. for breeding) that is not occupied during the rest of the year, and there is no explanatory reason for their absence then.

In this respect, Mediterranean gulls remarkably have held breeding nuclei, over several seasons, in spaces that were not occupied during the wintering season, in the years before, during or after the establishment of the colony: 10-15 bp in 2003 & 2004 in Santa Pola (Ramos & Arroyo 2005) and up to 63 bp in 2008 in Albufera de Valencia, where breeding started in 2001 (Dies & Dies 2004).

THE TWO-STEP PROCESS OF HABITAT SELECTION

When the selection of a wintering area is not genetically determined (Alerstam *et al.* 2003), the individual decision to settle in a given area may be influenced by internal factors, such as previous experience (Wolf *et al.* 2009), or, externally, by the cues given by conspecifics (Doligez *et al.* 2003) present in the area already. In any case, the group decision to settle in a given region must necessarily precede the individual decision to follow conspecifics, so it is interesting to investigate how this happens.

Results show that the group does not settle in any area chosen at random, but has a preference for areas of extensive beaches, with high marine productivity and a hinterland of dry cultivation. This complex landscape is generally associated with low-lying coastland in the vicinity of large river systems, such as the Ebro and Rhone. However, the same conditions may be found away from river systems, and wintering populations of Mediterranean gulls regularly occur in Malta, Sicily, Tunisia, Málaga (southern Spain) and other areas far from fluvial habitats (Baccetti & Smart 1999, García *in press*).

The atypical combination of apparently disconnected variables obtained in the results points to the species favouring to settle in those environments that offer multiple options, rather than being linked to a single, straightforward strategy. This is coherent with the unusually wide spectrum of recorded food items and the fact that they can all occur in temporary superabundance (Table I in Annex). It is perhaps in this context, as well, that spatial aggregation and social foraging become advantageous. Buckley (1997) showed that, for colonially-breeding seabirds, spatial concentration was favoured when food patches were sufficiently large or short-lived that intraspecific competition was ameliorated.

Therefore, the group initially settles in a favourable environment and, through social enhancers, must attain its optimal size. Familiarity with the site, along with spatial aggregation and conspecific attraction, represents an advantage for social foragers (Brown 1998, Brown *et al.* 2008), and is probably relevant in this case. Noticeably, the population has individuals with ample previous experience in the wintering area, because they visited one or several of its sites repeatedly through the years (Table VI in Annex). They must contribute, in this way, to making food-searching more efficient, so their role must be important to increase the overall fitness.

EVIDENCE AGAINST PREVIOUS ASSUMPTIONS

None of the analysis carried out selected the availability of fish discards as an explanatory variable of the observed distribution. This is contrary to the initial assumption, based on the available bibliography (Isenmann 1976, Carrera *et al.* 1981, Carrera 1987), which highlighted the importance of fish discards as the main source of food in the winter season – if there were geographical differences in such availability, they should reflect in the distribution and numbers of birds. However, neither TOTAL_CATCH nor No._VESSELS had a significant role in any of the analyses.

There are only two possible inferences from that: (a) fish discards are a readily available food source along the geographical gradient, and are therefore not limiting, and (b) fish discards represent an important food source (as proven by multiple observations in the study area) but are only a fraction of the gulls' winter diet. The birds must be able to seek other options, and the possibility to do so is central to the presence of Mediterranean gulls in the area.

It has also been suggested that the presence of Mediterranean gulls wintering in an area might be conditioned by the existence of inland freshwater reservoirs. Direct observation confirms that the birds make an intensive use of reservoirs in some localities (embalse de Riudecanyes near Cambrils, embalse de la Viñuela near Málaga), gathering there in very large numbers in the evening before moving back to roost at sea. However, at other sites (e.g. Vilanova i la Geltrú) they do not seem to make use of the available reservoirs. Results show that the linear distance to a reservoir is not an explanatory variable, as it does not appear with significance in any of the analyses. The longest distance to a reservoir from any of the sites is 55.02 km, and the 75% percentile lies at 38.52 km. This is well under an hour's flight for a gull.

SETTLING IN AN IMPERFECT ENVIRONMENT

Several of the variables analysed show seasonal patterns of variation, some features being totally unavailable or non-existent during parts of the year. Most remarkably, beaches are completely taken over by humans in late July-August, when the gulls arrive after breeding. For several weeks, *available* beach length (one of the five variables selected by the model) is reduced to almost nil. The physical space is there, but it cannot be occupied by the birds. Mediterranean gulls cannot begin to use the beach (for loafing, resting, sleeping, preening, etc.) until late September-October. They have to resort to alternative, perhaps suboptimal, places and thus concentrate on a few rooftops and on inland fields near the port where they feed. It is paradoxical that a significant feature for the selection of habitat is inaccessible at the time when settling occurs. Only birds that are familiar with the site can decide to settle in an environment that is temporarily imperfect, and expect it to gain quality as the season advances. Additionally, less experienced birds may be driven by their innate tendency to associate with conspecifics and use them as indicators of habitat quality (Donahue 2006).

V. Conclusions

Selection of winter habitat is as critical for individual fitness as is the selection of habitat for breeding. The distribution of birds in this part of the year reflects their preferences for certain features, or combinations of features, that will provide them with the necessary resources not only to survive the winter months but to do so in the best possible condition. The observed distribution of Mediterranean gulls is coherent with their strategy as social foragers dependent on the existence of multiple alternatives in the places they choose to live. It is a combination of habitats lying in close proximity, a characteristic trait of traditional Mediterranean coastal landscapes, that forms their preferred environment.

The species' long-term persistence in a part of a territory that has undergone substantial transformations has been favoured by a strong social bond based upon three aspects of their behaviour: site-fidelity, individual experience (conditional on longevity) and conspecific attraction. Together, they contribute to making the area attractive for settling, from the social as well as from the ecological point of view.

The long-term viability of this population is surely dependent on the continuation of this combination of traits: multiple feeding options on both the marine and the hinterland sides, and the presence of conspecifics in sufficient numbers, in a form of positive density dependence or component Allee effect (Courchamp *et al.* 2008). The maintenance of those favourable conditions should be incorporated into the species' conservation plans.

VI. Further research

The spatial distribution of Mediterranean gulls in winter will be further investigated as part of my Ph.D. thesis on "*Importance and functioning of wintering areas: the Mediterranean gull as a case study*", under the direction of Dr. Meritxell Genovart and Dr. Giacomo Tavecchia of the Population Ecology Group, IMEDEA (CSIC-UIB).

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ANNEX:

Table I – Food items and trophic levels: a list of food items taken regularly by *Larus melanocephalus* in various areas and seasons, with indication of the habitat where they occur and their trophic level.

Food	Main component	Species (if known)	Habitat	breeding	post-br.	winter	Trophic level	Sources
Barley	seed	*Hordeum vulgare*	arable fields		■		Producer – primary	Milchev et al. (2000)
Wheat	seed	*Triticum sp.*	arable fields		■		Producer – primary	Milchev et al. (2000)
Sunflower	seed	*Helianthus annuus*	arable fields (summer) port docks (winter)		■	■	Producer – primary	Milchev et al. (2000), own data
Ragwort	seed	*Senecio sp.*	arable fields (weed)		■		Producer – primary	Milchev et al. (2000)
Bread	seed (product)		urban parks	■	■		Producer – primary	R. Flamant, *pers.comm.*, S. Sales, *in litt.*
Grape	fruit	*Vitis vinifera*	vineyards		■		Producer – primary	Milchev et al. (2000)
Olive	fruit	*Olea europea*	olive groves			■	Producer – primary	Baccetti & Smart (1999), own data
[European] Plum	fruit	*Prunus domestica*	orchards		■		Producer – primary	Milchev et al. (2000)
Oriental Bittersweet	fruit	*Celastrus orbiculatus*	orchards / gardens		■		Producer – primary	Milchev et al. (2000)
Earthworm	entire animal	*Lumbricus terrestris* *Allolobophora*	arable land, orchards, meadows, pastures	■		■	Detritivore	R. Flamant, *pers.comm.*, S. García, *pers.comm.*, Goutner (1994)
Land snail	entire animal (incl. shell)	*Theba pisana*	arable land, meadows		■		Consumer – primary	own data
Marine bivalves	entire animal (incl. shell)	Veneroida: *Tellina, Donacilla, Spisula,*	sea-shore	■	■			Goutner (1994), Milchev et al. (2000)
[Italian] locust	entire animal	*Calliptamus italicus*	grassy vegetation		■		Consumer – primary	Milchev et al. (2000)
Mole cricket	entire animal	*Gryllotalpa gryllotalpa*	arable land, meadows, pastures	■			Consumer – primary & secondary	Goutner (1994)
Ants	entire animal (incl. flying ♂)	*Messor, Formica, Myrmica*	arable land, meadows, pastures	■	■		Consumer – primary	Goutner (1994), Carrera (1986?)
Shield bugs	entire animal	Scutelleridae	arable land, orchards, meadows, pastures	■			Consumer – secondary	Goutner (1994)
Beetles	entire animal	Coleoptera: Carabidae, Tenebrionidae, Curculionidae	arable land, orchards, meadows, pastures	■	■	■?	Consumer – primary & secondary	Milchev et al. (2000), Goutner (1994)
Sand-hopper	entire animal	Isopoda: Talitridae	sea-shore	■	■		Detritivore	Goutner (1994), Milchev et al. (2000)
Mud shrimp	entire animal	Decapoda: *Upogebia sp.*	discard?	■		■	Scavenger	Goutner (1994), own data
Fish (fresh & brackish water)	entire animals, discards	*Carassius auratus, Rutilus rutilus, Neogobius sp., Perca fluviatilis, Mesogobius batrachocephalus*	wetlands, lagoons, estuaries	■	■		Consumer – secondary	Goutner (1994), Milchev et al. (2000)
Fish (marine)	discards	*Syngnathus sp., Anthias anthias, Scorpaena sp., Symphodus sp., Ophidion sp., Pleuronectes sp.*	fishing ports		■	■	Consumer – secondary	Goutner (1994), Milchev et al. (2000), own data
Land Vertebrata	young & small birds, small rodents, shrews	*Sylvia, Phylloscopus, Carduelis, Crocidura, Mus, Microtus*	arable land, orchards, meadows, pastures		■		Consumer – primary & secondary	Milchev et al. (2000)

TABLE II – Number of wintering *Larus melanocephalus* in each locality, as derived from official winter census data and bibliography, including ornithological yearbooks for all regions (see below for sources). "-- " indicates that the site was not covered in general survey for that particular year, while absence of sign indicates lack of (relevant) observations, *i.e.* the species was not seen; "+" indicates the species was present but not counted.

FISHING PORT	Lat. ° N	**1977**	**1979**	**1980**	**1981**	Log_{10}	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	Log_{10}
Sête	43.40		>500	++		3		--	533	2500				3
Agde	43.29		50-100	+		2		170	300	--				2
Port la Nouvelle	43.02		0-10	+		1		15	1	--	25			1
Port-Vendres	42.52					0								0
Llançà	42.37			0	0	0			0	0		0	0	0
Port d la Selva	42.34			0	0	0			0	0		0	0	0
Roses	42.25			0	0	0			0	0		0	0	0
l'Escala	42.12			--	0	0			--	0		0	0	0
Palamós	41.84			0	0	0			2	0		0	32	0
St Feliu G.	41.78			0	0	0			0	0		--	--	0
Blanes	41.67			31	15	1	400		550	12		--	--	2
Arenys d Mar	41.58			--	20	1	--		9	1175		--	--	2
Mataró	41.53			--	10	1	--		15	9		--	--	1
Barcelona - Llobregat	41.38	1270	3066	1250	832+	3	439	1120	1274	83	--	1176	--	3
Vilanova i G.	41.21	--	--	175	100	2	272		854	750	3900	1022	--	3
Torredembarra	41.13	--	5	--	--	1	800		200	70	--	--	--	2
Tarragona	41.11	--	190	10	100	2	2560		0	0	4110	--	--	3
Cambrils	41.06	--	175	+	700	2	--		25000	19150	--	4560	--	4
l'Ametlla d Mar	40.88	5720	4230	7500	2300+	4	--		*[1]	*[1]	*[1]	*[1]	15520	4
l'Ampolla	40.81	*[2]	*[2]	*[2]	*[2]	3	--		*[1]	*[1]	*[1]	*[1]	870	3
St Carles d R.	40.62	*[2]	*[2]	*[2]	*[2]	3	--		*[1]	*[1]	*[1]	*[1]		3
Vinaròs	40.47			600	1300	3	--	0	97	--	+	+		3 *[3]
Benicarló	40.41			40	175	2	--	0	0	--	+	+		3 *[3]
Peñíscola	40.36	1400	--	4100	3255	3	--	940	1030	900	+	+		3 *[3]
Castellón	39.97		150	1155	2148+	3	--	347	305	--	2000	+		3 *[3]
Borriana	39.86			500	307	2	--	163	0	+	237	2000		2 *[3]
Sagunto	39.65			0	0	0	--							0
Valencia	39.45			0	2	0								0
Cullera	39.17			0	--	0							0	0
Gandía	38.99			0	--	0							0	0
Denia	38.84					0							0	0
Jávea	38.80					0							0	0
Calpe	38.64					0			0	0	0		0	0
Altea	38.59					0			0	0	0		0	0
Benidorm	38.53					0			0	0	0		0	0
Villajoyosa	38.51					0			0	0	0		0	0
Alicante	38.33					0			0	0	0		0	0
Santa Pola	38.19					0			0	0	0		5	0
Torrevieja	37.97					0			0	0	0		0	0
Ibiza	38.91					0			0	0	0		0	0

FISHING PORT	Lat. ° N	1977	1979	1980	1981	Log_{10}	2002	2003	2004	2005	2006	2007	2008	Log_{10}
St Antoni	38.98					0								0
Formentera	38.73					0								0
Palma	39.57					0								0
Andratx	39.55					0								0
Sóller	39.80					0								0

NOTES:

Log_{10} – Mediterranean gull population size for each locality, according to the following (logarithmic) scale: (see text for details)
0 - 4 ind: 0; 5 - 49 ind: 1; 50 - 499 ind: 2; 500 - 4999 ind: 3; 5000 - 49999 ind: 4

*[1] - Figures for 3 ports (Ametlla de Mar, l'Ampolla & Sant Carles de la Ràpita) grouped under general heading 'Delta de l'Ebre' in surveys, with:
2004 – 35000; 2006 – 14652; 2007 – 8106

*[2] - Figures for 2 ports (l'Ampolla & Sant Carles de la Ràpita) grouped under general heading 'Delta de l'Ebre' in surveys, with:
1977 – 900+; 1979 – 1600

*[3] - Tirado (2009), in a general review of the status of the species in Castellón, Valencia & Alicante, gives following average winter figues:
Vinaròs – 1000-3000; Benicarló – 1000-3000; Peñíscola – 600-3200; Castellón – 1000-1300; Borriana – 1000-1300; other ports – 0

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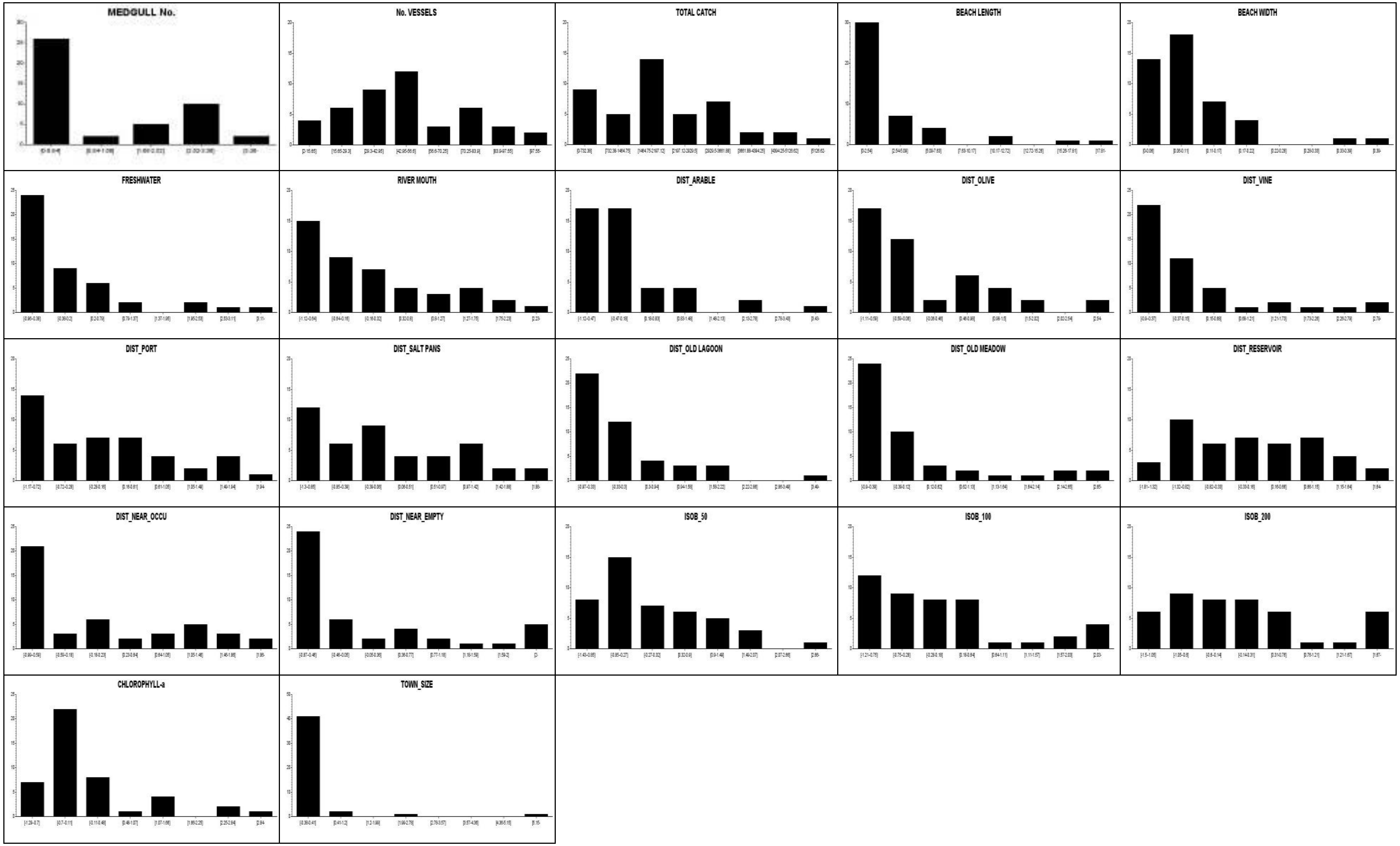
Table III – List of the variables measured, with their corresponding description and biological significance for the species. Notice that, for some variables, it was the distance to the resource that was measured (and, therefore, the larger distance to the resource gave the highest values).

VARIABLE name	Avg.	Var.	S.D.	C.V. %	Min.	Max.	Range	Description	Variable measured & biological significance
MEDGULL No.	1.11	2.01	1.42	127.6	0	4	4	Total number of *Larus melanocephalus* present in site – average of mid-winter counts 2002-2008 (log scale)	Main (dependent) variable
No. VESSELS	48.18	650.24	25.5	52.93	2	106	104	Total number of active fishing vessels registered in fishing port	Indicates activity of fishing port & food availability (discards)
TOTAL CATCH	2108.09	$1.83 \cdot 10^6$	1354.69	64.26	0	5580	5580	Total amount (Tm) of fish catch unloaded	Indicates availability of food (discards)
BEACH LENGTH	3.14	17.49	4.18	133.06	0	19.38	19.38	Total length of [continuous] beach in town	Species gathers on beaches for resting & other purposes
BEACH WIDTH	0.1	0.01	0.08	83.25	0	0.42	0.42	Maximum beach width	Species gathers on beaches for resting & other purposes
FRESHWATER	1.37	1.96	1.4	102.31	0.03	6.22	6.19	Distance to nearest freshwater source, usually on beach	Species makes ample use of freshwater pools & streams, particularly for bathing after having fed
RIVER MOUTH	11.01	92.28	9.61	87.23	0.26	35.3	35.04	Distance to nearest river mouth of any size	Measures distance to potential source of freshwater & food
DIST_ARABLE	2.01	2.39	1.55	77.09	0.28	7.93	7.65	Distance to nearest arable land	Measures distance to inland habitat used by species for feeding
DIST_OLIVE	8.77	53.32	7.3	83.29	0.68	29.69	29.01	Distance to nearest olive groves	Measures distance to inland habitat used by species for feeding
DIST_VINE	7.21	39.22	6.26	86.89	1.56	26.71	25.15	Distance to nearest area of vineyard	Indicates potential foraging site (vineyard)
DIST_PORT	29.82	636.54	25.23	84.61	0.4	85.56	85.16	Distance to nearest commercial port	Indirect availability of food source (seeds)
DIST_SALT PANS	72.38	3075.56	55.46	76.62	0.23	191.98	191.75	Distance to nearest [operative] salt pans	Species known to concentrate on salt pans where they occur
DIST_OLD LAGOON	13.28	176.06	13.27	99.93	0.39	64.88	64.49	Distance to [past or persistent] littoral lagoon	Known to frequent littoral lagoons in other regions; past sites included in case individuals/population might conserve memory of habitat
DIST_OLD MEADOW	7.07	57.16	7.56	106.86	0.3	29.49	29.19	Distance to [past or persistent] hallophytic meadow	Known to frequent hallophytic meadows in other regions; past sites included in case individuals/ population might conserve memory of habitat
DIST_RESERVOIR	26.69	211.44	14.54	54.49	0.39	55.02	54.63	Distance to nearest freshwater reservoir	Species uses some reservoirs for bathing & social function
DIST_NEAR_OCCU	82.88	5875.97	76.65	92.49	6.67	245.16	238.49	Distance (by sea) to nearest harbour where *Larus melanocephalus* present -- occupied sites --	Aggregated distribution (occupied sites)
DIST_NEAR_EMPTY	59.13	3933.69	62.72	106.08	4.69	200.37	195.68	Distance (by sea) to nearest harbour with no *Larus melanocephalus* present -- empty sites--	Aggregated distribution (empty sites)
ISOB_50	10.71	37.97	6.16	57.52	1.88	29.3	27.42	Distance to nearest point with -50 m isobath	Extension of continental shelf
ISOB_100	30.1	457.31	21.38	71.05	4.2	79.7	75.5	Distance to nearest point with -100 m isobath	Extension of continental shelf
ISOB_200	40.31	542	23.28	57.75	5.4	85.6	80.2	Distance to nearest point with -200 m isobath	Extension of continental shelf
CHLOROPHYLL-a	0.89	0.22	0.47	52.44	0.29	2.39	2.1	5-year (2003-08) average value of winter (nov-apr) Chl-a concentration ($mg \cdot m^{-3}$) in 12-nm radius around fishing harbour (data from 0.1 degree squares as obtained from OBPG SeaWIFS)	Indirect measure of primary productivity
TOWN_SIZE	101557.78	$7.01 \cdot 10^{10}$	264818.76	260.76	947	1595110	1594163	Total (human) population size of the municipality where the port is situated	Proxy for anthropic disturbance (dogs, walkers, sunbathers, etc.)

Fig. 2 – Frequency histograms of the 22 variables used for the analysis, after standardisation. Only a few variables are normally distributed; the rest are not suitable for ANOVA.



Correlation values for 22 variables (20 degrees of freedom): P = 0.01 ; r = 0.537
P = 0.05 ; r = 0.423

Table V. Spearman correlation matrix of the 22 variables

	MEDGULL No.	No. VESSELS	TOTAL CATCH	BEACH LENGTH	BEACH WIDTH	FRESHWATER	RIVER MOUTH	DIST_ARABLE	DIST_OLIVE	DIST_VINE	DIST_PORT	DIST_SALT PANS	DIST_OLD LAGOON	DIST_OLD MEADOW	DIST_RESERVOIR	DIST_NEAR_OCCU	DIST_NEAR_EMPTY	ISOB_50	ISOB_100	ISOB_200	CHLOROPHYLL-a	TOWN_SIZE
MEDGULL No.	**1**	0.3404	0.2752	0.2614	0.2143	0.1799	-0.0482	-0.0704	-0.1702	-0.1837	-0.3358	-0.0678	-0.2341	-0.1388	0.2536	-0.8011	0.8323	0.2778	0.3741	0.3471	0.6821	0.0026
No. VESSELS	0.3404	**1**	0.4991	0.1903	0.2282	0.0323	-0.2380	-0.0583	0.0989	-0.0530	-0.3581	-0.0587	-0.2712	0.0443	0.1594	-0.2117	0.2744	0.2581	0.1998	0.1432	0.4939	0.0376
TOTAL CATCH	0.2752	0.4991	**1**	-0.1660	-0.2912	0.0745	-0.1022	-0.0792	-0.2420	-0.2535	-0.1196	-0.1232	0.1102	0.0576	0.0269	-0.0225	0.2055	-0.0344	-0.0846	-0.1061	0.0201	0.0130
BEACH LENGTH	0.2614	0.1903	-0.1660	**1**	0.7248	0.2487	-0.3539	0.1912	0.2720	0.2120	-0.2464	0.2004	-0.4050	-0.3493	0.1910	-0.3133	0.1393	0.2783	0.2652	0.1835	0.2689	0.2408
BEACH WIDTH	0.2143	0.2282	-0.2912	0.7248	**1**	0.2089	-0.2824	0.2512	0.3896	0.1788	-0.2998	0.3006	-0.3224	-0.2967	0.0034	-0.3253	0.1779	0.2596	0.2501	0.2432	0.4427	0.2893
FRESHWATER	0.1799	0.0323	0.0745	0.2487	0.2089	**1**	-0.0328	0.2648	-0.0042	0.0303	-0.0084	0.1475	-0.1549	0.0581	0.2548	-0.2922	-0.0261	-0.2177	-0.1217	-0.0443	0.1280	-0.0850
RIVER MOUTH	-0.0482	-0.2380	-0.1022	-0.3539	-0.2824	-0.0328	**1**	-0.0483	-0.3373	-0.3532	0.1838	-0.2975	0.0908	0.1019	-0.1765	0.1415	0.0235	0.0042	-0.1099	-0.1426	-0.1357	-0.3926
DIST_ARABLE	-0.0704	-0.0583	-0.0792	0.1912	0.2512	0.2648	-0.0483	**1**	0.2564	0.3653	-0.0868	0.0442	-0.2228	-0.1474	-0.0104	0.1417	-0.0633	-0.0482	0.1548	0.1864	0.0510	0.3937
DIST_OLIVE	-0.1702	0.0989	-0.2420	0.2720	0.3896	-0.0042	-0.3373	0.2564	**1**	0.6762	-0.3349	0.1917	-0.0138	-0.0197	0.0054	0.1446	-0.0706	0.2253	0.0832	0.1211	0.0225	0.4952
DIST_VINE	-0.1837	-0.0530	-0.2535	0.2120	0.1788	0.0303	-0.3532	0.3653	0.6762	**1**	-0.0827	0.3893	0.0883	-0.0269	0.2155	0.0797	-0.1578	-0.0447	-0.0992	0.0091	-0.1351	0.3789
DIST_PORT	-0.3358	-0.3581	-0.1196	-0.2464	-0.2998	-0.0084	0.1838	-0.0868	-0.3349	-0.0827	**1**	0.0870	0.1531	0.0388	-0.1162	0.2171	-0.3607	-0.3245	-0.1551	-0.1709	-0.2584	-0.3783
DIST_SALT PANS	-0.0678	-0.0587	-0.1232	0.2004	0.3006	0.1475	-0.2975	0.0442	0.1917	0.3893	0.0870	**1**	0.1806	0.2152	0.0605	-0.2790	-0.2316	-0.3721	-0.4590	-0.4375	-0.0803	0.2419
DIST_OLD LAGOON	-0.2341	-0.2712	0.1102	-0.4050	-0.3224	-0.1549	0.0908	-0.2228	-0.0138	0.0883	0.1531	0.1806	**1**	0.5385	-0.2518	0.2385	-0.2658	-0.3214	-0.3289	-0.2909	-0.5067	0.0995
DIST_OLD MEADOW	-0.1388	0.0443	0.0576	-0.3493	-0.2967	0.0581	0.1019	-0.1474	-0.0197	-0.0269	0.0388	0.2152	0.5385	**1**	-0.1134	0.0065	-0.2217	-0.1859	-0.3068	-0.2922	-0.2074	-0.0986
DIST_RESERVOIR	0.2536	0.1594	0.0269	0.1910	0.0034	0.2548	-0.1765	-0.0104	0.0054	0.2155	-0.1162	0.0605	-0.2518	-0.1134	**1**	-0.3817	0.2322	0.2837	0.1921	0.2997	0.2974	-0.1017
DIST_NEAR_OCCU	-0.8011	-0.2117	-0.0225	-0.3133	-0.3253	-0.2922	0.1415	0.1417	0.1446	0.0797	0.2171	-0.2790	0.2385	0.0065	-0.3817	**1**	-0.5862	-0.2275	-0.2549	-0.2698	-0.6791	0.1421
DIST_NEAR_EMPTY	0.8323	0.2744	0.2055	0.1393	0.1779	-0.0261	0.0235	-0.0633	-0.0706	-0.1578	-0.3607	-0.2316	-0.2658	-0.2217	0.2322	-0.5862	**1**	0.4037	0.3325	0.3153	0.6402	0.0031
ISOB_50	0.2778	0.2581	-0.0344	0.2783	0.2596	-0.2177	0.0042	-0.0482	0.2253	-0.0447	-0.3245	-0.3721	-0.3214	-0.1859	0.2837	-0.2275	0.4037	**1**	0.6453	0.6183	0.5288	-0.0252
ISOB_100	0.3741	0.1998	-0.0846	0.2652	0.2501	-0.1217	-0.1099	0.1548	0.0832	-0.0992	-0.1551	-0.4590	-0.3289	-0.3068	0.1921	-0.2549	0.3325	0.6453	**1**	0.9478	0.5959	0.0493
ISOB_200	0.3471	0.1432	-0.1061	0.1835	0.2432	-0.0443	-0.1426	0.1864	0.1211	0.0091	-0.1709	-0.4375	-0.2909	-0.2922	0.2997	-0.2698	0.3153	0.6183	0.9478	**1**	0.5522	0.0209
CHLOROPHYLL-a	0.6821	0.4939	0.0201	0.2689	0.4427	0.1280	-0.1357	0.0510	0.0225	-0.1351	-0.2584	-0.0803	-0.5067	-0.2074	0.2974	-0.6791	0.6402	0.5288	0.5959	0.5522	**1**	-0.0536
TOWN_SIZE	0.0026	0.0376	0.0130	0.2408	0.2893	-0.0850	-0.3926	0.3937	0.4952	0.3789	-0.3783	0.2419	0.0995	-0.0986	-0.1017	0.1421	0.0031	-0.0252	0.0493	0.0209	-0.0536	**1**

Table VI – Winter philopatry and individual experience. Occurrence at different sites in the study area of 25 Mediterranean gulls *Larus melanocephalus* that were >6 years old in 2005 (estimated generation length is 6 yrs, BirdLife Int. 2004), at the onset of the present study. Observation effort was unequal across sites and between years. Site fidelity is conditional on survival.

Ring ID.	Year ringed	Country ringed (age)	2005 age	2005/06 sites	2006 age	2006/07 sites	2007 age	2007/08 sites	2008 age	2008/09 sites
blue A24	1990	Italy (pull.)	15	VNG, TAR	16	VNG	17	VNG, TAR, CAM	18	VNG
blue B34	1991	Italy (pull.)	14	VNG, CAM	15	VNG	16	VNG, CAM		
blue B62	1991	Italy (pull.)	14	VNG	15	VNG	16	VNG	17	VNG
blue B64	1991	Italy (pull.)	14	CAM	15	CAM	16	CAM		
blue E43	1992	Italy (pull.)	13	CAM, VNG			15	CAM		
blue S09	1992	Italy (pull.)	13	TAR, CAM, VNG	14	VNG	15	VNG, CAM	16	VNG
blue S25	1992	Italy (pull.)	13	CAM	14	VNG	15	VNG, TAR	16	VNG
blue X29	1993	Italy (pull.)	12	VNG	13	VNG	14	VNG	15	VNG
blue X25	1994	Italy (pull.)	11	VNG	12	VNG	13	VNG, CAM	14	CAM, VNG
blue Y71	1994	Italy (pull.)	11	TAR, CAM	12	TAR, VNG, CAM	13	CAM	14	VNG
red H994	1999	Hungary (ad.)			>10	VNG	>11	VNG		
black 6A3	1997	Greece (pull.)	8	TAR, VNG	9	VNG	10	VNG		
blue IAJV	1997	Italy (pull.)	8	CAM	9	CAM	10	CAM	11	VNG
blue IASX	1997	Italy (pull.)	8	CAM	9	VNG	10	VNG		
black P3H	2000	Ukraine (ad.)	>7	CAM	>8	CAM	>9	CAM		
black P6N	2000	Ukraine (ad.)	>7	CAM, AMT	>8	CAM				
black P8K	2000	Ukraine (ad.)	>7	VNG, CAM	>8	VNG				
blue IBKD	2001	Italy (ad.)	>6	CAM, VNG			>8	VNG	>9	CAM
blue IBNJ	2000	Italy (>2cy)	>6	TAR, VNG	>7	VNG	>8	VNG	>9	VNG, TAR
blue IBPH	2000	Italy (>2cy)	>6	VNG, CAM	>7	VNG	>8	VNG, TAR	>9	VNG
black 4E7	1999	Greece (pull.)	6	CAM			8	VNG, CAM	9	VNG
black 1L8	1999	Greece (pull.)	6	TOR	7	VNG	8	VNG	9	VNG, CAM
black 2L1	1999	Greece (pull.)	6	VNG, CAM	7	VNG	8	VNG, CAM	9	VNG
white 4AH	1999	Belgium (pull.)	6	VNG, TAR, CAM	7	VNG	8	VNG	9	VNG
blue IFVH	1999	Italy (pull.)	6	VNG, TAR	7	VNG				

AMT = Ametlla de Mar; CAM = Cambrils; TAR = Tarragona; TOR = Torredembarra; VNG = Vilanova i la Geltrú