



Presence, richness and extinction of birds of prey in the Mediterranean and Macaronesian islands

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ABSTRACT

Aim We analyse modern patterns of richness, presence and extinction of birds of prey (Accipitiformes and Falconiformes) in the Mediterranean and Macaronesian islands, using an integrated approach involving both biogeographical and human-induced factors.

Location Forty-three islands grouped into nine Mediterranean and Macaronesian archipelagos.

Methods Information about 25 species breeding during the past century and their fate (permanence or extinction) was compiled from the literature and regional reports. Jaccard's similarity index and cluster analyses were applied to define island assemblages. In order to detect the factors driving richness, presence and extinction, generalized linear models (GLM) were applied to 32 explanatory variables, evaluating location, physiography, isolation of island, taxonomic affinities and life-history patterns of the raptor species.

Results Islands belonging to the same archipelago clustered when raptor assemblages were compared, revealing a marked biogeographical signal. Species richness was influenced by island area and accessibility from the continent (explained deviance of 51% in the GLM). Models of the probability of presence (explained deviance of 32%) revealed positive influences of migratory patterns (maximum for partial migrants), size of distribution areas and proximity to main migration routes. The model for probability of extinction explained only 8% of the deviance. It revealed that populations living on islands with a high density of human population were more prone to disappear. Also, raptors depending on human resources had more risk of extinction.

Main conclusions Basic predictions of island biogeography can explain current patterns of raptor richness in the study area despite millennia of intense humanization processes. Colonization success appears to depend on life-history traits linked to migratory and dispersal strategies, whereas body-size constraints are not influential. Additionally, our results reveal the importance of species-based analyses in studies of island biogeography.

Keywords

Extinction, generalized linear modelling, island biogeography, Macaronesia, Mediterranean, raptors, species richness.

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INTRODUCTION

Island biogeography (MacArthur & Wilson, 1963, 1967) has been one of the most widely discussed aspects of modern ecological theory. Classically, its core centres on species richness, which is dependent on patch size (island area) and

degree of isolation. Thus distance to the continent determines probability of arrival, whereas island area influences probability of extinction. Subsequent predictions derived from these central arguments have been broadly documented and proven for very different taxonomic groups (see Ricklefs & Lovette, 1999; Johnson *et al.*, 2000 for reviews). On the other

hand, many aspects of the theory of island biogeography and, in particular, the concept of equilibrium, have been deeply criticised (see Brown & Lomolino, 1998; Walter, 2004 for reviews). It has also been argued that approaches based on comparisons involving different taxonomic groups have overlooked fine-tuning mechanisms determining colonization and extinction events. In particular, the probability of island colonization may be dependent on a species' life-history characteristics, particularly dispersal capacity (Fernández-Palacios & Andersson, 1993). On the other hand, the permanence or extinction of a local population can be influenced by species-specific factors such as body size and degree of ecological specialization: large organisms at the top of food chains are more prone to suffer declines with environmental changes (Peltonen & Hanski, 1991; Alcover & McMinn, 1994; Rosenzweig & Clark, 1994; Millien-Parra & Jaeger, 1999). Thus analyses focusing on phylogenetically closely related groups should be preferred to avoid the largely irrelevant variance inherent in joint treatment of different groups of taxa (Carrascal & Palomino, 2002). In addition, when factors related to the life history of each species are considered, it is possible to determine species-based colonization and extinction patterns which, in the end, may model the composition and assembly of insular communities (Lomolino, 2000).

Anthropogenic disturbance may have a deep impact on species richness through the modification of some intrinsic island characteristics such as habitat abundance and diversity (Russell *et al.*, 2004). Its effects, however, may vary depending on scale. It is well known that humanization of island systems has widely altered the initial structure and richness of avian communities worldwide. Direct persecution, habitat destruction and facilitation of biological invasions are the main consequences following human settlement on islands. They bring about processes of extinction of local endemism and the expansion of alien species (Chown *et al.*, 1998). For instance, in the Pacific tropics as many as 2000 bird species were lost after human colonization (Steadman, 1995), and temperate insular systems have suffered a parallel impoverishment (Milberg & Tyrberg, 1993; Alcover *et al.*, 1998; Palmer *et al.*, 1999). Birds of prey live on most islands of the world, with the sole exception of the Antarctic continent (White & Kiff, 2000). Frequently, diversity in birds of prey is high in comparison with other taxonomic groups because birds of prey typically have good flight abilities, permitting many species to reach oceanic islands far from continental regions. Unlike other taxonomic groups which may have been constrained by strict ecological requirements and/or specific dispersal constraints, birds of prey, at least in temperate regions, tolerate moderate habitat transformations driven by human activities (Rodríguez-Estrella *et al.*, 1998), although species of large body size may be more prone to suffer negative effects because of their conservative life-history traits (Alcover & McMinn, 1994; White & Kiff, 2000). This scenario makes birds of prey an appropriate tool for the study of biogeographical patterns and the interaction between intrinsic factors linked to island characteristics and

those related to transformations derived from human activities.

In this paper we examine the factors conditioning species composition and richness of birds of prey in the Mediterranean islands and Macaronesia. These regions are considered 'biodiversity hot-spots' due to their high rates of endemism (Covas & Blondel, 1998; Juan *et al.*, 2000). This variety is particularly outstanding in birds of prey: up to 26 species can be found in the region, with some islands having had more than 15 breeding species. Islands of the region show very different degrees of human transformation, which allows us to deal with the above-mentioned questions. Two groups of hypotheses are tested in this study. The first group is in relation to the basic principles of island biogeography theory. We expect that island size, habitat complexity and degree of isolation from the mainland will influence species richness. Accordingly, richness is expected to increase with island area and proximity to the mainland. Within this general scenario we also test whether, as predicted, there are more similarities in the composition of communities of birds of prey between islands belonging to the same archipelago than between archipelagos. Second, we test how a species' life-history characteristics affect the probability of presence and extinction after controlling for island size and isolation. We predict that: (1) small body-sized raptors should be found more frequently in insular systems due to their relatively high population turnover compared with large body-sized raptors (Newton, 1979); (2) because of the 'rescue' effect there is a greater probability of finding species on islands if there is a large population on a neighbouring area of mainland (Brown & Kodrick-Brown, 1977; Sarà & Morand, 2002); (3) probability of extinction should be higher for large-bodied species with low population turnover; and (4) species directly benefiting from human-induced transformations will show lower probabilities of extinction.

MATERIALS AND METHODS

Study area

The study encompasses 43 islands of at least 100 km² in the Mediterranean Sea and Macaronesia (Appendix 1; Fig. 1). The selection comprises all major island groups and archipelagos with a broad range of geological age, from 20 Myr (late Miocene) to 0.8 Myr (Pleistocene). Both progressive isolation and divergent evolution have taken place, mainly after the glaciations of the Northern Hemisphere and desertification of the African Continent. Consequently these islands have different climates and vegetation. Macaronesian archipelagos exhibit the largest environmental gradient and vegetation ranges. Laurel forest formations dominate in the Azores, Madeira and on the northern slopes of the western Canary Islands, whereas semi-desert, succulent scrub occupies the southern parts of the western islands and all the eastern islands of the latter archipelago (Fernández-Palacios & Andersson, 2000). The Mediterranean islands

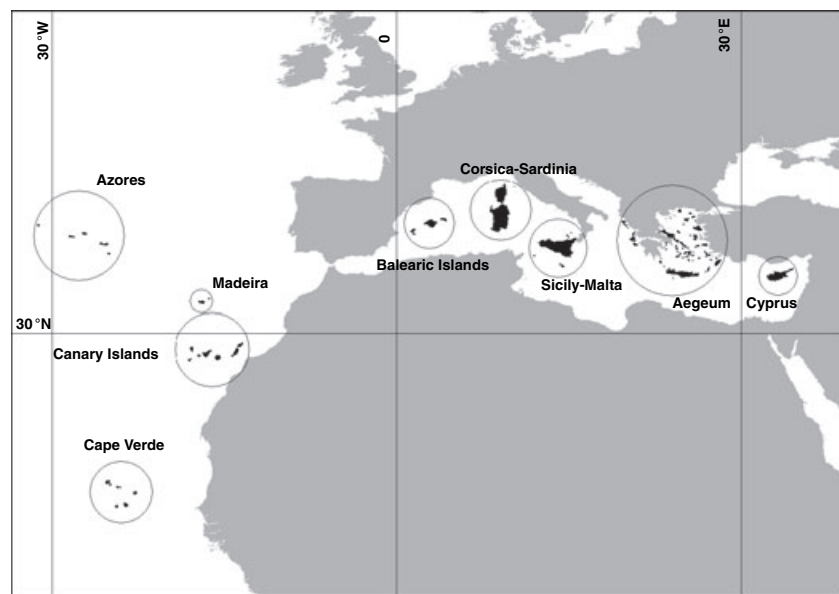


Figure 1 Geographical setting of study area, and grouping of 43 islands studied into nine archipelagos. Macaronesia: Azores, Madeira, Canary Islands and Cape Verde; Mediterranean: Balearic Islands, Corsica–Sardinia, Sicily–Malta, Aegeum and Cyprus.

have a relatively homogeneous climate with scarce rainfall and more xeric vegetation; the observed variations are mainly determined by altitudinal gradients (Covas & Blondel, 1998). Humanization has been very important all over, but whereas the islands of the Mediterranean were settled by humans between 12,000 and 9000 yr BP (but see Ramis *et al.*, 2002), Macaronesian archipelagos were colonized only from 2500 yr BP (Canaries) to 500 yr BP (Azores, Madeira and Cape Verde).

Birds of prey

Our main objective was to determine factors influencing raptor richness, presence and extinction on the islands of the Mediterranean Basin and Macaronesia. To accomplish this goal, we compiled data generated during the twentieth century. Literature about ornithological surveys in the study area prior to this period is extremely scarce, so it was not feasible to extend our analyses to factors operating before the twentieth century. The possibility of using sub-fossil data to look at factors operating on a larger time-scale was discarded because reliable palaeontological information is scarce and varies among islands. In addition, bone remains of large species appear more frequently (Alcover & McMinn, 1994; Rando, 2002), therefore sub-fossil data were considered to be misleading and biased.

Information was gathered from general sources (Cramp & Simmons, 1980; Hagemeyer & Blair, 1997), monographic revisions (Muntaner & Mayol, 1996) and unpublished regional reports. We considered only those islands for which there is a good amount of ornithological literature. All the potential breeding species are included in the analyses. We considered potential breeders to be those species that have been found during the past century breeding in an area of around 1500 km from the island. The only exception was Eleonora's falcon (*Falco eleonora*), because of its unique ecology and the virtual

absence of continental populations (Cramp & Simmons, 1980).

Geographical pattern

The convenience of including geographical variables in the study was checked using faunistic similarity tests. Islands were grouped according to (1) 'true' Mediterranean and Atlantic archipelagos, or (2) 'groups' of islands that are geographically close (< 100 km).

Association patterns among islands and archipelagos were inspected first, using Jaccard's similarity index (Jaccard, 1901). This index considers the proportion between localities where two species are found and the total number of localities where at least one of them is found. This index is commonly used in ecological studies and was selected for its easy interpretation, independence of negative matches, symmetry and homogeneity properties (Janson & Vegelius, 1981). Dice's index (Dice, 1945), with similar mathematical properties (but in which matches are double-weighted) was also calculated since the use of alternative measurements of association is recommended (Hubálek, 1982). Similarities were transformed to distances and the relationships among islands were visualized through a neighbour-joining reconstruction (Saitou & Nei, 1987) in which the branch lengths are meaningful. Robustness of the nodes of the topology was assessed through bootstrapping (Felsenstein, 1985) after 1000 resamplings. The analysis was performed in MATLAB and the scripts are available from the authors on request.

Response variables

Three response variables were defined, as follows.

1. Species richness: the number of species that bred on each island during the past century. A species was computed as if it was recorded breeding on an island for a period of at least 10 continuous years.

2. Probability of presence: *a priori*, we considered potential colonizers to be those species having continental populations within a radius of 1500 km of each island. This is the largest distance found between neighbouring populations of the same species in the study area (between populations of red kite, *Milvus milvus* in the archipelagos of Canary Islands and Cape Verde; Cramp & Simmons, 1980). On each island a potential colonizing species was characterized as 1 if it had been recorded breeding in the island during the past century, or 0 if not. For this analysis, African species linked to the tropical rain forest were excluded.

3. Probability of extinction: for each species and for a given island, an extinction event was computed as 1 when the species was extinct in that island. Value 0 was assigned to species that have maintained populations to the present.

Explanatory variables

Island characteristics

We used total area, geographical location (latitude) and maximum altitude as geographical variables that could influence richness, presence and extinction events (Table 1). The latter variable is a good predictor of habitat diversity (Carrascal & Palomino, 2002). We evaluated the accessibility of the island to the birds of prey through a set of variables measuring the distance one bird has to travel to reach the island. We first considered the possibility of reaching the island from the mainland by the shortest, most direct flight or, alternatively, by the same route but following narrower straits. Additionally, we measured the distance from the island to the

Table 1 Explanatory variables used to characterize Mediterranean and Macaronesian Islands and raptor species (see Materials and methods for information sources)

Variable	Units
Island	
1 Island code (Appendix 1)	
2 Archipelago code (Fig. 1; Appendix 1)	
3 Biogeographical region: (1) Mediterranean; (2) Macaronesia (Fig. 1)	
4 Latitude	Degrees
5 Number of islands (> 100 km ²) in the archipelago	
6 Island area	km ²
7 Human density	Inhabitants km ⁻²
8 Maximum altitude	m
9 Minimum distance to continent	km
10 Minimum distance to nearest coast (island or continent)	km
11 Minimum sum of width of marine channels necessary to cross to reach island following route with less flight above sea	km
12 Maximum width of marine channels to cross to reach island, following route as variable (10)	km
13 Number of marine channels to cross to reach island, following route as variable (11)	
14 Land occupied by 'open' habitats (cultures, grazing, shrubs)	%
15 Land occupied by urban areas	%
16 Geographical position with respect to migration routes: (1) within a principal route; (2) within a secondary route; (3) far from main and secondary routes	
17 Presence of top-predator birds of prey (golden eagle, Bonelli's eagle, goshawk): (1) present; (2) absent	
Species	
18 Species code (Appendix 1)	
19 Taxonomic position: (1) Accipitridae; (2) Falconidae	
20 Distribution area (number of 5 × 5 km squares) occupied by species in a 500 km radius	
21 General distribution: (1) Palearctic; (2) African; (3) both	
22 Migratory pattern: (1) resident; (2) long-distance migrant; (3) partial migrant	
23 Adult mean body weight	g
24 Nest site habitat: (1) tree; (2) cliff; (3) ground	
25 Reproductive strategy: (1) solitary; (2) colonial	
26 Median clutch size	
27 Length of incubation period	Days
28 Length of nestling period	Days
29 Sexual maturity	Years
30 Foraging habitat: (1) open; (2) semi-open; (3) woods	
31 Affinity to human activities: (1) breeding in buildings; (2) feeding on livestock carcasses; (3) without direct affinity	
32 Population trend in Western Palearctic during twentieth century: (1) without reduction in breeding area; (2) reduction of breeding area < 50%; (3) reduction of breeding area > 50%	

three main migratory routes crossing the Western Palearctic: Gibraltar–Western African coast, Messina, and the Bosphorus (Berthold, 2001). We also evaluated the presence of top-predator raptors as an indication of well-structured food webs (Newton, 1979). Finally those variables related to human pressure on island ecosystems, such as population density and land use, were evaluated from sources that had compiled information from the past decade (Table 1), as there is an almost total lack of information for previous times. Although potentially biased (some islands are suffering accelerated transformations), it seemed better to have an estimator of human-induced transformations than to ignore their possible effects. Statistics on human populations were obtained from state general sources. Land uses were obtained from the CORINE Land Cover database (CEC 1999) by using the XTools extension (available at http://www.odf.state.or.us/DIVISIONS/management/state_forests/GIShome.asp) of ArcView GIS 3.2.

Species characteristics

The taxonomic categories family (Accipitridae vs. Falconidae) and species were codified. Body size, breeding performance, and foraging and migratory habits described the life history of each species. We also quantified the abundance of each species in surrounding areas of different radii as an estimate of the probability of 'rescue' events. Finally, we considered whether the species uses buildings for nesting and/or usually consumes by-products of human activities (e.g. livestock carcasses) to evaluate the effects of association with human activities.

Statistical analyses

Initially, we analysed a possible phylogenetic effect and investigated whether family or species categories should be included in further analyses. We performed a GLM using SAS macro GLMMIX (Littell *et al.*, 1996) to identify the taxonomic level (family or species) at which most of the variation occurs in the response variables probability of presence and extinction (Figuerola, 2000). The analysis included family and species nested within family as random effects. Both models showed that phylogenetic relationship explained only 28% and 24% of the original deviance in the probabilities of presence and extinction respectively. In both analyses most of the variation was explained by species (accounting for 28% and 26% of the original deviance in the analysis of presence and extinction, respectively), while family accounted for only 4% and 11% respectively. Consequently only species identity was included in further analyses as a random variable to control for phylogenetic effects.

The main analyses were performed applying generalized linear mixed model (GLMM), which allowed dissection of the relative contribution of island intrinsic characteristics and species-specific life-history traits from a joint analysis of geographical, ecological and human-related factors. This kind

of approach is uncommon in biogeographical research (Covas & Blondel, 1998; Burbidge & Manly, 2002). We fitted the mixed models by PROC MIXED in SAS when the response variable was normally distributed. Appropriate link functions and error structures for normal and binomially distributed data were implemented. When necessary, species, island and archipelago were treated as random terms. Each explanatory variable (Table 1) and their interactions were fitted to the observed data following a forward stepwise procedure, which results in the most adequate model for explaining variation in the response variable where only significant effects are retained (Forero *et al.*, 2002). Special attention was paid to potential interactions between biogeographical region (Mediterranean and Macaronesia) and the explanatory variables, to determine whether there was a differential response between these two zones. Finally, higher polynomial models were also fitted to account for potential nonlinear relationships.

The specific characteristics of each fitted model were as follows.

1. Species richness: a GLMM with normal error and identity link function was fitted for the 17 variables related to island characteristics (Table 1). Archipelago was fitted as a random term.
2. Presence: a GLMM with binomial error and logistic link function was fitted for the presence (1) or absence (0) of each species in each island (Appendix 1). All 32 explanatory variables were included (Table 1). Species, archipelago and island nested in archipelago were considered as random terms.
3. Extinction: a GLMM with binomial error and logistic link function was fitted for the extinction (1) or permanence (0) of the breeding populations (Appendix 1). Variables and statistical treatments were similar to those of the former analysis.

RESULTS

Raptor richness

A total of 25 species of birds of prey were recorded breeding in the 43 different islands studied (Appendix 1). If we consider a total of 49 species breeding in a radius of 1500 km of the study island, only 51% of these continental species have managed to establish breeding populations in the Mediterranean and Macaronesian islands during the past century. Twenty one of the species have a distribution restricted to Europe and the African North Sahara, and four are distributed through Europe and Africa (including the sub-Saharan region). None is distributed exclusively in sub-Saharan Africa: 24 species breeding in that region have never been found nesting in islands of the study area. Consequently only species with partial or total circummediterranean distribution were considered in further analyses. The number of breeding species by island ranged from 1 (only the European buzzard, *Buteo buteo* is present in the islands of the Azores) to 18 in Sicily, with a median value of four species per island (Appendix 1).

Geographical pattern

The island assemblages based on Jaccard's index and Dice's index were almost identical. Results derived from Jaccard's index (having a higher bootstrap support) are shown in Fig. 2. In the resulting topology all three Atlantic archipelagos (the Azores, Canary and Cape Verde Islands) were recovered in clearly distinguished clusters. But whereas the Azores Islands had no structure, the Canarian and Cape Verde archipelagos showed strong internal structure. On the other hand, only two main groups could be defined among the Mediterranean islands (eastern vs. western). Interestingly, the Balearic Islands cluster closer to the Atlantic archipelagos (Canaries and Cape Verde) than to other Mediterranean islands. Bootstrap values support only those nodes in the topology defining each of the Atlantic archipelagos (although the Canary islands appear in two groups), the two largest islands of the Balearics and, finally, a group made up of Sicily together with Corsica and Sardinia (Fig. 2).

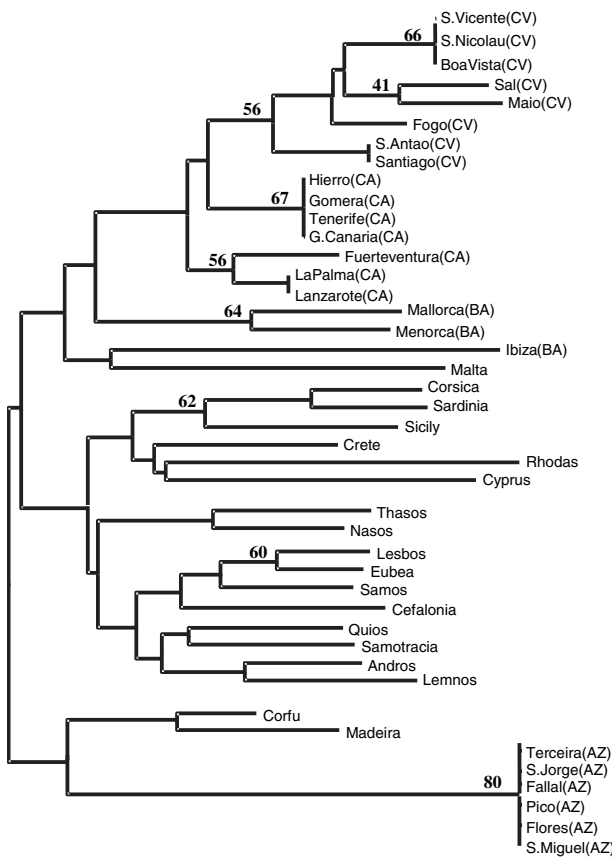


Figure 2 Similarities in bird of prey guild composition among 43 islands studied from the Mediterranean and Macaronesia. Topology obtained after a neighbour-joining distance reconstruction based on Jaccard's similarity index. Bootstrap values after 1000 replicates. Archipelagos: CV, Cape Verde; CA, Canary Islands; BA, Balearic Islands; AZ, Azores.

Species richness

After controlling by archipelago ($Z = 1.20, P = 0.11$), the GLMM explained up to 51.5% of the initial deviance and included two main explanatory variables: island area and width of the largest marine channel necessary to cross to reach the island. Species richness increased with island area, and decreased with distance to the mainland (Table 2).

Probability of presence

The two random effects species ($Z = 2.83, P = 0.002$) and island nested in archipelago ($Z = 1.95, P = 0.002$) had significant effects, but not archipelago alone ($Z = 1.28, P = 0.1$). After controlling by these variables, the best-fit model explained up to 32% of the initial deviance (Table 3). This indicates that the probability of presence on an island increases with island area and with proximity to a migration route. The effect of the migratory habits of a species was more significant: partial migrants were more prone than migrant or sedentary species to maintain populations on islands. In

Table 2 Results of generalized linear mixed model on species richness of birds of prey in the islands of the Mediterranean and Macaronesia ($n = 43$)

	Parameter estimate	Standard error	F	P
Intercept	7.01	0.98		
Island area	0.0005	0.0001	41.73	0.0001
Width of sea channel*	-0.0062	0.0021	8.43	0.007
Explained deviance (%)	51.5			

*Width of largest sea channel necessary to cross to reach island.

Table 3 Results of generalized linear mixed model for probability of presence on Mediterranean and Macaronesian islands by birds of prey with populations in a 1500 km radius

	Parameter estimate	Standard error	F	P
Intercept	-2.97	1.00		
Migratory status			22.71	< 0.0001
Sedentary	-3.57	0.55		
Migrant	-2.84	0.87		
Partial migrant	0.00			
Distribution area (500 km radius)	1.50	0.12	12.11	< 0.0001
Island area	1.5×10^{-4}	0.00	3.83	0.0001
Migratory ways			6.09	0.0023
Principal way	1.47	0.96		
Secondary way	-0.57	0.98		
Out of way	0.00			
Presence of large raptors			5.35	0.0209
Absent	-1.08	0.47		
Present	0.00			
Explained deviance (%)	32.0			

addition, species with broad distribution areas in the Western Palaearctic (measured in 500 km radius) showed higher probabilities of presence. Finally, the probability of presence was positively related to the existence of top-predator raptors.

Probability of extinction

In 53% of the islands studied, at least one species became extinct or suffered > 50% decline in population size (and/or breeding area) during the past century (Appendix 1). The median value was two extinctions per island. Cyprus and San Vicente (Cape Verde) were the islands with the greatest number of extinct species (four). Mean rates of extinction for the Canarian and Cape Verde archipelagos were 29% and 43% respectively. Mediterranean islands showed higher rates: the mean value was 23%, but reaching 50% in Cyprus and 100% in Malta (Appendix 1).

After controlling by species ($Z = 1.74$, $P = 0.04$), archipelago ($Z = 0.51$, $P = 0.3$) and island nested in archipelago ($Z = 1.38$, $P = 0.08$), the model explained only 8% of the original deviance (Table 4). The GLMM showed that raptor populations had a higher probability of extinction when their distribution area in neighbouring western Palaearctic areas (radius 500 km) was small. In addition, islands with dense human populations were more prone to suffer extinction events. Finally, species depending on human resources for feeding (livestock carcasses) and breeding (buildings) had a higher risk of extinction.

DISCUSSION

The similarity indexes showed a fairly important biogeographical signal in the composition and structure of guilds of birds of prey on the Mediterranean and Macaronesian islands (Fig. 2). This result justifies the consideration of geographical variables in further analyses. Nevertheless, the length of branches and bootstrap values support such a structure only for the Atlantic archipelagos and the Balearics, and a group made up of Sicily, Corsica and Sardinia in the Western Mediterranean Sea. The association among the other Mediterranean islands, partic-

ularly in the Eastern Mediterranean, was much weaker (Fig. 2). This pattern indicates the relative importance of historical and species-specific characteristics (such as dispersal capacity) over linear measures of distance (Fernández-Palacios & Andersson, 1993) in understanding island similarities, particularly in the Mediterranean Sea. The Atlantic archipelagos show higher stability in their species composition (lower turnover) which may be clearly related to the much higher speciation rate found on them. As many as 11 endemic subspecies of birds of prey have been recognized in Macaronesia, contrasting with only three (*Accipiter gentilis arragoni*, *Accipiter nisus wolterstorffi* and *Buteo b. arragoni*) found in the Mediterranean (all on Corsica).

Relatively high species turnover in the Mediterranean islands, promoted by shorter distances to the mainland, would have hampered any structuring of the guild, as shown by the topology. Thus a relatively high turnover rate of colonization/extinction episodes would have been an important factor determining faunal composition on the Mediterranean islands. There are many reports of occasional breeders (e.g. Bannerman & Bannerman, 1983) on these islands, events that are probably underestimated since they are difficult to detect. The shallow differentiation between Eastern and Western Mediterranean islands (although not supported by bootstrap) could be due to the presence in the former group of species showing only an eastern distribution that do not reach the western side of the Mediterranean.

Many studies have shown a close relationship between species richness and island area (Temple, 1981; Thiollay, 1997; Brown & Lomolino, 1998; Whittaker, 1998; Millien-Parra & Jaeger, 1999). This relationship may be due to the positive relationships of island area, either with total habitat availability or with habitat structure and diversity (Williams, 1964; Carrascal & Palomino, 2002). Distinguishing these related factors is difficult, but possible through our modelling approach. Intermediate steps in the construction of the model showed a significant and positive effect of maximum altitude (an indicator of habitat diversity: Fernández-Palacios & Andersson, 1993; Carrascal & Palomino, 2002) on species richness. However, this effect disappeared when island area was included in the model. Birds of prey living in temperate areas show coarse-grained habitat selection (Sánchez-Zapata & Calvo, 1999) because their numbers are largely dependent on the total extension of suitable land. Thus island-dwelling birds of prey in temperate areas appear to behave differently from those living in tropical zones, which are more dependent on small-scale habitat features (Thiollay, 1997).

Our results also show that richness decreases with isolation (width of sea barrier), as predicted by the theory of island biogeography. Water masses may constitute important barriers for birds of prey, and the lack of thermal currents on the sea may limit the displacement of large and medium-sized species (Pennycuik, 1972). Migrating raptors travel from Europe to Africa across the Mediterranean Sea mainly through the narrower straits (Gibraltar and the Bosphorus) to minimize flying over open sea (Berthold, 2001). However,

Table 4 Results of generalized linear mixed model for probability of extinction of birds of prey in islands of the Mediterranean and Macaronesia during the twentieth century

	Parameter estimate	Standard error	F	P
Intercept	-2.29	0.96		
Human density	0.004	0.001	10.46	0.0016
Dependence on humans			6.60	0.0019
Nest sites (buildings)	0.77	1.26		
Food (livestock carcasses)	3.60	1.05		
No dependence	0.00			
Distribution area (500 km radius)	-0.71	0.26	7.29	0.0079
Explained deviance (%)	8.0			

part of the migratory flow reaches Africa through the Italian Peninsula and the strait of Sicily, which is 140 km wide. This indicates that raptors are also able to cross quite large bodies of water. The regular recording of non-breeding individuals and migratory groups on islands situated far away from the continent is evidence supporting the fact that water masses do not represent absolute geographical barriers for raptors. As many as 18 species of non-breeding birds of prey have been recorded on the Canary Islands; six are considered as regular visitors (*Milvus migrans*, *Circus aeruginosus*, *Circus cyaneus*, *Circus pygargus*, *Hieraetus pennatus*, *Falco subbuteo*: Martín & Lorenzo, 2001). A similar picture is found in the Balearics, where up to seven non-breeding raptor species can be observed regularly on these islands, mainly during migration (Bannerman & Bannerman, 1968). It is likely that water straits act as semi-permeable barriers, creating a metapopulation structure that may determine low probabilities of colonization of appropriate habitats and lands beyond the barrier (Serrano & Tella, 2003).

The lack of a significant effect of body size in the probability of presence model does not support the arguments that restrict the distribution of large-body raptors to islands close to mainland (Alcover & McMin, 1994). Species such as the Egyptian vulture (*Neophron percnopterus*) are able to reach islands as distant from the continent as Cape Verde (600 km). However, the probability of presence was higher for species with partial migration patterns. These species may have more flexible phylopatric behaviour on the basis of their adaptation to unstable environments (Hamilton & May, 1977). Such flexibility may favour colonization of islands by individuals arriving hazardingly during their migratory trips. The link between migration and probability of presence is shown again by our results, indicating the role of the island's vicinity to the main migratory routes crossing the study area. In addition, probability of presence was positively influenced by the existence of the species in an area of 500 km radius around the island. Larger areas (and consequently populations) may determine not only greater possibilities of reaching the island (Sarà & Morand, 2002), but also a higher probability of persistence (post-colonization) through a 'rescue effect' (Brown & Kodrick-Brown, 1977). Finally, a positive influence of the presence of top-predator birds of prey was found, indicating that islands with complex food webs are more able to sustain breeding raptors.

Extinction rates on some islands have been high during the past century, especially for islands in some of the Macaronesian archipelagos such as Cape Verde. However, the low deviance explained by our model (8%) indicates that these events may either depend on other factors, different from those analysed, or be modelled by stochastic events (demographics, environmental, genetic, etc.) as is the rule for small, isolated populations (see Meffe & Carroll, 1994 for review). It is interesting to note that extinctions appear to be more probable on islands with dense human populations, which probably reflects direct persecution.

Furthermore, and contrary to our prediction, species directly dependent on human activities are more prone to

suffer population declines, and extinction probability did not depend on body size. These results can be derived from the fact that species in contact with humans are more susceptible to persecution. Scavengers are often affected by indirect poisoning derived from persecution of livestock predators. This is considered to be the principal cause of the increasing rarity of red kites (*M. milvus*) on Cape Verde and the Canary and Balearic Islands, Egyptian vultures on Cape Verde and the Canary Islands, and cinereous (*Aegypius monachus*), griffon (*Gyps fulvus*) and bearded (*Gypaetus barbatus*) vultures on Sardinia, Sicily and Crete (Hiraldó *et al.*, 1979; Muntaner & Mayol, 1996; Hille & Thiollay, 2000; Xirouchakis *et al.*, 2001; Donazar *et al.*, 2002). Our results underline that generalizable conservation strategies are not adequate for endangered birds of prey of the Mediterranean and Macaronesian islands. An increasing number of projects, such as those funded by the European Union, have been directed towards conservation of some of the last insular populations of cinereous, bearded and Egyptian vultures (European LIFE Nature Database; <http://europa.eu.int/comm/life/home.htm>). It seems clear that these projects must be based on careful evaluation of ecological and human-related factors potentially limiting each local population (Donazar *et al.*, 2002).

In conclusion, our results reveal that long-term and intense humanization of Mediterranean and Macaronesian islands has not altered the general patterns predicted by the island biogeography theory: the richness of birds of prey depends on island area and distance to continental source populations. It is also remarkable that the two regions did not differ in the trends observed (all the interactions were not significant). This suggests that our findings can probably be generalized to other insular systems. Habitat requirements of birds of prey in temperate insular biomes appear to be low, which should increase the survival of their populations. The models highlight the importance of species-based analyses in studies of island biogeography: species identity explained an important part of the observed variability in the probability of presence (Lomolino, 2000). Species' inherent features are determining, but do not appear to be linked to fixed life-history traits such as those imposed by body size. Flexibility in behavioural patterns appears to be of greater importance. In particular, interspecific variability in the flexibility of dispersal and migratory strategies may be important in explaining arrival and permanence in insular systems (Rosenzweig, 1995; Owens *et al.*, 1999).

ACKNOWLEDGEMENTS

We thank R. Barone, C. J. Palacios, V. Penteriani, P. Beja, P. J. Paes de Faria, A. C. Pereira, F. de Pablo, A. Corso and S. Xirouchakis for unpublished information on raptor status on several islands of the study area, and R. E. Strauss for MATLAB programmes. O. Ceballos contributed to formulating the work, and J. L. Tella, D. Serrano, M. Palmer and two anonymous referees discussed and improved the manuscript. Rachel Atkins and Lauren Bortolotti gently corrected the English style. The Consejería de Medio Ambiente del Cabildo

Insular de Fuerteventura, the Viceconsejería de Medio Ambiente del Gobierno de Canarias, and Projects REN 2000-1556 GLO and CGL2004-00270 funded this research. M.G.F. was supported by a RyC contract of the Spanish MCyT.

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Editor: José María Fernández-Palacios

Appendix 1 Presence/absence (1/0) of breeding bird of prey populations in 43 islands of the Mediterranean Basin and Macaronesia during the twentieth century. Species with currently extinct populations are shown in bold. Number of species* also indicated by island (richness) and number and percentage of extinctions. First two columns indicate codes for each island (CI) and archipelago (CA)†. General bibliographic sources are detailed in Materials and methods. See last column and footnotes for regional studies

CI†	CA†	Ph	Pa	Mm	Mg	Ha	Gb	Np	Gf	Am	Cg	Cp	Ca	Ag	An	Ab	Bb	Br	Ac	Hp	Hf	Ft	Fn	Fs	Fb	Fp	No. species*	No. extinct	% Extinct	Source‡	
Ibiza	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0.0	1	
Mallorca	2	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	1	10	1	10.0	1	
Menorca	3	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	7	0	0.0	1	
Corsica	4	2	1	0	1	0	1	0	0	0	1	1	1	1	0	1	0	1	0	0	0	1	0	1	0	1	13	1	7.7	2	
Sardinia	5	2	1	0	1	0	1	0	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1	1	0	1	17	4	23.5		
Sicily	6	3	1	0	1	1	0	1	1	1	1	1	1	0	1	0	1	0	1	0	1	1	1	1	1	1	19	4	21.0	3	
Malta	7	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	3	3	100.0	4	
Crete	8	4	1	0	0	0	1	1	0	0	0	1	1	0	1	1	1	1	1	1	0	1	1	1	0	1	14	1	7.1	5	
Rhodus	9	4	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	9	1	11.1	6, 7	
Lesbos	10	4	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	15	1		6	
Chios	11	4	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	9	1		6	
Corfu	12	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	4	1		6	
Euboea	13	4	0	1	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	14	1		6	
Andros	14	4	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0	0	1	1	1	0	1	9	1		6	
Lemnos	15	4	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	1	1	1	0	1	8	1		6	
Thasos	16	4	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	1	1	0	1	1	9	1		6	
Samos	17	4	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	1	1	1	1	1	1	12	1		6	
Cephalonia	18	4	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	0	1	0	1	10	1		6	
Naxos	19	4	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	1	1	0	1	1	8	1		6	
Samothrace	20	4	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	1	1	0	0	1	6	1		6	
Cyprus	21	5	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	8	4	50.0	8	
La Palma	22	6	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	0	1	6	2	33.3	9	
Hierro	23	6	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	7	2	28.6	9	
Gomera	24	6	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	7	2	28.6	9	
Tenerife	25	6	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	7	2	28.6	9	
Gran Canaria	26	6	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	7	3	42.9	9	
Lanzarote	27	6	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	6	1	16.7	9	
Fuerteventura	28	6	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	5	1	20.0	9	
Madeira	29	7	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	3	0	0.0	10	
San Miguel	30	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0.0	10	
Terceira	31	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0.0	11	
San Jorge	32	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0.0	11	
Faial	33	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0.0	11	
Pico	34	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0.0	11	
Flores	35	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0.0	11	
St Antao	36	9	1	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	7	1	14.3	12
San Vicente	37	9	1	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	6	4	66.7	12	

