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Explanations for bird species range size: ecological correlates and phylogenetic effects in the Canary Islands.

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ABSTRACT

Aim To explore the determinants of island occupancy of 48 terrestrial bird species in an oceanic archipelago, accounting for ecological components while controlling for phylogenetic effects.

Location The seven main islands of the Canary archipelago.

Methods We obtained field data on density, habitat breadth and landscape distribution in Tenerife, Fuerteventura and La Palma, trying to sample the whole availability of habitats and the gradient of altitudes. In total 1,715 line transects of 0.5 km were carried out during the breeding season. We also reviewed the literature for data on occupancy, the distance between the Canary Islands and the nearest distribution border in the mainland, body size and endemicity of the 48 terrestrial bird species studied. Phylogenetic eigenvector regression was used to quantify (and to control for) the amount of phylogenetic signal.

Results The two measurements of occupancy (number of occupied islands or 10x10 km UTM squares) were tightly correlated and produced very similar results. The occupancy of the terrestrial birds of the Canary Islands during the breeding season had a very low phylogenetic effect. Species with broader habitat breadth, more intense preferences for urban environments, smaller body size, and lower degree of endemicity had a broader geographical distribution in the archipelago, occupying a larger number of different islands and 10x10 UTM squares.

Main conclusions The habitat generalist species with a tolerance for novel urban environments tend to be present in more islands and to occupy more area, while large-sized species that are genetically differentiated within the islands are less widespread. Therefore, some properties of the ranges of these species are explicable from basic biological features. The positive relationship with local abundance, previously uncovered in continental studies, was not found, probably because it relies on free dispersal on continuous landmasses that may be short-circuited in oceanic island scenarios.

Keywords

Abundance, birds, body size, Canary Islands, habitat breadth, macroecology, occupancy, phylogenetic effect, urban preferences.

Running title: bird range size in the Canary Island

INTRODUCTION

Understanding why species are more or less broadly distributed within their geographical limits is one of the cornerstones of macroecology and biogeographical ecology, and has spurred a large number of studies that attempt to identify prevailing patterns, infer the underlying processes, and use the findings to forecast future changes under global change (e.g. Channell & Lomolino, 2000; Gaston *et al.*, 2000; Linder *et al.*, 2000; Böhning-Gaese *et al.*, 2006; Hawkins & Diniz-Filho, 2006). The extension of the geographical range also has important consequences for the conservation of biodiversity, as this is one of the primary variables determining the endangered status of the species (IUCN Red List classification, IUCN, 2001). Several analyses have studied the correlation between ecological and life-history traits with population size, density and body mass (Gaston, 1996, 2003; Gaston & Blackburn, 2000), or niche breadth and niche position (Fernández & Vrba, 2005; Harcourt, 2006). Evolutionary effects on interspecific differences in range occupancy have also been analysed, dealing with the phylogenetic conservatism of this trait (Waldron, 2007). Nevertheless consistencies in ecological, life history and phylogenetic correlates have not always been found, which illustrates that predicting the fate of species across different taxa and geographical scenarios on the basis of simple traits is not always possible due to the highly contingent nature of evolution and geography (see Böhning-Gaese & Oberrath, 1999; see Duminil *et al.,* 2007).

With few exceptions (Gottelli & Graves, 1990; Thiollay, 1997; Foufopoulos & Ives, 1999; Dennis *et al.*, 2000; Jones *et al.*, 2001) this research has been carried out largely in continuous continental areas. Insular systems offer an additional complication in macroecological studies because the range must be measured on disjoint geographical entities (i.e. islands), where three distinct types of phenomena acquire fundamental relevance. First, current range depends on the past events of island colonization, and on the local persistence and dispersal of populations between islands. Second, island populations may rapidly adapt to local conditions and differentiate into new taxa, which would initially have smaller ranges and perhaps later extend and eventually contract again afterwards following a taxon cycle (Ricklefs & Bermingham, 2002; Millien, 2006). Finally, species may be freed from the pressure of competitors and predators and expand their realized niches, which could improve their ability to colonize new areas (for example, via character release, Blondel *et al.*, 1988; Grant, 1998). Thus, the occupancy of the different islands within an archipelago may be a rather stochastic phenomenon, because the arrival is mediated by chance, and the subsequent population dynamics of the species most probably operate under novel constraints, where abiotic factors and biotic interactions can be totally different from those in source regions.

In such a discontinuous geographical scenario, the number of occupied islands may provide a reasonable measure of the geographical extent, which substantially differs from the classical measure of the area over which the species actually occurs. This is because several islands within an archipelago may be the result of different geological events, of different age, area, landscape heterogeneity, and distance to the continent. Thus, the distribution over an extensive area in only one large island may not imply such a high colonization success as the occupation of a similar area dispersed over several small islands (see also Hurlbert & White, 2007 for a discussion on this topic). On the other hand, the study of ecological and life history correlates of the occupancy of island faunas is of great interest because due to the small areas of islands with respect to continental land masses, many endemic species should be considered as endangered according to IUCN Red List distribution criteria on range size (IUCN, 2001). Taking into account that distribution within archipelagos is subjected to dispersal limitations from the continental sources and local demographic processes within different islands, it is probable that not all species have the same ability to thrive and persist irrespective of human perturbations (Steadman, 2006). This probability of persistence, and thus the geographical extent within archipelagos, may have an evolutionary basis (i.e., phylogenetic niche conservatism), being phylogenetically structured. Hence, the ability to colonize and thrive in a wide array of different islands has not been found to be arbitrarily distributed along an evolutionary tree, but rather it is concentrated in certain clades (Foufopoulos & Ives, 1999; Sol *et al.*, 2002). Conversely, it may not be phylogenetically structured as a consequence of random sampling from the continental fauna pool, highlighting the role of stochasticity in the dispersal-colonization-extinction process (Juan *et al.*, 2000).

In this paper we analyse the interspecific variation in occupancy of the avifauna of the Canary Islands. This archipelago is composed of seven main islands of volcanic origin. They are located in the northeast Atlantic Ocean and show a broad range of variation in many environmental and geological traits (geological age, distance to the continent, area, altitude, climate, and vegetation). The bird fauna of the Canary Islands is typically Palaeoarctic, although its geographical position coincides with the south-western limit of this biogeographical region (Kunkel, 1976; Clarke *et al.*, 2006). In insular systems such as these, the ecological patterns commonly found in continental areas and their proposed explanatory hypotheses may be altered due to the stochastic nature of colonization from the continental source, the processes of adaptive evolution and extinction (Juan et al., 2000) and the intensive human influence within the islands (e.g. Rando, 2002).

We study and discuss several potential correlates of occupancy, such as body size, population density, habitat breadth, tolerance for human disturbances (agriculture and urbanism) and the distance of the Canary Islands to the distribution limits of the species in the continent. All of these variables have been claimed to affect the geographical range of species according to alternative hypotheses with contrasting supporting evidence (see Gaston 2003 for a review). Also, these potential determinants of occupancy are analysed within a phylogenetic framework, in order to control for the potential degree of non-independence among species due to common descent.

Thus, our main aim is to explore the determinants of occupancy in an oceanic archipelago scenario, estimating the influence of ecological factors, whilst accounting for phylogenetic inertia and endemicity. We quantify the effect of these different factors, discuss their relative merits to explain occupancy of the terrestrial bird species in the Canary Islands, and argue the reasons why island scenarios may provide results contrasting with those from continental studies.

METHODS

Study area

We obtained data on occupancy, body size, abundance, habitat breadth, landscape distribution and endemicity for 48 terrestrial bird species that breed in the Canary Islands (27º30’-29º30’N and 13º20’-18º15’W). The seven main islands comprise a wide range of environmental conditions, distances to mainland and habitats. Island area ranges from 2059 km^2 (Tenerife) to 273 km^2 (El Hierro). The minimum distance to the nearest mainland (north-western Africa) varies from 96 km for Fuerteventura, to 417 km for La Palma. Fuerteventura, Lanzarote and Gran Canaria have an ancient geological history (15-20 million years old respectively) while El Hierro and La Palma are the youngest in the archipelago (1-2 million years). Fuerteventura and Lanzarote are the most arid and low islands (less than 800 m a.s.l., and 300 mm of precipitation per year) with a predominance of semi-desert landscapes and woodlands almost completely absent, while Tenerife and La Palma reach higher altitudes (more than 2400 m a.s.l., and have extensive areas with more than 600 mm of precipitation per year) and have a widespread representation of native pine and evergreen (‘*laurisilva’*) forests (although natural cover have been much reduced since humans occupied the islands, Walter and Breckle, 2002; De Nascimento *et al.*, in press). Habitat diversity in these islands is tightly related to their maximum altitude, ranging from the highest figures of Tenerife, La Palma and Gomera, to the lowest values in Fuerteventura. See Juan et al. (2000), Fernández-Palacios & Martín-Esquivel (2001) for more details on island characteristics.

Bird data

Bird surveys were carried out during the breeding season in 2002-2003 (Tenerife), 2005-2006 (Fuerteventura) and 2007 (La Palma), in an attempt to sample the whole availability of habitats and the gradient of altitudes. Field work was conducted from March to April, depending upon the geographical variation in the breeding phenology of the birds in these three islands (beginning earlier at lower altitudes and in the dry Fuerteventura, then at higher altitudes and in the more western, oceanic, islands). The survey method was the line transect, frequently used in extensive assessments of abundance, general distribution patterns and habitat preferences of birds (Bibby *et al.*, 2000).

A total of 1,715 line transects of 0.5 km (measured by means of portable GPSs) were made (Tenerife: n=592, Fuerteventura: n=686, La Palma: n=437; Fig. 1). The transects were carried out on windless and rainless days, walking cross-country or by little-used dirt tracks at a low speed (1-3 km/h approximately), during the 4 hours after dawn and the 2.5 hours before dusk. From this sampling we estimated densities (i.e., abundance per unit area) correcting for the detectability of the species by using the perpendicular distances to the birds (Buckland *et al.*, 2001). Several variables used to characterize the 0.5 km transects were obtained, averaging three estimations (at 125, 250 and 375 m within the line transect) on 25-m radius circular plots. Three of them were used in this paper: 1) altitude above sea level (measured with GPS receptors), and coverage of 2) urban areas (buildings, paved streets) and 3) any agricultural land-use (coverages were estimated by eye).

These transects cover the wide variation of climate, altitude, anthropogenic impact, habitat structure and floristic characteristic of the environments available for terrestrial birds in the Canary archipelago. Bird transects were stratified *a-priori* in 36 major habitat types according to overall vegetation and topographic characteristics: 12 in Fuerteventura (Fv), 14 in Tenerife (Tf) and 11 in La Palma (LP). These habitats included the following environments: urban habitats, various kinds of agricultural areas, pasturelands, two kind of euphorbia shrublands according to altitudinal distribution and vegetation cover, and lava fields with very low vegetation cover in the three islands; evergreen (‘*laurisilva*’) forests, tall heathlands, two pine forests according to altitudinal location, and high altitude scrublands (>2500 m a.s.l.) in Tf and LP; sandy areas covered with grasses, forbs and small shrubs (‘*jable*’), semi-desert lowland areas, arid scrublands in mountain areas both with low and high shrub cover, and riparian dwarf woodlands of *Tamarix canariensis* only in Fv; poorly vegetated subalpine areas (above 2500 m a.s.l.) only in Tf.

Response and explanatory variables

We quantified the occupancy in the Canary Islands in two ways. First, we calculated the area of occurrence as the number of 10x10 km Universal Transverse Mercator squares occupied by each species in the seven main islands of the Canary archipelago (according to the most recent breeding bird atlas of Spain: Martí and Del Moral, 2003). Second, we noted the number of occupied islands (one to seven), which is a measure of the extent of occurrence considering the very different geographic, orographic, climatic and landscape characteristics of the islands within the archipelago (see Appendix S1 in Supplementary Material).

We estimated the maximum density recorded in the 36 major habitat types censused, as a measure of the maximum ecological abundance a species can attain in its most favourable environment in the Canary Islands. We also estimated the maximum ecological density of each species within each island, with the 12 habitats distinguished in Fuerteventura, 14 habitats in Tenerife and 11 habitats in La Palma (see Appendix S2 in Supplementary Material). The average altitudinal distribution of each species in the archipelago was estimated as the average altitude of the samples where the species was observed (weighted by the number of birds recorded in each 0.5 km transect). Finally, the affinity for novel environments of anthropogenic origin in the Canary Islands was also calculated as the weighted average (by the number of birds recorded in each transect) of the cover of urban and agricultural habitats (see above) in the transects where the species were recorded.

Niche breadth of habitat distribution in the Canary archipelago was calculated considering a re-arrangement of habitat types in 9 categories that account for more than 95% of the terrestrial surface of the Canary Islands: urban environments, agricultural areas, pine forests, evergreen arboreal vegetation (‘*monteverde*’; laurel forests and tall heathlands), lowland semi-deserts, euphorbia scrublands, other shrublands in mountain areas (below 800 m a.s.l.), high altitude scrublands (>2500 m a.s.l.), and subalpine barren areas (above 2500 m a.s.l.). In the following analyses we used the maximum densities recorded in these main habitat categories. Habitat breadth (HB) of species was calculated following the Levins index, divided by the number of habitat categories considered (Levins, 1968):

$HB = [(\Sigma p_i^2)^{-1}]/9$

where p_i is the proportion of the density for each species measured in the habitat i (dividing density in habitat i by the sum of all maximum densities recorded in the nine main habitat categories). This index ranges between 1 (evenly distributed across the nine habitats) and 1/9 (only present in one habitat). Habitat breadth in each island was also calculated for the species (see Appendix S2 in Supplementary Material), using the same index and considering the habitats distinguished in Fuerteventura (12), Tenerife (14) and La Palma (11).

The taxonomic status of each species was assessed with the recent compendium of bird natural history for the Canary Islands (Martín & Lorenzo, 2001), other more recent reports (Kvist *et al.*, 2005; Packert *et al.*, 2006), and with unpublished data from the regional government (J.L. Martín-Esquivel, *pers. com.*). An ordinal categorical variable measuring the degree of endemicity was created, assigning the value 2 to endemic species, 1 to endemic subspecies, and 0 for all other species, whether native or recently introduced.

To take into account the range position of the study species, we estimated the distance between the Canary Islands and the nearest distribution border of the native species in the mainland from the distribution maps in the Western Palaearctic (Perrins, 1998). This measurement could not be obtained for three recently introduced species from Argentina, India and Southern Africa (*Myiopsitta monachus, Psittacula krameri* and *Streptopelia roseogrisea*, respectively), nor for the ten endemic species of Macaronesia (Madeira, Azores and Canary Islands; *Apus unicolor*, *Columba bollii*, *C. junoniae, Anthus berthelotii, Saxicola dacotiae, Phylloscopus canariensis, Regulus teneriffae, Cyanistes teneriffae, Fringilla teydea* and *Serinus canaria*).

Finally, body mass was used to account for several aspects related to life-history (Peters, 1983), habitat use (Polo & Carrascal, 1999), flight performance (Ellington, 1991; Spaar, 1997), population density and the extent of occurrence (see review by Gaston & Blackburn, 2000). Body mass of species was obtained from published literature (Perrins, 1998) as the mean weight of males and females, or as the average value of body weight range in spring and summer. In some instances where body mass was not available (*Apus unicolor*, *Columba bollii* and *C. junoniae*), it was calculated by means of allometric relationships among closely related species of the Southwestern Palaearctic, using tarsus and wing lengths as predictors (R^2>0.90).

Statistical methods

We used phylogenetic eigenvector regression (PVR) to quantify the amount of phylogenetic signal and to correct for this signal in analysing the relationship between occupancy and ecological and biogeographical variables (Diniz-Filho *et al.*, 1998; Diniz-Filho & Torres, 2002). In order to perform the PVR, we first created a matrix of pairwise phylogenetic distances between the 48 species and used it to carry out a Principal Coordinates Analysis (PCoA). The axes of the PCoA account for the bird phylogeny. We selected the first four axes (PVR components) using the broken-stick rule to parsimoniously summarize the phylogenetic signal present in the data.

The phylogenetic hypothesis used was taken from Sibley and Ahlquist (1990), based on DNA-DNA hybridisation data. Although more recent phylogenies (eg., Barker et al., 2004; Fain & Houde, 2004; Ericson et al., 2006) show several regions of the Sibley and Ahlquist phylogeny to be misleading, these discrepancies do not affect the phylogenetic hypothesis used in this study for the analysed species. Accordingly, the matrices of phylogenetic distances between the 48 bird species are nearly identical considering Sibley and Ahlquist (1990) or the more recent literature sources (Mantel test of correlation between matrices: $r=0.94$, $P<0.001$). Moreover, Sibley and Ahlquist's (1990) work is the only one that provides a topology for all the families and genera used in this study and seems to be well resolved above the subfamily level (Mooers & Cotgreave, 1994). Because deltaT_{50}H values provided by Sibley and Ahlquist (1990) do not establish unequivocally the evolutionary time elapsed between species and nodes, and between nodes (Mooers & Cotgreave, 1994), alternative distance matrices can be designed by transforming the distances to test phylogenetic effects. Therefore, we have carried out the phylogenetic analyses with the original distances (d_{ij} between species i and j), the squared transformed matrix (d_{ij}^2; to decrease independence among contemporary tip species), and the square-rooted distances ($d_{ij}^{0.5}$; to increase independence among contemporary tip species). Working with these extreme phylogenies allowed us to test the robustness of phylogenies when using inaccurate branch length information (Martins & Garland, 1991).

A first assessment of the phylogenetic signal in the data (R^2, variance explained by the phylogenetic hypothesis) was made by linear regression of the study variables on the selected eigenvectors. This analysis was carried out using the first four PVR components obtained with the phylogenetic distance matrix using original, squared and square-rooted distances. Second, a multiple regression analysis was used, regressing the number of occupied Canary Islands (the response variable; log-transformed) upon the explanatory variables and the four phylogenetic PVR components. A type-III sum of squares for variance partitioning was used. Species body mass, maximum ecological density and midpoint altitude were log-transformed, while for habitat breadth and average urban and agriculture cover the angular transformation was used (arcsin square-root [x_i], x_i being a number ranging between 0 and 1). The degree of endemicity was included as an ordinal predictor. Finally, the maximal regression model that includes all the predictors was reduced with stepwise regression, where alternative models were compared with the version of AIC corrected for small sample sizes (S-PLUS function stepAIC.c by Spencer Graves, available at www.prodsyse.com).

In order to determine the relative merits of the alternative explanations for the occupancy we followed a variance partitioning scheme (see Fig. 2 and Borcard *et al.*, 1992; Heikkinen *et al.*, 2004 for similar approaches; Carrete *et al.*, 2007; Diniz-Filho & Bini, 2008). We divided the explanatory variables into three sets: (1) the four phylogenetic eigenvectors and the endemicity, (2) the maximum ecological density and the body mass, and (3) the midpoint altitude, the urban cover, the agricultural cover and the habitat breadth. Then we built multiple linear regressions models with each of these sets on their own as well as three other models combining sets (1+2), (1+3), (2+3) and, lastly, the maximal model with the full set of variables. The first three models allow the estimation of the fraction of the variance that can be attributed to evolutionary effects (set 1), life-history traits (set 2) and to habitat use (set 3), while the rest serve to calculate the phylogenetically structured effects (sets 1+2 and 1+3), the concomitant effects of life-history and habitat use patterns (set 2+3), and the maximum explanation attainable (sets 1+2+3). Pure and joint fractions were estimated by simple algebra with the R^2 of the models. For example, the portion of variance in the extent of occurrence attributed to pure evolutionary effects was calculated as the R^2 of the maximal model (built with sets 1+2+3) minus the R^2 of the regression built with sets (2+3).

The effect of the distance between the Canary Islands and the nearest distribution border in the European or African mainland on the species' geographical ranges in the Canary Islands was tested by means of the correlation between the logarithm of these geographical distances and the residuals of the maximal regression model. Multiple regression analyses were carried out using STATISTICA 6.0 (Statsoft, 2001). Residuals were checked for normality, patterns of relationship of residuals and predictions of the regression models (to identify deviations of the assumption of linearity), and for influence and outlier data points using Cook's distance and leverage. We also tried alternative Poisson regressions with the response variables (generalized linear models with Poisson errors and with log link function), but they resulted in a worse fit to the data (overdispersion parameter φ highly deviated from unit and poorer residual plots), so we based our analyses instead on general linear regression.

RESULTS

Phylogenetic effects

The Principal Coordinates Analysis on the original distance matrix resulted in 37 eigenvectors. We selected the first four eigenvectors, which accounted for 68% of the total variation observed in the original distances in the phylogenetic matrix. The first eigenvector mainly separates the Passeriformes from the remaining species. The second eigenvector clearly separates the Columbiformes from a large clade composed by Falconiformes, Galliformes, Charadriiformes, Coraciiformes and Piciformes, which is again classified into two groups by the third eigenvector (Falconiformes and Charadriiformes vs. Galliformes, Coraciiformes and Piciformes). Finally, the fourth eigenvector introduces subtle differentiations between the clades previously defined by the first three eigenvectors. The alternative phylogenetic hypotheses using square or square-root transformations of original phylogenetic distances produced similar results (square-rooted distances: 56% of explained variation from original phylogeny; squared distances: 72%).

Neither measure of occupancy (number of occupied islands or 10x10 km UTM squares) regressed significantly on the phylogenetic eigenvectors (Table 1). Similarly, average position in the altitudinal gradients of the islands, distance to the nearest mainland distribution border, habitat breadth and preference for areas devoted to agriculture did not show any appreciable amount of phylogenetic signal. The occupation of urban environments and, most notably, body mass and maximum ecological density in the Canary Islands, showed a marked phylogenetic effect accounting for 21-57% of the variation in actual observed interspecific variation. These results hold irrespective of the phylogenetic distances used in the analyses (i.e. original, squared or square-rooted). Therefore, results obtained with the original phylogenetic distances are presented in the following paragraphs for the sake of simplicity.

Archipelago occupancy

The maximal model (i.e. using the full set of predictor variables) for the extent of occurrence using the number of occupied islands was significant ($F_{11,36}$=3.03, P=0.006) and explained 48.1% of the variation in the data (Table 2). Controlling for phylogenetic effects in both the response and explanatory variables, the number of occupied islands in the Canary archipelago was positively influenced by habitat breadth and negatively affected by body size of terrestrial birds (both at $P<0.05$). The degree of endemicity (with a negative effect) approached significance ($P=0.060$).

Most of the variation in occupancy was explained by the simple effects of variables describing the species habitat use (20.1%) and, to a lesser extent, the evolutionary effects and life-history variables alone (15.8% and 8.3%, respectively; Figure 2). The joint effects were low, and two resulted in negative values, which show low interaction effects between the sets of variables. There were no relevant phylogenetically structured effects (i.e., there is a lack of high positive joint effects with phylogeny).

All of the similar plausible regression models (those with ΔAIC<2; Table 3) incorporated the degree of endemicity, body mass and habitat breadth, reinforcing their prominent role in determining the extent of distribution in the Canary Islands. Inclusion of urban cover and agricultural cover is more debatable, as these terms are in only some of the best models, all of which are equally plausible. The model with the lowest AIC, included body size, habitat breadth, the degree of endemicity and the average urban cover of the preferred habitat (the latter approaching significance at P=0.057) plus the phylogenetic eigenvectors PVR1 and PVR4 (R^2=0.461, $F_{6,41}$=5.84, P=0.0002; see Tables 2 and 3).

The residuals from the maximal model were uncorrelated with the nearest distance to the mainland distribution border of the native species (r=0.061, n=35, P=0.727).

Both measures of occupancy (number of occupied islands and 10x10 km UTM squares) are highly correlated (r=0.744, n=48, P<0.001). Indeed, the results were very similar regardless of the variable used. The best subset model obtained for the number of occupied 10x10 km UTM squares is very close to the one for the number of occupied islands (compare with results in the right side of Table 2). The regression model was highly significant ($F_{6,41}$=19.98, P<0.001, R^2=0.745), with very significant negative associations with the degree of endemicity (β=-0.31, P=0.001) and body mass (β =-0.41, P=0.002), and positive relationships with habitat breadth (β =0.78, P<0.001) and the average urban cover of the preferred habitat (β =0.19, P=0.038), after controlling for the phylogenetic vectors PVR1 (P =0.117) and PVR4 (P =0.007).

To summarize, the occupancy of the terrestrial birds of the Canary Islands during the breeding season shows a very low phylogenetic effect. Those species with broader habitat breadth (Fig. 3), smaller body size, lower endemism score, and (marginally) more intense preferences for urban environments had a broader geographical distribution in the archipelago, occupying a larger number of different islands.

Within-island occupancy

Table 4 shows the relationships between the area of occupancy (measured as the number of occupied 10x10 km UTM), the abundance and the breadth of habitat of the species in Fuerteventura, Tenerife and La Palma, after controlling for the phylogenetic effects accounted for by the vectors PVR1 to PVR4. The other five variables included in Table 2 were not considered here due either to the lack of information or variation across islands (for variables endemicity and body mass), or to sample size deficiencies that prevented the estimation of accurate averages for some species (for variables midpoint altitude, urban cover and cover of agricultural areas).

The effect of phylogeny was very low, reaching significance only in Fuerteventura Island (again the vectors PVR1 and PVR4). Habitat breadth had a consistent positive and significant influence in the three islands. The maximum ecological density had a positive influence on area of occupancy in the three islands, although it only reached the significance level in Fuerteventura.

DISCUSSION

The two measurements of occupancy of the species examined in this study were tightly correlated and produced very similar results, although the amount of variance explained by the ecological and phylogenetic correlates was larger for the area of occurrence (73%) than for the number of different islands on which the species were present (47%). Nevertheless, it can be argued that the number of occupied islands is a better measurement of the geographical extent of a species within archipelagos (although more difficult to model) than the number of geographical spatial units occupied (e.g., number of UTM squares of 10x10 km), because it is more closely related to demographic processes and ecological niche. For example, although two species may show the same area of occurrence in an archipelago, one could inhabit several habitats on a single homogeneous large island (e.g., *Saxicola dacotiae*, which occupies 28 10x10 km UTM squares in the dry habitats of Fuerteventura) while the other could be restricted to fewer habitats on several islands (e.g., *Scolopax rusticola*, which occupies 29 squares on five islands). The number of occupied islands is a rough index of eurytopicity both at the landscape (habitats available and occupied on different islands) and geographical scales (occupation of different islands according to their size, altitudinal gradients, and distance from the mainland), and summarizes the species' ecological ability to colonize and persist under a wide array of environmental conditions.

Niche-based characteristics may explain patterns of distribution and abundance from the level of local habitats to that of geographical ranges (Gaston *et al.*, 1997b). High range occupancy is frequent in species that are common and tolerate a relatively wide range of ecological conditions (Swihart *et al.*, 2003; Böhning-Gaese *et al.*, 2006;

Hurlbert & White, 2007). Consistently, a direct measure of ecological width of the terrestrial bird species of the Canary Islands (habitat breadth) is tightly correlated to occupancy measured for the entire archipelago, either as the number of occupied islands or as 10x10 km UTM squares. Moreover, this relationship is also found within each of the three studied islands. The regional range size of a species has frequently been explained by the species habitat breadth or position in such a way that those species with larger realized niche breadths, or those occupying common and extensive habitats, are in turn more widespread (Gaston & Blackburn, 2000; Gaston, 2003). Being of volcanic origin, the Canary Islands differ in age, size, topography and habitat types, and this variability provides a wide range of highly contrasting environmental conditions to which species must adapt, such that eurytopic or tolerant species are more likely to inhabit a wide array of different habitats and to establish populations on several islands.

On the other hand, the maximum ecological density attained in the preferred habitat did not enter the best subset models for occupancy over the entire archipelago (Table 3), and was not significantly related to area of occupancy at the within-island level in Tenerife and La Palma. These results are also consistent with observations of birds in continental areas (see also arguments for the lack of this association in Blackburn *et al.*, 2006; Reif *et al.*, 2006; Symonds & Johnson, 2006). Interestingly, the explanations of the abundance-range relationship based on local population dynamics rely on the ability of the species to disperse and colonize new areas (Watkinson *et al.*, 2003), and these processes may be disrupted in insular contexts.

Barriers to dispersal could elucidate the effect of abundance on range size because individuals in local dense populations could colonize new areas (thus creating the positive relationship between local abundance and range size) only if they are first able to disperse to such new areas. Within a single island, such barriers to dispersal do not exist, and thus if the same processes driving continental occupancy-abundance relationships are at work, one would expect a positive relationship between the density and the number of UTM squares occupied on that island. This relationship is positive and attains significance only in the most homogeneous and arid of the islands (Fuerteventura; Table 4). Nevertheless, if these occupancy-abundance relationships are not stronger than the archipelago-wide relationship, then it may be due not only to barriers to dispersal, but possibly to other features either of the species or the region. This would be the case in the more heterogeneous islands of Tenerife and La Palma, in which the great environmental heterogeneity (both in habitat types and in altitudinal belts) provides many opportunities for local adaptations and specialization, resulting in high ecological densities in more productive environments (e.g., laurel forests; e.g., Carrascal *et al.*, 1992; Valido *et al.,* 1994 for the Canary Common Chaffinch).

The association between the extent of the geographical range and body size of species is controversial, with very contrasting patterns depending on the taxonomic and geographic scenarios examined (see review by Gaston, 2003). The relationship between occupancy and body size for terrestrial bird species in the Canary Islands was significant and negative for both the number of occupied islands and the occurrence in UTM squares. This association may be founded in the widely recognised influence of body mass on population size and life history traits. Thus, body mass and abundance are usually negatively correlated in birds (Gaston & Blackburn, 2000), especially if maximum ecological densities in the preferred habitats are considered at the regional scale (Carrascal & Tellería, 1991). These two variables were significantly correlated in the Canary Islands: smaller birds reached larger densities in their preferred habitats than did larger terrestrial birds (β = -0.48, $F_{1,42}$=12.89, P<0.001 in the regression analysis controlling for the four phylogenetic vectors). A high population density, combined with the intense allometric relationship of body mass in birds with some demographic parameters, such as fecundity or age at first breeding attempt (Peters, 1983; Brown *et al.*, 2004; Hendriks, 2007), decreases the probability of local extinctions that are especially adverse on small islands, and for those stenotopic species restricted to some particular habitats of reduced extent (Reynolds, 2003).

Large body size is apparently a common correlate of present extinction susceptibility in many vertebrate groups (Purvis *et al.*, 2003; Brook & Bowman, 2005) and especially in birds (Gaston & Blackburn, 1995; Owens & Bennett, 2000). Large-sized species usually have ‘slow’ life cycles (i.e., they produce small numbers of offspring at a late age) and often live at low densities (Gaston & Blackburn, 2000; Reynolds, 2003). If they have restricted geographical ranges, it is probable that declining abundances and range sizes mediated by habitat loss or mortality render them more susceptible to local extinctions that would result in their extirpation from small islands. In insular volcanic environments the probability of catastrophic natural phenomena is high (e.g., volcanic eruptions, storms) and the influence of human impacts are proportionally higher due to the small area (Whittaker & Fernández-Palacios, 2007; Fernández-Palacios & Whittaker, 2008). Several examples illustrate this pattern of body size and extinction in the Canary Islands (Rando *et al.*, 1999; Martín & Lorenzo, 2001; Rando & Alcover, 2008). *Puffinus holeae* (ca. 700 g), *P. olsoni* (ca. 350 g) and *Coturnix gomerae* (probably ca. 150 g) are three large endemic Canarian species considered extinct as a result of past anthropogenic activities. Conversely, the only evidence of a historic extinction of a small endemic Canarian species is that of *Emberiza alcoveri* (ca. 37 g), probably caused by the reduction of laurel forests, and the introduction of terrestrial predators. On the other hand, four out of five large terrestrial bird species breeding in the Canary Islands have experienced severe conservation problems or local extinction in the past 50 years: the Houbara bustard (*Chlamydotis undulata*, 1200-2400 g), and the large-sized birds of prey *Milvus milvus, Buteo buteo* and *Neophron percnopterus* (550-2200 g, Martín & Lorenzo, 2001; Gangoso *et al.*, 2006). The sole Canary endemic extinct in recent historical times is the Canary Islands Oystercatcher *Haematopus meadewaldoi* (perhaps 600-800 g). All of these species reached very low maximum ecological densities (lower than 1.2 birds / km^2) and have body masses larger than 600 g. Conversely, not one small species (i.e., <20 g, 13 spp) has become extinct since the mid 20th century on any of the Canary Islands nor have any been recognized as threatened on the Canary red list of birds (http://www.gobiernodecanarias.org/cmayot/medioambiente/biodiversidad/centinela/main.do). The only exceptions within medium-sized terrestrial bird species (i.e., 20-750 g, 31 spp) are the locally threatened *Calandrella rufescens* in Tenerife (23 g) and the endemic *Fringilla teydea polatzeki* (30 g) in Gran Canaria, with their status mainly attributed to the lack or recent loss of adequate habitat.

From the two measures of habitat use related to human impact (agriculture and urbanism), only the cover of urban structures in the areas where the species were present was directly related to occupancy. Although this effect is quite obvious with alien species or with those that have recently colonized the islands (e.g., *Psittacula krameri, Myiopsitta monachus, Streptopelia roseogrisea, Streptopelia decaocto, Passer hispaniolensis*), it also affects several native birds principally inhabiting natural environments, such as *Phylloscopus canariensis, Cyanistes teneriffae* or *Motacilla cinerea canariensis*. This is in agreement with a previous study (Palomino & Carrascal, 2005) which found that the overall proportion of bird species from the regional pool ‘captured’ by urban environments is higher on the island of Tenerife than on the mainland (Central Spain), concluding that the avifauna of the Canary Islands is more prone to occupy the novel urban environments. Urban environments are recent, artificial habitats and are structurally similar between the islands. Hence, species having traits that enable them to become ‘urban exploiters’ should increase their geographical extent in the archipelago in parallel to urban sprawl (Kark *et al.*, 2007). On the contrary, those species that are unable to take advantage of the urban environments (‘urban avoiders’) have a restricted extent of occupancy in the archipelago. Future landscape planning associated with urbanization (a common threat to coastal habitats) should be carefully considered, since the impact of increased urban sprawl would lead to even greater restriction of distributions of ‘urban avoider’ species.

Species from mountain areas have less potential habitat available than those living in lowland areas simply because of the conic shape of mountains (high-altitude belts have smaller surfaces than lower-altitude belts). Therefore, bird species inhabiting areas at higher altitudes should have smaller occupancies, which lead to smaller population sizes and could thus render them more prone to local extinctions (O'Grady *et al.*, 2004). This prediction is not supported by bird populations in the Canary Islands. This counterintuitive result is the consequence of the lack of mountain or alpine bird species in the avifauna of this region (Martín & Lorenzo, 2001), located at a great distance from the large alpine areas of the Western Palaearctic. Indeed, the bird species that reach higher altitudes in the Canary Islands are those with broad altitudinal ranges and mainly distributed in lowland areas (Carrascal & Palomino, 2005).

The Canary Islands are located at the south-western limit of the Western Palaearctic, and thus biogeographical factors may also be important in explaining interspecific variation in range sizes. Species should be more prevalent towards the centre of the range than towards its periphery because the probability of encountering a site meeting their ecological needs should decrease with increasing distance from the 'optimal' core area (Brown 1984). This paper does not support the predicted association as the residuals from the maximal model in Table 2 were uncorrelated to distance to the continental distribution border. A possible explanation for this lack of association is that the Canary archipelago has highly contrasting environmental conditions and a large number of available habitats for colonizers as a result of the wide altitudinal range and the considerable climate variation, providing many distinct ecological opportunities for the bird fauna.

Endemic island birds can exhibit niche release and develop local adaptations that enable them to exploit a wider spectrum of resources and habitats than their continental counterparts (the niche expansion hypothesis; Lack, 1969; Blondel *et al.*, 1988; Owens *et al.*, 2006), particularly if they are highly mobile species such as birds. Consequently, endemic species, having had enough time to undergo this process, would colonize a larger area (Fjeldsaå & Lovett, 1997, but note, however, that niche expansion could be an entirely plastic response of the species occurring on an ecological timescale). Alternatively, endemic taxa are older colonizers or have evolved more rapidly than non-endemics, in either case having developed phenotypic changes in response to the novel environments on the islands (Millien, 2006). These changes could fine-tune the species to particular insular habitats, generating local adaptations that would limit their potential distribution area. Our results support the latter scenario, as we found a negative relationship between endemicity and range size: endemic taxa occupied fewer islands and 10x10 km UTM squares. A possible explanation is that successful recent colonizers have not had the time to differentiate, adapt and specialize to very particular environments. On the contrary, several other taxa have apparently radiated rapidly, differentiating into recognized species or sub-species that become restricted to a few habitats and islands.

In conclusion, the occupancy of bird species in the Canary Islands, an oceanic archipelago, correlates positively with habitat breadth (and to a lesser extent with preferences for urban environments) and negatively with the degree of endemicity and body size. Consequently, the generalist species with a tolerance for novel urban environments tend to be present on more islands (or to occupy a greater area), while the larger species that have at least partially differentiated within the islands are less widespread. We did not find the positive relationship with local abundance previously shown in continental studies, most likely because it relies on free dispersal over continuous landmasses, and thus may be disrupted in island scenarios. Therefore, the range of a species –even across limited areas such as an archipelago– is at least partly determined by basic biological features and is irrespective of anthropogenic alterations to the habitat.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1 Study variables used to explore the determinants of range size for 48 bird species in the Canary Islands.

Appendix S2 Maximum ecological density (Dmax; birds/km^2), habitat breadth, and number of occupied 10x10 km UTM squares for 48 bird species in three Canary Islands.

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Table 1. Phylogenetic signal in the study variables used in subsequent analyses. We show the explained variance (R^2 in percentage) and p-value (*P*) for the multiple linear regression models of each variable on the first 4 eigenvector extracted from the Principal Coordinates Analysis performed on the phylogenetic matrix, using original, square and square-root transformed phylogenetic distances. Sample size is n=48 for all variables except for the nearest distance to the mainland distribution border where n=35. *: log-transformed. †: using the angular transformation.

	Original		Square		Square root	
Variable	R^2	*P*	R^2	*P*	R^2	*P*
Occupied islands*	4.2	0.759	5.2	0.669	3.6	0.803
Occupied 10x10 km UTM squares*	13.0	0.189	6.9	0.534	13.2	0.182
Maximum ecological density*	50.6	<0.001	51.0	<0.001	51.3	<0.001
Body mass*	57.2	<0.001	57.0	<0.001	57.2	<0.001
Urban cover†	31.8	0.002	20.7	0.037	34.6	<0.001
Cover of agricultural areas†	10.7	0.289	12.0	0.231	10.8	0.287
Midpoint altitude*	13.0	0.188	10.8	0.283	14.8	0.135
Habitat breadth†	7.6	0.485	4.9	0.694	7.7	0.474
Nearest distance to the mainland distribution border*	3.5	0.895	7.7	0.647	2.6	0.395

Table 2. Summary table for the maximal model explaining the extent of occurrence as the number of islands occupied ($F_{11,36}$=3.03, P=0.006). For each variable it is shown the fitted standardized regression coefficient (β) and its corresponding significance (F and P values for partial effects). It is also shown the model with the lower Akaike's Information Criterion (see table 3). Between square brackets are shown the set of variables describing [1] evolutionary effects, [2] life-history traits and [3] habitat use.

	Maximal model			Best subset model		
	β	*F*	*P*	β	*F*	*P*
PVR1 [1]	-0.35	3.86	0.057	-0.34	4.29	0.045
PVR2 [1]	-0.04	0.06	0.801			
PVR3 [1]	-0.03	0.05	0.831			
PVR4 [1]	-0.36	6.88	0.013	-0.34	7.61	0.009
Endemicity (0-non, 1-sub spp, 2-spp) [1]	-0.34	3.77	0.060	-0.36	7.72	0.008
Body mass [2]	-0.49	5.19	0.029	-0.48	7.53	0.009
Maximum ecological density [2]	-0.06	0.08	0.780			
Midpoint altitude [3]	0.06	0.16	0.688			
Urban cover [3]	0.26	2.76	0.105	0.25	3.82	0.057
Cover of agricultural areas [3]	0.14	1.00	0.325			
Habitat breadth [3]	0.41	9.82	0.003	0.44	12.72	0.001

Table 3. Alternative models for the extent of occurrence of terrestrial bird species in the Canary Islands (measured as the number of occupied islands) ordered by the value of the AIC criterion (with small sample correction). Only those models with an increase in the AIC statistic lower than 2 are shown (see ΔAIC figures).

Model	AIC	ΔAIC
pvr1 + pvr4 + endemicity + body mass + urban cover + habitat breadth	62.94	0.00
pvr1 + pvr4 + endemicity + body mass + habitat breadth	63.85	0.90
pvr4 + endemicity + body mass + urban cover + habitat breadth	64.62	1.67
pvr1 + endemicity + body mass + urban cover + habitat breadth	64.72	1.78
pvr1 + pvr4 + endemicity + body mass + urban cover + cover of agricultural areas + habitat breadth	64.79	1.85

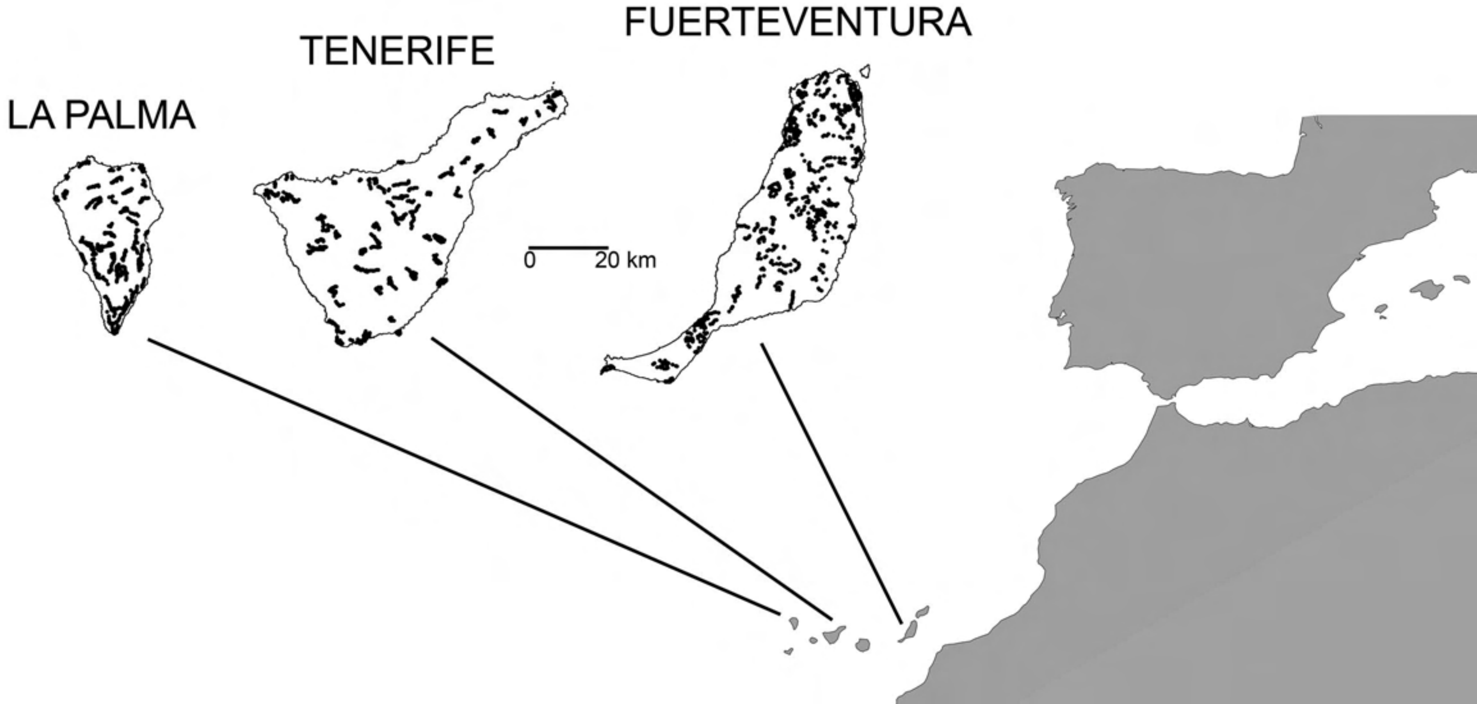
Table 4. Multiple regression analyses showing the relationship between the number of 10x10 km UTM occupied and the maximum ecological density and habitat breadth of the terrestrial birds in Fuerteventura (31 species), Tenerife (39 species) and La Palma (31 species), controlling for the phylogenetic effects PVR1-PVR4. For each variable the standardized regression coefficient (β) and its corresponding significance (*F* and *P* values for partial effects) are shown.

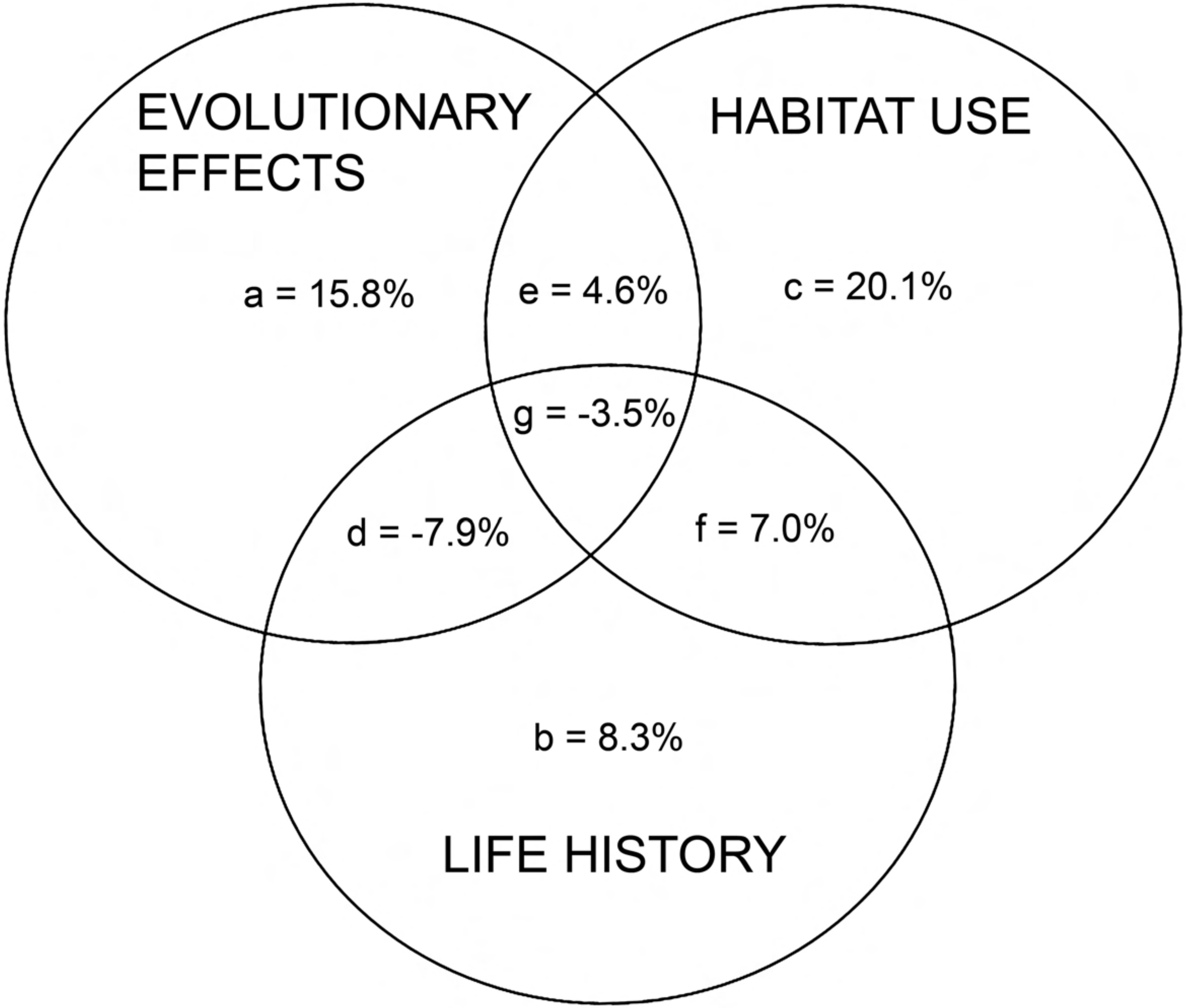
	Fuerteventura			Tenerife			La Palma		
	β	F	P	β	F	P	β	F	P
PVR1	-0.35	7.87	0.010	-0.10	0.56	0.461	0.07	0.17	0.686
PVR2	-0.19	1.99	0.171	-0.04	0.07	0.800	0.25	1.96	0.174
PVR3	-0.23	4.14	0.053	0.01	0.00	0.947	0.19	2.17	0.154
PVR4	-0.25	5.05	0.034	-0.14	1.42	0.242	0.12	0.82	0.374
Maximum ecological density	0.34	5.84	0.024	0.10	0.51	0.480	0.25	1.29	0.267
Habitat breadth	0.88	49.49	<0.001	0.75	38.85	<0.001	0.59	17.15	<0.001

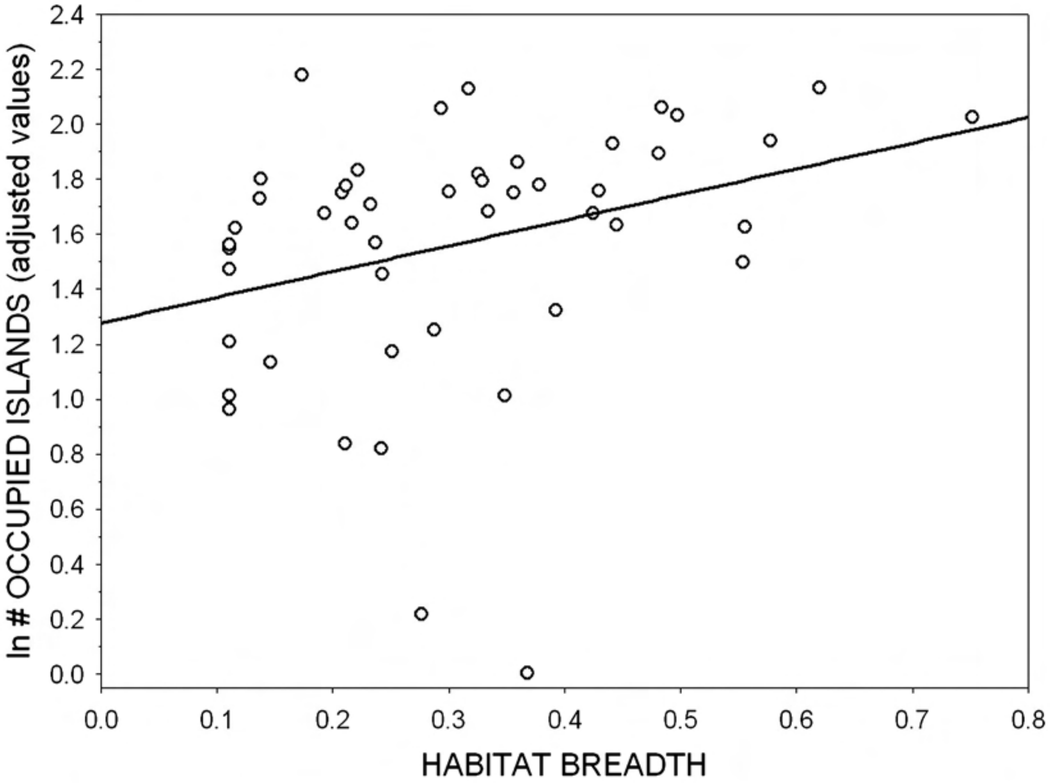
Figure 1. The three study islands within the Canary archipelago. Each dot positions the centre of the 0.5 km transects done to survey bird species.

Figure 2. Variation partitioning for the extent of occurrence (number of islands occupied) among evolutionary (phylogenetic eigenvectors and endemicity), life-history (body mass and maximum ecological density) and habitat use (midpoint altitude, habitat breadth and cover of urban and agricultural areas) components.

Figure 3. Relationship between the number of islands occupied by terrestrial birds in the Canary Islands and their habitat breadth. Habitat breadth is measured using the distribution of maximum densities measured in the nine main habitats defined in the Canary Islands (see Methods). The Y-axis shows the partial effects for habitat breadth (that is, it shows the response variable modelled with the maximal model in Table 3, excluding the habitat breadth term).


LA PALMA
TENERIFE
FUERTEVENTURA
0
20 km


EVOLUTIONARY EFFECTS
HABITAT USE
a = 15.8%
e = 4.6%
c = 20.1%
g = -3.5%
d = -7.9%
f = 7.0%
b = 8.3%
LIFE HISTORY


ln # OCCUPIED ISLANDS (adjusted values)
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
HABITAT BREADTH

Species	# 10x10 km UTM squares occupied	# islands occupied	Maximum ecological density (birds/km^2)	Body mass (g)	Urban cover (%)	Agricultural areas cover (%)	Midpoint altitude (m)	Habitat breadth	Distance to continental border (km)	Endemicity
Accipiter nisus	46	5	0.42	204.0	0.67	13.72	1166.68	0.33	115	1
Alectoris barbara	99	7	14.08	480.0	0.68	10.92	390.82	0.29	115	0
Anthus berthelotii	142	7	64.47	16.5	0.58	22.46	582.22	0.58		1
Apus unicolor	138	7	61.82	28.8	7.98	66.62	417.79	0.38		1
Bucanetes githagineus	72	6	45.99	18.1	0.47	22.24	232.54	0.42	115	0
Burhinus oedicnemus	74	7	3.51	461.0	0.16	34.06	190.12	0.32	115	1
Buteo buteo	99	6	1.10	806.5	1.28	21.54	467.02	0.50	685	1
Calandrella rufescens	56	4	94.02	23.3	0.00	35.42	165.75	0.29	115	0
Carduelis cannabina	105	7	63.15	17.6	4.78	59.63	470.66	0.33	115	1
Carduelis carduelis	55	7	2.71	16.0	13.29	52.23	299.64	0.19	293	0
Carduelis chloris	51	6	3.65	26.5	36.95	54.24	516.43	0.24	327	0
Chlamydotis undulata	22	2	1.00	1245.0	0.00	29.60	155.16	0.21	115	0
Columba bollii	22	4	58.34	286.0	0.04	0.24	878.34	0.14		2
Columba junoniae	23	4	42.93	328.7	0.24	5.66	938.51	0.21		2
Columba livia	149	7	130.72	216.0	25.53	41.77	340.44	0.36	115	0
Corvus corax	90	7	1.23	1250.0	0.13	14.57	537.85	0.62	203	0
Coturnix coturnix	43	7	13.40	98.4	0.50	75.79	253.04	0.21	274	0
Cursorius cursor	29	4	5.43	108.0	0.00	0.00	86.97	0.11	115	0
Cyanistes teneriffae	94	7	71.51	11.3	3.61	9.66	864.54	0.48	374	2
Dendrocopos major	20	2	6.66	80.7	0.00	0.00	1629.25	0.11	438	1
Erithacus rubecula	54	5	88.27	16.7	0.30	5.09	953.40	0.33	342	1
Falco pelegrinoides	58	7	0.38	469.8	0.00	0.92	115.40	0.17	165	0
Falco tinnunculus	142	7	3.59	174.5	3.62	35.84	623.96	0.75	127	1
Fringilla coelebs	44	5	112.01	23.0	0.31	3.37	1001.87	0.23	269	1
Fringilla teydea	18	2	37.73	30.1	0.00	0.00	1563.33	0.11		2
Lanius excubitor	77	4	6.76	63.5	1.27	15.30	278.28	0.55	115	1
Miliaria calandra	58	7	49.92	43.0	0.36	97.35	637.95	0.12	343	0
Motacilla cinerea	78	4	12.49	18.0	20.67	62.22	393.84	0.25	215	1
Myiopsitta monachus	22	5	111.52	102.0	57.59	0.00	119.09	0.11		0
Neophron percnopterus	13	2	0.30	2035.0	0.00	24.29	193.15	0.35	115	1
Passer hispaniolensis	129	7	406.62	27.0	39.09	21.70	171.53	0.22	115	0
Petronia petronia	34	5	165.18	31.0	0.25	100.00	699.04	0.11	270	0

Phylloscopus canariensis	94	5	248.08	7.7	4.45	24.26	811.16	0.56		2
Psittacula krameri	15	4	7.52	90.0	51.93	29.57	251.10	0.15		0
Pterocles orientalis	24	2	6.74	474.0	0.00	14.64	145.51	0.24	115	0
Pyrrhocorax pyrrhocorax	17	1	21.64	321.5	4.21	22.38	1110.28	0.37	418	0
Regulus teneriffae	40	4	210.10	5.8	0.24	0.25	1059.41	0.24		2
Saxicola dacotiae	28	1	26.39	16.5	0.00	7.34	269.05	0.28		2
Scolopax rusticola	29	5	2.28	305.0	0.00	0.00	1017.32	0.22	1291	0
Serinus canarius	96	7	128.21	15.3	6.75	61.48	677.37	0.43		1
Streptopelia decaocto	108	7	240.15	196.0	52.67	17.05	200.07	0.14	250	0
Streptopelia roseogrisea	41	6	38.78	141.5	83.60	1.46	266.42	0.11		0
Streptopelia turtur	118	7	39.58	125.0	4.44	31.52	489.13	0.36	177	0
Sylvia atricapilla	82	5	48.35	22.3	11.29	55.71	477.55	0.39	433	0
Sylvia conspicillata	137	7	37.68	9.5	0.53	19.87	323.74	0.44	115	1
Sylvia melanocephala	100	7	52.48	11.2	1.77	30.77	390.35	0.30	115	0
Turdus merula	87	5	130.24	86.1	4.78	24.59	764.82	0.44	283	1
Upupa epops	104	7	3.75	59.8	3.31	20.95	169.67	0.48	361	0

Appendix S1. Study variables used to explore the determinants of range size for 48 bird species in the Canary Islands. Range size is measured as the number of occupied 10x10 km UTM squares or the number of occupied islands. The explanatory variables are as in table 1. Units for quantitative variables are between brackets, while the index of habitat breadth ranges from 0 to 1 (evenly distributed across the main nine habitats defined for the archipelago) and the index of endemicity from 0 (non-endemic or introduced taxa) to 2 (endemic especies). We assigned missing data to the nearest distance to the mainland distribution border for macaronesian endemics, and for recently introduced species whose distribution ranges are outside the Palaearctic region.

	# 10x10 km UTM squares			Maximum ecological density			Habitat breadth		
	FV	TF	LP	FV	TF	LP	FV	TF	LP
Accipiter nisus	0	17	11	--	0.4	0.4	--	0.14	0.41
Alectoris barbara	23	30	15	9.4	14.8	3.5	0.41	0.17	0.31
Anthus berthelotii	30	37	15	5.4	53.3	64.5	0.77	0.45	0.20
Apus unicolor	24	39	16	--	--	61.8	--	--	0.49
Bucanetes githagineus	29	5	0	46.0	6.1	--	0.62	0.11	--
Burhinus oedicnemus	27	8	4	3.6	1.6	0.4	0.51	0.09	0.18
Buteo buteo	23	28	13	0.8	2.0	0.5	0.44	0.27	0.53
Calandrella rufescens	26	5	0	94.2	--	--	0.54	--	--
Carduelis cannabina	24	32	13	22.5	63.1	16.3	0.55	0.18	0.26
Carduelis carduelis	7	15	4	2.8	1.9	--	0.19	0.20	--
Carduelis chloris	4	21	6	--	3.7	--	--	0.16	--
Chlamydotis undulata	15	0	0	1.2	--	--	0.23	--	--
Columba bollii	0	11	7	--	35.9	58.3	--	0.14	0.14
Columba junoniae	0	9	9	--	13.8	42.9	--	0.07	0.27
Columba livia	31	39	17	13.7	121.2	117.9	0.21	0.31	0.45
Corvus corax	26	16	13	0.7	0.1	1.2	0.81	0.07	0.31
Coturnix coturnix	9	8	9	13.4	4.4	0.4	0.24	0.07	0.18
Cursorius cursor	21	1	0	5.4	--	--	0.20	--	--
Cyanistes teneriffae	11	35	13	16.8	71.6	29.2	0.34	0.56	0.46
Dendrocopos major	0	12	0	--	6.7	--	--	0.14	--
Erithacus rubecula	0	20	11	5.5	88.3	6.6	0.16	0.33	0.30
Falco pelegrinoides	8	16	9	0.4	--	0.1	0.16	--	0.09
Falco tinnunculus	28	38	15	2.9	2.7	3.6	0.32	0.64	0.73
Fringilla coelebs	0	13	12	--	33.4	112.7	--	0.22	0.29
Fringilla teydea	0	13	0	--	37.7	--	--	0.16	--
Lanius excubitor	26	15	0	6.8	2.5	--	0.80	0.30	--
Miliaria calandra	18	13	6	4.3	49.9	--	0.21	0.09	--
Motacilla cinerea	0	34	15	--	7.4	12.5	--	0.31	0.29
Myiopsitta monachus	2	9	1	111.5	5.7	--	0.08	0.07	--
Neophron percnopterus	12	0	0	0.3	--	--	0.39	--	--
Passer hispaniolensis	30	33	7	46.6	154.0	14.6	0.24	0.08	0.10
Petronia petronia	0	7	3	--	165.2	--	--	0.08	--
Phylloscopus canariensis	0	36	16	--	122.3	248.8	--	0.65	0.74
Psittacula krameri	2	4	0	7.0	7.5	4.8	0.11	0.07	0.09
Pterocles orientalis	21	0	0	6.7	--	--	0.43	--	--
Pyrrhocorax pyrrhocorax	0	0	17	--	--	21.6	--	--	0.40
Regulus teneriffae	0	18	11	--	22.0	146.5	--	0.24	0.34
Saxicola dacotiae	28	0	0	26.4	--	--	0.39	--	--
Scolopax rusticola	0	12	8	--	2.3	2.5	--	0.07	0.20
Serinus canarius	5	34	16	4.0	128.2	124.8	0.33	0.38	0.52
Streptopelia decaocto	23	31	8	24.2	115.5	54.3	0.12	0.07	0.17
Streptopelia roseogrisea	7	10	2	3.6	38.8	1.0	0.08	0.07	0.09
Streptopelia turtur	19	36	13	39.6	18.7	6.4	0.18	0.45	0.52
Sylvia atricapilla	0	33	14	2.9	3.3	48.4	0.17	0.40	0.51
Sylvia conspicillata	32	35	13	37.7	8.7	11.7	0.57	0.45	0.22
Sylvia melanocephala	15	33	14	46.8	23.0	52.5	0.21	0.41	0.27
Turdus merula	0	33	15	1.7	127.6	13.2	0.08	0.37	0.55
Upupa epops	26	26	5	3.8	0.7	--	0.81	0.27	--

Appendix S2. Maximum ecological density (Dmax; birds/km^2), habitat breadth, and number of occupied 10x10 km UTM squares for 48 bird species in three Canary Islands. The index of habitat breadth ranges from 0 to 1 (evenly distributed across habitats; 12 habitats distinguished in Fuerteventura, 14 in Tenerife and 11 in La Palma). FV: Fuerteventura; TF: Tenerife; LP: La Palma. The double dash “--“ shows that the species was absent in the island or we were unable to obtain reliable data for it.