



Ecological traits influence the current distribution and range of an island endemic bird

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ABSTRACT

Aim The aim of this paper is to investigate the causes of the current restricted distribution of a narrow-range endemic bird species, the Canary Islands stonechat, *Saxicola dacotiae*.

Location Eastern islands of the Canary Islands archipelago.

Methods We compared climatic patterns (temperature and rainfall), habitat and microhabitat structure, food availability during a full annual cycle, and the abundance of native avian competitors and predators inside and outside the species' range. Three study areas, located in similar habitats on nearby islands, were studied: northern Fuerteventura, close to the northern border of the species' range; southern Lanzarote, 22 km from the nearest site occupied by stonechats; and the Lobos islet, 10 km from the nearest occupied site and 2 km from the coast of Fuerteventura.

Results The cover of suitable habitats (slopes with high cover of large shrubs, stony fields and ravines) and microhabitats (shrubs and boulders) and the abundance of arthropods during the breeding period of Canary Islands stonechats were lower outside than inside the species' range. Temperature, rainfall and the abundance of competitors and predators inside and outside the species' range did not differ significantly.

Main conclusions Ecological requirements explaining the distribution of the Canary Islands stonechat within its range seem to be the main factor hindering its settlement on nearby islands. Geological and palaeoclimatic processes, as well as past and current human impact, could also have constrained the distribution of this narrow-range endemic bird species.

Keywords

Canary Islands, Canary Islands stonechat, food availability, habitat structure, island biogeography, limited dispersal, range limits, *Saxicola dacotiae*.

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INTRODUCTION

Understanding the factors that determine the distribution and abundance of species has long been a central aim in ecology (Andrewartha & Birch, 1954; Cody, 1985; Wiens, 1989; Boyce & McDonald, 1999). The distribution and abundance of organisms are conditioned by selective pressures such as the quantity and quality of habitat, the presence of competitors, predators and parasites, and the willingness to colonize new areas beyond range limits, and also by present or past climatic and geological processes (Newton, 2003). In general, studies on bird biogeography postulate that biotic interactions (e.g.

competition, predation, etc.) and habitat characteristics such as vegetation cover and structure limit the distributions of species at small scales, whereas abiotic factors (basically climatic) are the primary forces explaining the distribution and abundance of species at large scales (Watson, 1964; Newton, 2003).

Island communities are characterized by a higher number of endemic taxa than mainland communities per unit area. Since many island organisms have long been isolated and entire populations are often restricted to a limited area, it is possible to determine which ecological and evolutionary processes could account for entire distribution ranges (Grant, 1986,

1998; Whittaker, 1998; Emerson, 2002). Island colonization by any species is essentially a stochastic process. However, the reasons why island species are restricted to specific islands can be approached through evolutionary and ecological studies. Many studies carried out on island biogeography have analysed the relationships between specific island characteristics such as size, age and habitat diversity and the number of species living there (MacArthur & Wilson, 1967; Chown *et al.*, 1998; Whittaker, 1998; Ricklefs & Lovette, 1999; Selmi & Boulinier, 2001; Carrascal & Palomino, 2002). Fewer studies have tested different hypotheses to explain the patterns of distribution and abundance of either single species or entire bird communities within their ranges (Carrascal, 1987; Blondel *et al.*, 1988; Carrascal *et al.*, 1992; Latta *et al.*, 2000). Only a handful of papers have addressed the question of the absence of insular species outside their current distribution range on the basis of ecological factors, despite the interest of this topic from both conservation and evolutionary standpoints (Steadman, 1995; Komdeur *et al.*, 2004). Several hypotheses proposed to account for the presence, absence or abundance of island birds in mainland habitats have been developed, for example competitive exclusion, species-specific habitat preferences, and rates of predation and parasitism (Grant & Abbott, 1980; Carrascal *et al.*, 1992; Woodworth, 1997), whereas other hypotheses are classical features of insular faunas, such as species poverty, density compensation and niche expansion (MacArthur *et al.*, 1972; Wright, 1980; Blondel *et al.*, 1988; Nogales & Hernández, 1994).

The Canary Islands form a volcanic archipelago comprising seven main islands and several islets, which have emerged during various eruptive episodes since the Miocene (Carracedo & Day, 2002; Fig. 1). The volcanic activity and habitat diversity of an island have important implications for the establishment and diversification of the colonizing species arriving there (Juan *et al.*, 2000; Emerson, 2003). From an ornithological perspective, the Canary Islands provide an exceptional opportunity for the study of biogeographical patterns, as they are

inhabited by more than 30 endemic subspecies and by five endemic bird species (Martín & Lorenzo, 2001; Martí & del Moral, 2003). Of these avian endemics, the Canary Islands stonechat, *Saxicola dacotiae* (Meade-Waldo, 1889) has the most restricted distribution, being present only on Fuerteventura. Moreover, declining populations in the last 20 years have led to a reclassification of the species from 'Near Threatened' to 'Endangered' (Illera, 2004a). The Canary Islands stonechat did have a wider distribution in the past, as a small population described as the endemic subspecies *S. d. murielae* lived in the islets north of Lanzarote (Alegranza and Montaña Clara) until at least 1913 (Bannerman, 1913). Later expeditions conducted to find individuals of this subspecies were unsuccessful, and this population was declared extinct in 1990 (Martín *et al.*, 1990). Several recent records in the southern part of Lanzarote Island, located less than 11 km from Fuerteventura and with an apparently similar habitat, suggest that this species is capable of making inter-insular movements (Martín & Lorenzo, 2001), although no breeding outside of Fuerteventura has been recorded. Therefore, this bird species, which not only colonized the Canary Island archipelago but also radiated into two endemic subspecies, could be undergoing a reduction of its range as a result of current, but unknown, environmental factors.

The main objective of this study was to determine the likely causes for the absence of the Canary Islands stonechat from the nearby island of Lanzarote and Lobos islet. Apart from their theoretical interest, any findings will be useful for developing conservation strategies aimed at reverting the recent deterioration of the conservation status of the species (Illera, 2004a). The basis of our investigation was the premise that factors influencing patterns of distribution, abundance and reproductive success within the species' range (i.e. the island of Fuerteventura; Illera, 2001; Illera & Díaz, in press) could also explain its absence on nearby islands. We expected that there would be less suitable habitat and microhabitat cover and a lower abundance of arthropods outside compared with inside

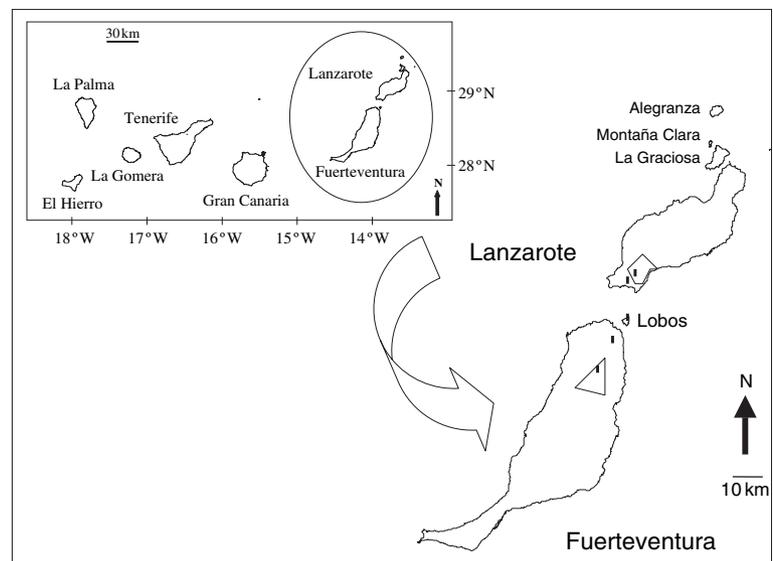


Figure 1 Map of the Canary Islands, indicating the study areas in Fuerteventura and Lanzarote. Bars indicate weather stations.

the species' range, as well as differences in climatic regimes between occupied and unoccupied islands. In addition, we tested whether other processes explaining the presence and/or absence of local bird populations (see Cody, 1985; Wiens, 1989; Newton, 1998, and references therein) could limit the distribution of the Canary Islands stonechat. Specifically, we compared the abundance of native avian competitors and predators inside and outside the stonechat's natural range. Berthelot's pipit, *Anthus berthelotii*, is a potential competitor, as it is the only other species that forages in similar habitats and feeds on prey of similar type and size to that of the stonechats (Martín & Lorenzo, 2001; J.C.I., pers. obs.). Predators of the Canary Islands stonechat include the endemic subspecies of the southern grey shrike, *Lanius meridionalis koenigi*, and the Eurasian kestrel, *Falco tinnunculus dacotiae*, both of which prey on adult birds, fledglings or nestlings (Martín & Lorenzo, 2001). It has been suggested that the presence of kestrels and shrikes negatively affects the density (Suhonen *et al.*, 1994; Hromada *et al.*, 2002) and annual fecundity (Scheuerlein *et al.*, 2001) of other *Saxicola* species. Lower abundances of competitors and predators were expected in Fuerteventura than in Lanzarote and Lobos. We did not test for differences in the abundance of exotic species such as goats, which decrease habitat quality for the Canary Islands stonechat in Fuerteventura (Illera, 2001), or feral cats, which are opportunistic nest predators (Illera & Díaz, in press). It is known that the feral populations of goats and cats are in fact larger in Fuerteventura than in Lobos and Lanzarote (Gobierno de Canarias, 2004; Nogales *et al.*, 2004), except for feral cats in Lanzarote and Fuerteventura, where no data are available. The potential factors influencing the Canary Islands stonechat range limits considered in this study are difficult or impossible to manipulate and replicate at the proper spatial and temporal scales, for either logistic or ethical reasons. Therefore, we could not estimate formally the relative contributions of each factor, or test for potential interactions between factors (i.e. food availability and abundance of competitors). These factors impose limits to the interpretation of the results obtained, a shortcoming that is intrinsic to many coarser-scale biogeographic analyses (Brown, 1995).

STUDY AREA

Fuerteventura and Lanzarote are the oldest islands of the archipelago, including emerged volcanic formations dated 22 and 15.5 Ma, respectively (Carracedo & Day, 2002). They are also the closest to the African mainland (100 and 140 km, respectively). Fuerteventura is the second largest island of the archipelago, with an area of 1660 km², while Lanzarote is the fourth largest, with an area of 846 km². The islands are separated by a narrow and shallow stretch of sea some 11 km wide (Fig. 1). Lobos is a 4.68-km² islet situated between Fuerteventura (2 km) and Lanzarote (8 km).

The study areas in Lanzarote and Fuerteventura were chosen according to their geographic proximity (northern Fuerteventura and southern Lanzarote), their similarity regarding the

extent of the two habitat types selected by Canary Islands stonechats in Fuerteventura (stony field and ravine habitats; Illera, 2001), and their similar altitude (200 m a.s.l. on average). The size of the study areas of Fuerteventura and Lanzarote were 51 and 45.16 km², respectively (Fig. 1). The whole area of Lobos islet was included as a third study area because of its geographic location between the other two (Fig. 1). The Fuerteventura area is occupied by stable populations of stonechats (Illera, 2004b), and all recent sightings of this species outside its known range were obtained in the Lanzarote area. Vegetation is sparse and dominated by xeric shrublands, with the few native trees (mainly *Tamarix* spp.) restricted mostly to ravines. Dominant shrubs are *Launaea arborescens*, *Euphorbia obtusifolia*, *Euphorbia balsamifera*, *Sal-sola vermiculata*, *Lycium intricatum*, *Nicotiana glauca* and *Kleinia neriifolia*. Small tracts of salt-marshes in Lobos are covered by *Sarcocornia fruticosa*, *Limonium tuberculatum* or *Chenoleoides tomentosa*. These plants also occur in Fuerteventura and Lanzarote, but outside the study areas.

Stonechat natural history

The Canary Islands stonechat is a small passerine (10.9–14.1 g; $n = 125$; J.C. Illera, unpubl. data). Two subspecies have been described: *Saxicola dacotiae dacotiae* lives on Fuerteventura Island, whereas *S. d. murielae*, now extinct (Martín *et al.*, 1990), occurred on the small islets of Alegranza and Montaña Clara (north of Lanzarote). It is a typical sit-and-wait forager, which scans for its prey from high perches such as boulders and shrubs (Illera, 2001). Its diet includes a wide range of ground arthropod groups such as Coleoptera, Hymenoptera and Lepidoptera (Martín & Lorenzo, 2001; pers. obs.). The species is distributed throughout Fuerteventura, but only in places with specific habitat and microhabitat characteristics (Illera, 2001). Specifically, it appears to prefer ravines and slopes covered with shrubs and is absent from sandy habitats and recent lava flows at the landscape scale, and it selects steep slopes and high covers of boulders and shrubs at the microhabitat scale (Illera, 2001). The population has been estimated at 650–850 pairs (Bibby & Hill, 1987). The species is sedentary and territorial, and adults are site- and mate-faithful year-round (Illera, 2005; J.C. Illera & M. Díaz, submitted). Birds start to breed in their first year (Illera & Atienza, 2002), with the start and duration of the breeding season and the reproductive effort depending proximately on rainfall and ultimately on food (arthropod) availability (Illera & Díaz, in press). The abundance of ground arthropods also influences microhabitat selection (Illera, 2001).

METHODS

Climate

We compared rainfall and temperature patterns among islands using records from weather stations of the Spanish Meteorological Institute located within or close to the study areas

(Fig. 1). We used the records of the three stations located within each study area to analyse rainfall patterns. Owing to gaps or differences in the time series available, we only analysed the rainfall series from 1992 to 2002, i.e. full series from the same years, in order to avoid biases in the interpretation of comparisons. Few meteorological stations recorded temperature, and none were situated within the study areas, so we had to use data (only full series from the same years) from the closest stations (7 and 3 km away from the study areas of Fuerteventura and Lanzarote, respectively; Fig. 1). No temperature data are available for Lobos.

Habitat

Our main objective was to test for differences in habitat and microhabitat between study areas (islands) by comparing a standardized set of variables describing the habitats occupied by the Canary Islands stonechat within its current distribution range (Illera, 2001). We used visual estimates after a period of training. This method has been widely used for determining bird habitat preferences in structurally simple habitats (e.g. Larsen & Bock, 1986; Illera, 2001; Serrano & Astrain, 2005; Tellería *et al.*, 2005; Seoane *et al.*, 2006). In brief, the estimates were standardized during 1 day of training using a tape measure (for cover estimation) and compass and protractor (for slope estimation) in circles of 25-m radius. The three islands are structurally simple (i.e. semiarid habitats with sparse shrubby vegetation), and all estimates were recorded by the same person (J.C.I.) to minimize any observer bias. We characterized microhabitat structure in Fuerteventura between 28 August and 5 September 2002 along random transects 1000 m long established in seven localities of the study area. We visually estimated seven ground-cover variables and mean slope (Table 1) on 70 circular sample units of 25-m radius. Circular sample units within each transect were spaced 200 m apart. The same procedure was followed in Lanzarote. The 70 circular sample units were obtained in five localities within the study area from 8 to 11 September 2002, and in two additional localities from 16 to 18 November 2002. We characterized the microhabitat structure of the Lobos islet by means of 25 circular sample units of 25-m radius located along five random

transects 500 m long; they were obtained from 3 to 16 January 2001. Since sandy habitats occurred only in Lobos and they are not occupied at all by the Canary Islands stonechat (Illera, 2001), we excluded the sample units in this habitat from further analyses of differences in microhabitat structure in order to avoid sampling artefacts.

We characterized landscape structure by estimating covers of four variables: stony fields and ravine habitats, and slopes having > 15% or < 15% shrub (≥ 25 m tall) cover (hereafter slopes with or without shrubs, respectively). Values of variables were visually estimated from both maps (covers of stony fields and ravines) and field visits (cover of slopes with and without shrubs). We measured cover in 18 circular sample units, of 1-km radius randomly chosen along transects, where we characterized microhabitat structure, avoiding sample overlap (all units were located to the nearest metre using GPS), in both Fuerteventura and Lanzarote. In Lobos we took eight circular sample units of 500-m radius chosen randomly (without area overlap) using a 1:25,000 map. The eight samples included more than 85% of the surface of the islet.

Arthropods

We estimated the availability of arthropods on the ground throughout the whole annual cycle (pre-breeding, breeding and post-breeding periods) of the Canary Islands stonechat. Lanzarote was sampled in May, September and November 2001, and in February and May 2002, and Lobos in January, April, August and November 2001. Fuerteventura was sampled monthly over three years (2001–2003) in the localities where we measured habitat and microhabitat structure. Thus, comparisons between Fuerteventura and the two other islands using data taken in the same months were always possible.

To assess food availability we used the direct observation method. This involves counting all invertebrates ≥ 1 mm present on the ground and low vegetation within 0.5 m \times 0.5 m wooden frames for 2 min. We took arthropod samples every 100 m along randomly sited line transects of 1000 m (Fuerteventura and Lanzarote) or 500 m (Lobos). We obtained 120 monthly sample units in four localities in the Fuerteventura study area, and 90 sample units in four localities in Lanzarote, with the exception of May 2001, when only 30 sample units were recorded. Finally, at Lobos we took 50 sample units monthly, except during January 2001, when we took 97 samples. Samples were obtained in the morning during the first fortnight of every month, avoiding rainy, very cloudy or windy days in order to eliminate biases resulting from weather-induced changes in arthropod mobility or detectability (Ausden, 1996).

Bird abundance

We recorded the abundances of Berthelot's pipits, southern grey shrikes and Eurasian kestrels over two years. We carried out bird censuses in five localities in the Fuerteventura study area in the periods 21 March–8 April 2002 and 29 April–8 May

Table 1 Variables used to characterize the structure of the microhabitat on the three study islands. All variables were measured in circular plots of 25-m radius

Variable	Description
SHRUB1	Cover of shrubs < 0.25 m tall (%)
SHRUB2	Cover of shrubs between 0.25 and 0.50 m tall (%)
SHRUB3	Cover of shrubs > 0.50 m tall (%)
Soil	Bare ground cover (%)
Grass	Grass cover (%)
Stone	Cover of stones < 0.25 m height (%)
Boulder	Cover of stones > 0.25 m height (%)
Slope	Average slope (°)

2003. In Lanzarote, we counted birds in the periods 1–3 May 2002 and 15–16 May 2003 in the same four localities as where we measured the abundance of arthropods. We carried out a census on Lobos islet on 26 May 2003 only. We used the line-transect method (Bibby *et al.*, 2000), recording all birds detected by sight or sound inside and outside 25-m-wide belts on either side of randomly established 500-m line transects. Because Eurasian kestrels have wide territories and their nests are built in places easy to locate, we counted all pairs present in the localities where censuses of pipits and shrikes were carried out. Censuses were performed from dawn to noon, avoiding rainy and very windy or cloudy days.

Statistical procedures

We tested for differences in temperature patterns by means of Student’s *t*-tests on log-transformed mean monthly temperatures. Rainfall patterns were analysed by means of one-way ANOVAS on square-root-transformed monthly rainfall, followed by *a posteriori* Scheffé’s tests for significant differences between groups. Two MANOVAS on arc-sin-transformed data were used to test for differences in microhabitat and landscape characteristics between Fuerteventura and Lanzarote and between Fuerteventura and Lobos, followed by the corresponding one-way ANOVAS in the case of significant multivariate differences (Scheiner, 1993). Mann–Whitney tests were used to compare arthropod availability and abundance of shrikes among islands, whereas a Student’s *t*-test was used for Berthelot’s pipit abundance as the original data were normally distributed. All analyses were performed with the SPSS 12.0 statistical package.

RESULTS

Precipitation and temperature

Total annual rainfall differed significantly among islands ($F_{2,18} = 9.75, P = 0.001$). Significant differences resulted from the lower annual rainfall in Lobos (Scheffé test, $P < 0.05$ for Lobos–Lanzarote and Lobos–Fuerteventura comparisons). However, monthly differences among islands were not significant (one-way ANOVAS, $P > 0.05$ for all months). Monthly changes in temperature were similar in Fuerteventura and Lanzarote. Differences were not significant for mean annual temperature ($t_{10} = 0.34, P = 0.74$) or for monthly means for any month ($P > 0.05$). Although no temperature data are available for Lobos, its location between Fuerteventura and Lanzarote (Fig. 1) makes it highly unlikely that temperature patterns would differ from those of either large island.

Habitat structure

Fuerteventura vs. Lanzarote

Microhabitat structure differed significantly among islands (Wilks’ lambda = 0.57, d.f. = 8,131; $P < 0.001$). Habitat traits

accounting for these differences were the covers of medium-sized shrubs (SHRUB2; $F_{1,138} = 32.3; P < 0.001$), small-sized shrubs (SHRUB1; $F_{1,138} = 21.33; P < 0.001$), bare ground (SOIL; $F_{1,138} = 10.3; P < 0.01$), boulders (BOULDER; $F_{1,138} = 7.66; P < 0.01$), stones (STONE; $F_{1,138} = 4.8; P = 0.03$) and tall shrubs (SHRUB3; $F_{1,138} = 5.0; P = 0.03$). Overall, microhabitats in Lanzarote had lower shrub and boulder covers and higher stone cover than in Fuerteventura (Table 2), indicating that habitat suitability for the Canary Island stonechat is lower in Lanzarote than in Fuerteventura.

Significant differences in the landscape were also found between the two islands (Wilks’ lambda = 0.39, d.f. = 3,32; $P < 0.001$). Habitat traits accounting for these differences were the extents of slopes without shrubs ($F_{1,34} = 34.21; P < 0.001$) and of slopes with shrubs ($F_{1,34} = 18.59; P < 0.001$). Fuerteventura presented a much larger area of slopes with high shrub cover than Lanzarote (Table 3); again, this finding indicates lower habitat suitability in Lanzarote.

Table 2 Mean (\pm SE) values (untransformed) for the microhabitat variables measured on circular samples of 25-m radius in each study area and island

Variable	Fuerteventura (n = 70)	Lanzarote (n = 70)	Lobos (n = 25)
SHRUB1 (%)	2.47 \pm 0.30	1.11 \pm 0.19	0.28 \pm 0.12
SHRUB2 (%)	9.57 \pm 0.57	5.14 \pm 0.53	5.12 \pm 0.68
SHRUB3 (%)	8.01 \pm 0.72	5.96 \pm 0.57	5.20 \pm 1.15
Soil (%)	22.01 \pm 1.57	29.17 \pm 1.58	11.52 \pm 2.48
Grass (%)	14.08 \pm 1.15	11.23 \pm 1.18	0.20 \pm 0.08
Stone* (%)	39.01 \pm 1.39	44.56 \pm 1.87	68.04 \pm 4.43
Boulder† (%)	4.83 \pm 0.59	2.83 \pm 0.42	9.64 \pm 3.30
Slope‡ (°)	10.72 \pm 0.61	10.48 \pm 0.71	9.16 \pm 2.42

n, Sample size.

*Habitat trait selected negatively (Illera, 2001). See text for further details.

†Habitat trait selected positively inside the distribution range.

Table 3 Mean (\pm SE) values (untransformed) for the habitat variables measured on circular samples of 1-km radius in each study area and island. Lava and sand fields did not occur in the study areas of Fuerteventura and Lanzarote

Variable	Fuerteventura (n = 18)	Lanzarote (n = 18)	Lobos (n = 8)
Ravine (%)	2.86 \pm 0.15	2.05 \pm 0.15	0.37 \pm 0.16
Stony field (%)	97.19 \pm 0.15	97.95 \pm 0.15	12.69 \pm 10.95
Slope without shrubs (%)	8.70 \pm 1.20	60.36 \pm 3.59	1.25 \pm 0.82
Slope with shrubs* (%)	54.67 \pm 3.0	20.08 \pm 1.97	0.87 \pm 0.87
Lava field (%)	–	–	31.68 \pm 11.6
Sand field (%)	–	–	8.43 \pm 5.93

n, Sample size.

*Habitat trait selected positively inside the distribution range (Illera, 2001). See text for further details.

Fuerteventura vs. Lobos

The Lobos islet is composed mainly of lava fields, and to a lesser extent of stony fields and sandy habitats, while the proportion of ravine habitats is very small. All of the above habitats greatly influenced the microhabitat and landscape structure of Lobos (Table 3). At the microhabitat scale, significant differences were found compared with Fuerteventura (Wilks' lambda = 0.16, d.f. = 8,86; $P < 0.001$). The covers of herbs (GRASS; $F_{1,93} = 112.6$; $P < 0.001$), stones (STONE; $F_{1,93} = 65.5$; $P < 0.001$), small-sized shrubs (SHRUB1; $F_{1,93} = 42.7$; $P < 0.001$), medium-sized shrubs (SHRUB2; $F_{1,93} = 22.7$; $P < 0.001$) and bare ground (SOIL; $F_{1,93} = 20.12$; $P < 0.001$) were the habitat traits accounting for these differences. Out of the three microhabitat variables selected by the Canary Islands stonechat in Fuerteventura (i.e. boulder and stone covers and slope; Illera, 2001), only the cover of boulders was greater in Lobos than in Fuerteventura (Table 2).

The landscape structure also differed significantly between the two islands (Wilks' lambda = 0.11, d.f. = 4,21; $P < 0.001$). Lava fields and sandy habitats were excluded from the analysis because they were not represented in the study area of Fuerteventura. Habitat traits accounting for differences between islands were the covers of stone fields ($F_{1,24} = 149.34$; $P < 0.001$), slopes with shrubs ($F_{1,24} = 56.30$; $P < 0.001$), and ravines ($F_{1,24} = 38.74$; $P < 0.001$). Covers of these habitat types were lower in Lobos than in Fuerteventura (Table 3).

Arthropod availability

Seasonal changes of the arthropod community showed similar patterns among islands, with an increase in the number of arthropods after rainfall in December–February and a decrease after the end of the rainy season. Differences between the winters of 2001 and 2002 in Fuerteventura were a result of the fact that the first study year (2001) was rather dry whereas the second (2002) could be considered as normal (Illera & Díaz, in press). Significant differences among islands were found during the period of maximum abundance. For Fuerteventura vs. Lanzarote: $Z = -6.18$, $P < 0.001$ for December 2001; and $Z = -2.76$,

$P = 0.006$ for February 2002. For Fuerteventura vs. Lobos: $Z = -2.69$, $P = 0.007$ for January 2001, with larger abundances in Fuerteventura than in Lanzarote and Lobos during this critical period and no differences outside it ($P > 0.05$; Fig. 2).

Bird abundance

No significant differences in the abundance of any bird species were found between the two study years ($P > 0.05$; Table 4). Abundances of Berthelot's pipits and southern grey shrikes were always larger in Fuerteventura than in Lanzarote and Lobos, although these differences were not significant (Table 4). Lobos was sampled in 2003 only, but it is unlikely that abundances (or absences, as was the case for southern grey shrikes) would have changed significantly between years, as suggested by the lack of between-year changes in the two nearby large islands (Table 4). Abundances of Eurasian kestrels were the same in Fuerteventura and Lanzarote for the two years, as a single pair was resident in each of the study localities (five and four individuals in Fuerteventura and Lanzarote, respectively). The presence of a pair was also recorded in Lobos in 2002, but not in 2003.

DISCUSSION

Ecological traits influencing the current distribution and range of the Canary Island stonechat

Our original premise was that ecological constraints within the current range of the Canary Islands stonechat influence their distribution and range limit. This study suggests that habitat, microhabitat and food availability are the most probable main factors explaining their patterns of distribution and abundance, reflecting basic biological requirements for suitable places for nesting and foraging (Illera, 2001). Habitat and microhabitat structure differed among occupied and unoccupied nearby islands, and such differences indicated lower habitat suitability for the Canary Islands stonechat inside than outside the range at both the microhabitat and the landscape scale (Illera, 2001). The Canary Islands stonechat times its breeding according to

Figure 2 Monthly availability of arthropods (mean + SE) in each study area. Differences between pairs of islands in each month were tested by means of the Mann–Whitney U -test ($*P < 0.01$; $**P < 0.001$). Arrows indicate the breeding periods of Canary Islands stonechats in Fuerteventura (Illera & Díaz, in press).

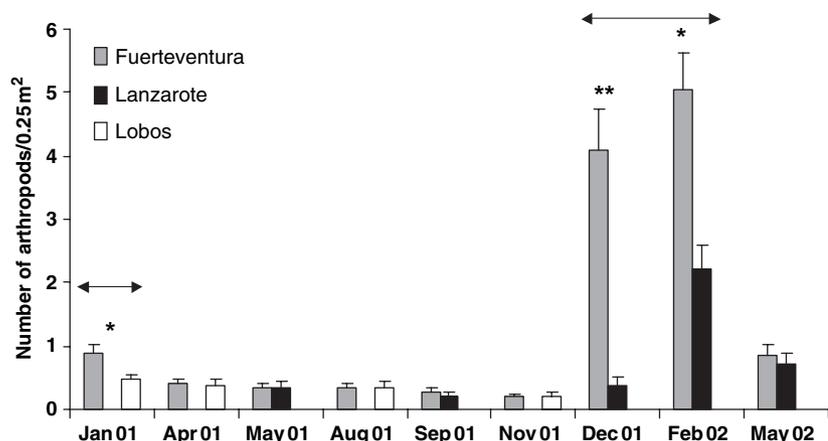


Table 4 Breeding densities (no. birds/10 ha \pm SE) of Berthelot's pipits (*Anthus*) and southern grey shrikes (*Lanius*) on each island for each study year. Results of tests for pairwise between-island comparisons are also shown. The Lobos islet was censused in 2003 only. See text for further details

	FV	LZ	Lobos	FV-LZ	P	FV-Lobos	P
<i>Anthus</i> 2002	9.34 \pm 1.39 (<i>n</i> = 20)	7.24 \pm 2.01 (<i>n</i> = 18)		<i>t</i> = 0.87	0.39		
<i>Anthus</i> 2003	8.70 \pm 1.37 (<i>n</i> = 20)	6.70 \pm 1.13 (<i>n</i> = 19)	4.00 \pm 2.73 (<i>n</i> = 6)	<i>t</i> = 1.11	0.27	<i>t</i> = 1.61	0.12
<i>Lanius</i> 2002	4.09 \pm 1.85 (<i>n</i> = 20)	2.93 \pm 1.11 (<i>n</i> = 18)		<i>U</i> = 178	0.94		
<i>Lanius</i> 2003	2.22 \pm 1.28 (<i>n</i> = 20)	1.51 \pm 0.71 (<i>n</i> = 19)	0.00 \pm 0.00 (<i>n</i> = 6)	<i>U</i> = 189	0.99	<i>U</i> = 48	0.24

n, Number of 500-m line transects performed on each island (FV: Fuerteventura; LZ: Lanzarote).

winter rains in Fuerteventura, since primary productivity and food availability pulse after such rains (Illera & Díaz, in press). Although rainfall patterns did not differ between islands, the increase in arthropod abundance after rains was different inside from that outside the Canary Islands stonechat's range, leading to lower food availability in Lanzarote and Lobos than in Fuerteventura during the Canary Islands stonechat's breeding. Therefore, our results seem to suggest that ecological constraints (i.e. differences in habitat quality and food availability) within the species' range also influence the location of range limits, explaining why Canary Islands stonechats have not settled on Lobos or Lanzarote. Our results seem to be in agreement with the niche model proposed by Brown (1984) to explain range limits. This model postulates that satisfaction of the ecological requirements of a species decreases towards the edges of its range.

Climate, and particularly rainfall, is strongly correlated with arthropod availability in Fuerteventura, both between years and within a given year (Illera & Díaz, in press). Nevertheless, climatic differences between inside and outside the distribution range were not associated with the geographic location of the range limit (Watson, 1964; Newton, 2003). Lobos islet was drier than Fuerteventura both during 1992–2002 and in 2001 (18.0 mm vs. 40.2 mm), a result that was in agreement with lower arthropod availability in Lobos than in Fuerteventura. In contrast, Lanzarote received more rainfall than Fuerteventura both during the year when arthropod availability was measured (2002; 127.0 mm vs. 87.0 mm) and during the time series available (158.01 \pm 23.71 mm vs. 120.61 \pm 17.48 mm), although this latter difference was not statistically significant. Lower arthropod availability in Lanzarote than in Fuerteventura in spite of similar or higher rainfall could be a result of lower amounts of vegetation cover (Table 3). Human impact since the first inhabitants of the Canary Islands established stock-breeding (goats and sheep) and agriculture has been stronger in Lanzarote than in Fuerteventura (Reyes-Betancort *et al.*, 2001; Criado & Atoche, 2003). Heavy grazing pressure for centuries and clearance of the native semiarid shrub vegetation seems to have accelerated erosive processes acting on both slope and ravine habitats in Lanzarote, a fact that could explain its lower carrying capacity for both arthropods and Canary Island stonechats.

Competitive interaction within foraging guilds (Repasky & Schluter, 1994; Gross & Price, 2000) and predation risk (Suhonen *et al.*, 1994; Norrdahl & Korpimäki, 1998; Hromada

et al., 2002) have been suggested as the main factors determining presence and abundance of bird species in mainland sites, but these factors could be much less important in species-poor island bird communities. We did not find any evidence of interspecific competition and predation risk shaping the range limits of the Canary Island stonechat. On the contrary, both Lanzarote and Lobos seem to support similar or lower densities of Berthelot's pipits and southern grey shrikes than Fuerteventura. Moreover, other studies carried out on passerine birds in the Canary Islands found that habitat structure and food availability explained patterns of distribution and abundance better than the abundance of potential competitors (Carrascal, 1987; Carrascal *et al.*, 1992; Valido *et al.*, 1994). Low predation pressure was a typical ecological trait of many islands, including the Canary Islands, until the introduction of feral predators (mainly cats and black rats, *Rattus rattus*) by people (Steadman, 1995; Nogales *et al.*, 2004). However, it should be borne in mind that, in the absence of manipulative experiments of potential competitors and predators and/or controlled translocations of our target species, the influence of these processes in determining the species' limit cannot be completely excluded.

Historical processes constraining range limits in the eastern Canary Islands

Canary Island stonechats had a wider distribution within the archipelago in the past, so a full understanding of their current restricted distribution requires the consideration of the geological and palaeoclimatic processes that have affected the eastern Canary Islands (Fuerteventura, Lanzarote and all its surrounding islets) since they emerged. In fact, complex patterns of colonization, speciation, extinction and recolonization linked to these historical processes have been revealed for the Canary Islands during the past two decades (e.g. Juan *et al.*, 2000; Emerson, 2002). The Canary Islands stonechats diverged from their sister taxon, the common stonechat *S. torquata*, c. 1.3–1.7 Ma (Wink *et al.*, 2002), considerably later than the emergence of the eastern Canary Islands. The eastern islands form one large volcanic unit elongated in a SW–NE direction. They are based on a submarine platform less than 200 m deep and are separated by shallow waters (the mean depth of the underwater saddle connecting the eastern islands is 40 m; Carracedo & Day, 2002). During the Quaternary glaciations, the sea level was much lower than today (Pirazzoli,

1991), and Lanzarote, Fuerteventura and their surrounding islets formed a single large island (García-Talavera, 1997; Carracedo & Day, 2002). The Canary Islands stonechat and all species living in the eastern Canary Islands could potentially have occupied the whole island, as has been postulated for other archipelagos such as New Zealand, Japan and Northern Melanesia (Whittaker, 1998; Mayr & Diamond, 2001; Newton, 2003). This idea is supported by the large number of endemic taxa currently shared by the eastern islands as compared with the remaining Canary Islands (see Izquierdo *et al.*, 2001 for a full list). The large eastern island comprising present-day Lanzarote, Fuerteventura and their surrounding islets was fragmented 18,000 years ago, after the end of the last glacial period, when the sea rose to current levels (Pirazzoli, 1991). Thereafter, it is likely that gene flow between populations of Canary Island stonechats was reduced, as suggested by the presence of two subspecies.

During the eighteenth and nineteenth centuries, the Canary Islands suffered a period of intense volcanic activity. The negative consequences on the distributions of animal and plant communities could have been of a similar magnitude to those that occurred in other eruptive episodes, as has been demonstrated for the nearby island of Gran Canaria after the Roque Nublo eruptive period (Pestano & Brown, 1999; Emerson, 2003; Gübitz *et al.*, 2005). The most important historical volcanic eruption for the Canary Islands occurred in Lanzarote in 1730–36, covering one-third of the island in lava. This eruption, together with secular human impact (Reyes-Betancort *et al.*, 2001), could have driven remnant populations of Canary Islands stonechats in Lanzarote to extinction, although no fossil records are available to support this hypothesis. Small populations of the endemic subspecies *S. d. mureliae* remained on the islets of Montaña Clara and Alegranza, north of Lanzarote, until the beginning of the twentieth century. The extinction of this subspecies was apparently the result of a combination of natural factors (i.e. a series of consecutive dry years) and the negative effects of introduced mammals (goats, rabbits and cats). Alien predators may drive small populations restricted to islets to extinction, although their effects on large populations on large islands are usually less severe (see Nogales *et al.*, 2004), which could help to explain why Fuerteventura populations have survived in spite of large populations of feral mammals.

Implications for conservation

In summary, our results indicate that, although apparently similar, Fuerteventura, Lanzarote and Lobos islands differ in the abundance and distribution of a number of critical stonechats habitats. We conclude, therefore, that autoecological factors such as food availability and habitat quality seem to have been the main factors hindering the settlement of all the Canary Islands by stonechats. Differences between islands could be related to secular intensive management and heavy grazing pressure, which are more evident on the smallest islands of Lanzarote and Lobos.

Three clear conclusions with implications for conservation can be drawn from our results. First, direct destruction or alteration of habitats can cause stonechat populations to decrease or to become extinct (Illera, 2004a). Second, heavy grazing pressure can lead to a degradation of habitat via a decrease in the available vegetation cover and an acceleration in soil erosion, both of which can decrease food availability. Finally, our results emphasize the need to carry out detailed studies on habitat suitability for future plans of population reintroduction or reinforcement, focused specifically on habitat and microhabitat structure and arthropod availability. This information can be used as an aid to develop specific management plans to maintain these habitat traits in order to prevent further reductions in the Fuerteventura populations. On this basis, we suggest that a priority in the conservation of stonechats in the Canary Islands should be the complete removal of or a significant reduction in the number of feral goats (Illera, 2004a).

ACKNOWLEDGEMENTS

This study was partially funded by the Canary Islands Government. The Cabildo of Fuerteventura kindly provided logistic support during our study in the Lobos Natural Park. We would especially like to thank Matías Benítez and David Chacón for their hospitality during fieldwork in Lobos. Juan Carlos Rando provided the GPS. José Luis Tella and two anonymous referees made useful suggestions on a first draft of this paper. Iain Barr kindly corrected the spelling. J.C.I. is also indebted to José Ramón Rodríguez for excellent accommodation in Lanzarote and warm friendship.

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Editor: Jon Sadler