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## Original article

# Site fidelity in the Canary Islands stonechat *Saxicola dacotiae* in relation to spatial and temporal patterns of habitat suitability

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## ARTICLE INFO

## Article history:

Published online 13 February 2008

## Keywords:

Arid ecology

Canary Islands stonechat

Fuerteventura

Habitat quality

Site faithfulness

*Saxicola dacotiae*

Semiarid habitat

Spatial homogeneity

## ABSTRACT

We investigate the degree of territory faithfulness of the Canary Islands stonechat *Saxicola dacotiae*, an endemic bird species of the semi-arid island of Fuerteventura (Canary Islands, Spain), and the spatial and temporal variability of habitat traits related to its breeding success over its whole distribution range. Between 1998 and 2003 we monitored the spatial location of individually marked birds to determine whether they were site faithful. We also analysed the spatial and temporal variability of the abiotic (rainfall) and biotic (food availability, abundance of avian predators and competitors, and nest predation) factors that may influence breeding success in this species. Canary Islands stonechats were strongly site faithful. Out of 106 individuals, 86 (81.0%) were re-sighted during the whole study period, and most re-sightings (76; 88.4%) were in the territory where they were initially caught. Dispersal events were rare both within (1%) and between ( $\leq 6\%$ ) consecutive years, and detectability of colour-ringed birds was as high as 87%. No significant spatial variation of abiotic and biotic factors affecting success was found at a range of spatial scales. Low spatial variance in the habitat characteristics determining reproductive success could have favoured site fidelity in this species, as costs associated with changing site would not be compensated for by significant increases in survival or breeding prospects in new territories. Strict protection of the areas already occupied by this “Endangered” narrow range endemic bird would be the most effective way of preserving it, due to its strict habitat and microhabitat requirements and its strong site fidelity.

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## 1. Introduction

Mobile individuals must decide where to live. The frequency with which this decision has to be made can vary from once only to repeatedly over the lifetime of an individual. The decision of where to live will be constrained by evolutionary or

ecological factors such as morphological design, abundance and quality of food, availability of breeding sites or presence of competitors, predators and parasites (Cody, 1985; Stephens and Krebs, 1986; Wiens, 1989; Newton, 1998).

Birds are highly mobile organisms. Nevertheless, individuals that show site fidelity by returning to their breeding or

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doi:10.1016/j.actao.2008.01.003

wintering territories year after year have been recorded in many species of migratory birds (e.g. Cuadrado et al., 1995; Latta and Faaborg, 2001; Pyle et al., 2001; Hoover, 2003). Site fidelity is predicted to be maintained by various benefits including pairing with a familiar partner (Schieck and Hannon, 1989), or because familiarity with an area can improve the ability of individuals to escape predators, to forage successfully, or to identify better nesting sites (Greenwood and Harvey, 1982; Shields, 1984; Stamps, 1995; Schjørring et al., 2000). Furthermore, site faithful individuals may benefit from the presence of familiar neighbours, as the costs of territorial defence (time spent singing or fighting) has been shown to increase when neighbours change (Falls and McNicholl, 1979; Ydenberg et al., 1988; Eason and Hannon, 1994).

In spite of these advantages, if fitness benefits obtained on the current breeding site are low (i.e., low reproductive success), then individuals are predicted to change breeding site in favour of sites where fitness prospects may be better. Many studies have found that low breeding success decreases site fidelity and that individuals tend to return to sites where they have bred successfully (Beletsky and Orians, 1991; Switzer, 1997a; Blums et al., 2002; Hoover, 2003). The most accepted behavioural rule for site fidelity is that individuals should choose to stay in their territories if the previous breeding attempt was successful ("win-stay") or to switch to a new nest site if their reproductive success was low ("lose-switch"; Switzer, 1993; Schmidt, 2001, 2004).

Apart from previous experience, the decision to stay or leave a site will be influenced by the costs associated with moving to, and settling into, unfamiliar territories (Switzer, 1993; Jakob et al., 2001; Yoder et al., 2004), and on whether the benefits of moving compensate for these costs. Nevertheless, the costs and benefits of this trade-off in relation to environmental heterogeneity have, so far, rarely been explicitly addressed (Switzer, 1997b). Most empirical studies on the site fidelity of birds have been carried out on migratory species with wide distribution ranges (references above). High spatial variability in the quality of unoccupied territories is taken for granted for these species, and such variance can compensate for moving and settling costs. However, this may not be the case for sedentary species with narrow ranges. Strong site fidelity may be maintained in these species if spatial variability in habitat characteristics associated to fitness is low, even in the face of high temporal variability in breeding success and territory quality (Switzer, 1993).

We monitored the spatial location of individually marked Canary Islands stonechats, *Saxicola dacotiae*, a bird species endemic to the semi-arid island of Fuerteventura (Canary Islands, Spain), from 1998 to 2003. Apart from documenting whether birds were faithful to their territories, the goal of this study was to analyse the spatial and temporal variability of the abiotic (rainfall) and biotic (food availability, abundance of avian predators and competitors, and nest predation) factors that determine the among-year variability in breeding success of this species (Illera and Díaz, 2006). Low spatial variability in these factors over the distribution area of the species is predicted to be associated with site faithfulness, whereas high spatial variability would preclude it if breeding success or habitat quality varies in time (Switzer, 1993).

## 2. Material and methods

### 2.1. Species and study area

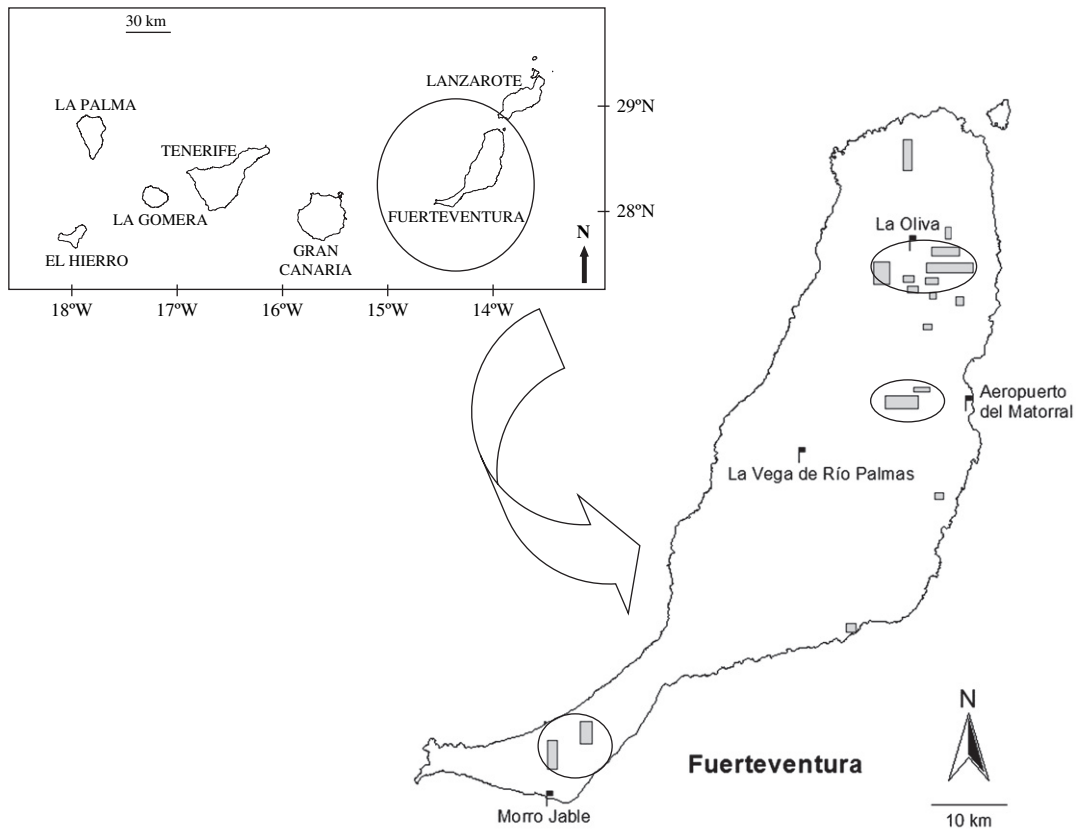
The Canary Islands stonechat is a small passerine endemic to the Fuerteventura Island. It breeds across the entire island where suitable habitat occurs, favouring ravines and slopes covered by boulders and shrubs and avoiding sandy areas and recent lava flows. Habitat and microhabitat selection depend on food (arthropod) availability and presence of perches and suitable nest sites (Illera, 2001). Canary Island stonechats are strictly sedentary. Individuals pair up and establish territories and then defend them against conspecific intruders year round (Illera, 2004a). Territory shapes are irregular, and sizes can vary among breeding seasons but rarely exceed an area of 250 m in radius (around 20 ha; Illera, 2004a). The breeding period extends from December to April (Illera and Díaz, 2006). In wet years, pairs breed over more extended periods and lay two clutches, whereas in dry years they breed only once or not at all. The number of fledglings is mostly determined by nest predation and breeding effort (which is positively related to rainfall; Illera and Díaz, 2006).

The Canary Islands are a volcanic archipelago located in the north-eastern Atlantic Ocean, 100 km west of mainland Africa. It comprises seven main islands and several islets that emerged during different eruptive episodes from the Miocene to the present (Carracedo and Day, 2002). Fuerteventura is the island closest to the mainland, the oldest (c. 22 million years old; Carracedo and Day, 2002), and the second largest (1659.71 km<sup>2</sup>; Fig. 1). Its topography is mostly low and flat (c. 200 m a.s.l.), with a maximum elevation of only 807 m. The climate is semi-arid. Rainfall (143 mm/year on average) is strongly seasonal, with most rain falling during the autumn/winter months. Monthly rainfall records were obtained from four weather stations located close to the field sites (Fig. 1). Mean monthly temperatures varied between 19 °C in January and 21 °C in August (Marzol-Jaén, 1984). The vegetation is dominated by sparse and xerophytic shrubland (Rodríguez et al., 2000).

### 2.2. Ringing and monitoring of Canary Islands stonechats

We ringed and monitored birds from December 1998 until March 2002 in 17 localities randomly distributed over the northern, central and southern parts of the island (Fig. 1). Birds were caught with clap-nets placed below foraging perches using *Tenebrio molitor* larvae as bait. Each individual was ringed with a unique combination of an aluminium ring (Spanish Environmental Ministry) and two colour rings. Ringed birds were released at the point of capture which was located to the nearest meter using a Global Positioning System.

We monitored birds each month using observations made along 1-km line transects and random visits made throughout the island. Transects were performed either in the morning (from 08:00 until 12:00) or during the afternoon (from 16:00 until 19:00), avoiding rainy, very windy and cloudy days. We chose the transect approach because it is a suitable method for detecting birds in open landscapes such as those of



**Fig. 1** – Map showing the field sites (ellipses) and weather stations (flags) on Fuerteventura Island. Rectangles show the areas where birds were trapped. Rectangle size indicates the number of individual Canary Islands stonechats ringed during the study period. Measurements of arthropod availability and monthly linear transects for monitoring Canary Islands stonechats were carried out in focal areas (inside ellipses) located in the northern, central and southern parts of the island (see Section 2 for further details).

Fuerteventura (Bibby et al., 2000) and facilitates the inspection of large numbers of stonechat territories. Transects were monitored monthly, from December 2000 until June 2003, at three field sites on Fuerteventura covering the whole island and including many different populations (Fig. 1). Field sites, that include 10 different focal areas, were established in zones where high numbers of birds were colour-ringed (Fig. 1). Within focal areas, transects were established aiming at crossing the largest number of territories of Canary Islands stonechats, and they were separated by 1–6 km within each focal area. Four focal areas at the northern field site were monitored monthly along three transects each (except in July, September and October 2002). Within the central field site one focal area was monitored along two transects (February 2001–June 2002) and two focal areas along two transects each (September 2001–June 2002). The southern field site was monitored at three focal areas with two transects each (September 2001–June 2002). Besides these study plots, more than 500 other potential breeding localities throughout the whole island were visited at least once looking for marked Canary Islands stonechats during the six study years.

Canary Islands stonechats sometimes forage in adjacent territories, but intruders are pursued and expelled by the owner as soon as they are detected (Illera, 2004a). We

monitored individuals for at least 11 min to distinguish these ephemeral intrusions from territory changes. Territory boundaries usually coincide with those of neighbouring pairs. We considered a bird as site unfaithful if it spent more than 10 min foraging outside a 350 m radius around the place where it was caught. As most individuals were sighted several times, we could determine if they were caught close to the territory border, and we could then correct for the spatial location of their territories to determine site faithfulness.

Changes in the population size of Canary Islands stonechats over the study years (2000–2002) were monitored in three focal areas in the northern field site (Fimbapaire, Espigón de la Mesa and Valle Chico). We established line transects covering the whole focal area. Transects were run up to four times per week during the pre-breeding period. Observations of individually marked birds were mapped during each visit. The number of breeding territories was established from the observations and from additional confirmatory visits where required.

### 2.3. Food availability

The Canary Islands stonechat is a sit-and-wait insectivorous bird that detects prey from perches and hunts for them mainly

on the ground (Illera, 2001). Food availability was evaluated by counting all arthropods  $\geq 1$  mm found during 2 min of careful examination of the ground and low vegetation within 0.5 m  $\times$  0.5 m quadrats. One millimetre is the minimum prey length of the common stonechat *Saxicola torquata* (Martínez-Cabello et al., 1991), a sister species of the Canary Islands stonechat. Quadrats were located at 100-m intervals along fixed 1000-m line transects that were monitored monthly over the three years. Line transects were randomly established within the three field sites on Fuerteventura (Fig. 1) and they always crossed territories of the Canary Islands stonechats. The northern field site was monitored from December 2000 until June 2003 (no data were collected in July, August and October 2002) with a total of 12 transects (120 samples) at four focal areas. The central field site comprised two transects monitored from February 2001 till June 2002 in one focal area, and six transects in other two focal areas (two transects per focal area) monitored from September 2001 until June 2002. The southern field site included six transects in three focal areas (two transects per focal area) monitored from September 2001 until June 2002.

Temporal patterns of arthropod availability in the north of the island have been analysed elsewhere, showing strong seasonal and annual variation that were closely related to rainfall patterns (Illera and Díaz, 2006). In the present study spatial patterns of arthropod availability were analysed following a two-tier approach: among and within focal areas. The spatial variability among focal areas (i.e., at the scale of the distribution range of the species) was analysed with data taken in 2002, when northern, central and southern field sites were sampled throughout the year. The spatial variability within focal areas (i.e. at a scale closer to territory size) was tested each month in each focal area by analysing the variation in numbers of arthropods among transects. Estimates of variability at these two scales (among areas and among transects within areas) could be considered as conservative estimates of variability among individual territories, as such territories were crossed by transects established to measure food abundance. We did not measure arthropod abundance within territories because (a) sampling would have caused too much disturbance for territory holders belonging to an endangered species, and (b) no other environmental factor considered could be measured at this fine scale apart from breeding success.

#### 2.4. Abundance of avian competitors and predators

The only potential competitor of the Canary Islands stonechat is Berthelot's pipit *Anthus berthelotii*, an insectivorous bird endemic to the Macaronesian archipelagos which feeds almost exclusively on the ground, picking invertebrates while walking or snatching them from the air (Martín and Lorenzo, 2001). The southern grey shrike *Lanius meridionalis koenigi* and the Eurasian kestrel *Falco tinnunculus dacotiae* are potential predators of nests, juveniles and adults. The abundance of pipits, shrikes and kestrels was estimated during the breeding seasons of 2002 (late March to early April) and 2003 (late April to early May) at five focal areas (Fimbapaire, Vallebrón, Valle Chico, Espigón de La Mesa and Valle de Juan Pablo). These focal areas were within the northern field site where the

abundance of arthropods was measured. The abundances were estimated by counting all competitors or predators within and outside 25-m-wide belts at both sides of 20 randomly established 500-m line transects (Bibby et al., 2000). Surveys were performed early in the morning (from 08:00 until 10:00), avoiding rainy, very windy and cloudy days. Because Eurasian kestrels have large territories and build nests easy to locate, we were able to directly count pairs present in the same focal areas where censuses of pipits and shrikes were carried out.

#### 2.5. Nest predation

Introduced feral cats, *Felis catus*, were the main predators of stonechat nests (67% of predation events; Illera and Díaz, 2006). Nest predation rates (i.e. proportion of nests predated) were obtained by means of weekly monitoring of the nests of 78 pairs during the full breeding cycle. Nest predation was monitored during three study years (2001–2003) in 12 focal areas throughout Fuerteventura in order to analyse its spatial and temporal variability. Four sites were monitored during all study years, three in two years and five in only one year. The numbers of sites and pairs included in different years were 9 and 32 in 2001, 8 and 27 in 2002 and 6 and 28 in 2003.

#### 2.6. Statistical analysis

The spatial and temporal variability of rainfall were analysed by a two-way ANOVA with log-transformed monthly rainfall as the dependent variable and year and location as random factors. Variability in mean monthly abundance of arthropods among focal areas were analysed by a one-way ANOVA with square-root transformed number of arthropods per sample as the dependent variable and focal area—the four northern focal areas, the pooled average of all central and the pooled average of all southern focal areas—as a random factor (pooling was necessary due to missing data from some months in some focal areas). Differences in variability among focal areas were tested by means of a one-way ANOVA with Box-Cox transformed monthly coefficients of variation (CV) of the number of arthropods per sample as the dependent variable and locality (pooled as above) as a random factor. Variability in numbers of arthropods within each focal area was analysed by Kruskal-Wallis and Mann-Whitney tests. The temporal and spatial variation in the number of competitors and predators were analysed by means of either a Friedman test (southern grey shrikes) or a two-way ANOVA (Berthelot's pipits; original data were normally distributed) with number of birds per transect as the dependent variable, year as a random factor and focal area as a fixed factor. Densities of Canary Islands stonechats were also analysed by means of a Friedman test. Nest predation rates were compared among sites (i.e. to test spatial variability) pooling all depredated nests by site, and years (i.e. to test temporal variability) pooling all depredated nests by year, by means of G-tests using the Williams' correction when d.f. = 1 (Fowler et al., 1998). Means are given with  $\pm$ SE unless otherwise stated. All statistical analyses were performed with the SPSS 12.0 statistical package.

### 3. Results

#### 3.1. Bird banding and monitoring

Overall, 106 individual Canary Island stonechats were caught and banded across Fuerteventura between 1998 and 2002 (Fig. 1). Out of these, 86 (81%) were observed in subsequent years while the remaining 20 (19%) were not seen again. These latter cases could be assumed to have been due to the death of individuals rather than to long-distance movements, as indicated by the large monitoring effort we carried out. The remaining 86 birds could be monitored for 1 year (38 birds; 44.2%), 2 years (33; 38.4%), 3 years (14; 16.3%) and up to 4 years (1 bird; 1.1%) after their release. Only 10 individuals (11.6%) were recorded outside their former territories (6 males and 4 females). These individuals were observed to move between 400 and 1500 m. Only one female moved during the breeding season (see below), whereas the rest of individuals dispersed outside the breeding season. Annual dispersal rates were low: 0% (1999/2000), 4% (2000/2001), 6% (2001/2002), 2% (2002/2003). We could estimate when individuals moved in seven cases. Two males moved during December 2000, one female left its territory between October and December 2000, two birds (male and female) moved between March and April 2001, and one female deserted its male in February 2002. This male moved in October 2002 and was faithful to its new territory until the end of this study (June 2003). The three remaining cases involved birds that moved from their place of capture at an unknown date before the following breeding season. Young birds usually stay in the parental territories for a year, from fledging in January–April until they are expelled by their parents at the beginning of the next breeding season in December–January (29 of 32 families; 90.6%). The remaining three cases of juvenile dispersal (3 of 32 families; 9.4%) were due to the expulsion of fledglings from the first clutch at the time of laying a second clutch within the same breeding season.

#### 3.2. Spatial and temporal patterns of habitat suitability

Rainfall patterns, as well as being seasonal, were strongly variable among years during the study period ( $F_{2,6} = 11.39$ ,  $P = 0.01$ ). However, these patterns were consistent across the whole island, with no significant spatial variability ( $F_{3,6} = 0.94$ ,  $P = 0.48$  for the effect of location and  $F_{6,133} = 0.38$ ,  $P = 0.89$  for the year by location interaction).

No significant differences among focal areas in mean arthropod availability were detected ( $F_{5,49} = 0.48$ ,  $P = 0.79$ ). No significant focal area effects on variability in arthropod numbers were found either ( $F_{5,49} = 0.26$ ,  $P = 0.93$ ), although average variability within focal areas was moderate (mean CV = 179.71). The spatial variability within focal areas was very low during the three years studied. Significant differences ( $P < 0.05$ ) were only found in 19 out of the 155 locality-months analysed (Table 1).

The number of predators did not vary significantly either spatially or temporally. All focal areas were occupied by a single pair of Eurasian kestrels over the study period. The density of southern grey shrikes did not differ significantly among

**Table 1 – Results for among-transect comparisons within each focal area for all months of study. Mann–Whitney (U) or Kruskal–Wallis ( $\chi^2$ ) tests were used depending on whether two or more transects were carried out in each focal area, respectively. Only significant results ( $P < 0.05$ ) are shown. N, number of months analysed in each focal area**

	Field site	N	Significance tests
Fimbapaire	Northern	28	Dec 01: $\chi^2 = 13.7$ , $P = 0.003$ Mar 02: $\chi^2 = 8.3$ , $P = 0.04$ Feb 03: $\chi^2 = 7.9$ , $P = 0.05$
Vallebrón	Northern	28	Mar 01: $\chi^2 = 8.9$ , $P = 0.03$
Valle Juan Pablo	Northern	28	Apr 03: $U = 25.0$ , $P = 0.04$
Espigón de la Mesa	Northern	25	Dec 01: $U = 13.0$ , $P = 0.003$ Feb 02: $U = 14.5$ , $P = 0.007$ Jan 03: $U = 17.5$ , $P = 0.012$ Feb 03: $U = 5.0$ , $P = 0.001$ Mar 03: $U = 10.0$ , $P = 0.02$ Jun 03: $U = 24.0$ , $P = 0.02$
Triquijviate	Central	15	Jun 01: $U = 19.0$ , $P = 0.01$ Aug 01: $U = 30.0$ , $P = 0.03$
Bco. Jeney	Central	9	Dec 01: $U = 21.0$ , $P = 0.025$ Apr 02: $U = 21.5$ , $P = 0.02$
Morro Tinajas	Central	7	None
Bco. Mal Nombre	Southern	8	Dec 01: $U = 8.5$ ; $P = 0.001$
Bco. Vinámar	Southern	4	None
Bco. Esquinzo	Southern	7	Jan 02: $U = 14.5$ ; $P = 0.006$ Mar 02: $U = 4.0$ ; $P = 0.000$

focal areas ( $\chi^2_4 = 3.18$ ,  $P = 0.53$ ) or years ( $\chi^2_1 = 1.00$ ,  $P = 0.32$ ; Table 2). The density of potential competitors (Berthelot's pipits) did not differ significantly among localities or years either ( $F_{4,4} = 1.01$ ,  $P = 0.50$  for the effect of focal area,  $F_{1,5} = 0.30$ ,  $P = 0.61$  for the effect of year, and  $F_{4,30} = 1.07$ ,  $P = 0.39$  for the focal area by year interaction; Table 2). Densities of Canary Islands stonechats did not vary significantly among focal areas ( $\chi^2_2 = 2.67$ ,  $P = 0.26$ ) or among study years ( $\chi^2_2 = 2.36$ ,  $P = 0.31$ ). The mean density was 0.08 territories/10 ha (range: 0.04–0.1).

Overall, 37 out of the 128 nests monitored were preyed upon, mainly during the nestling stage. Nest predation rates did not differ significantly among sites within a given breeding period (2000–2001:  $G^2_2 = 2.56$ ,  $P = 0.28$ ; 2001–2002:  $G^2_3 = 2.51$ ,  $P = 0.47$ ; 2002–2003:  $G^2_1 = 2.85$ ,  $P = 0.09$ ) or among breeding periods ( $G^2_2 = 2.94$ ,  $P = 0.23$ ). Mean predation rates (%) were  $42.23 \pm 13.52$ ,  $36.12 \pm 7.32$  and  $20.25 \pm 11.95$  for 2000–2001, 2001–2002 and 2002–2003, respectively. No individual or pair ( $n = 26$  pairs) moved after suffering predation events. Finally, nine pairs that did not breed at all during the breeding period of 2000–2001, probably because of low food availability in that dry year, remained site faithful until the next breeding season.

### 4. Discussion

Canary Islands stonechats showed strong site fidelity both within and among breeding periods along a 6-year study period. Most birds were not monitored during the whole period, as they were also ringed during the study, so that we cannot rule out completely episodes of site unfaithfulness by these birds either before being marked or after finishing this study. However, such unnoticed episodes should have been

**Table 2 – Densities (No. birds/10 ha  $\pm$  S.E.) of Berthelot's pipits (*A. berthelotii*) and southern grey shrikes (*L. meridionalis*) according to study years and localities. *n*, number of 500-m line transects**

	2002		2003	
	<i>A. berthelotii</i>	<i>L. meridionalis</i>	<i>A. berthelotii</i>	<i>L. meridionalis</i>
Fimbapaire ( <i>n</i> = 4)	13.59 $\pm$ 4.21	4.84 $\pm$ 3.46	8.85 $\pm$ 3.16	1.09 $\pm$ 1.09
Vallebrón ( <i>n</i> = 6)	7.84 $\pm$ 2.19	2.39 $\pm$ 1.68	7.11 $\pm$ 2.99	5.33 $\pm$ 3.95
Valle J. Pablo ( <i>n</i> = 4)	10.61 $\pm$ 1.39	4.00 $\pm$ 4.00	9.98 $\pm$ 3.39	2.00 $\pm$ 2.00
E. de la Mesa ( <i>n</i> = 4)	3.31 $\pm$ 2.07	0.00 $\pm$ 0.00	9.65 $\pm$ 3.71	0.00 $\pm$ 0.00
Valle Chico ( <i>n</i> = 2)	14.82 $\pm$ 1.17	16.00 $\pm$ 16.00	8.75 $\pm$ 0.27	0.00 $\pm$ 0.00

extremely rare, as shown by the low frequency of dispersal events recorded both within (1%) and between ( $\leq 6\%$ ) consecutive years. For this reason, we think that between-years rates of dispersal are a fair estimate of individual dispersal rates (i.e., “true” site fidelity if such rates are low), that could not be computed accurately because most birds were not monitored during its whole lifetime.

An important potential bias to our estimates of dispersal rates is the detectability of marked birds. We assumed that birds that were not detected the following year were dead rather than having migrated permanently to another locality on the basis of the huge monitoring effort made throughout the whole distribution range of the species (448 km of transects plus more than 500 other localities visited throughout Fuerteventura). No individual undetected the following year was detected afterwards. Temporal emigration within the same year could also produce underestimates of the between-years dispersal rates because these events are not included in the annual dispersal rates and could result in overestimates of site fidelity. Nevertheless, only one bird was not seen in its territory during one year but was detected again in it in the following, which could mean either temporal emigration or that it was not detected in spite of being there. These data, together with missed birds that were detected afterwards in their territories within the same year, gave a recapture probability (or detectability) as high as 87% using the classic Cormack–Jolly–Seber model (Illera and Díaz, unpublished data). Hence, low detectability of marked birds could not account for the low dispersal rates recorded, supporting a high site faithfulness in Canary Islands stonechats.

Site faithfulness was independent of reproductive success, as no individual or pair that suffered nest predation or did not breed due to low food availability moved afterwards. The breeding success of Canary Islands stonechats is mostly determined by rainfall-mediated food availability and nest predation (Illera and Díaz, 2006). The low spatial variability of these factors within a given year, together with low spatial and temporal variation in the abundance of potential competitors or predators, suggests that the likelihood of finding vacant territories of higher (or lower) quality than the year's average would be low. In this scenario, the small potential increase in success gained in a new territory may not compensate for the costs of changing territories. Such costs include the increased probability of predation while moving and, because Canary Islands stonechats defend territories all year round, the costs of establishing in a new territory in terms of fighting costs and decreased time available for foraging (Switzer, 1997b; Jakob et al., 2001; Yoder et al., 2004).

The number of clutches, and clutch size of individual pairs, varies among years in relation to the strong among-years differences in food availability closely related to rainfall (Illera and Díaz, 2006). Rainfall and arthropod abundance did not vary significantly at the scale of the distribution area of the species (i.e., among focal areas). Variation among transects within focal areas (i.e., at a scale closer to that of individual territories) was also usually not significant, with the exception of the Espigón de la Mesa focal area, where six out of the 25 months studied showed significant spatial variation, including three consecutive months of 2003 (Table 1). However, no site unfaithfulness was recorded for this area and period.

Nest predation reduced the breeding success of individual pairs, but the chance of a nest being depredated did not differ significantly among either focal areas or years (see also Illera and Díaz, 2006). The identity, distribution and predatory behaviour of the main nest predators, feral cats, could explain this lack of spatial and temporal pattern of nest predation. After their introduction centuries ago cats are now widely distributed over Fuerteventura Island, and locate nests (and many other prey; see Nogales et al., 2004 and references therein) essentially at random. Hence, moving to other territory after suffering nest predation would not decrease the subsequent risk of nest predation compared to staying in the same territory. Being site faithful independently of past reproductive success may thus be an optimal strategy for the Canary Islands stonechat due to the low spatial variability of relevant abiotic and biotic factors (Shields, 1984; Switzer, 1993; Stamps, 1995). Low spatial variability occurred at the scales of the whole distribution range (all factors), focal areas occupied by stable populations (food availability) or even individual territories (nest predation).

If most individuals are site faithful, colonisation of vacant territories must depend on juvenile dispersal. Juveniles experience a partial moult between March and July, so that they may look like adults unless carefully handled and examined (Illera and Atienza, 2002). On this basis, the two site unfaithful males recorded in December 2000 and the female recorded in October–December 2000 could have been dispersing juveniles (unfortunately, they were not aged upon capture). The two birds (male and female) that moved between March and April 2001 were settled on an ephemeral food source, a little rubbish dump with plenty of arthropods within an area of lava flows with low food availability (Illera, 2001). The dump was closed just before the birds left the territory, suggesting a cause-effect relationship. The remaining two cases of territory movement were due to an exceptional case of divorce described in more detail in Illera (2005). The female paired with

a neighbouring unpaired male in February 2002 after successfully rearing three chicks. The divorced male was unable to attract another female and moved to a new territory in October, where it paired in the breeding season of 2002–2003. This male was faithful to its new territory until June 2003, despite a breeding success of zero after suffering two consecutive nest predation events.

Overall we conclude that, once a Canary Islands stonechat acquires a territory, it usually stays there for life. This site faithfulness was related to the low spatial variability of environmental factors determining breeding success. The few cases of adult dispersal recorded seemed to have been forced by specific adverse conditions. Overall, our findings on site fidelity (this paper) and breeding success (Illera and Díaz, 2006) suggest that Canary Islands stonechats have evolved strategies to adjust their life cycles to the temporal variability of habitat quality (“sit and wait breeding”) rather than assessing and responding to the spatial variability of habitat quality, as predicted by models on performance-based attraction or presence and number of conspecific models (Doligez et al., 2003, 2004; Serrano et al., 2001, 2004).

Finally, if site fidelity is associated with the spatial homogeneity of Fuerteventura Island, it could be expected similar results in other species with similar requirements inhabiting this island or other islands with similar ecological conditions. Low spatial variability of habitat suitability may thus also explain the low variability in the abundance of Berthelot’s pipits found in this study.

## 5. Implications for conservation

The Canary Islands stonechat is a narrow-range endemic bird which has been listed as “Endangered” because of the increasing destruction and alteration of its habitats by tourism developments and/or overgrazing (Illera, 2004b). Because of the stonechats’ specific habitat and microhabitat requirements (Illera, 2001) and its strong site fidelity (this paper), strict protection of the areas it already occupies appears to be the most effective way of preserving this species. As most of our focal areas were outside the Important Bird Areas (IBA) network previously to this study, it is now necessary to map the distribution of this species and include it in the IBA network. The year-round site fidelity and habitat requirements of this species may facilitate this task as predictive distribution maps based on relevant habitat features extracted from land use maps can be developed (Bustamante and Seoane, 2004; Seoane et al., 2004).

## Acknowledgements

We are grateful to José Luis Tella, David Serrano, David S. Richardson and two anonymous referees for helpful comments and suggestions on the manuscript. D.S. Richardson helped with the spelling. Juan Carlos Rando provided the GPS. Juan Carlos Atienza and Ángel Moreno helped during ringing sessions. J.C.I. thanks Manuel Nogales for continuous encouragement during his PhD work. This study received

partial financial support by the Regional Government of the Canary Islands. Birds were ringed with official permit of the Regional Government. Dámaso Santana and Nemesio Hernández (Cabildo de Fuerteventura) provided the worms needed for trapping birds.

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