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Original article

Plasticity of nest-site selection in the trumpeter finch: A comparison between two different habitats

Rafael Barrientos*, Francisco Valera*, Andrés Barbosa, Carmen M. Carrillo, Eulalia Moreno

Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas, CSIC, General Segura 1, Almería E-04001, Spain

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A B S T R A C T

In habitats with more predators, a species is expected to breed in safer sites and be less successful than in predator-impoverished habitats. We tested this hypothesis by studying nest-habitat selection and nest predation in two populations of Trumpeter finch (*Bucanetes githagineus*). One breeds in a predator-rich habitat (Tabernas, Iberian Peninsula), and the other is found on an island with fewer predators (La Oliva, Canary Islands). In both localities, we studied the features of nests in two different substrates, on the ground and in cliffs, including visibility and position in the cliff. We measured the habitat characteristics in a series of plots around the ground nests and compared them to random points. We also studied the influence of nest features and habitat selection on predation of both nest types. Trumpeter finches built more nests in cliffs in Tabernas, probably because there are more cliffs available there. In this locality, the patches selected for ground nesting had below-average vegetation cover, lower vegetation height, and were on steeper slopes. In La Oliva, they selected above-average vegetation height and steeper slopes. Cliff nests were less predated than ground nests in La Oliva, but not in Tabernas. The only variable that affected survival rates in Tabernas was the height of vegetation around ground nests, with nests in lower vegetation having higher survival rates. These results suggest that locality-related differences in habitat selection by vegetation height could be related to the different predator assemblages present in any given area, though we cannot rule out confounding influences of other differences between the two sites.

1. Introduction

Nest predation is one of the main factors determining avian fitness (Martin, 1993) and it is also a strong selective pressure affecting the life history of prey, as it is a severe primary cause of breeding failure (Martin, 1993). There are many studies in the literature on how nest predation influences various breeding traits, such as nest size, (López-Iborra et al., 2004), clutch size (Martin, 1993, 1995; Yanes and Suárez, 1997; Eggers et al., 2006), parent nest visitation rates (Eggers et al., 2005), duration of nestling period (Martin, 1993, 1995; Yanes and Suárez, 1997) or breeding dispersal distances (Hakkarainen et al., 2001). Nest predation rates vary among habitats and nest sites, and one of the highest is for ground-nesting birds breeding in open lands (Martin, 1993; Yanes and Suárez, 1995). This is because nest predation varies with nest attributes. For example, brood loss is much higher amongst open-nesters than cavity-nesters (Martin and Li, 1992). Moreover, the simplicity of open land makes nest concealment more difficult.

Although behavioural responses can reduce nest predation (Remeš, 2005), nest location is considered the main adaptive response to this selective pressure (e.g., Yanes and Oñate, 1996; Yanes et al., 1996; Penloup et al., 1997; Mezquida and Marone, 2002). Predation rates can vary with predator presence or abundance, both locally and on a larger scale (Sæther, 1996; Penloup et al., 1997; Schmidt and Ostfeld, 2003). Potential nest predation can also differ predictably among localities (Martin, 1995) as sites with more predators are expected to undergo higher predation rates, determining nest-habitat selection both at territorial (Söderström, 2001; Nordström and Kopimäki, 2004; Roos and Pärt, 2004; Fontaine and Martin, 2006) and microhabitat scale (Forstmeier and Weiss, 2004; Eggers et al., 2006). Furthermore, different predators may induce birds to select for different nest attributes. For instance, some vegetation cover around the nest can be enough to prevent nest predation when predators use visual cues, but this same cover may not be enough for evading predators that employ olfactory cues (Martin and Joron, 2003).

Islands are not as rich in native vertebrates as the mainland is, due to both limited colonization by non-avian vertebrates and to

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* Corresponding authors. Tel.: +34 950 281 045; fax: +34 950 277 100.
E-mail addresses: rafabarri@hotmail.com (R. Barrientos), pvalera@eeza.csic.es (F. Valera).

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the settlement limitation of predators which require large areas to survive (reviewed in Blondel, 2000). The under-representation of predators in most island biotas leads to them having generally lower rates of nest predation (e.g., George, 1987; Martin and Joron, 2003) as well as relaxation in antipredatory behaviour of the prey (reviewed in Blondel, 2000). Consequently, a comparison of mainland and island nest-site selection presents a natural experiment especially well suited to studying the responses of nesting birds to predator pressure. To our knowledge, this biogeographical approach has been relatively little explored to date (but see Martin and Joron, 2003).

We compared two populations of the Trumpeter finch (*Bucanetes githagineus*), a dryland open-nester passerine. One, on the mainland, is in the Tabernas Desert (Southeast continental Spain) and the other, on an island, at La Oliva, Fuerteventura Island (Canary Islands). The mainland population faces a predator-rich assemblage, whereas the island population breeds in an area with fewer predators (Palomo and Gisbert, 2002; Martí and del Moral, 2003; Pleguezuelos et al., 2004; Nogales and González, 2005; pers. obs.). The trumpeter finch is particularly well suited for this study because of its exceptional trait of commonly nesting in two very different types of sites: (i) nests built directly on the ground, often partially concealed under stones or shrubs; and (ii) nests built in cliffs, often in cavities, and less commonly on shelves (Manrique et al., 2003). We could therefore expect finches to select safer nest sites (e.g., cliffs) in the locality with more predators. Our aim was to study the response of nesting trumpeter finches to habitat characteristics and potential nest predation. Our three-fold approach compared (i) nest attributes by type (ground vs. cliff) and by population (island vs. mainland). In ground nests, we studied (ii) whether habitat around the nest differed from random habitat available in the rest of the locality (i.e., nest-site selection) and whether nest-site selection patterns differ between localities. Finally, we analysed (iii) whether nest-site selection affects survival rates. In ground nest-site selection, we expected differences in habitat selection between localities according to their different predator assemblages (Söderström et al., 1998; Martin and Joron, 2003), since nest-site selection is adjusted to the current predation risk (Forstmeier and Weiss, 2004; Eggers et al., 2006). In Tabernas, where the predator community is richer, we particularly expected finches to select those nest sites that would facilitate escape from predators (Yanes and Oñate, 1996). In contrast, at La Oliva, less predator pressure probably leads to different antipredatory responses (Blondel, 2000), including nest-site selection. Finally, since nest-site selection can influence nest predation rates (Martin, 1988, 1995; Yanes et al., 1996; Clark and Shutler, 1999; but see Mezquida and Marone, 2002; Mezquida, 2004), we expected certain habitat features to affect nest survival rates.

2. Materials and methods

2.1. Study species and area

The trumpeter finch is a small (around 21g) passerine distributed over the warm arid regions of the Middle East, North Africa, Southeast Iberian Peninsula and the Canary Islands (Cramp and Perrins, 1994). The total nesting period is about 25–30 days (Barrientos et al., 2007) and at least some pairs lay two clutches per season, which extends from February to July in continental Spain (Barrientos et al., 2007) and from January to May in the Canary Islands (Martín and Lorenzo, 2001).

In the mainland locality (Tabernas Desert, 37° 02′ N, 2° 30′ W, Almería, Southeast Iberian Peninsula), the study area was monitored from February to August 2004 and 2005. Most of the Iberian population is probably concentrated in our study site (Carrillo et al., 2007). This area is characterized by a network of ravines and particularly abundant cliffs alternating with dry riverbeds, and badlands with a high percentage of bare ground and abrupt slopes. The area has a semiarid Mediterranean climate, with mean annual precipitation of less than 250 mm. The locality studied has two deep gullies, one wider than the other. Vegetation is concentrated at the bottom of the ravines and is dominated by perennial grasses like *Stipa tenacissima* and *Lygeum spartum*, and xerophytic shrubs like *Launaea arborescens*, *Limonium tabernense*, *Salsola genistoides*, *Artemisia barrelieri*, and *Anabasis articulata*. This type of habitat is common throughout the arid Southeast of the Iberian Peninsula (Peinado et al., 1992).

The breeding biology of the island population was monitored in La Oliva (Fuerteventura, 28° 41′ N, 13° 52′ W, Canary Islands) from January to April 2005. The study area consists of two wide valleys dominated by a volcanic landscape with few cliffs, but with steep slopes at mid height on hillsides. Volcanic rocks spread over the area cover 85% of the surface (Illera, 2001). The area has a semi-desert climate with an annual precipitation of 145 mm. Vegetation is highly conditioned by overgrazing by goats (Gangoso et al., 2006), and plant development is higher up on abrupt slopes. The vegetation is mainly composed of six xerophytic shrub species: *L. arborescens*, *Salsola vermiculata*, *Suaeda spp*., *Euphorbia regis-jubae*, *Lycium intrincatum* and *Nicotiana glaucax* (Illera, 2001).

Potential nest predator richness and abundance differ widely between the two study areas, the main difference being the absence of reptiles in La Oliva (Table 1). The predator assemblage in Tabernas is well represented and can be considered representative of arid regions in the Southeast Iberian Peninsula, where snakes, rodents and wild carnivores are the most important potential nest predators (Palomo and Gisbert, 2002; Martí and del Moral, 2003; Pleguezuelos et al., 2004). In contrast, at La Oliva, the only native predator of relative importance is the grey shrike (*Lanius meridionalis*). The two most important predators, Barbary ground squirrels (*Atlantoxerus getulus*) and domestic cats (*Felis silvestris catus*), are both naturalized species (Nogales and González, 2005; Medina et al., 2008; Medina and Nogales, 2009). Consequently,

Table 1
Abundance of potential nest predators in the study areas. Key: – absent, * present, ** common, *** abundant and **** highly abundant. Data from Palomo and Gisbert (2002), Martí and del Moral (2003), Pleguezuelos et al. (2004), Nogales and González (2005) and own data.

Predator species	Abundance	
	Tabernas	La Oliva
Reptiles		
Malpolon monspessulanus	****	–
Elaphe scalaris	***	–
Coluber hippocrepis	**	–
Lacerta lepida	*	–
Birds		
Falco tinnunculus	*	*
Lanius meridionalis	*	**
Lanius senator	*	–
Corvus monedula	*	–
Corvus corax	–	*
Mammals		
Atlantoxerus getulus	–	****
Vulpes vulpes	*	–
Martes foina	***	–
Meles meles	**	–
Felix silvestris catus	–	****
Rattus sp.	–	*
Mus domesticus	*	*
Mus spretus	*	–
Eliomys quercinus	**	–

these predators are linked to human habitats like, for instance, agricultural terraces in the case of squirrels (López-Darias and Lobo, 2008).

2.2. Nests surveys

Nests were found by following parents with a telescope from observation sites or just by chance while walking. We studied 25 nests in Tabernas in 2004 and 24 in 2005, and 55 were monitored in La Oliva in 2005.

Visits to the nests were limited to disturb the breeding pairs as little as possible (mean number of visits per nest was 3.5 in Tabernas and 4.1 in La Oliva). Nestlings observed less than two days before the expected fledging date or parents feeding fledglings close to the nest were considered evidences of successful broods (Martin, 1993). Nests where at least one of the young fledged were considered successful. Nest predation was assumed when eggs were found broken or chicks were found dead or disappeared before hatching or fledging and were not found alive close to the nest (see Barrientos et al., 2007 for details). To ascertain the effect of researchers' visits on nest predation, the visitation rate was calculated as the number of visits between the date when nest was found and the next-to-the-last visit (since the effect of the last visit cannot be evaluated) divided by the number of days between these two dates. In successful nests, the last visit was two days before the expected fledging date. As reported for other arid bird species (e.g., Lloyd et al., 2000 and references therein), our results suggest that the visitation rate did not influence nest predation (based on nests with predation/success outcome and at least two visits, logistic regressions: Tabernas: $\chi^2_1 = 0.9$; $n = 25$; $P = 0.34$; La Oliva: $\chi^2_1 = 0.3$; $n = 36$; $P = 0.58$).

2.3. Nest features and site

Nest *visibility* was estimated in degrees (0–360°) of habitat without bushy vegetation or large stones within a 3-m radius around the nest. We used a protractor placed on the nest to project the imaginary 3-m long lines and estimate the degrees of habitat free of obstacles that would prevent seeing a potential predator from the nest. We also measured *lower height*, the distance (if any) from the nest to the cliff base, and *upper height*, the distance (if any) from the nest to the cliff top. Based on these features, the nests could be classified as *cliff nest* (lower and upper height > 0) or *ground nest*. None of the variables measured for cliff nests (visibility, upper height, lower height) or ground nests (visibility) differed between years in Tabernas (cliff nests, *t*-tests: $P > 0.10$ in all the cases, $n_{2004} = 9$, $n_{2005} = 18$, data not shown; ground nests: Mann–Whitney U test: $P > 0.10$, $n_{2004} = 16$, $n_{2005} = 6$, data not shown). Based on the consistency of the patterns found, we were able to pool data from both years in Tabernas.

2.4. Nest-site habitat selection in ground nests

We studied ground nest-site selection on the basis of three variables: *percentage of vegetation cover*, *maximum vegetation height* (in centimetres) and *substrate slope* (in degrees, i.e., 0–90). These variables were measured in 2×2-m squares at four positions around the nest (see Fig. 1). The down-slope square was labelled the *front square* and the up-slope square, the *back square*. Four squares were delimited 5 m and 15 m away from the nest (N, S, E and W in both cases) and averaged for one *square* 5 m *away* and one *square* 15 m *away*, respectively. Any square 5 or 15 m away that fell on a cliff was discarded.

Since we found no interannual differences in any of the variables measured in any of the positions sampled in Tabernas (i.e., front, back, 5 m and 15 m squares away, Mann–Whitney tests, $P > 0.05$ in all cases; data not shown), 2004 and 2005 data were pooled. To identify habitat selection, habitat characteristics near the nest must be compared to the general habitat. We therefore measured the same variables at random points placed from 50 to 200 m from the nearest nest. In heterogeneous habitats like ours, measures can vary widely in small spaces. For instance, the 2×2-m square at a random point could be in a riverbed, often less than 2 m across, with plenty of vegetation, and the rest of the plot dominated by abrupt slopes with no vegetation. To avoid such biases, we replicated every random point four times at every cardinal point 15 m from the centre. The data from these five squares were averaged in one for every variable at every *random point*. In Tabernas, we measured 26 random points in 2005, but were unable to collect random habitat data in 2004, so we used data from a previous year (2003, $n = 16$ random points), as there were no statistical interannual differences in the variables studied between 2003 and 2005 (*t*-Student tests, $P > 0.10$ in the three variables). Features were therefore measured for a total of 49 nests in Tabernas and 55 in La Oliva and at 42 random points in Tabernas and 60 in La Oliva.

In Tabernas, the soil is sandy and slopes are steep. Consequently, measuring the habitat around the nests erodes the ground and leaves easy tracks for nest predators in the study plots. Habitat features were therefore measured at the end of each breeding season to avoid human-mediated nest predation. Season-dependent differences in the measured variables were assumed negligible because: i) the vegetation-related variables measured in our arid habitat are mainly related to the occurrence and density of shrubs, which are less seasonally dependent than herbaceous vegetation, ii) seasonal effects (e.g., vegetation growth) are very likely consistent throughout the study area, and we therefore do not expect them to affect the outcome of this study. In La Oliva, where volcanic soil consistency minimizes the impact of research activity, we measured habitat features just after breeding in each nest.

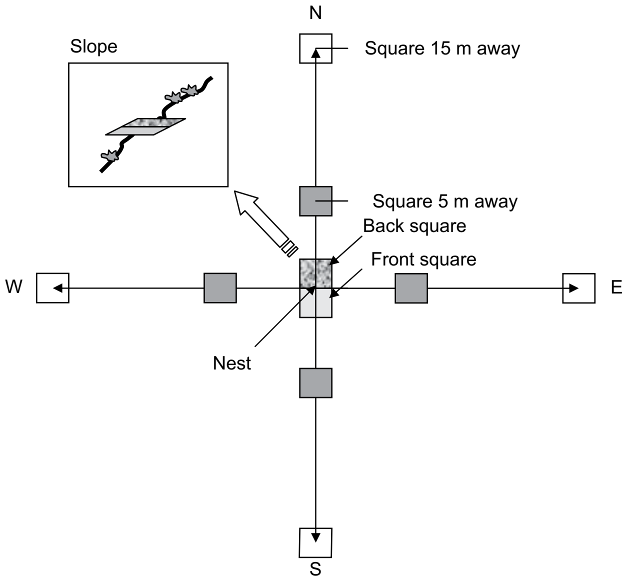

Fig. 1. Sampling distribution around the nests. Predictor variables were measured in *front* and *back squares* placed just down-slope and up-slope from the nest (see detail), respectively. *Square* 5 m *away* was the average of the predictor variables measured in four squares at the 4 cardinal points 5 m from the nest. The same methodology was repeated for the *square* 15 m *away*.

2.5. Nest predation and the influence of nest-habitat selection

Seven nests with unknown outcome in Tabernas and 4 in La Oliva, 6 abandoned nests in Tabernas and 8 in La Oliva, and one more nest in Tabernas in which chicks died of starvation were excluded from the predation analyses. The predation rate was therefore calculated with information from 35 nests in Tabernas and 43 in La Oliva. Predation rates were calculated separately overall and for ground and cliff nests. First, the predation rate was calculated as the number of predated nests divided by the total number of nests (i.e., predated or successful). Second, for more realistic information on predation rates, we calculated daily survival rates (hereafter DSRs) with the program MARK (Rotella, 2009; see also Dinsmore et al., 2002; Rotella et al., 2004). The use of survival analysis reduced our sample size, as this analysis requires at least two visits to a nest to be included in the calculations. Therefore, DSR was calculated for 28 nests in Tabernas and 43 in La Oliva. Data are presented for the whole nesting period, assuming that all nests in the sample have the same DSR every day (Rotella, 2009). DSRs were assessed: i) by locality, including both nest types; and ii) differentiating between cliff and ground nests within and between localities.

To study how nest-habitat selection and nest features influence DSRs, we separated cliff and ground nests because of their differential accessibility to predators. In cliff nests, we studied the influence of nest features (i.e., visibility, lower and upper height) on DSRs. In ground nests, we studied the influence of visibility and habitat variables that were statistically significant in the nest-site selection study (see Results). When a predictor variable taken at different distances from the nest differed from the one found for the random points, but not among those distances themselves (e.g., maximum vegetation height similar in front, back, 5-m and 15-m squares, but all of them different from the random squares), they were averaged before entering the variable in the models.

2.6. Statistical analyses

The percentage difference between cliff and ground nests was examined between years in Tabernas and between localities using 2×2 contingency tables with the Yates correction. Differences in visibility and upper and lower heights between nest types and/or localities were verified by *t*-tests after checking normality and homocedasticity, or by Mann–Whitney U-tests. The percentage of vegetation cover was transformed using the arcsine-square-root transformation. Differences in response variables over the distance from the nest were tested by ANOVA and a posteriori Tukey test. DSR was calculated with the constant model implemented in the program MARK (Rotella, 2009). Survival rates were compared for population and nest type by chi-square analyses using CONTRAST software (Hines and Sauer, 1989). We used the program MARK to evaluate the set of potential nest predation influence models. This software uses maximum likelihood estimation and the Akaike Information Criterion (AIC) to identify the model best explaining (i.e., having the lowest AIC; Rotella, 2009) nest predation with the predictors considered.

3. Results

3.1. Nest sites and features

Trumpeter finches nested in cliffs and on the ground in both study areas, but the percentages were very different. In Tabernas, 9 out of 25 nests (36%) in 2004 and 18 out of 24 (75%) in 2005 (between-years, $\chi^2 = 6.0$, d.f. = 1, $P = 0.01$) were built in cliffs, whereas in La Oliva only 5 out of 55 (9.1%) were. The percentage of nests in cliffs was significantly smaller in La Oliva than in Tabernas, even when compared to the year when the percentage of cliff nests in Tabernas was lower (2004) ($\chi^2 = 6.9$, d.f. = 1, $P = 0.01$).

The upper height in cliff nests did not differ between localities (mean ± SE, 388.5 ± 86.5, $n = 27$, in Tabernas vs. 230.0 ± 93.0, $n = 5$, in La Oliva; Mann–Whitney U test, $Z = 0.6$, $P = 0.55$), however, the lower height was significantly greater in Tabernas (655.6 ± 122.6, $n = 27$) than in La Oliva (172.0 ± 20.8, $n = 5$; Mann–Whitney U test, $Z = 2.0$, $P = 0.047$).

Within localities, visibility did not differ between cliff and ground nests in Tabernas (*t*-test, $t = 0.6$, $P = 0.57$, $n = 27$ and 22, respectively), although it did in La Oliva (Mann–Whitney U-test, $Z = 2.8$, $P < 0.01$, $n = 5$ and 50, respectively), where cliff nests had a wider field-of-view (Fig. 2). Cliff nest visibility was similar in Tabernas and in La Oliva (Mann–Whitney, $Z = 0.7$, $P = 0.48$, $n = 27$ and 5, respectively) (Fig. 2). In contrast, ground nests had more visibility in Tabernas than in La Oliva (*t*-test, $t = 5.6$, $P < 0.0001$, $n = 22$ and 50, respectively) (Fig. 2).

3.2. Nest-habitat selection in ground nests

In Tabernas, we found significant differences in the three variables measured for distance from the nest compared to the random points. Specifically, vegetation cover was lower both in the front squares and in the squares 5 m away than at the random points ($F_{4,125} = 6.8$; $P < 0.0001$; see Fig. 3a for Tukey test significance). Maximum vegetation height also differed by position ($F_{4,125} = 13.9$; $P < 0.0001$; Fig. 3b) along an increasing gradient from front squares to random points. In contrast, the slope gradient decreased from the front squares to random points, as front squares, back squares and squares 5 m away had higher slopes than random points ($F_{4,125} = 8.8$; $P < 0.0001$; Fig. 3c).

In La Oliva, ANOVA results showed no statistical differences in vegetation cover ($F_{4,255} = 0.2$; $P = 0.94$; Fig. 3a). In contrast, both maximum vegetation height ($F_{4,255} = 15.4$; $P < 0.0001$; Fig. 3b) and substrate slope ($F_{4,255} = 6.9$; $P < 0.0001$; Fig. 3c) differed significantly, as vegetation height was lower in the random points than at any point around the nest, and the slope was more abrupt in the squares 5 m and 15 m away than at the random points.

3.3. Nest predation and influence of nest-habitat selection

Overall nest predation was 62.9% (22 out of 35 nests) in Tabernas and 53.5% (23 out of 43) in La Oliva. In Tabernas, 47.1% (8 out of 17) of cliff nests and 77.8% (14 out of 18) of ground nests were predated, whereas in La Oliva none of the four cliff nests and 58.9% (23 out of 39) of ground nests were predated. Previous survival analyses with the program MARK allowed us to pool Tabernas data from 2004 and

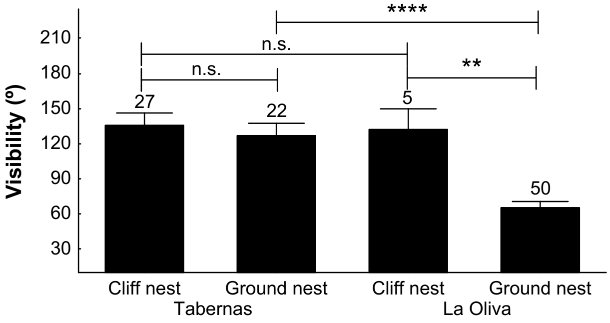

Fig. 2. Differences in visibility from the nest (mean ± SE) for different nest types and localities. Asterisks mark the significance levels as follows: ns, not significant; **, $P < 0.01$; ***, $P < 0.001$. Sample size is shown above bars.

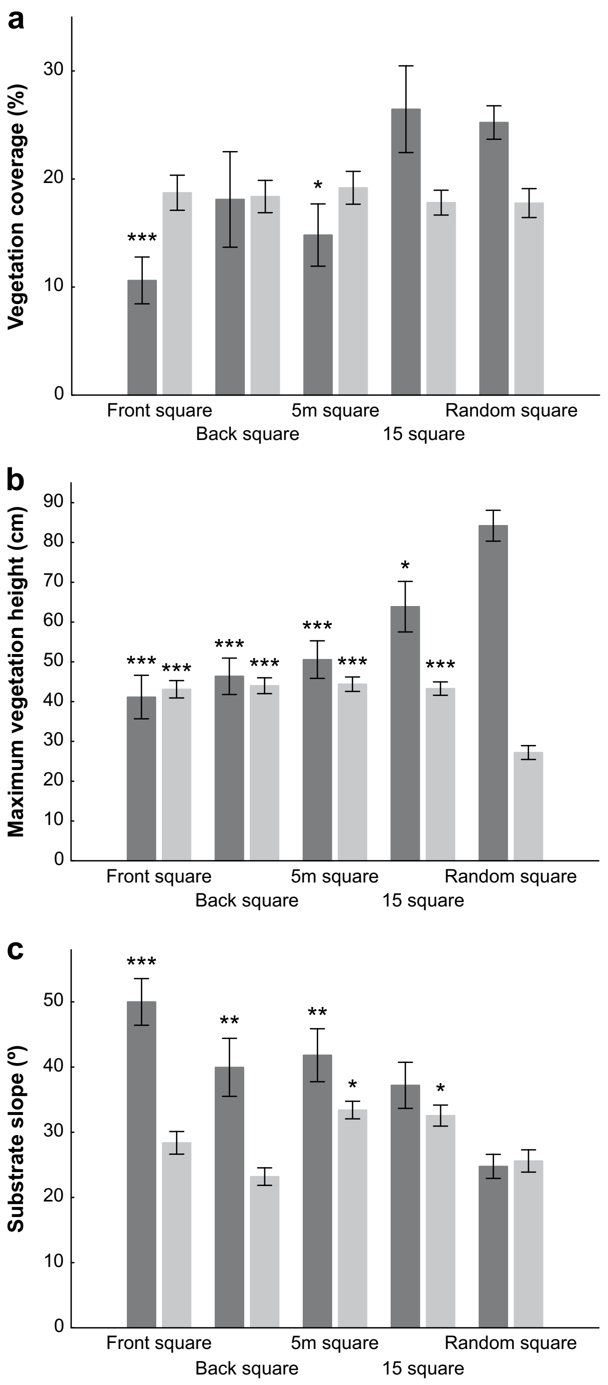

Fig. 3. Percentage of vegetation cover (3a), maximum vegetation height (3b) and substrate slope (3c) in Tabernas (dark-grey bars) and La Oliva (light-grey) at locations measured around trumpeter finch nests (see Fig. 1). Data are expressed as mean ± SE. Sample sizes: 22 sampling sites around the nest and 42 random points in Tabernas and 50 sampling sites around the nest and 60 random points in La Oliva. Asterisks mark the Tukey test significance level between a certain square and the random point as follows: *, $P < 0.05$; **, $P < 0.01$ ***, $P < 0.001$.

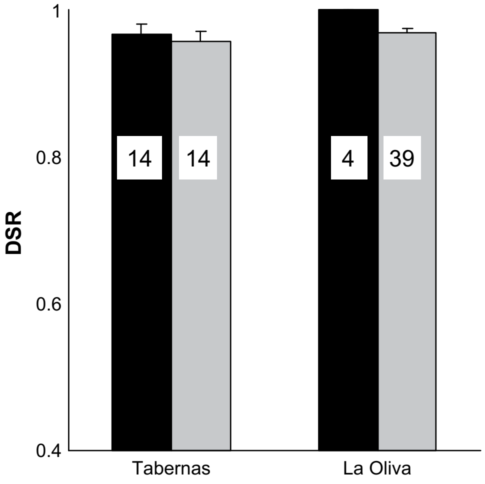

Fig. 4. DSR calculated using survival analyses with program MARK for cliff (black) and ground (grey bars) trumpeter finch nests in Tabernas and in La Oliva. Standard errors are also shown over the bars as well as the sample sizes inside them.

2005 as there were no significant annual differences in overall DSR (presented as DSR ± SE; total nests in 2004, 0.956 ± 0.012, $n = 18$ vs. total nests in 2005, 0.970 ± 0.015, $n = 10$; $\chi^2 = 0.5$, d.f. = 1, $P = 0.47$) or by nest-site (cliff nests in 2004, 0.958 ± 0.024, $n = 6$ vs. cliff nests in 2005, 0.972 ± 0.016, $n = 8$; $\chi^2 = 0.2$, d.f. = 1, $P = 0.63$; ground nests in 2004, 0.955 ± 0.015, $n = 12$ vs. ground nests in 2005, 0.963 ± 0.037, $n = 2$; $\chi^2 = 0.0$, d.f. = 1, $P = 0.84$). Survival analyses showed similar overall DSR in Tabernas and La Oliva (0.961 ± 0.010, $n = 28$ vs. 0.972 ± 0.006, $n = 43$; $\chi^2 = 0.9$, d.f. = 1, $P = 0.35$). DSR in nests built on cliffs was not statistically different from those built on the ground (Fig. 4) in Tabernas (0.966 ± 0.014, $n = 14$ vs. 0.956 ± 0.014, $n = 14$; $\chi^2 = 0.3$, d.f. = 1, $P = 0.61$), but was higher in cliff nests in La Oliva (1.000 ± 0.000, $n = 4$ vs. 0.968 ± 0.007, $n = 39$; $\chi^2 = 20.9$, d.f. = 1, $P < 0.0001$). The DSR in cliff nests was significantly higher in La Oliva than in Tabernas ($\chi^2 = 5.9$, d.f. = 1, $P = 0.02$), and similar in ground nests between localities ($\chi^2 = 0.6$, d.f. = 1, $P = 0.44$).

Our results for cliff nests in Tabernas show that no model explained more than the simpler intercept-only model, which means that none of the three variables (i.e., visibility, lower and upper height) affected DSR. In La Oliva, it is worth mentioning that all the cliff nests with known outcome were successful ($n = 4$), so the influence of their traits on DSR could not be evaluated. For ground nests in Tabernas we used visibility, percentage of vegetation cover (averaged for the front and 5-m squares), the maximum vegetation height (averaged from the front, back, 5-m and 15-m squares) and the slope (averaged for the front, back and 5-m squares) as predictors. The model with the lowest AIC included only the maximum vegetation height, for which the DSR was higher in those nests with lower vegetation. The predictors used for ground nests in La Oliva were visibility, maximum vegetation height (averaged for front, back, 5-m and 15-m squares) and the substrate slope (averaged for 5-m and 15-m squares). Our results showed that no model received more support than the simpler intercept-only model for La Oliva ground nests.

4. Discussion

Trumpeter finches build their nests in two very different locations, on the ground and in holes in cliffs, a plasticity that is unusual among passerines (Martin and Li, 1992), including related species (Khoury et al., 2009). Wide field of view is a typical trait of cliff nests due to their height above the ground. Cliff nests are therefore expected to have more visibility than ground nests, as was the case in La Oliva. However, in Tabernas, trumpeter finches selected places for ground nests with visibility similar to cliff nests, in patches of lower-than-average vegetation and with below-average cover. In contrast, at La Oliva, nests were located in patches with taller than average vegetation. In both localities, finches built their ground nests on steeper slopes than the mean available. Whereas the nest type had no clear influence on DSR in Tabernas, it was decisive in La Oliva, since there was less nest predation in cliffs (although our sample was small). The only habitat variable that had an influence on DSR was the vegetation height around the ground nests in Tabernas. Interestingly, DSRs in nests surrounded by taller vegetation were lower.

Nesting in inaccessible cliffs is probably advantageous on the continent where predators are numerous (Boulinier et al., 2008), or on islands where there are a significant number of introduced predators, as cliffs provide protection against predators that cannot fly or climb, reducing the number of potential predators and nest predation (Penloup et al., 1997). We found no predated cliff nests in La Oliva (although the number of cliff nests was low), probably for their protection against introduced predators. On the other hand, data from Tabernas suggest that in localities occupied by a wide variety of predators and hunting strategies, this protection is not enough (see also Mezquida, 2004). The absence of clear differences in predation rates between the two nest types (i.e., cliff and ground) is the most likely explanation for the widespread use of both nest emplacements in Tabernas. However, we may have underestimated breeding success in cliff nests, as we could not monitor nests built inside inaccessible cavities (6 out of 7 cliff nests with unknown outcome in Tabernas) and, therefore, the nests with the best protection due to their inaccessibility were not analysed. In fact, the number of predated nests in Tabernas did not differ between cliff and ground (Chi-Square with Yates correction, 8 nests predated out of 17 in cliff vs. 14 out of 18 in ground, $\chi^2 = 2.3$, d.f. $= 1$, $P = 0.13$), whereas, assuming that all 6 nests with unknown outcome were successful, nest predation would be lower in cliff nests (Chi-Square with Yates correction, 8 out of 23 vs. 14 out of 18, $\chi^2 = 5.9$, d.f. $= 1$, $P = 0.02$).

The availability of suitable nesting places is a key factor in interpreting population differences in the percentage of nest types (i.e., hole in cliff vs. ground). There are more cliffs in Tabernas (15.7% of the squares sampled, $n = 667$), which is likely to facilitate the choice of a cliff and also make it easier to find higher available cavities than in La Oliva (2.4%, $n = 740$). Although we did not study cliff characteristics, other authors have shown that larger cliffs provide more potential nest sites (e.g., Blanco et al., 1998). Such local features could explain the difference in percentages of cliff nests in the two localities, as birds in Tabernas would have had more holes to choose for. The reasons for the inter-year variability in the proportion of nest types in Tabernas are unknown. Finally, in Tabernas, other species, like rock sparrows *Petronia petronia* and Spanish Sparrows *Passer hispaniolensis* also nest in cliffs in the study area and could compete for holes with trumpeter finches, although both sparrow species are less abundant than finches (pers. obs.). In this sense, it is worth mentioning that during our study we only observed one case of interaction, when a pair of Spanish sparrows bred in a crack where a pair of trumpeter finches had previously bred successfully.

Once finches had decided to breed on the ground, or had been forced to because there were no cliffs, they built their nests in patches of vegetation of similar height in the close vicinity of the nest in both localities (see Fig. 3b), involving opposing vegetation height selection patterns in every site. Whereas in Tabernas, birds selected for nest sites with vegetation lower than randomly available, in La Oliva, where vegetation in random points was lower than in Tabernas, they selected for areas where bushes were taller than random. The selection of vegetation cover is more refined in Tabernas, as there is a gradient from the front square to the random point, whereas in La Oliva there are no significant differences among the squares around the nest. This result is especially meaningful, as the only variable that affected DSR in ground nests in Tabernas was vegetation height, which suggests that those pairs that did not find a sufficiently clear patch to nest in experienced higher predation risk. Finally, at both localities, finches selected for nest places that were steeper than random. In La Oliva, whereas trumpeter finches selected for steeper hillsides (represented by squares 5 m and 15 m away) as nesting places, they built their nests in small depressions in these hillsides (front and back squares had slopes similar to the random ones). Stones, commonly used by finches to hide their nests in La Oliva (41 out of 50 ground nests were at least partly under stones), are more abundant in these hollows (pers. obs.). Nest concealment with stones is easier in the rocky habitat at La Oliva (74.0% of ground surface covered by rocks; see also Illera, 2001) than in Tabernas, which is sandy (only 23.7% stone cover). However, the concealment of nests with stones, which contributed to reducing the field of view in La Oliva, seemed to be actively selected against in Tabernas, since finches here placed the nest at the edge of shrubs or rocks (if any), whereas in La Oliva they hid the nest well inside them (pers. obs).

One explanation for differences in nest-habitat selection and nest features found between localities could be the presence of different predator assemblages in the locality. Different predators locate nests by different methods and sensory cues (visual, olfactory, thermal or acoustic). This suggests that, since defence strategies are predator-specific (Halupka, 1999), the composition of a current predator assemblage could induce both different nest-site selection and nest features in breeding birds (Söderström et al., 1998; Martin and Joron, 2003). Ricklefs (1989) suggested that different nest sites are probably vulnerable to different predators depending on their hunting strategies and their sensory inputs. In Tabernas, the predator community is rich and most species (i.e., reptiles, rodents, stone martens or foxes) do not use visual approaches. Furthermore, reptiles (essentially diurnal), a significant group of potential predators in this locality, are absent in La Oliva. We therefore suggest that in Tabernas, ground-nesting finches build their nests in clear patches to ensure a wide field of view to detect potential predators and escape as soon as possible in order to make nest detection more difficult, as movement of the escaping parent is essential to attracting predators (Yanes and Oñate, 1996). Consistent with our explanation is the fact that nests surrounded by taller vegetation in Tabernas had lower DSRs. Also consistent with this interpretation is the assumption that poor fitness from brood loss is not as dramatic as death of the incubating female, because reproductive success in birds is strongly related to lifespan (Magnhagen, 1991; Schieck and Hannon, 1993). Thus, finding a patch with low vegetation may also be essential to guaranteeing parent survival. In contrast, at La Oliva, where the predator pool is poorer, finches hide their nests on hillsides with tall vegetation and usually under stones. Nest concealment is an optimal antipredatory strategy in the presence of visually oriented diurnal predators like shrikes, squirrels or crows (Martin and Joron, 2003; Eggers et al., 2006). Remaining silent in a well-hidden nest would also be optimal for evading predators that employ acoustic cues, like cats, which along with squirrels, are the most common predators in La Oliva. In this sense, in his study on ecological shifts in island birds, Martin (1992) suggested that island populations are often relatively isolated genetically, and that this allows island birds to develop responses to local environmental conditions more closely than mainland populations, and can therefore respond better to habitat particularities. This could be also the case of trumpeter finches breeding in La Oliva, as Barrientos et al. (2009) found that at present, Fuerteventura finches are genetically differentiated from those in North Africa and the Iberian Peninsula. Nevertheless, it would be interesting to test our explanation in future experimental studies, as we only found one variable (maximum vegetation height) related to DSR. Furthermore, other factors (e.g., breeder experience, different second clutch rates between populations, changes in predator density during the season, etc) not studied here could be influential as well.

Absence of clear relationships between nest-habitat variables and predation is not uncommon in ornithological literature (e.g., Mezquida and Marone, 2002; Forstmeier and Weiss, 2004; Mezquida, 2004). A likely explanation for the lack of more significant results in our localities is that none of the above-mentioned predators specialize in the trumpeter finch, but are incidental predators (Vickery et al., 1992). While hunting for other prey, they may occasionally encounter and depredate trumpeter finch broods. This type of incidental predation, which does not alter predator foraging behaviour (Vickery et al., 1992), might constrain a hypothetical build-up of defences (i.e., increased importance of habitat selection for predation avoidance), because there is no predator nest searching pattern. Furthermore, nest-site selection strategies vary only when costs and benefits associated with nesting at different sites vary consistently (Forstmeier and Weiss, 2004). A second explanation for the absence of more significant predation avoidance could be that wide predator diversity (with highly diverse predation strategies) causes high nest predation regardless of nest-habitat selection, simply because a safe nest place is difficult to find (Mezquida, 2004). Furthermore, high densities of a single predator may also cause similar breeding failure. For instance, even though dusky warblers *Phylloscopus fuscatus* build their nests higher above the ground when the density of their main predator is greater, predation rates are still higher because of this stronger predation pressure (Forstmeier and Weiss, 2004).

5. Conclusion

Our data show that trumpeter finches may nest in two very different types of nest-site, ground and holes in cliffs. While in one study area, La Oliva, nesting in cliffs increased nest success, in the other, Tabernas, no difference was found. Our results also show that trumpeter finches select different patterns of vegetation height with respect to the general habitat in different areas when nesting on the ground. In Tabernas, they tend to build their nests in patches with lower-than-average vegetation, whereas in La Oliva the nests are in patches with higher-than-average vegetation. At least in Tabernas, this habitat selection seems suitable, as nests in patches of lower vegetation had higher survival rates. It is worth noting that these opposing patterns lead to similar habitat use in two sites with very different habitat availability. We hypothesize that this differential nest-site selection could be aimed at reducing the current predation risk generated by the different predator assemblages present in any given area, although, as pointed out in other studies, the efficiency of this habitat selection is reduced under high predation risk.

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