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Distribution and abundance patterns of a newly colonizing species in Tunisian oases: the Common Blackbird *Turdus merula*

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We investigated distribution and abundance patterns of a recently arrived species in the oases of southern Tunisia: the Common Blackbird *Turdus merula*. In this system, we expected that the vegetation structure and geographical locations of oases would have played an important part in shaping the patterns of oasis occupancy and local abundance. Using data collected at 53 oases during two breeding seasons, we found that Blackbird occurrence in a given oasis depended mainly on its presence at neighbouring oases. However, vegetation structure did not prove to be a relevant predictor of Blackbird occurrence. Within occupied oases, local abundance was associated with vegetation structure, namely with the diversity and abundance of the two lowest vegetation layers: fruit trees and herbaceous plants. The presence of Blackbirds at neighbouring oases was not found to account for local abundance. Overall, our results suggest that the distribution and abundance of this newly colonizing species in the southern Tunisian oasis system are influenced by processes acting at two different spatial scales. Landscape-scale processes (i.e. dispersal and colonization from nearby occupied oases) are likely to play an important role in shaping the pattern of oasis occupancy, whereas local-scale factors seem to be more relevant in determining the abundance of locally established populations.

Understanding the factors affecting the distribution and abundance of species living in patchy environments has long been a major question in pure and applied ecology. As habitat quality may affect the feeding and reproductive success of species (Newton 1998), investigations of this issue first focused on the association between species and local habitat conditions (e.g. Verner *et al.* 1986). However, larger-scale processes are increasingly recognized as relevant determinants of distribution and abundance of subdivided populations (Wiens 1995, Bolger *et al.* 1997). At the landscape scale, metapopulation processes (Levins 1969, 1970, Hanski 1999) are reported to play a major role in the survival of local and regional populations, and in shaping patterns of patch occupancy and local abundance (Verboom *et al.* 1991, Hinsley *et al.* 1995, Newton 1995). The relative importance of local-scale vs. landscape-scale processes in determining the presence or absence of a species and the abundance of local populations may depend on the features of the considered patch system and species. This is particularly important to disentangle in the case of a species that has reached a new area, as this may provide important information on the origin and dynamics of biodiversity within this area. We found such an example in the Common Blackbird *Turdus merula* breeding in the oases of southern Tunisia.

Tunisian oases are isolated seminatural wood-lots surrounded by an inhospitable desert matrix and within which vegetation is composed of three main layers: palm trees, fruit trees and herbaceous plants. This vegetation has produced a microclimate that contrasts sharply with the harsh climatic conditions of the desert environment (Riou 1990, Kassah 1996). This vegetation has favoured the establishment of

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some non desert-adapted Palearctic bird species, such as the Orphean Warbler *Sylvia hortensis*, Spotted Flycatcher *Muscicapa striata*, Blue Tit *Parus caeruleus*, Woodchat Shrike *Lanius senator*, Chaffinch *Fringilla coelebs*, European Serin *Serinus serinus* and Blackbird (Selmi 2000). In previous papers, we have suggested that dispersal and metapopulation processes have played a major role in shaping oasis breeding bird communities (Selmi *et al.* 2002, Selmi & Boulinier 2003a). Oases may have received bird colonizers from the forests of northern and central Tunisia, and the exchange of species between these seminatural habitat patches may have affected the present distribution and abundance of these non desert-adapted species (Selmi 2001). However, these processes have not been investigated at the level of individual species, and there is a need for detailed information on the ecological factors and processes affecting species' distribution and the abundance of local populations. Such information is essential in developing a conservation plan for the endangered biodiversity within this man-made system (Kassah 1996, Selmi & Boulinier 2003a). Here, we investigate this issue using data on the distribution and abundance of the Blackbird, a recent colonist in the oasis system. The Blackbird was restricted to northern and central Tunisia (Thomsen & Jacobsen 1979, Mayaud 1988) until the early 1990s when it became a resident breeder in some oases of southern Tunisia (Selmi 2000).

In this system we expected that the occurrence and abundance of non-desert species, such as the Blackbird, would depend on the habitat quality (i.e. vegetation structure) within oases. Moreover, given that the Blackbird has recently reached the oasis system, we expected that the probability of its occurrence in a given oasis would depend on its occurrence in neighbouring oases. That is, some oases may act as sources of colonizers to others, and the proximity to occupied oases may be an important predictor of occurrence probability, independently of local habitat conditions. To test these predictions, we investigated spatial autocorrelation in the observed occurrence and local abundance of this species, and we used regression models to assess the significance of vegetation structure and relative geographical location of oases in predicting the occurrence probability and abundance within local populations.

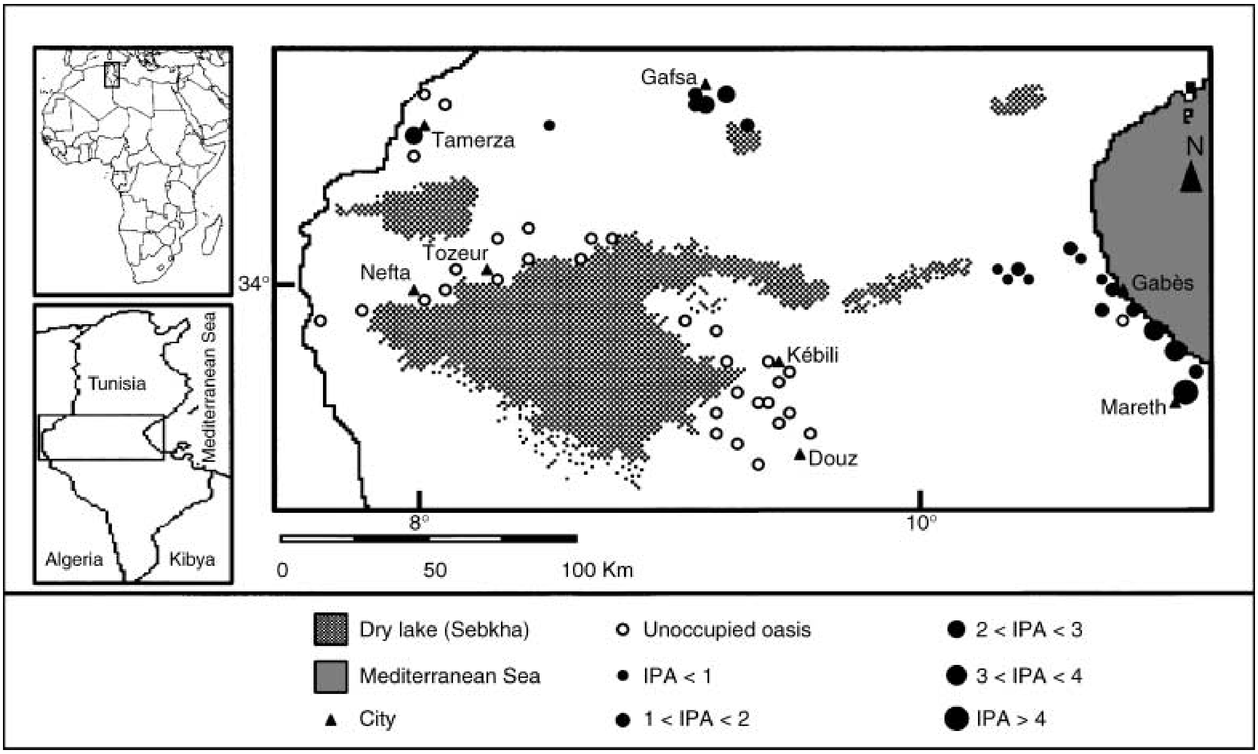

Figure 1. Map of southern Tunisia showing the geographical location of sampled oases with indication of Blackbird local abundance. IPA = abundance index.

METHODS

Data collection

Our work was carried out at 53 oases in southern Tunisia (Fig. 1). Oasis size ranges from 23 to 973 ha, and distance to the next nearest oasis varies from 1 to 31 km. From April to May 1999, the vegetation in each of these 53 oases was sampled by measuring seven vegetation variables in ten 400-m^2 quadrats (20 m × 20 m): density of palm trees (plants/400 m^2), cover of palm trees (%), total number of fruit tree species, density of fruit trees (plants/400 m^2), cover of fruit trees (%), total number of herbaceous plant species and cover of herbaceous plants (%). Squares were uniformly spaced along a line transect, with a between-square distance varying with oasis size: 100 m in large oases (> 100 ha) and 50 m in small ones (< 100 ha). The cover values for palm trees and fruit trees were measured directly in each quadrat. However, the cover of herbaceous plants was estimated visually. All estimations were conducted by the same observer (S.S.) in order to avoid observer bias (Prodon & Lebreton 1981).

Blackbird populations were surveyed during the breeding seasons of 1998 and 1999 using the 'IPA' method (Blondel *et al.* 1970, 1981). One IPA survey consists of performing two partial unlimited-distance counts of 20 min each at the same point, but at two different sampling periods in the breeding season. By according a score of 1 to each possible breeding pair detected (a singing male or an observed pair or family group), and a score of 0.5 to each recorded single individual (a bird seen or a call heard), and by retaining the highest sum of scores between the two partial counts, we obtained an abundance index of the species from each double count (Blondel *et al.* 1970, 1981). In order to use the results of this survey method for comparing the abundance of different local populations, we standardized count conditions. All counts were conducted by the same observer (S.S.), early in the morning (from 30 min after sunrise to 3 h after sunrise) and only under ideal meteorological conditions. Given the large number of sampled oases and the frequency of windy days on which counts could not be conducted, only one IPA survey (two partial counts) was carried out per oasis during the breeding season of 1998. In 1999, we conducted one IPA survey per oasis at 25 oases, but we were able to carry out five IPA surveys at five different points at each of 28 oases including all those where Blackbirds had previously been recorded. Points were carefully selected to be surrounded by a vegetation representative of the oasis habitat, including the three different layers characterizing the oasis habitat (palm trees, fruit trees and herbaceous vegetation). We used the mean of these five IPAs as an abundance index of the Blackbird. We are aware that any difference in the detectability of Blackbirds between oases may constitute a source of bias for the survey results (Farnsworth *et al.* 2002). However, in a related study we investigated species detectability in the subsample of 28 oases where counts were conducted on five points, and we found a high frequency of detection of Blackbirds at all oases where the species occurred (Selmi & Boulinier 2003b).

Data analyses

Given that the original vegetation variables were correlated, we first conducted a principal component analysis (PCA) to summarize the vegetation data into two independent factors. This analysis was carried out on the average value of each variable for each oasis.

We investigated spatial autocorrelation in our response variables (Blackbird presence/absence and local abundance) and explanatory variables (vegetation descriptors and oasis size) by using correlograms (Oden & Sokal 1986, Legendre & Fortin 1989). For each variable, we plotted a correlogram in which Moran's (1950) spatial autocorrelation coefficients were plotted on the ordinates against equidistant geographical distance classes between pairs of oases on the abscissa. In order to assess the significance of correlograms, we used the Bonferroni correction for multiple tests. These analyses were carried out using 'R' statistical package (Legendre & Vaudor 1991).

We used stepwise logistic regression to assess the relative strength of the association between Blackbird presence or absence and a set of four explanatory variables: vegetation descriptors (PC1 and PC2), oasis size and an autocorrelation term (called *Autocor*), which expresses the potential influence of occupation patterns in neighbouring oases. This autocorrelation term was calculated for each oasis using the method proposed by Augustin *et al.* (1996). For oasis 'i', the autocorrelation term is: $Autocor_i = \Sigma w_{ij} y_j / \Sigma w_{ij}$, where w_{ij} is the weight given to oasis 'j' calculated as the inverse of the geographical distance between oases 'i' and 'j' and y_j is the response in oasis 'j' (0 if the species is absent and 1 if it is present). For a given oasis, *Autocor* may take a value near 1 if the Blackbird occurs in all neighbouring oases and a value near 0 if the Blackbird occurs only in the more distant oases.

We first regressed the presence/absence of the Blackbird on vegetation descriptors and oasis size (log-transformed). The autocorrelation term was then added to the list of explanatory variables, and the analysis was rerun. This analysis was carried out using the LOGISTIC procedure of the SAS statistical package (SAS 1998), which also allowed us to compare the relative fit and predictive ability of the two models (with and without the autocorrelation term), using Akaike's Information Criterion (Burnham & Anderson 1998) and concordance scores (see also Bolger *et al.* 1997).

Variation in the abundance index (log-transformed) among local populations was analysed using a multiple regression to test for the effects of vegetation descriptors, oasis size (log-transformed) and the spatial autocorrelation term. As for the logistic regression, we first used a model without the autocorrelation term and then, in a second model, we added the autocorrelation term as a covariate. We then compared the fit of the two models to our data using Akaike's Information Criterion. For this analysis, we used the MIXED procedure of the SAS statistical package (SAS 1998).

RESULTS

The first two factors extracted from the PCA of the seven original vegetation variables accounted for 80% of the variance in the original data set (PC1: 50%; PC2: 30% of the variance of the original data set). PC1 was positively correlated with the density ($r = 0.9193$, $P < 0.001$), cover ($r = 0.8918$, $P < 0.001$) and number ($r = 0.8208$, $P < 0.001$) of fruit tree species, and with the cover ($r = 0.7120$, $P < 0.001$) and number ($r = 0.7433$, $P < 0.001$) of herbaceous plant species, but it was negatively correlated with palm tree cover ($r = -0.3550$, $P < 0.01$). This component can be interpreted as an axis of increasing diversity of the two lowest vegetation layers (fruit trees and herbaceous plants). PC2 was positively correlated with the density ($r = 0.9525$, $P < 0.001$) and cover ($r = 0.8844$, $P < 0.001$) of palm trees, but negatively correlated with the number of herbaceous plant species ($r = -0.3854$, $P < 0.01$). It mainly summarized the abundance of the palm tree layer. These vegetation descriptors, as well as oasis size did not show significant positive spatial autocorrelation at the first distance class (Fig. 2). This suggests that neighbouring oases are not more similar to one another in terms of habitat conditions than are more distant oases. Neighbouring oases do not necessarily provide similar habitat conditions for birds, and similarity in habitat conditions among oases does not depend on the distance separating them.

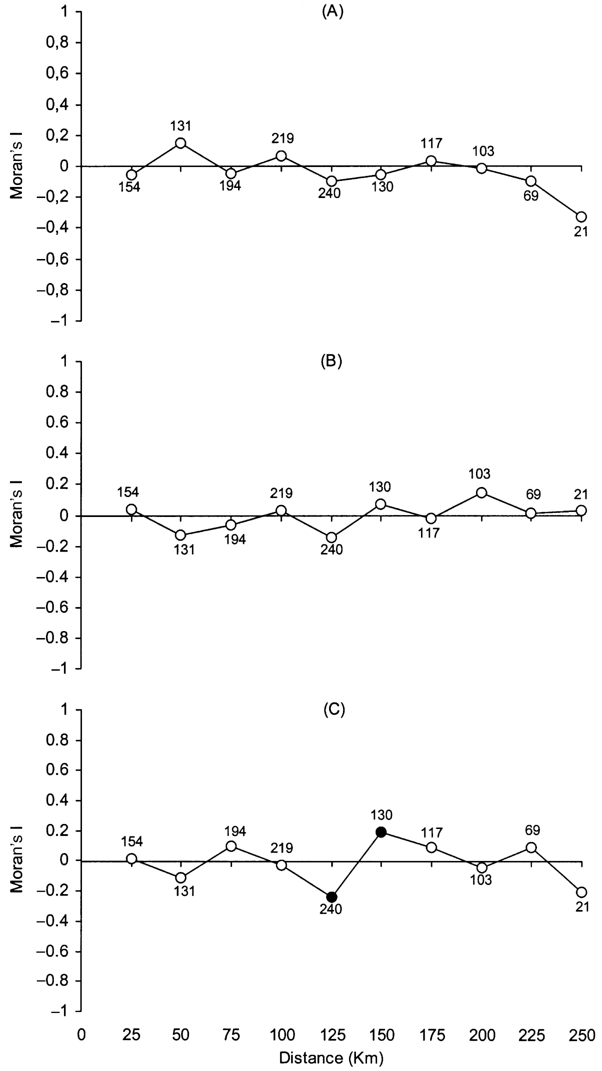

Figure 2. Correlograms of PC1 (a), PC2 (b) and oasis size (c) among the 53 sampled oases. Oases are grouped by ten equidistant classes. Values on correlogram points represent the frequencies of classes. Black symbols represent significant Moran's I values at the corrected Bonferroni level (0.05/10 = 0.005).

With regard to the Blackbird distribution, no difference was found between 1998 and 1999. In both years, Blackbirds were recorded in 21 oases, corresponding to an occupancy of 40% (Fig. 1). The correlogram of Blackbird occurrence in the oasis system was significant at the 0.05 level (Fig. 3), suggesting that local Blackbird populations are spatially dependent on each other. Of considerable importance is the highly significant positive autocorrelation for

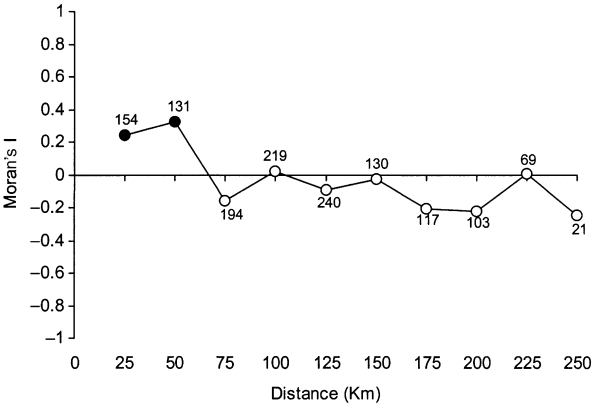

Figure 3. Correlogram of Blackbird presence/absence among the 53 sampled oases. Oases are grouped by ten equidistant classes. Values on correlogram points represent the frequencies of classes. Black symbols represent significant Moran's I values at the corrected Bonferroni level (0.05/10 = 0.005).

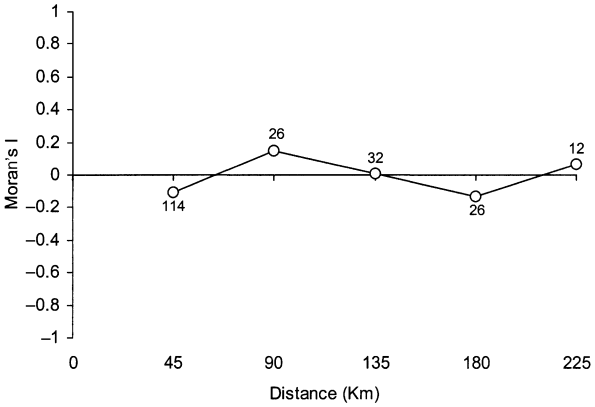

Figure 4. Correlogram of Blackbird abundance among the 21 occupied oases. Oases are grouped by ten equidistant classes. Values on correlogram points represent the frequencies of classes. No Moran's I value was significant at the corrected Bonferroni level (0.05/5 = 0.01).

low distances, which shows that the probability of Blackbird occurrence in a given oasis is related strongly to its presence in the closer neighbouring oases.

The results of the logistic regression analysis (Table 1) show that the model with the autocorrelation term was more appropriate for estimating the occurrence probability of the Blackbird than the model without the autocorrelation term. Indeed, incorporating information on the relative location of oases (autocorrelation term) as a covariate improved the fit of the model to the data, as the comparison of AIC values shows. Based on concordance scores, the association between the occurrence probabilities predicted by the model and the observed occurrence was improved by 15% when the spatial autocorrelation in Blackbird presence was taken into account. These results also suggest that the probability of Blackbird occurrence in a given oasis was principally related to its occurrence in the neighbouring oases, which is consistent with the results of the spatial autocorrelation analysis. Oasis size was not found to have a significant effect, whereas the diversity of fruit trees and herbaceous plants (PC1) and the abundance of palm trees (PC2) were both at the margin of significance (Table 1).

With regard to the local abundance of Blackbirds in the 21 oases where they occurred, we found that the mean abundance index varied between 0.4 and 5.8. The results of spatial autocorrelation analysis show that local abundance was not autocorrelated (Fig. 4), suggesting that oases close to each other

Table 1. Summary of the results of stepwise logistic regression of presence/absence of Blackbird in the oasis system (n = 53 oases) on vegetation descriptors (PC1 and PC2) and oasis size (log-transformed), using a model without an autocorrelation term and a model with an autocorrelation term (*Autocor*). AIC = Akaike's Information Criterion (smallest AIC is better).

	AIC	First variable entered	Second variable entered	Third variable entered	Concordance (%)
Model without an autocorrelation term:	53.396	PC1	–	–	84.4
Estimate ± se		−2.0681 ± 0.6573	–	–	
Score χ^2		16.8272	–	–	
P		0.0001	–	–	
Model with an autocorrelation term (*Autocor*):	26.864	Autocor	PC1	PC2	97.2
Estimate ± se		−12.2825 ± 4.0795	−3.0678 ± 1.7238	−1.2588 ± 0.8596	
Score χ^2		38.4620	2.9399	2.4593	
P		0.0001	0.0864	0.1168	

Table 2. Results of regression analyses of local abundance index (log-transformed) of Blackbirds in the 21 oases in which they occur on vegetation descriptors (PC1 and PC2) and oasis size (log-transformed), using a model without an autocorrelation term and a model with an autocorrelation term of species occurrence (*Autocor*). AIC = Akaike's Information Criterion (smallest AIC is better).

	AIC	*df*	Estimate (± se)	Type III *F*	*P*
Model without an autocorrelation term:	39.0783				
Oasis size		17	0.0863 (± 0.1252)	0.48	0.4997
PC1		17	0.8211 (± 0.2965)	7.67	0.0131
PC2		17	0.0205 (± 0.1439)	0.02	0.8883
Model with an autocorrelation term (*Autocor*):	37.2248				
Oasis size		17	0.0938 (± 0.1309)	0.51	0.4840
PC1		17	0.7932 (± 0.3178)	6.23	0.0239
PC2		17	0.0060 (± 0.1613)	0.00	0.9971
Autocor		17	–0.3001 (± 0.9730)	0.10	0.7617

may support different-sized Blackbird populations. The results of the multiple regression analysis of Blackbird local abundance on vegetation descriptors and oasis size suggest that taking into account the relative location of oases by adding the autocorrelation term of Blackbird occurrence (*Autocor*) to the list of explanatory variables did not improve the fit of the regression model to data. AIC values for both models (with and without autocorrelation term) were not very different (Table 2). Local abundance was primarily associated with the diversity of fruit tree and herbaceous plant layers (PC1), whereas no significant effect was found for oasis size, abundance of palm trees (PC2) and the relative location of oases. This suggests that local habitat conditions within occupied oases were more likely to determine the local abundance of Blackbirds than was the proximity to a possible source of colonizers. This may explain the absence of autocorrelation in local abundance (Fig. 4).

DISCUSSION

The distribution of Blackbirds in southern Tunisian oases was found to exhibit significant spatial autocorrelation. Blackbirds occupy oases close to each other, and the probability of occurrence of this species in a given oasis is strongly related to its presence in the nearest neighbouring oases. Interestingly, this pattern does not seem to be a direct consequence of an autocorrelation in oasis characteristics. Indeed, climatic conditions are relatively homogeneous among oasis zones in southern Tunisia, in that all oases receive an average annual rainfall of less than 200 mm, with an average annual temperature ranging between 19.2 and 20.9 °C (Henia 1993, Kassah 1996). Moreover, no significant autocorrelation was found for oasis size, nor for vegetation structure, which we expected to be major factors affecting occurrence probability of this non desert-adapted species. This finding is consistent with the results of the logistic regression of Blackbird presence/absence. Indeed, the proximity to occupied oases, which can be considered as possible sources of colonizers, was the most relevant predictor of Blackbird occurrence probability, whereas oasis size and vegetation structure were not significant. However, within occupied oases Blackbird abundance was strongly related to vegetation structure, namely to the abundance and diversity of the two lowest vegetation layers (fruit trees and herbaceous plants). The distance to occupied oases was not a good predictor of local abundance, which is also shown by the non-significant spatial autocorrelation for local abundance.

Our work shows that the distribution and abundance of Blackbirds in the oases of southern Tunisia are influenced by processes acting at two different spatial scales. At the local scale, the density and diversity of the two lowest vegetation layers (fruit trees and herbaceous plants) affect the abundance of established local populations. This relationship was expected as herbs and grasses affect the food supply directly for this species, which feeds predominantly on invertebrates during the breeding season (Greenwood & Harvey 1978, Snow & Perrins 1998). Moreover, Blackbirds require small trees and bushes with relatively dense vegetation for nesting (Hatchwell *et al.* 1996, Snow & Perrins 1998). In this context, it should be noted that all Blackbird nests we found in the occupied oases were on the branches of fruit trees, mainly on Olive *Olea europea* and Pomegranate *Punica granatum* trees, between 1.20 and 3.85 m from the ground. Our observations also suggest that breeding territory selection is based on fruit tree density, herbaceous plant cover, but also on the existence of at least one palm tree (generally exceeding 5 m in height) that males use as a perch for singing and territory guarding.

In southern Tunisian oases, trees are likely to play an important role for non desert-adapted species, such as the Blackbird, as they maintain the climatic contrast between the oasis interior and the desert environment: the 'oasis effect' (Riou 1990). Indeed, tree cover may reduce wind intensity and retain higher humidity and lower temperatures within oases compared with the surrounding desert. However, small local Blackbird populations were found in some oases where local conditions (diversity and cover of fruit trees and herbaceous plants) seemed unsuitable. Furthermore, many potentially suitable oases did not support local Blackbird populations. These observations were supported by the results of the logistic regression of presence/absence, which suggested that the probability of Blackbird presence in a given oasis did not depend on vegetation structure but instead on the proximity of occupied oases. This could also be interpreted as evidence of the occurrence of 'suitable but empty habitat patches' for Blackbirds in the oasis system, and suggests that colonization from nearby occupied suitable oases (possible sources) may have increased the probability of establishment of a local population at a given oasis, regardless of the habitat conditions. It is well known that this species is a short-distance colonizer (Greenwood & Harvey 1976, 1982, Paradis *et al.* 1998), and this supports our argument. Thus, the distribution of Blackbirds in Tunisian oases appears to be the expression of landscape-scale processes, rather than of local-scale processes. Dispersal and the exchange of individuals between nearby oases (probably in a source-sink manner) are likely to play a major role in shaping future occupancy and abundance patterns of the Blackbird at southern Tunisia oases. A long-term study of the local dynamics, dispersal and genetic structure would tell us more about the origin and regional survival of the Blackbird in this area at the margin of its geographical range. For instance, we might determine whether oases act as sources or sinks for such species.

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