DOES NEST PREDATION AFFECT NEST-SITE SELECTION IN LARKS?

Miguel YANES and Juan J. OÑATE

INTRODUCTION

Nest predation is one of the main factors determining avian reproductive strategies (Lack, 1968; Ricklefs, 1969). One adaptive response to it is nest-site selection as slight differences in the area around the nest may result in different nest predation rates. Such is the case with, for example, habitat structure around the nest (Martin & Roper, 1988; Clark & Nudds, 1991; Li & Martin, 1991; Mankin & Warner, 1992; Riley et al., 1992) or distance to the ecosystem edge (Rodenhoushe & Best, 1983; Small & Hunter, 1988).

Ground nesting birds experience high nest predation, especially those that breed in shrub and grassland habitats (Martin, 1993; Yanes & Suárez, 1995). In holarctic shrubsteppe, nest predation rates reach values of over 60%, although they vary a lot with area and year (Rotenberry & Wiens, 1989; Suárez & Manrique, 1992). Changes in management may even increase rates to values around 90% (Suárez et al., 1993). In this paper we analyze the effect of predation on lark’s nest habitat selection, in an area of very high nest predation, in order to test the hypothesis that nest predation is a selective pressure shaping nest-site selection in order to reduce nest predation risk.

STUDY AREA AND METHODS

STUDY AREA

The study was carried out in the Ornithological Reserve of «Las Amoladeras», Almería, SE Spain (36°50’ N, 2°25’ W, 0-50 m asl); a 850 hectare shrubsteppe with a semi-arid Mediterranean climate (mean annual rainfall of 250-300 mm). Most of it is a plain with thin vegetation consisting of chamephytes such as Teucrium belion, Helichrysum stoechas, Thymelaea hirsuta and Haloxylon articulatum, and, to a lesser degree, grasses as Stipa tenacissima and Ammophila arenaria. However, there is also an extensive abandoned Agave spp. plantation and stands of a larger bush called «Azufaifo» Ziziphus lotus grow locally.


The reserve is partially bordered by two large « ramblas » (dry rivers) and crossed by other smaller ones. These ramblas, Agave plantations and azufaifo stands contain all the fox dens in the study area (Yanes et al., in press). Red Foxes *Vulpes vulpes*, together with feral Dogs *Canis familiaris*, are the main nest predators in the study area (Yanes & Suárez, in press). Others are Bastard Snake *Malpolon monspessulanus*, Horseshoe Snake *Coluber hippocrepis*, Ladder Snake *Elaphe scalaris*, Eyed Lizard *Lacerta lepida*, Hedgehog *Erinaceus europaeus* and Great Grey Shrike *Lanius excubitor*.

The bird community is very poor in species, larks being the dominant ones (Tellería et al., 1988). Thekla Lark *Galerida theklae* and Lesser Short-toed Lark *Calandrella rufescens* are the only species that are relatively numerous. Their high nest predation rates do not appear to be affected by researcher visits (Westmoreland & Best, 1985; Major, 1990), because i) in other years no relationship was observed between monitoring frequency and nest predation (Suárez & Manrique, 1992), and ii) no differences were noted in a series of experiments with artificial nests monitored daily and unmonitored ones (Suárez et al., 1993).

**NEST-SITE HABITAT MEASUREMENTS**

Habitat features of 150 nests were measured (75 of Thekla Lark, 75 of Lesser Short-toed Lark) and 75 random sites. For each species 60 nests were predated and 15 successful. The nests were found using random field itineraries and visual observation of adult behaviour over three years (1992-94). The random points were taken in the same years, at 60 m intervals along random linear tracks.

Habitat characteristics were estimated in a circle centred on the nest or the random point during the nesting periods. Two circle sizes were considered: a small 1.5 m radius one, in the immediate vicinity of the nest, and a large 15 m radius territorial one. Using the method proposed by Prodon (1976), we estimated on both scales the overall area covered by: shrubs < 20 cm high (variable S20 on small scale and L20 on large scale), between 20-40 cm (S24 and L24), > 40 cm (S40 and L40), grasses (SGR and LGR), open ground (SBG and LBG) and rock (SRO and LRO). The chosen height of the shrubs for the variables corresponds to the most frequent sizes in the area. On the large scale we also considered two other variables: distance to a « clearing » of bare ground or rocky substrate of over 6 m² (CLE) and the distance to the shrubsteppe edge (EDG). Edge was taken to mean the boundary of the ramblas, the Agave plantations and the high azufaifo stands.

**STATISTICAL ANALYSES**

To summarize habitat characteristics, the variables were reduced to two orthogonal axes using principal component analysis (PCA). Two series of PCAs were carried out to discover the possible existence of (i) nest-site habitat selection and (ii) habitat differences in successful and predated nests. First two PCAs, one on each scale, small and large, including all nests (both successful and predated) of both species and random points were carried out. Secondly, another two PCAs for each species, one on each scale but differentiating successful and predated nests, were carried out. The differences in the principal component scores between these groups were analyzed using an analysis of variance (ANOVA). To compare the scores of the two species one with another and of one with the random sites,
a Tukey HSD multiple comparison was carried out. The variables were transformed prior to the PCA: the arcsine transformation was used for variables expressed as percentages, and the logarithmic transformation was applied to the remaining ones.

Moreover, we made individual comparisons of the untransformed habitat variables for species vs random sites and for successful vs predated nests, using the Mann-Whitney U test. The SYSTAT statistical package was used for all statistical analyses (Systat, 1992).

RESULTS

NEST-SITE SELECTION

The first small scale PCA axis orders the nests and random points along a gradient from places dominated by herbs to areas covered mostly with rock and low shrubs. The PCA scores for the nests and random points on this axis differ according to group (ANOVA, F ratio = 7.377; p < 0.01); there are significant differences between Lesser Short-toed Lark nests and random sites, but there are no differences between species neither between random sites and Thekla Lark nests, although in this last case the probability is near to significance level (Table 1).

The second axis orders the vegetation along a complexity gradient from areas with high shrubs to areas with more bare ground. In this case also the differences are significant (F ratio = 7.107; p < 0.01), due to the segregation of the nests of the different species and of Lesser Short-toed Lark compared with the controls (Table 1). These first two axes together accounted for 53.3 % (30.6 and 22.7 %, respectively) of the variance of the original six variables.

| TABLE I |

**Probability values of the differences between PCA scores according to the Tukey HSD multiple comparison.**

<table>
<thead>
<tr>
<th></th>
<th>Thekla Lark vs L. Short-toed Lark</th>
<th>Thekla Lark vs Random sites</th>
<th>L. Short-toed Lark vs Random sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small scale</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Axis I</td>
<td>0.240</td>
<td>0.069</td>
<td>0.000</td>
</tr>
<tr>
<td>Axis II</td>
<td>0.001</td>
<td>0.779</td>
<td>0.011</td>
</tr>
<tr>
<td>Large scale</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Axis I</td>
<td>0.556</td>
<td>0.809</td>
<td>0.005</td>
</tr>
<tr>
<td>Axis II</td>
<td>0.000</td>
<td>0.017</td>
<td>0.001</td>
</tr>
</tbody>
</table>

The configuration of the large scale PCA axes is similar to that of the previous ones. On the first axis the variables of greatest weight are the low matorral and least distance to the clearing in relation to pasture cover. However, there are no
Figure 1. — Ordering on both scales according to the PCA scores for the nests of the two larks and random points. Circles: Thekla Lark; Squares: Lesser Short-toed Lark; Points: Random sites.
differences between groups (F ratio = 1.395; p > 0.05), whether they are nests or random points (Tab. I). The second axis ranks the points from areas covered in matorral of medium or large size to those with a greater area of open land. Unlike the first there are important differences between groups (F ratio = 27.289; p < 0.01); not only are the species clearly separated one from another but also from the random sites (Table I). The variance accounted for by the two axes of the eight initial variables is 51.8% (28.1 and 23.7%, respectively). The arrangement of both species' nests and random points in the space formed by PCA axes, for the small scale as for the large one, is shown in shown in Figure 1.

Considering the variables individually, Lesser Short-toed Lark is the species showing the most marked nest-site selection: all the variables on the small scale and over half on the large scale differ significantly from the random sites (Table II). Thekla Lark is the most eclectic when choosing a nest-site, tending to select only sites far from the shrubsteppe edge, with greater rock cover in the immediate vicinity of the nest and with few high shrubs on both scales (Table II). The greatest differences between species occur on the large scale (Table II).

### TABLE II

Mean ± sd of considered habitat variables in random sites and nests. All variables are expressed as percentages, with the exception of CLE and EDG which are expressed by meters. Only significant differences according to the Mann-Whitney U test are indicated. a: Thekla Lark vs Lesser Short-toed Lark; b: Thekla lark vs random; c: Lesser Short-toed Lark vs random. *= p < 0.05; **= p < 0.01.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Random (n = 75)</th>
<th>Thekla Lark (n = 75)</th>
<th>L. Short-toed Lark (n = 75)</th>
<th>Signif. differences</th>
</tr>
</thead>
<tbody>
<tr>
<td>S20</td>
<td>8.5 ± 10.2</td>
<td>10.4 ± 9.1</td>
<td>9.6 ± 7.0</td>
<td>b*, c**</td>
</tr>
<tr>
<td>S24</td>
<td>7.1 ± 10.2</td>
<td>6.5 ± 7.0</td>
<td>3.1 ± 4.9</td>
<td>a**, c*</td>
</tr>
<tr>
<td>S40</td>
<td>4.1 ± 10.4</td>
<td>1.1 ± 3.2</td>
<td>0.5 ± 1.9</td>
<td>b**, c***</td>
</tr>
<tr>
<td>SGR</td>
<td>20.9 ± 21.4</td>
<td>19.8 ± 20.9</td>
<td>13.2 ± 14.8</td>
<td>c</td>
</tr>
<tr>
<td>SBG</td>
<td>44.5 ± 21.1</td>
<td>41.3 ± 17.8</td>
<td>52.1 ± 16.5</td>
<td>a**, c*</td>
</tr>
<tr>
<td>SRO</td>
<td>14.8 ± 18.0</td>
<td>20.6 ± 19.5</td>
<td>20.2 ± 16.2</td>
<td>b*, c**</td>
</tr>
<tr>
<td>L20</td>
<td>10.1 ± 7.0</td>
<td>8.7 ± 6.0</td>
<td>9.9 ± 5.5</td>
<td>a**</td>
</tr>
<tr>
<td>L24</td>
<td>9.3 ± 6.5</td>
<td>10.0 ± 5.6</td>
<td>7.6 ± 5.6</td>
<td>a**</td>
</tr>
<tr>
<td>L40</td>
<td>8.2 ± 7.6</td>
<td>5.2 ± 5.3</td>
<td>3.0 ± 3.7</td>
<td>a*, b**, c**</td>
</tr>
<tr>
<td>LGR</td>
<td>22.7 ± 19.5</td>
<td>20.3 ± 16.8</td>
<td>14.3 ± 14.0</td>
<td>a*, c**</td>
</tr>
<tr>
<td>LBG</td>
<td>34.6 ± 16.5</td>
<td>36.5 ± 13.6</td>
<td>42.7 ± 11.9</td>
<td>a**, c***</td>
</tr>
<tr>
<td>LRO</td>
<td>15.3 ± 13.7</td>
<td>20.0 ± 16.6</td>
<td>22.4 ± 13.5</td>
<td>c**</td>
</tr>
<tr>
<td>CLE</td>
<td>4.3 ± 9.3</td>
<td>4.5 ± 5.5</td>
<td>5.4 ± 10.6</td>
<td>a**, b*, c**</td>
</tr>
<tr>
<td>EDG</td>
<td>108.3 ± 117.0</td>
<td>140.1 ± 121.1</td>
<td>224.7 ± 172.7</td>
<td>a**, b*, c**</td>
</tr>
</tbody>
</table>

**SUCCESSFUL VS PREDATED NESTS**

The results obtained in the PCAs for the two species and scales indicate that there are no differences between predated and successful nests. In Thekla Lark, the scores for both types of nests did not differ one from the other, neither on the small scale (F ratio = 0.027 and 0.010, I and II axes, respectively; p < 0.05; 53.9 %
incorporated variance) nor on the large scale (F ratio = 0.001 and 0.397; p < 0.05; 51.2%). In Lesser Short-toed Lark the results are very similar, there not being any differences on the small scale (F ratio = 0.002 and 0.079, I and II axes, respectively; p < 0.05; 54.4% incorporated variance) or large scale (F ratio = 0.620 and 0.110; p < 0.05; 49.1%).

Neither are there differences in the habitat nest-site variables of predated or successful nests in both species. In Thekla Lark none of the variables showed significant differences in predated or successful nests, and in Lesser Short-toed Lark only the distance to "clearing" was significantly greater in predated nests (Table III). This difference is contrary to what is in theory expected for more exposed nests (Martin & Roper, 1988; Riley et al., 1992) and may be due to a stochastic effect: out of 24 variables, 12 of each species, it is easy for one of them to be different in the sample despite not being so in the population.

**Discussion**

Both lark species have clear preferences in nest-site habitat characteristics. They are more pronounced in the case of the Lesser Short-toed Lark, which only lives in arid and semi-arid areas (Cramp, 1988). The Thekla Lark, on the other hand has a wider habitat choice that even includes wooded areas, thus revealing a greater flexibility in nest-site selection. However, due to the evolutionary pressure of nest predation, both species can be expected to show a common tendency to nest
in safe sites. They thus share common features in nest-site selection, which are linked to factors that determine nest predation. On the one hand, they tend to avoid both large and small areas of tall scrub, as well as the proximities of shrubsteppe boundaries. On the other hand, both select areas with more rock and low scrub in the immediate vicinity of the nest.

Tall shrubs are used by the Great Grey Shrike as look-out perches, while Red Foxes, dogs, Eyed Lizards and snakes are often more abundant in dry river beds and stands of Yucca, which they use as refuges. The proximity of visually oriented predator perches (Erikstad, 1982) and the border of the ecosystem (Rodenhouse & Best, 1983) may increase ground nest predation. Both species thus seem to select sites with an apparently lower risk of nest predation.

The two lark species in this study are capable of producing 3 or more clutches in one breeding season, with which they increase their probability of offspring survival. Moreover, lifetime reproductive success in birds depends fundamentally on lifespan (e.g. Newton, 1989). For these reasons, nest loss is not as disastrous as the death of the incubating female (Rands, 1989; Magnhagen, 1991; Schieck & Hannon, 1993). From this perspective, both species’ small-scale preference for areas with more rock and low shrub cover can be understood. Open rocky areas increase the female’s field of vision from the nest, and low shrub, apart from helping to conceal the nest, does not block the female’s escape should a predator appear. In fact, out of a total of 297 predated nests found during the course of a more extensive study on the reproductive ecology of these species, only three females had been caught: two Lesser Short-toed Larks (1.5% of predated nests of the species), and one Thekla Lark (0.6%, Yanes, unpublished).

The existence of certain characteristics of the area around the nest that affect the nest predation risk has been proven for other birds (Martin & Roper, 1988; Li & Martin, 1991; Riley et al., 1992). We did not, however, find differences in habitat characteristics between successful and predated nests of either of these larks (see also Schieck & Hannon, 1993).

The main lark nest predator in the study area was the Red Fox. The fox density in the area is high, between 0.6 and 1.0 dens with young/km² depending on the year (Yanes et al., in press). Paradoxically, bird predation rates in this Bird Reserve are extremely high—beyond the level of population stability (Yanes & Suárez, in press). This might well be hindering the discernment of current hypothetical effects of the habitat characteristics on nest predation rates. Local considerations aside, however, the selective pressure of nest predation on the larks has been high in evolutionary time, as they are ground nesting species in predominantly shrubsteppe environments (Yanes & Suárez, 1995). Under this high predation regime, locations that facilitate nest predation and especially the capture of the incubating female, are counter-adaptive. They have thus probably been eliminated evolutively, or at least highly attenuated in the population. Under these conditions, it is logical that differences cannot be found now between the habitat characteristics of successful and predated nests of both larks. Subsequent studies in other localities and lark species should confirm this pattern.

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**SUMMARY**

Nest-site selection may affect nest predation rates. In this paper we analyse nest-site habitat selection in the Thekla and Lesser Short-toed larks, and compare the habitats of successful and predated nests. Both species have a preference for safe sites. At present, however, there are not habitat differences between successful and predated nests. This is probably because nest predation has acted as an extremely high selective pressure on ground nesting steppe birds. We may thus assume that nest placements which facilitate predation must have been eliminated by this pressure in evolutive time.

**RÉSUMÉ**

Le choix de l’emplacement du nid peut influencer le taux de prédation des nids. Dans ce travail on analyse la sélection par l’Alouette pispolette *Calandrella rufescens* et le Cochevis de Thékla *Galerida theklae* de l’habitat dans lequel ces espèces placent leurs nids, et on compare l’habitat des nids selon qu’ils ont ou non été couronnés de succès. Pour les deux espèces il existe une sélection en faveur des sites les plus sûrs. Néanmoins, il n’y a aucune différence dans l’habitat des nids pillés ou non. Cela est probablement dû à ce que la prédation des nids a provoqué une pression sélective très forte pour les oiseaux de steppe nichant au sol. Les emplacements qui faciliteraient la prédation du nid ont été éliminés par cette pression en temps évolutif.

**REFERENCES**


