NEST-SITE SELECTION AND NESTING SUCCESS OF LITTLE OWLS (*ATHENE NOCTUA*) IN MEDITERRANEAN WOODLAND AND OPEN HABITATS

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ABSTRACT.—We studied nest-site selection by Little Owls (*Athene noctua*) in two Mediterranean habitats, a holm oak (*Quercus rotundifolia*) woodland (36 nests during 1997–99) and a steppe-like area (37 nests during 1997–99), in southern Portugal, by comparing macrohabitat and microhabitat characteristics of used nests to those of randomly-selected nest sites. In the woodland area, predator presence seemed to be the main factor that influenced nest-site selection by owls. In the steppe area, a large number of alternative cavities around a nest appeared as the most important variable associated with nest-site selection. At this site, size of stones in stone piles also seemed to influence nest-site selection; owls nested in piles with larger than average stones. We also found tree girth was positively associated with nesting success in the woodland area. Larger trees held more complex cavities that may have improved the ability of adults and offspring in escaping from predators. Other variables, such as distance to human habitations and the orientation of nest-site entrance might have influenced nesting success as well. Predation risk and the internal features of nest cavities were the most likely factors affecting nest-site selection and nesting success of Little Owls in Mediterranean habitats.

KEY WORDS: *Little Owl; Athene noctua; habitat selection; Mediterranean region; predation risk; reproductive success.*

SELECCIÓN DE SITIO-NIDO Y ÉXITO EN LA ANIDACIÓN DE LOS MOCHUELOS (*ATHENE NOCTUA*) EN BOSQUES Y HABITATS ABIERTOS DEL MEDITERRÁNEO

RESUMEN.—Estudiamos la selección de sitios nido para los Mochuelos (*Athene noctua*) en dos hábitats del Mediterráneo, un bosque de roble acebo (*Quercus rotundifolia*), con 36 nidos durante 1997–99, y un área de características esteparias (37 nidos durante 1997–99) en el sur de Portugal, para comparando las características de macro y micro hábitat entre nidos y puntos seleccionados aleatoreamente. En el área boscosa, la presencia de depredadores parece ser el principal factor que influyó en la selección de sitios nido por parte de los búhos. En el área de estepa, un gran numero de cavidades alternativas alrededor del nido parece ser la variable mas importante asociada con la selección del sitio-nido. En esta área, el tamaño de las rocas en la pila de piedras parece influenciar la selección de los sitios nido: los búhos anidaron en pilas con piedras mas grandes que el promedio. En el área boscosa, encontramos una relacíon positiva entre el diámetro del tronco, y el éxito en la anidación. Los árboles más grandes proveen mayor complejidad que puede haber mejorado la habilidad de los adultos y su prole para escapar de los depredadores. Otras variables, tales como la distancia a las habitaciones humanas y la orientación de la entrada de los sitios nido pudieron igualmente haber influenciado el éxito en la anidación. Los riesgos de depredación y las características internas de las cavidades de los nidos probablemente fueron los factores que más afectaron la selección de sitios nido y el éxito en la anidación de los Mochuelos en los hábitats del Mediterráneo.

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Nest-site selection is a key component of habitat selection by birds (Hildén 1965), with important consequences for survival and reproduction of individuals (Cody 1985). Nest predation is a major cause of reproductive loss in birds and is often considered as a strong selective force in the evolution of nesting and dispersal strategies (e.g., Newton 1979, Martin 1992, 1995, Hakkarainen et al. 2001). To reduce the risk of nest predation and losses due to adverse weather, birds have adopted strategies such as cavity nesting (e.g., von Haartman 1957). Consequently, cavity nesters often have higher breeding success than open-nesting species (e.g., Lack 1954, Nice 1957, Peterson and Gauthier 1985, Korpimäki 1987).

Nevertheless, high nest predation rates have also been recorded in some hole-nesting species (e.g., Flegg and Cox 1975, Dunn 1977, Eriksson 1979, Sonerud 1985b), and thus additional tactics to minimize nest predation and increase offspring production might be expected to influence nest-site selection of cavity-nesting birds. Nest-site variables, such as cavity dimensions, volume, height, and depth might be important (e.g., Stauffer and Best 1982, Van Balen et al. 1982, Peterson and Gauthier 1985, Belthoff and Ritchison 1990) and influence reproductive success (e.g., Karlsson and Nilsson 1977, Nilsson 1984, Korpimäki 1985, Rendell and Robertson 1989, Valkama and Korpimäki 1999). Microhabitat variables, such as tree species and density (Swallow et al. 1986) or the vegetation surrounding the cavity (McCallum and Gehlbach 1988, Valkama et al. 1995, Valkama and Korpimäki 1999) may also affect nest-site selection.

The Little Owl (*Athene noctua*) is a small owl mainly associated with farmland and open woodland habitats, where it breeds mostly in holes in trees, but it also uses cavities in stone piles and buildings, or even holes in the ground (Schönn et al. 1991, Génot and Van Nieuwenhuyse 2002). Over the last decades, Little Owl populations have declined severely throughout most of Europe, and the species is now listed as a "SPEC 3" species (i.e., a species whose global populations are not concentrated in Europe, but which have an unfavourable conservation status in Europe; Tucker and Heath 1994). This decrease has been caused by habitat changes due to intensification of agriculture, including elimination of nest sites, a decrease in prey abundance, and detrimental effects of pesticides on breeding success (Schönn et al. 1991, Exo 1992,

Tucker and Heath 1994, Génot and Van Nieuwenhuyse 2002).

Although several studies have described nest sites used by Little Owls, very few authors paid attention to nest-site selection strategies (Génot and Van Nieuwenhuyse 2002), particularly in steppe-like habitats. To our knowledge, only Juillard et al. (1992) and Centili (2001) reported on nest characteristics in steppe habitats, but they did not compare used nest-sites with available cavities, and thus provided no information on nest-site selection.

In western and central European farmland, where mechanization and intensification of agriculture has led to the scarcity of nest-sites, erection of nest-boxes has been adopted successfully to increase or maintain local populations of Little Owls (Kneule and Michels 1994, Bultot et al. 2001). However, in Mediterranean habitats of southern Europe, where the species is still relatively abundant, habitat features, and particularly nest sites, may be managed adequately for conservation. Therefore, our aim was to investigate features linked to nest-site selection by Little Owls in two different types of Mediterranean habitat. With this study, we collected data to develop management guidelines for the conservation of Little Owls. Furthermore, because individuals should prefer nest-site features that increase reproductive success (Alatalo et al. 1984, Leonard and Picman 1987, Milks and Picman 1994), we also examined relationships between nest-site variables and nesting success of owls.

METHODS

Study Areas. The study was conducted in two areas located approximately 22 km apart, in the Baixo Alentejo province, Southern Portugal: Cabeça da Serra (37°37'N, 8°09'W) and S. Marcos da Atabueira (37°42'N, 7°50'W) Cabeça da Serra comprised 5.6 km² of very open old holm oak (*Quercus rotundifolia*) woodland. The area is used as pasture for cattle or cereal cultivation and a small part is covered by a young plantation of stone pine (*Pinus pinea*). The density of Little Owls in this area is very high, with ca. 7 pairs/km² (R. Tomé unpubl. data). S. Marcos da Atabueira is a steppe-like area of 15.7 km² and is also used for cattle pasture and cereal cultivation. Trees are absent, with the exception of a small (<0.3 km²) plantation of blue gum (*Eucalyptus globulus*). Most of the area is managed for nature conservation. Little Owl population is less dense than in Cabeça da Serra, with ca. 2.3 pairs/km² (R. Tomé unpubl. data).

Nest-sites and Random Cavities. We searched for nests of Little Owls during the breeding seasons of 1997–99 Nest sites were mainly located by following male owls taking prey to incubating or brooding females, or young. In other cases, we detected nests by checking cavities in

places where adult birds were often observed. We measured several features of each nest site, including characteristics of the surrounding habitat. Depending on whether the nest was located in a tree or in a stone pile, the two main nesting environments for Little Owls in the study areas, we identified the tree species and measured its diameter at 1.40 m (diameter at breast height, DBH), tree height, and stone pile height, length, and width. Type of stone pile ("tower," "collapsing tower," "wall," hide for hunters, simple aggregation of stones, collapsed pile, and pile partially buried on the ground) and stability (two classes: stable, if the pile could support a person without threatening collapse; unstable, if it could not) were also classified. Mean dimensions (long and short diameters) of stones composing stone piles were determined by measuring ten stones. For nest-site entrances, we measured height (distance to the ground), long and short diameters, inclination (in degrees, corresponding 0° to a horizontal entrance and 90° to a vertical one) and orientation. For nests in trees, coverage (percent of the entrance covered by leaves or branches when viewed from 10 m, from the direction of the entrance) and site (trunk, base of branch, branch) in the tree were determined. For nest sites with more than one entrance hole, we measured the hole most often used (in all cases only one entrance hole was observed to be used). We also checked for the existence of alternative entrance holes to the same nest and for the presence of potential predator sign (e.g., feces of mustelids, foxes, rats or jewelled lizards [*Lacerta lepida*]).

We measured additional features within a 100-m radius of the nest site. We recorded the number and type of available perches and the number and type of available nesting cavities. We considered as perches any structure with a minimum height of 50 cm, because owls often hunted from perches this low. Each tree or stone pile was considered as one perch, irrespective of the number of possible individual perch sites (for instance, branches) it contained. Potential nesting cavities were defined as having a minimum depth of 50 cm and dimensions that appeared large enough for Little Owls (i.e., an opening greater than 8 cm in diameter; see also Juillard 1980, Exo 1981, Génot 1990, and Belthoff and Ritchison 1990 for the Eastern Screech Owl [*Otus asio*]). A tree or stone pile with at least one suitable cavity was considered as one available nesting site even if it had additional cavities. Other habitat features that were recorded included type of habitat and distance from the nest to the nearest road, pathway, human habitation, reservoir, and permanent stream. Distance measurements were made with the help of aerial photographs (1:15 000). Sample sizes of the variables were not equal, because it was impossible to measure all characteristics of some nests (for example, we could not be sure about the nest entrance in stone piles in some cases).

In the woodland area, 36 nests were found in 26 territories during the study period. Three different nests were used in one territory and two different nests were used in seven territories. In the steppe area, 37 nests were found in 30 territories. Two different nests were used in seven territories throughout the study. As in some other studies (e.g., Belthoff and Ritchison 1990, Sedgwick and Knopf 1990), we included all the different nests found,

because at least one of the parent owls changed in most of the territories during the study period (R. Tomé unpubl. data).

We selected 22 locations randomly for each study area and plotted these on a map with a numbered grid (e.g., Titus and Mosher 1981). Once random points were located in the field, the nearest available nesting cavity (same criteria as above) that was unused during the study period was chosen for comparison with occupied nests, and the same measurements taken.

Nesting Success. We recorded the success or failure of each nesting attempt whenever possible. This variable was 1 in cases where at least one juvenile fledged, or 0 in cases of no fledglings. Due to the depth and shape of the nest cavities, it was difficult to confirm the cause of failure in many cases (Glue and Scott 1980). Failure was ascribed to predation in cases where eggs disappeared or when we found destroyed eggs or the remains of nestlings.

Data Analysis. We compared nest-site variables between used and random cavities using parametric or nonparametric tests. Likewise, we compared variables in successful and unsuccessful nests. In three cases (one in the woodland area and two in the steppe area), nest sites were included in both categories, because they were successful and unsuccessful in different years. Continuous variables that met assumptions of homoscedasticity and normality were compared using t-tests. Variables that violated the assumptions were $\log_e$- or square-root transformed prior to analysis (Sokal and Rohlf 1981, Zar 1996), or were analyzed using Mann-Whitney U-tests. For categorical variables, contingency analyses were used to compare relative frequencies of used nests versus random cavities (Zar 1996). Mean cavity-entrance orientation ($\bar{a}$ ± angular deviation) and its dispersion (r) were calculated for both used nests and random cavities, and Rayleigh's tests (Zar 1996) were used to determine if a significant mean population existed in either sample Differences in mean directions of entrance holes between used nests and unused cavities were examined using the nonparametric Watson's test (Zar 1996).

We used logistic regression to evaluate simultaneously the effect of different variables and their interactions on the nest-site selection and then on nesting success. These analyses treated the dependent variables as binary response variables (1 = used nest, 0 = random point and 1 = successful nest, 0 = failed nest, respectively). All variables that had a univariate P-value <0.25 were entered in the initial multivariate model, together with their first-order interactions (Hosmer and Lemeshow 1989). Nonsignificant interactions and main effects were gradually removed from the model, starting from the least significant variable. In this way, only significant main effects and interactions were included in the final model (Christensen 1990, Tremblay et al. 1997, Valkama et al. 1998). We decided not to pool data from both study areas in the analyses, because the different nature of tree and stone pile cavities resulted in basic scale and categorical differences among most variables measured. Data were analysed using SPSS statistical package (Norusis 1993)

RESULTS

Nest-site Characteristics and Nest-site Selection. Thirty-three out of the 36 nests in the woodland

Table 1. Characteristics measured in nests and random sites in the woodland area. Variables in bold with univariate P-values <0.25 were included in the full logistic regression model. DBH is diameter at breast height.

	NESTS MEAN ± SE	N	RANDOM SITES MEAN ± SE	N	UNIVARIATE P-VALUE
Tree					
DBH (m)	**0.67 ± 0.16**	**30**	**0.74 ± 0.19**	**21**	**0.125**
Height (m)	6.33 ± 1.98	30	6.36 ± 1.89	21	0.946
Entrance					
Height (m)	1.94 ± 0.85	34	1.79 ± 1.13	22	0.700
Long diameter (cm)	21.70 ± 12.63	33	19.14 ± 11.01	22	0.399
Short diameter (cm)	**15.15 ± 9.00**	**33**	**12.20 ± 7.07**	**22**	**0.177**
Inclination (°)	52.03 ± 28.31	32	56.59 ± 34.55	22	0.597
Cover (%)	8.75 ± 26.70	32	3.10 ± 13.08	21	0.487
Surroundings (100-m radius)					
No. of perches	**42.42 ± 40.07**	**36**	**29.95 ± 24.25**	**22**	**0.210**
No. of cavities	**4.56 ± 3.17**	**36**	**3.18 ± 2.36**	**22**	**0.074**
Trees/ha	**4.34 ± 5.09**	**36**	**3.45 ± 3.94**	**22**	**0.163**
Distances to					
Road (m)	821.39 ± 832.90	36	849.95 ± 810.89	22	0.804
Pathway (m)	114.15 ± 114.21	36	109.73 ± 91.11	22	0.972
Human[a] (m)	**805.25 ± 452.19**	**36**	**957.27 ± 449.85**	**22**	**0.195**
Reservoir (m)	790.47 ± 483.79	36	757.55 ± 473.95	22	0.903
Stream (m)	413.50 ± 240.50	36	399.59 ± 266.60	22	0.838

[a] Distance from the nest to the nearest human habitation.

area were located in trees. Two were in stone piles and one in a hole under a road. Entrance holes were located on average <2 m above the ground (Table 1). None of the continuous variables differed significantly between nests and randomly-selected unused cavities, although six variables had univariate P-values less than 0.25 and were entered in the initial logistic regression model (Table 1). Mean entrance orientation was 162° ± 73.1 (r = 0.19) for the nests and 175° ± 72.2 (r = 0.21) for the random cavities (Fig. 1a). None of the populations showed significant directionality (Rayleigh's test: Z = 1.16, P > 0.20 for nests; Z = 0.90, P > 0.20 for random sites) and there was no significant difference between the mean entrance orientation of nests and random cavities (U^2 = 0.01, P > 0.5).

Proportions of nests and random cavities did not differ significantly relative to the tree species, number of entrance holes, place of the entrance holes and habitat (Table 2). However, the proportion of nests where some predator signs were found was significantly smaller than at random sites (Table 2) and this variable was included in the initial logistic regression model.

In the steppe area, 36 nests were located in stone piles and one in a hole in a wall. Used stone piles were on average relatively large, although low, and the nest entrance was usually situated <0.5 m above the ground (Table 3). Mean stone dimensions were significantly larger in stone piles used for nests than in unused piles (long stone diameter: t = 3.09, P = 0.003; short stone diameter: t = 2.85, P = 0.006; N = 36 nests, N = 22 unused piles; Table 3). Likewise, the number of additional suitable cavities around nests was also significantly greater than around random sites (Mann-Whitney U-test, z = −2.57, P = 0.01; Table 3). Nests were also significantly closer to pathways than unused piles (t = −2.38, P = 0.021; Table 3). Long stone diameter (correlated with short stone diameter: Spearman r = 0.85, P < 0.001), the number of suitable cavities, and distance to pathways were entered in the initial logistic regression model, together with small entrance diameter, which also had a univariate P < 0.25 (Table 3). In this area, the mean entrance orientation was 34° ± 78.1 (r = 0.07) for nests and 253° ± 65.6 (r = 0.35) for random cavities (Fig. 1b). None of the populations showed significant directionality (Rayleigh's test: Z = 0.133, P > 0.50 for nests; Z = 2.50, P > 0.05 for
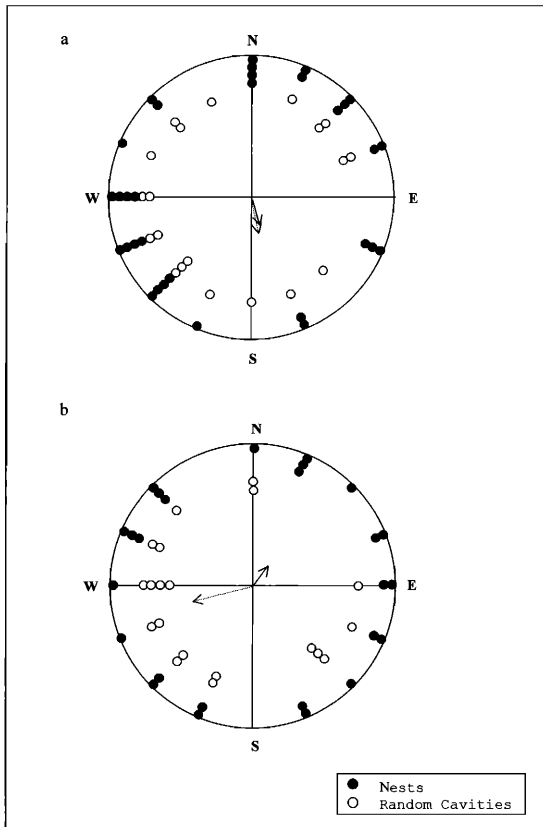
Figure 1. Cavity-entrance orientation of Little Owl nests (solid arrows) and randomly selected cavities (dashed arrows) in the (a) woodland and (b) steppe areas. Arrows represent mean direction for each distribution and their lengths correspond to the relative concentration (r, Zar 1996) of observations.

random sites) and there was no significant difference between the mean entrance orientation of nests and random cavities ($U^2 = 0.09$, $P > 0.20$). The proportions of nests and random cavities did not differ significantly relative to the stone pile type, stone pile stability, habitat, and predator presence (Table 4). The proportion of nests with more than one entrance hole was significantly greater than for random sites. Four of these categorical variables showed P-values <0.25 and were therefore included in the initial logistic regression model (Table 4).

Predator presence was the only variable to enter in the final logistic regression that modelled characteristics of nests and random sites in the woodland area ($\chi^2 = 4.44$, df $= 1$, $P = 0.035$). In the

steppe area, the number of suitable nesting cavities and the long diameter of stones in piles were the two variables entering the final model (number of cavities: $\chi^2 = 4.93$, df $= 1$, $P = 0.026$; long stone diameter: $\chi^2 = 3.62$, df $= 1$, $P = 0.057$).

Nesting Success. Of all nests with known output (46 nests), 26.1% failed in the woodland area. In the steppe area, this proportion was 33.3% ($N = 45$). Almost half (48%) of the failures could be attributed to predation, although it is likely that many of the remaining nest failures were due to this factor as well (e.g., nests that were abandoned during late phase of incubation or during the nestling period).

Five continuous variables showed univariate P-values lower than 0.25 when comparing differences between successful and unsuccessful nests in the woodland area (Table 5). In successful nests, DBH was significantly larger and nests were significantly further away from human habitation (Table 5). Mean entrance orientation was 264° ± 65.8 ($r = 0.34$) for successful nests and 25° ± 41.1 ($r = 0.74$) for nests that failed (Fig. 2). Successful nests did not show significant directionality (Rayleigh's test, $Z = 2.79$, $P > 0.05$), but entrance orientation in failed nests was significantly different from a homogeneous circular distribution (Rayleigh's test, $Z = 5.52$, $P < 0.002$). Mean entrance orientation of the two nest types differed significantly ($U^2 = 0.46$, $P < 0.01$). Habitat type was the only categorical variable with univariate P-value lower than 0.25 when comparing successful and unsuccessful nests (Likelihood Ratio $= 5.37$, df $= 2$, $P = 0.068$, $N = 37$).

In the steppe area, none of the measured variables showed significant differences between successful and unsuccessful nests. Only stone pile height (Mann-Whitney U-test, $z = -1.78$, $P = 0.075$, $N = 36$) and type of stone pile (Fisher's Exact Test, $P = 0.089$, $N = 36$) showed univariate P-values <0.25.

In the woodland area, only DBH was included in the final logistic regression model comparing the characteristics of successful and unsuccessful nests ($\chi^2 = 3.98$, df $= 1$, $P = 0.046$). Distance from nests to nearest human habitation was positively correlated with DBH (Pearson $r = 0.36$, $P = 0.0495$) and could be an alternative explanatory variable in the final model ($\chi^2 = 5.85$, df $= 1$, $P = 0.016$). In the steppe area, there were no significant main effects in the final model.

Table 2. Frequencies of categorical variables in nests and random sites in the woodland area. Differences were tested using χ^2 tests and Fisher's Exact Test. Variables in bold with univariate P-values <0.25 were included in the full logistic regression model. Habitat categories considered were: pasture during 3 yr (study period), young plantation during 3 yr, pasture during one part of the study, and cereal fields during another.

	NESTS (%)	RANDOM SITES (%)	TEST	P
Type of structure			Fisher's	0.75
Holm oak	29 (80.6)	17 (77.3)		
Other	7 (19.4)	5 (22.7)		
Number of entrances			Fisher's	1.00
1	28 (84.9)	19 (86.4)		
>1	5 (15.1)	3 (13.6)		
Entrance site			$\chi^2 = 2.50$	0.29
Trunk	9 (29.0)	9 (42.9)		
Base of branches	14 (45.2)	5 (23.8)		
Branches	8 (25.8)	7 (33.3)		
Habitat			$\chi^2 = 0.58$	0.75
Pasture	15 (41.7)	7 (31.8)		
Young plantation	6 (16.6)	4 (18.2)		
Pasture/cereal	15 (41.7)	11 (50.0)		
Predator			Fisher's	**0.04***
Absent	**25 (89.3)**	**7 (58.3)**		
Present	**3 (10.7)**	**5 (41.7)**		

* Significant, $P < 0.05$.

DISCUSSION

Nest-site Selection. According to our results, predator presence emerged as the main factor linked to nest-site selection by Little Owls in the woodland area. Predation has also been reported as one of the major factors affecting the breeding success of this owl (Exo and Hennes 1980, Schönn 1986), and the avoidance of predators was identified as one of the most important factors when selecting a nesting site for other cavity-nesting species (e.g., Rendell and Robertson 1989).

The main predators of Little Owl nests in our study areas were mammals such as the stone marten (*Martes foina*), the common genet (*Genetta genetta*), and the garden dormouse (*Eliomys quercinus*), as well as the jewelled lizard (Knötzsch 1978, Schönn 1986, Juillard et al. 1992, Génot 2001). All these species seek shelter and roost in cavities, and thus, include a number of cavities in their home ranges. By not nesting in trees used by predators, Little Owls probably reduce the chance of being killed by a predator. An alternative hypothesis is that owls use these sites, but are able to keep most predators away from their nests. Little Owls may attack predators near nests (Glutz and Bauer 1980,

Cramp 1985); however, our observations suggest that, at least toward a human intruder, they generally limited their nest-defense actions to a few alarm calls.

The large number of suitable natural cavities in the holm oak woodland of our study area makes it unlikely that nest-site availability was limiting the breeding density of Little Owls (Exo 1983, Loske 1986, Dalbek et al. 1999). This conclusion was supported by the low use of 50 nest boxes that were available in our 4-yr study. Only one box was occupied on three occasions, by a different owl pair. Because the use of nest-boxes often indicates nest-site limitation (e.g., Lundberg and Westman 1984, Brawn and Balda 1988, Knötzsch 1988, Exo 1992 for the Little Owl), this result supports the idea that nest sites are not limiting in our study area (Brush 1983), and that owls may be able to select nest sites that are relatively safe from predators. This suggestion was supported by our results on the frequency of nesting failure and nest predation, which were relatively low when compared to data from studies on the Little Owl in other parts of Europe (Glue and Scott 1980, Exo 1983, Juillard 1984, Schönn 1986, Génot 2001).

Table 3. Characteristics measured in nests and random sites in the steppe area. Variables in bold with univariate *P*-values <0.25 were included in the full logistic regression model.

	NESTS MEAN ± SE	N	RANDOM SITES MEAN ± SE	N	UNIVARIATE P-VALUE
Stone pile					
Long diameter (m)	8.66 ± 11.06	36	6.86 ± 5.34	22	0.569
Short diameter (m)	3.92 ± 2.00	36	4.40 ± 2.76	22	0.641
Height (m)	1.19 ± 0.74	36	1.14 ± 0.51	22	0.798
Stone					
Long diameter (cm)	**31.52 ± 9.19**	**35**	**25.08 ± 6.66**	**21**	**0.003**
Short diameter (cm)	19.85 ± 5.44	35	16.10 ± 3.84	21	0.006
Entrance					
Height (m)	0.45 ± 0.57	23	0.42 ± 0.29	22	0.532
Long diameter (cm)	21.32 ± 12.98	22	17.43 ± 10.92	22	0.257
Short diameter (cm)	**11.20 ± 5.11**	**22**	**9.05 ± 3.60**	**22**	**0.124**
Inclination (°)	71.82 ± 24.38	22	72.27 ± 28.48	22	0.542
Surroundings (100-m radius)					
No. of perches	25.84 ± 32.12	37	22.18 ± 28.81	22	0.446
No. of cavities	**2.92 ± 2.75**	**37**	**1.68 ± 1.73**	**22**	**0.010**
Distances to					
Road (m)	1428.43 ± 586.84	37	1333.77 ± 533.50	22	0.471
Pathway (m)	**141.68 ± 123.58**	**37**	**222.14 ± 128.54**	**22**	**0.021**
Human[a] (m)	1157.65 ± 404.89	37	1138.77 ± 394.99	22	0.862
Reservoir (m)	835.24 ± 363.79	37	729.05 ± 368.45	22	0.285
Stream (m)	704.81 ± 515.11	37	864.41 ± 581.23	22	0.277

[a] Distance from the nest to the nearest human habitation.

In the woodland area, none of the other nest-site characteristics appeared to influence nest-site selection by Little Owls. This should be interpreted with caution, however, because it is possible that "internal" characteristics of cavities (such as length and shape of access to the nest chamber or dimensions) may influence nest-site selection. Glue and Scott (1980) and Exo (1981) mentioned that Little Owls used mainly deep chambers, reached by long and winding passages (Schönn et al. 1991). These internal cavity dimensions were not measured in our study. Moreover, the fact that we restricted the selection of random cavities to ones that seemed suitable for owls increased the realism of the test, but reduced the likelihood of finding significant differences.

In the steppe area, the number of alternative suitable cavities emerged as the main variable explaining nest-site selection. Although Little Owls often show strong nest-site fidelity (with individual variation; Glue and Scott 1980, Glutz and Bauer 1980, Ullrich 1980, Exo 1981), they may benefit

from the inclusion of alternative suitable nesting cavities in their territories. In many species of birds (Jackson 1994, Marjakangas et al. 1997, Valkama et al. 1998), including cavity-nesters (e.g., Eriksson 1979, Dow and Fredga 1983, Sonerud 1985, Hakkarainen et al. 2001; but see Korpimäki 1987, 1993), individuals avoid breeding in sites where they have failed in previous attempts due to predation, probably because predators may revisit these sites. This could select for individuals that shift nest holes between breeding attempts. The inclusion of a large number of suitable cavities in a territory may also allow Little Owls to switch to alternative sites in the case of a stone pile collapse due to erosion, and provide alternative roosting places, both for adults and fledglings (Schönn et al. 1991, Short 1979, Sedgwick and Knopf 1990). The number of potential cavities was much larger in the woodland area than in the steppe area (on average almost the double number of suitable cavities) and probably decreased the importance of

Table 4. Frequencies of categorical variables in nests and random sites in the steppe area. Differences were tested using χ^2 tests and Fisher's Exact Test. Variables in bold with univariate *P*-values <0.25 were included in the full logistic regression model. Habitat categories considered were: pasture during 3 yr (study period) and used for agricultural crops in at least 1 yr.

	NESTS (%)	RANDOM SITES (%)	TEST	*P*
Stone pile type			Fisher's	**0.11**
"Built"	**5 (13.9)**	**7 (33.3)**		
Other	**31 (86.1)**	**14 (66.7)**		
Stone pile stability			$\chi^2 = 0$	1.00
Unstable	12 (42.9)	9 (42.9)		
Stable	16 (57.1)	12 (57.1)		
Number of entrances			Fisher's	**0.04***
1	**16 (80.0)**	**22 (100.0)**		
>1	**4 (20.0)**	**0 (0.0)**		
Habitat			$\chi^2 = 1.31$	**0.25**
Pasture	**17 (46.0)**	**6 (27.3)**		
Used for crops	**20 (54.0)**	**16 (72.7)**		
Predator			Fisher's	**0.15**
Absent	**7 (28.0)**	**7 (58.3)**		
Present	**18 (72.0)**	**5 (41.7)**		

* Significant, $P < 0.05$.

this variable in the final model for the woodland area.

According to our results, size of stones appeared to be an additional factor influencing nest-site selection in the steppe area, because stones in stone piles used for nesting were larger than stones in random sites. Larger stones probably create more internal cavities within piles (Juillard et al. 1992), and also deeper cavities that owls usually prefer (Glue and Scott 1980, Exo 1981, Génot 1990). The area of nest chambers in piles of large stones should also be bigger, and for many species of cavity nesters, this is often correlated with larger clutches and higher breeding success (e.g., Karlsson and Nilsson 1977, Korpimäki 1985, Rendell and Robertson 1989, Valkama and Korpimäki

Table 5. Continuous variables that differed between successful and failed nests by univariate *P*-values <0.25 in the woodland area, and were included in the full logistic regression model. Differences were tested using *t*-tests and Mann-Whitney *U*-tests.

	SUCCESSFUL NESTS MEAN ± SE	*N*	FAILED NESTS MEAN ± SE	*N*	TEST	*P*
Structure						
Tree DBH[a] (m)	0.71 ± 0.16	21	0.58 ± 0.01	10	$t = 2.87$	0.008*
Surroundings (100-m radius)						
Trees/ha	3.35 ± 2.42	26	6.48 ± 8.31	11	$U = 101.50$	0.167
Distances						
Road (m)	982.65 ± 843.53	26	613.73 ± 947.85	11	$U = 89.00$	0.073
Human (m)	926.85 ± 448.35	26	478.73 ± 275.48	11	$t = 3.71$	0.001*
Reservoir (m)	676.19 ± 438.01	26	1040.55 ± 491.61	11	$U = 85.50$	0.056

[a] DBH = Diameter at breast height.
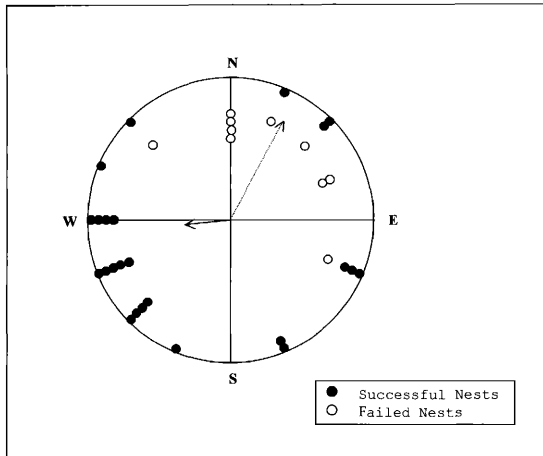* Significant, $P < 0.05$.

Figure 2. Cavity-entrance orientation of Little Owl nests with and without success in the woodland area. Arrows represent mean direction for each distribution and their lengths correspond to the relative concentration (r; Zar 1996) of observations. Solid arrow—successful nests; dashed arrow—failed nests.

1999). Finally, stone piles with larger stones are usually more recent, less prone to erosion, and thus, longer lasting (Juillard et al. 1992).

Although predator frequency (predator occurrence in random points of both areas) seemed to be similar between the two study areas, in the steppe area Little Owls are apparently less able to select nest sites without predators. The relative lack of suitable cavities in this area possibly increases the probability of occupation of the same stone piles by both owls and predators. The selection of cavities with more than one entrance (or exit) seemed to have some importance in this area (Glue and Scott 1980) and might be one strategy to reduce the risk of predation.

Nesting Success. Tree diameter appeared to be linked to the nesting success of Little Owls in the woodland area, because successful nests were located in trees with a greater DBH than failed nests. By using an infrared micro-camera on 26 nests, we observed that trees with a larger diameter seemed to hold deeper cavities, with more sinuous and complex access tunnels than smaller diameter trees. By nesting in trees with a larger girth, owls possibly reduce the probability of a nest being found by predators and may increase the ability of adults and offspring to hide or to escape once predators have found the nest. Other studies have also demonstrated an inverse relationship between

depth of nest cavity and losses due to predation (Moed and Dawson 1979).

Distance to human habitations appeared to be associated positively with nesting success in the study area, but as this variable was positively associated with tree diameter, this may not represent a cause-and-effect influence. Alternatively, the possibility that predators were more numerous near human habitations could account for the higher proportion of failed nests in those areas. However, no observations indicating obvious differences in predator density are available for our study area.

Entrances in the majority of failed nests in the woodland area were towards north or northeast, which may indicate that entrance orientation could have influenced nesting success. Prevailing winds and exposure to the sun may affect energy expenditure of adults and nestlings in some cavity-nesting species, and thus influence cavity entrance orientation (e.g., Lawrence 1967, Ricklefs and Hainsworth 1968, Inouye et al. 1981, Valkama and Korpimäki 1999). For many species of owls, cavity orientation seems to be unimportant (Forsman et al. 1984, Goad and Mannan 1987, McCallum and Gehlbach 1988, Belthoff and Ritchison 1990), while other Little Owl studies show that nest entrances may (Exo 1981, Génot 1990) or may not be (Juillard 1980) protected against wind and rain

Other variables related to nest sites might have influenced nesting success in both study areas and remained undetected. Some nests that failed very early in the breeding season may not have been detected resulting in some bias in our sample of failed nests. Although this could have hampered the identification of variables affecting nesting success, we believe that very few failed nests were missed and that it did not constitute an important bias.

Several studies have focused on the effects of large-scale and landscape variables on population dynamics of Little Owls (e.g., Van Nieuwenhuyse and Bekaert 2001, Van Nieuwenhuyse and Leysen 2001, Van Nieuwenhuyse et al. 2001, Ferrus et al. 2002). Our results show that smaller-scale features associated with nest sites may also be important and should be considered in management of Little Owl habitat. In particular, management guidelines directed towards Little Owl conservation in habitats such as the ones considered in this study could involve the preservation of large-diameter trees and stone piles made of larger stones, as well as

the maintenance of several alternative suitable cavities in the owl territories.

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