Bird Study (2004) **51,** 163–169

Habitat preferences for Long-eared Owls *Asio otus* and Little Owls *Athene noctua* in semi-arid environments at three spatial scales

JOSE ANTONIO MARTÍNEZ[1]* and IÑIGO ZUBEROGOITIA[2]
[1]C/ Juan de la Cierva 43, El Campello, E-03560, Alicante, Spain and [2]Lab. Zoología, Dpto. Zoología, Facultad de Ciencias, Universidad del País Vasco, Aptdo 644, E-48080, Bilbao, Spain

Capsule There is a relationship between owl numbers and the availability of the agri-forest patchwork.
Aims To model habitat preferences at three different scales of two predators largely neglected within the framework of Environmental Impact Assessment (EIA) studies.
Methods We studied habitat preferences of Long-eared Owls and Little Owls by comparing habitat composition around 28 and 78 occupied territories respectively with 55 non-occupied territories in Alicante (eastern Spain). Generalized linear models were used to examine patterns of habitat preference at three different spatial scales: nest-site, home range and landscape.
Results At the nest-site scale, Long-eared Owls preferred wooded areas with few paved roads while Little Owls preferred arid plantations. Furthermore, the probability of finding an occupied territory increased with the proximity of another occupied territory in the surroundings. The home range scale models mirror the feeding requirements of the owls. Thus, Long-eared Owls occupied areas with high percentages of forest, arid plantations, edges between these two land uses, short distances between nests, with presence of conspecifics and little human disturbance. Little Owls occupied arid plantations with high availability of linear structures and the proximity of villages. At the landscape scale, Long-eared Owls eluded extensive forests, and Little Owls preferred arid plantations.
Conclusions We suggest a hierarchical process of habitat selection for both owls regarding fitting trophic resources at the broadest scales and adequate sites for breeding and roosting at the smallest scale. EIA studies must consider that protecting small areas around single nests may not be an efficient conservation option compared with preserving clusters of territories for both species.

The choice of a suitable habitat is probably the result of the integration of different patches satisfying the different requirements of individuals (Orians & Wittenberger 1991). The multi-scale approach to the study of habitat selection is based on the conceptual framework suggested by Johnson (1980), whose basic assumption is that animals are capable of making decisions regarding resources at consecutively smaller scales. Consequently, general habitat selection can be regarded as a hierarchical process regarding, for example, a fitting patch for breeding at a small scale and suitable areas for foraging at a broader scale (Martínez *et al.* 2003a). The multi-scale approach may be specially useful to identify key factors involved in habitat preference of owls because they have large home ranges usually comprising different patches for breeding and foraging (Mikkola 1983).

In Alicante (eastern Spain), traditional arid plantations and large patches of scrubland and forests outside Natural Parks are threatened by urbanization plans despite their importance to raptor and owl populations. The main developments proposed are motorways, large housing developments, golf courses and large vegetable greenhouses. Environmental impact assessment (EIA) is mandatory prior to habitat alteration in Spain, but specialists face the problem that the choice of scale around nests determines the assessment of sensitive habitat features (Martínez *et al.* 2003b). Studies addressing this problem for large predators have singled out the importance of Mediterranean scrubland at different spatial scales (Rico *et al.* 2001, Martínez *et al.* 2003a). However, studies dealing with the habitat preferences for medium or small-sized listed predators inhabiting the agri-forest patchwork in Mediterranean Spain are lacking.

Here we aim: (1) to categorize relevant environmental

*Correspondence author. Email: qvcocotiers@hotmail.com

features affecting habitat preferences of two predators largely neglected within the framework of EIAs in spite of the fact that they are protected in Spain – Long-eared Owl *Asio otus* and Little Owl *Athene noctua* – at three different scales and (2) to assess the relative contribution of the different variables at each scale in order to get insight into the individual's perception of the environment.

METHODS

Study area

The study area in Alicante (southeast of Spain) ranged from the coast (southeast) to the province limit (northwest). The climate varies from semi-arid meso-Mediterranean in the southeast to sub-humid Mediterranean towards the northwest. Average annual rainfall is about 400 mm and annual average temperature is about 19°C. The northwest part of the study area is rugged, dominated by arid plantations, mainly abandoned Carob *Ceratonia siliqua*, Almond *Prunus amygdalus*, Olive *Olea europaea* plantations, vineyards, barley and sunflower cultures, scrubland and pine forests (*Pinus halepensis, Pinus pinea*). In the southeast, the ruggedness of the landscape is less than in the northwest, and the main land uses are dry and irrigated fields, mainly orange or lemon cultures, scrubland and coastal pine woodlots. Villages make up urbanized areas of the interior, while large urban developments distributed almost contiguously over the landscape prevail in the coast.

Survey methods

We located Long-eared Owls and Little Owls between 1997–2002 using the following methods: (1) listening to spontaneous vocalizations, (2) using playback of conspecifics (Centili 2001, Martínez *et al.* 2002), (3) listening to begging nestlings and (4) looking for nests and food remains. Habitat composition around 28 occupied Long-eared Owl nests and 78 Little Owl nests was compared with habitat composition around 55 non-occupied spots located at random. Random sites were located at a minimum distance of 3 km from each other or from occupied sites. All the 55 non-occupied random sites remained empty throughout the study period. Use of occupied sites varied annually between 86–100% (Little Owl) and 77–100% (Long-eared Owl). In order to study spatial distribution patterns we compiled data for all the study period (Newton 1991).

Selection of scales and variables

We used three different scales to study habitat preferences of owls. (a) Landscape scale: we tested for a possible response of the owls to habitat composition at a broad landscape level by choosing an area of 100 km^2 around nests (5.6 km radius around nests) (Martínez *et al.* 2003a). (b) Home range scale: the size of the home range was conservatively assumed for Little Owl to be a 30-ha circular plot around nests (309 m radius) (Génot & Wilhem 1993, Van Nieuwenhuyse & Bekaert 2002) and for Long-eared-Owl to be 742 ha (1537 m radius) (Galeotti *et al.* 1997a, Henrioux 2000). (c) Nest-site scale: the size of the nest-site scale was conservatively assumed for Long-eared Owl to be a 30-ha circular plot around nests (25% of the home range, 309 m radius) (Galeotti 1997a, Henrioux 2000) and for Little Owl to be 10.5 ha (35% of the home range, 182m radius) (Génot & Wilhem 1993, Van Nieuwenhuyse & Bekaert 2002).

We selected 37 environmental variables related to topography, human influence, land use and inter- and intra-specific interactions from aerial photographs and 1:5000 maps (Appendix).

Analytical procedures

Generalized linear models (GLMs) (McCullagh & Nelder 1989) were used to obtain mathematical descriptions of habitat selection by owls in an attempt to reduce the effect of covariance of explanatory variables.[a] We conducted three separate GLMs (stepwise forward method) for the environmental description of data. The presence of owls follows a binomial distribution (binary response variable: presence = 1, absence = 0). Therefore, we used a logit link (Bustamante 1997). Each explanatory variable and all possible interactions were fitted to the observations using the GENMOD procedure of the SAS package (SAS Institute 1996). Each variable was tested for significance in turn, and only those variables that contributed to the largest significant change in deviance were retained. Only variables significant at the 1% level were included in the models (Nicholls 1989). We also tested for quadratic functions in order to explore whether a higher order polynomial improved the models. We corrected for overdispersion when the value of the residual scaled deviance/residual degrees of freedom varied between 1 and 2 (Crawley 1993). The best models were selected by likelihood ratio tests for type I analysis (SAS Institute 1996). Kappa statistics (Titus *et al.*

1984) were used to test whether model discrimination significantly improved chance classifications.

RESULTS

Habitat preferences at the nest-site scale

Long-eared Owl

The habitat model at this spatial scale explained 61% of the original deviance. This model showed that the probability of finding an occupied territory increased with the amount of forest around nests, while it decreased with the extent of paved roads (Table 1). This model correctly classified 92.2% of the occupied territories and 89.1% of the unoccupied territories. This classification was 70.8% better than chance (Kappa test, $Z = 7.02$, $P < 0.0001$). Forest was the most important variable at this scale, accounting for 55.3 % of the explained deviance. It alone classified correctly 98% of occupied territories, but only 20% of the sites where Long-eared Owls were absent.

Little Owl

The habitat model at this spatial scale explained 53% of the original deviance. This model showed that the probability of finding an occupied territory increased with the amount of arid plantations around nests and when there was another occupied territory within the selected radius (Table 1). This model correctly classified 95.1% of the occupied territories and 94.3% of the unoccupied territories. This classification was 88.5% better than chance (Kappa test, $Z = 6.27$, $P < 0.0001$). Arid plantations was the most important variable at this scale, accounting for 72.4% of the explained deviance. It alone correctly classified 71% of occupied territories and 44% of the sites where Little Owls were absent.

Habitat preferences at the home range scale

Long-eared Owl

The probability of finding an occupied territory at this scale accounted for 96% of the original deviance. This model predicted high probabilities of presence of Long-eared Owls in areas with high percentages of forest, arid plantations, edges between these two land uses, short distances between nests and arid plantations and the presence of neighbours (Table 2). The probability of finding an occupied territory decreased with the amount of paved roads (Table 2). This model correctly

Table 1. Generalized linear models for the probability of presence of owls at the nest-site scale, using binomial error and logistic link.

	Long-eared Owl				Little Owl			
Parameter	Estimate	sd	χ^2	*P*	Estimate	sd	χ^2	*P*
Intercept	20.471	0.651			229.991	0.557		
Forest	0.072	0.011	50.21	0.000				
Arid plantations	–	–	–	–	0.034	0.05	32.111	0.000
Neighbours	–	–	–	–	0.027	0.002	23.22	0.000
Paved roads	–0.066	0.017	33.01	0.000	–	–	–	–
Residual deviance	40.281				41.021			

Table 2. Generalized linear models for the probability of presence of owls at the home range scale, using binomial error and logistic link.

	Long-eared Owl				Little Owl			
Parameter	Estimate	sd	χ^2	P	Estimate	sd	χ^2	P
Intercept	–9.781	1.455			–13.330	1.809		
Forest	0.202	0.004	668.552	0.000	–	–	–	–
Arid plantations	0.266	0.019	491.203	0.000	0.081	0.030	290.113	0.000
Arid plantations–forest edges	0.099	0.017	321.005	0.000	–	–	–	–
Linear structures	–	–	–	–	0.266	0.041	702.212	0.000
Neighbours	0.222	0.033	520.003	0.000	0.086	0.012	478.200	0.000
Distance to arid plantations	0.041	0.003	223.33	0.000	–	–	–	–
Distance to village or city	–	–	–	–	0.43	0.002	344.044	0.000
Paved roads	–0.044	0.004	337.721	0.000	–	–	–	–
Residual deviance	3.077				27.989			

Table 3. Generalized linear models for the probability of presence of owls at the landscape scale, using binomial error and logistic link.

	Long-eared Owl				Little Owl			
Parameter	Estimate	sd	χ^2	*P*	Estimate	sd	χ^2	*P*
Intercept	–1.336	0.611			–2.691	0.77		
Forest	– 2.18	0.001	44.452	0.000	–	–	–	–
Arid plantations	0.059	0.017	21.011	0.000	0.022	0.009	52.14	0.000
Residual deviance	52.777				65.003			

classified 99.3% of occupied territories and 98.7% of unoccupied cliffs. This classification is 96.7% better than chance (Kappa test, *Z* = 9.2, *P* < 0.0001).

Little Owl

The probability of having an occupied territory at this scale accounted for 70% of the original deviance. This model predicted high probabilities of presence of Little Owls in areas with high percentages of arid plantations, linear structures, the presence of neighbours and the vicinity of villages or cities (Table 2). The model correctly classified 64.6% of occupied territories and 78.7% of unoccupied territories. This classification is 89.5% better than chance (Kappa test, *Z* = 9.4, *P* < 0.0001).

Habitat preferences at the landscape scale

Long-eared Owl

The model for this scale accounted for 45.9% of the original deviance. Long-eared Owls showed a second-order response to the surface of forest (Table 3). The model also predicts occupancy of arid plantations (Table 3). The model at this scale correctly classified 92.2% of occupied cliffs and 75.5% of unoccupied territories, this classification being 81.2% better than chance (Kappa test, *Z* = 7.5, *P* < 0.0001).

Little Owl

The model for this scale accounted for 40.3% of the original deviance. The model predicts occupancy of territories in areas with arid plantations (Table 3). This GLM correctly classified 85.7% of occupied territories and 70.2% of unoccupied territories, this classification being 80.3% better than chance (Kappa test, *Z* = 7.8, *P* < 0.0001).

DISCUSSION

The probability of settlement of Long-eared Owls and Little Owls in our study area is largely dependent on the availability of the agri-forest patchwork (Tables 1–3). The positive response to the surface of forest from Long-eared Owls relates to the use of wick nests for breeding (Rico *et al.* 1991). For the Little Owl, the positive response to arid plantations seems to reflect the availability of Carobs and Olive trees (upon which they are largely dependent for breeding in this study area (Martínez & Zuberogoitia 2003a). It might also reflect the availability of old country houses and linear structures such as stone walls for breeding, most of which are in state of decay or dereliction. Little Owls also breed and roost in hollows in the banks of the ephemeral rivers criss-crossing the agri-forested patchwork. Occupied territories of Long-eared Owls occurred in areas with fewer paved roads than random sites (Martínez *et al.* 2003a).

Variables reflecting the feeding habits of the owls enter the models at the home range scale, namely the length of edges (Long-eared Owl) and the availability of linear structures (Little Owls). Moreover, Long-eared Owl nests were located closer to the forest edge than random sites. Indeed, distance to edges can influence egg-laying date, diet richness and diet diversity of owls because of the increased prey diversity in edges (Penteriani *et al.* 2001). In our study area, Long-eared Owls feed mainly on birds or small mammals inhabiting mainly edges or open areas (Rico *et al.* 1991). This suggests that owls benefit from exploiting both sides of the discontinuities between woodlots and arid plantations, which are also important perching sites for the Long-eared Owl while hunting. Little Owls feed mainly on insects, small mammals and lizards (unpubl. data) which inhabit mainly linear structures such as ditches, stone walls or tree lines (Exo & Hennes 1980, Van Nieuwenhuyse & Leysen 2001).

The length of paved roads within home ranges reduces the likelihood of having Long-eared Owl territories. Its is likely that owls avoid paved roads because of the risk of mortality or of the lack of prey, especially in areas where roads are numerous. It is possible that our models did not detect avoidance to large housing developments or unpaved roads due to the scarcity of large cities or highly developed pathway networks in the study area. However, no descriptors of environmental alteration enter the models for Little Owls. Furthermore, they seem to prefer the proximity of villages to less disturbed areas. The most parsimonious explanation to the increasing presence of Little Owls in some villages in Alicante is that they are forced to move to urbanized areas because of the fast disappearance of the arid plantations surrounding cities and villages, especially in coastal areas (Martínez & Zuberogoitia 2003a). Between 1996 and 1998, the number of territorial disputes (as measured by the number of diurnal spontaneous contests between males) in some villages increased fivefold, coinciding with a steep decline in the availability of the surrounding arid plantations. Between 1999 and 2002 diurnal spontaneous vocalizations in these villages decreased fourfold, coinciding with the replacement of the few remaining houses with Carob orchards by large buildings and gardens with young exotic trees (unpubl. data). This indicates changes in the amount of territorial disputes over the variable resources available in these villages by an increasing number of immigrants from the disappearing surroundings (Martínez & Zuberogoitia 2003b). Furthermore, four diurnal communal roosts of 9–15 Little Owls were recorded between 2000 and 2002 in the four remaining house gardens in arid plantations that underwent urbanization. No communal roosts have been reported in the literature for the Little Owl (Génot & Van Nieuwenhuyse 2002).

The probability of settlement of both species was positively related to the presence of neighbours (Tables 1 & 2). The aggregation of Little Owl territories can be a consequence of social interactions so that conservation efforts should focus on clusters rather than on single territories (Van Nieuwenhuyse & Bekaert 2002). However, clustering of Little Owl territories in our study area would be a consequence of the increasingly aggregated distribution of nesting and hunting areas resulting from major habitat changes. Long-eared Owls may be using the presence of conspecifics for assessing habitat suitability indirectly (Serrano *et al.* 2001). Furthermore, close nesting may favour helping behaviour at nests between related individuals (Galeotti *et al.* 1997b).

At the broadest scale, the second-order response to the surface of forests seems to indicate that Long-eared Owls are less likely to be found in large forests. One possible explanation is that the size/length of edges ratio in large homogeneous forests reduces the availability of profitable hunting grounds, as the length of edges between habitats is relatively small (Goszczynsk 1997).

It has been suggested that the relative importance of each environmental limiting factor could be related to the scale of selection, with more important factors driving preferences at the broadest scales (Rettie & Messier 2000, Martínez *et al.* 2003a). Our results show that selection of arid plantations persist over the three spatial scales for the Little Owl and over the broadest scales for the Long-eared Owl, while the amount of forest persists over the three scales for Long-eared Owls. This suggests that EIA studies that encourage preserving only small areas around single nests do not sufficiently meet the habitat requirements of these two species (Ferrus *et al.* 2002). Moreover, EIA studies should take into account the social interactions between neighbours that increase the probability of finding occupied territories (Galeotti *et al.* 1997b, Van Nieuwenhuyse & Bekaert 2002).

ACKNOWLEDGEMENTS

We are most indebted to Fernando Falcó, Luis Rico, Luis Fidel and HELIACA, who helped in the location of the owls. A previous study with David Serrano provided us with useful ideas for this study. Dries Van Nieuwenhuyse, John O'Halloran, Ken Norris, F. Henrioux and two anonymous referees made valuable comments on the manuscript. Jean-Claude Génot, Dries Van Nieuwenhuyse and Michael Exo provided us with relevant references.

ENDNOTE

a. GLMs allow for the use of appropriate error formulations from the exponential family distributions, hence avoiding some of the limitations of the conventional regression models. GLMs consists of a linear predictor, an error function and a link function. The linear predictor (LP) is defined as: $LP = a + bx_1 + cx_2 + \ldots$ where a is the intercept, $b, c\ldots$ are the parameter estimates to be obtained from the observed data, and $x_1, x_2, \ldots$ are the explanatory variables. The error and link functions depend on the nature of the data.

REFERENCES

Bustamante, J. 1997. Predictive models for Lesser Kestrel *Falco naumanni* distribution, abundance and extinction in southern Spain. *Biol. Conserv.* **80:** 153–160.

Centili, D. 2001. Playback and Little Owls *Athene noctua*: preliminary results and considerations. In Van Nieuwenhuyse, D. Leysen, M. &

Leysen, K. (eds) *The Little Owl in Flanders in Its International Context. Proceedings of the Second International Little Owl Symposium*, 16–18 March, 2001. *Oriolus* **67**(2–3): 88–93. Geraardsbergen, Belgium.

Crawley M.J. 1993. *GLIM for Ecologists*. Blackwell Scientific Publications, London.

Exo, K. & Hennes, R. 1980. Beitrag sur Populationsökologie des Steinkaizes – eine Analyse destscher un niederländischer Ringfunde. *Vogelwarte* **30:** 162–179.

Ferrus, L., Génot, J.C., Topin, F., Baudry, J. & Giradoux, P. 2002. Répartition de la Chevêche d'Athéna (*Athene noctua*) et variation d'echelle d'analyse des paysages. *Rev. Écol. Terre Vie* **57:** 39–51.

Galeotti, P., Tavecchia, G. & Bonetti, A. 1997a. Home-range and habitat use of Long-eared owls in open farmland (Po Plain, Northern Italy), in relation to prey availability. *J. Wild. Res.* **2:** 137–145.

Galeotti, P., Pilastro, A., Tavecchia, G., Bonetti, A. & Congiu, L. 1997b. Genetic similarity in long-eared owl communal winter roosts: a DNA fingerprint study. *Mol. Ecol.***6:** 429–435.

Génot, J.C. & Van Nieuwenhuyse, D. 2002. Little Owl *Athene noctua*. *BWP Update* **4:** 35–63.

Génot, J.C. & Wilhem, J.L.1993. Occupation et utilisation de l'espace par la Chouette chevêche *Athenenoctua* en Bordure des Vosges du Nord. *Alauda* **61:** 181–194.

Goszczynsk, J. 1997. Density and productivity of Common Buzzard *Buteo buteo* and Goshawk *Accipiter gentilis* population in Rongónw, Central Poland. *Acta Ornithol.* **32:** 149–155.

Henrioux, F. 2000. Home range and habitat use by the Long-Eared Owl in northwestern Switzerland. *J. Raptor Res.* **34:** 93–101.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61:** 65–71.

Martínez, J.A. & Zuberogoitia, I. 2003a. La urbanización litoral en Alicante reduce la población del Mochuelo Europeo (*Athene noctua*). *Quercus* **203:** 52.

Martínez, J.A. & Zuberogoitia, I. 2003b. *Las Aves Rapaces en los Mosaicos Agroforestales de Alicante y Valencia (I)*. Huuhkaja Ed., Alicante.

Martínez, J.A., Zuberogoitia, I., Colás, J. & Maciá, J. 2002. Use of recorded calls for detecting Long-eared Owls *Asio otus*. *Ardeola* **49:** 97–101.

Martínez, J.A., Serrano, D. & Zuberogoitia, I. 2003a. Predictive models of habitat preferences for the Eurasian Eagle Owl *Bubo bubo*: a multi-scale approach. *Ecography* **26:** 21–28.

Martínez, J.A., Martínez, J.E., Zuberogoitia, I., García, J.T., Carbonell, R., de Lucas, M. & Díaz, M. 2003b. La evaluación de impacto ambiental sobre las poblaciones de aves rapaces: problemas de ejecución y posibles soluciones. *Ardeola* **50:** 85–102.

McCullagh, P. & Nelder, J.A. 1989. *Generalised Linear Modelling*. Chapman & Hall, London.

Mikkola, H. 1983.*Owls of Europe*. Poyser, Carlton.

Newton, I. 1991. Habitat variation and population regulation in Sparrowhawks. *Ibis* **133:** 76–88.

Nicholls, A.O. 1989. How to make biological surveys go further with generalised linear models. *Biol. Conserv.* **50:** 51–75.

Orians, G.H. & Wittenberger, J.F. 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* **137:** 29–49.

Penteriani, V., Gallardo, M. & Roche, P. 2001. Habitat structure and prey density affect Eagle Owl *Bubo bubo* density and breeding performance: a case of intrapopulation heterogeneity. *J. Zool. Lond.* **257:** 365–372.

Rettie, W.J. & Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* **23:** 466–478.

Rico, L., Villaplana, F. & Vidal, A. 1991. *Estudio sobre el Búho chico (Asio otus) y el Cernícalo primilla (Falco naumanni) en la Provincia de Alicante*. Consellería de Medi Ambient, Alicante.

Rico, L., Martínez, J.A., Morán, S., Navarro, J.R. & Rico, D. 2001. Preferencias de hábitat del Águila-azor Perdicera *Hieraaetus fasciatus* en Alicante a dos escalas espaciales. *Ardeola* **48:** 55–62.

SAS Institute 1996. *SAS/STAT software: changes and enhancements through Release 6.11*. SAS Institute, Cary, NC.

Serrano, D., Tella, J., Forero, M. & Donázar, J. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *J. Anim. Ecol.* **70:** 568–578.

Titus, K., Mosher, J.A. & Williams, B.K. 1984. Chance corrected classification for use in discriminant analysis and ecological applications. *Am. Midland Nat.* **111:** 1–7.

Van Nieuwenhuyse, D. & Bekaert, M. 2002. An autologistic model for prediction of Little Owl (*Athene noctua*) suitability of landscape in East Flanders – evidence for socially induced distribution patterns of Little Owl. In *Raptors in the New Millennium. Proceedings of the World Conference on Birds of Prey and Owls, 2–8 April 2000:* 80–90. Reuven Yosef International Birding & Research Center in Eliat, Israel.

Van Nieuwenhuyse, D. & Leysen, M. 2001. Habitat typologies of Little Owls *Athene noctua* territories in Flanders (northern Belgium). In Van Nieuwenhuyse, D. Leysen, M. & Leysen, K. (eds) *The Little Owl in Flanders in Its International Context. Proceedings of the Second International Little Owl Symposium, 16–18 March, 2001, Geraardsbergen, Belgium. Oriolus* **67**(2–3): 72–83.

(MS received 25 March 2003; revised MS accepted 23 September 2003)

APPENDIX

Variables used to characterize centres of activity at the nesting, home range and landscape scales.

Physiography

RELIEF, measured as the number of 100-m contours cut by four lines starting from the centre of the area in directions N, S, E and W
MAXIMUM ALTITUDE, above sea level
MINIMUM ALTITUDE, above sea level
AVERAGE ALTITUDE, (maximum altitude + minimum altitude)/2
ALTITUDINAL DIFFERENCE, maximum altitude – minimum altitude

Human disturbance

UNPAVED ROADS, metres around the cliff
PAVED ROADS, metres around the cliff
DISTANCE TO NEAREST UNPAVED ROAD, in metres
DISTANCE TO NEAREST PAVED ROAD, in metres
DISTANCE TO THE NEAREST BUILDING, in metres
DISTANCE TO THE NEAREST CITY OR VILLAGE, in metres
NUMBER OF BUILDINGS

Land use (%)

FOREST
SCRUBLAND
ARID PLANTATIONS
IRRIGATED CULTURES
NON CULTIVATED LANDS
GRAVEL PITS
WATER
EPHEMERAL RIVERS
DISTANCE TO EACH LAND USE

Edges (m)

ARID PLANTATIONS–IRRIGATED CULTURES
IRRIGATED CULTURES–FOREST
IRRIGATED CULTURES–SCRUBLAND
ARID PLANTATIONS–FOREST
ARID PLANTATIONS–SCRUBLAND
FOREST–SCRUBLAND

Linear structures (m)

LENGTH OF DITCHES, STONE WALLS, AND TREE LINES

Intra-specific relationships

NEIGHBOURS, presence (1) or absence (0) of occupied territories of conspecifics in the circular sampling area

Inter-specific relationships

COMPETITORS, presence (1) or absence (0) of territories of occupied territories of the other species in the circular sampling area