HABITAT PREFERENCE MODELS FOR NESTING EAGLE OWLS *BUBO BUBO*: HOW MUCH CAN BE INFERRED FROM CHANGES WITH SPATIAL SCALE?

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SUMMARY.—*Habitat preference models for nesting Eagle Owls* Bubo bubo*: How much can be inferred from changes with spatial scale?*

Aims: To analyze whether habitat preference patterns of the Eagle Owl *Bubo bubo* change with spatial scale in an area of very high rabbit *Oryctolagus cuniculus* density as compared to an area of lower prey availability (Martínez *et al*., 2003a).

Location: An area of over 2,100 km^2 located in the province of Toledo, central Spain.

Methods: 17 habitat variables were measured around 100 nests that were occupied between 1999 and 2003 and around 100 random points at four spatial scales (circular areas of 250, 500, 1000 and 1,500 m of radius). The range of spatial scales was established on the basis of the observed high density of Eagle Owl nests in the study area, the second highest reported to date. Habitat features of occupied and random areas were compared by means of logistic regressions for each spatial scale. The possible effect of the spatial autocorrelation was assessed using as additional predictors all the terms of a cubic equation defined by the coordinates of the sampling points.

Results: Topographic irregularity and distance to the nearest stream were included into the models at all scales as the main predictors of the presence of Eagle Owl nests, classifying a high percentage of both random and occupied points. Percent correct classification of the models did not change across scales. Positive selection of areas with irregular topography and close to streams can be interpreted as due either to a choice of protected areas for nest location and/or of areas with high prey availability. At the 500 meters of radius scale the model included marginally the positive selection of areas with high covers of dehesa, a variable that may be interpreted in the same way that the selection for the two main predictors. Two terms (X and Y^2) of the cubic equation witch defined the spatial distribution of the nest and random points entered into all the models as relevant factors.

Conclusion: No hierarchical patterns of habitat preference were detected, contrasting with results from a previous study carried out in an area of lower rabbit abundance (Martínez *et al*., 2003a). This result may be related to the high abundance of rabbits in central Spain, witch would have lead to a preference for good nesting places rather than for areas with higher than average prey abundance. Methodological effects cannot be ruled out, however, in either this comparison or in multiscale habitat preference studies in general. Independent data on the foraging behavior of the involved species and/or on the fitness consequences of habitat selection would be necessary to ascertain whether results from multiscale studies truly reflect underlying biological processes (and what processes) or are biased by the parameter values of the modeling approach.

Key words: *Bubo bubo*, Eagle Owl, habitat preferences, land uses, multiple spatial scales, prey abundance, Spain, topography.

RESUMEN.—*Modelos de preferencia de hábitat para el Búho Real* Bubo bubo*: ¿Qué puede inferirse de cambios con la escala espacial?*

Objetivos: Analizar si las preferencias de hábitat del Búho Real *Bubo bubo* cambian con las escala espacial en un área de muy alta densidad de conejos *Oryctolagus cuniculus*, en comparación con lo que ocurre en un área de menor disponibilidad de presas (Martínez *et al*., 2003a).

Localidad: Un área de unos 2.100 km^2 en la provincia de Toledo, centro de España.

Métodos: Se midieron 17 variables en torno a 100 nidos ocupados entre 1999 y 2003 y 100 puntos elegidos al azar a cuatro escalas espaciales (áreas de 250, 500, 1000 y 1.500 m de radio). El rango de escalas se estableció sobre la base de la alta densidad de nidos de Búho Real en el área de estudio, la segunda mayor encontrada hasta la fecha. Las características del hábitat de los puntos ocupados y los puntos al azar fueron comparadas mediante regresiones logísticas para cada escala espacial. El posible efecto de la autocorrelación

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espacial fue evaluado utilizando como predictores adicionales todos los términos de una ecuación de tercer grado definida por las coordenadas X e Y de los puntos de muestreo.

Resultados: La irregularidad topográfica y la distancia a arroyos fueron incluidas en los modelos de todas las escalas como los principales predictores de la presencia de nidos de Búho Real, clasificando un elevado porcentaje tanto de puntos ocupados como de puntos al azar. El porcentaje de casos clasificados correctamente no varió con la escala. La selección positiva de áreas con altas irregularidades topográficas y cercanas a arroyos puede interpretarse como debida a una preferencia por zonas seguras para la nidificación y/o con alta abundancia de presas. A la escala de 500 metros de radio el modelo incluyó de modo marginalmente significativo la selección por áreas con una elevada cobertura de dehesas, una variable que puede ser interpretada en el mismo sentido que la selección de los dos predictores principales. Dos términos, X e Y^2, de la ecuación de tercer grado que define la distribución espacial de los nidos y los puntos al azar fueron incluidos en los modelos como predictores influyentes.

Conclusión: No encontramos un proceso de selección de hábitat jerárquico en nuestro área de estudio y para las escalas analizadas, en contraste con los resultados de un trabajo previo realizado en una zona con menor densidad de conejos (Martínez *et al*., 2003a). Este patrón puede estar ligado a la alta abundancia de conejos en el centro de España, que podría dar lugar a una búsqueda de puntos adecuados para la nidificación más que a una selección de características del hábitat relacionadas con la abundancia de presas. Sin embargo, no se puede descartar el efecto de la metodología empleada para analizar los cambios en las preferencias con la escala, ni en esta comparación ni en los estudios de preferencias a escalas múltiples en general. Se requiere por tanto información independiente sobre el comportamiento de búsqueda de alimento y/o sobre las consecuencias de las preferencias de hábitat sobre la eficacia biológica de los individuos para poder determinar si los patrones observados reflejan procesos biológicos reales (y qué procesos) o están influidos por el método general de análisis de los estudios multiescala.

Palabras clave: *Bubo bubo*, Búho Real, preferencias de hábitat, usos del suelo, multiples escalas espaciales, abundancia de presas, España, topografía.

INTRODUCTION

Habitat preference models have been extensively developed to define and analyze several components of habitat use by animals (Morrison *et al*., 1998). If such preference models have a causal basis (Seoane & Bustamante, 2001; Tyre *et al*., 2001), they have been proposed as one of the main tools for preserving endangered species, either as the best basis for developing habitat management strategies (Morrison *et al*., 1998) or to evaluate the impact of human activities (Martínez *et al*. 2003b, 2003c). Under these assumptions, a raising number of preference models on the nesting habitat (*e.g.* González *et al*., 1992; Donázar *et al*., 1993; Suárez *et al*., 2000; Ortego & Díaz, 2004), habitat use by immature individuals during natal dispersal (*e.g.* Ferrer & Harte, 1997) or foraging habitat (*e.g.* Tella *et al*., 1998) by raptors have been developed in Spain during the last years (reviewed in Martínez *et al*., 2003b). However, the interpretation of most of these models suffers from the caveat pointed out by Jones (2001) about the repeated conceptual confusion between habitat selection and habitat preferences. Habitat selection refers to a hierarchical process of behavioral responses that may result in a disproportionate use of habitats, which in turns influence the individuals' fitness (Block & Brennan, 1993), whereas habitat preference refers to the final pattern resulting from the habitat selection process. As individual decisions are constrained by ecological and evolutionary factors such as inter- and intraspecific competition, perceptual bias or site tenacity (Wiens, 1989), habitat preferences are only partially caused by habitat selection, so that interpreting habitat preference models as if they were habitat selection models is a conceptual mistake (Jones, 2001).

In spite of this basic criticism, the analysis of habitat preferences is still one of the main approaches to study the habitat selection process (Lawler, 1999; Martínez *et al*., 2003a), as far as its design takes into account the potential influences of ecological and evolutionary constraints (*e.g.* Pulido & Díaz, 1997; Díaz *et al*., 1998; Beutel *et al*., 1999). One way of doing this is to analyze how habitat preferences vary with spatial scale (*e.g.* Wiens *et al*., 1987; Lawler, 1999; Sánchez-Zapata & Calvo, 1999; Illera, 2001; Penteriani *et al*., 2001a; Martínez *et al*., 2003a). The rationale of this approach is

that animals are expected to make decisions regarding resources (food availability, nesting places, etc.) at different spatial scales that should be hierarchically integrated (Johnson, 1980; Lawler, 1999). For example, suitable nesting places may not be actually occupied because trophic resources would be too scarce or human disturbance too high in the areas surrounding such places. Changes (or lack of changes) in patterns of habitat preference across spatial scales may provide insights on what resources are critical at each scale (*e.g.* Martínez *et al.*, 2003a) as well as on the scale at which each species perceives its environment (*e.g.* Martínez & Zuberogoitia, 2004). These two factors are in the core of the causal link between patterns of habitat preference and the process of habitat selection (Johnson, 1980; Holling, 1992) since fitness consequences of habitat preferences are also scale-dependent (*e.g.* Misenhelter & Rotenberry, 2000), a fact linked with the different selection pressures to which individuals are to be exposed at each decision step in the hierarchical habitat selection process.

Habitat preferences of Mediterranean Eagle Owls *Bubo bubo* have been analyzed in Navarra (Donázar, 1988), Murcia (Martínez & Calvo, 2000; Sánchez-Zapata, *et al.* 1996), Alicante (Martínez *et al.*, 2003a) and Toledo (Ortego & Díaz, 2004) in Spain, as well as in another Mediterranean population (Penteriani *et al.*, 2001b), at a variety of spatial scales. All of them emphasize the importance of safe nesting places and rabbit *Oryctolagus cuniculus* abundance and distribution on habitat preferences and population densities of Eagle Owls. Only the recent paper by Martínez *et al.* (2003a) follows a multiscale approach, using a range of spatial scales established on the basis of a mixture of local and general knowledge on the ways Eagle Owls possibly perceive their environment. In this paper, the null hypothesis of a random occupancy of habitat at different spatial scales by Eagle Owls in central Spain will be tested, established on the basis of the distribution of owl nests in the study area. Specifically, it will be tested whether habitat preferences vary with spatial scale, as reported by Martínez *et al.* (2003a), and what the potential is for these changes (or lack of them) to infer the likely causes of the observed preferences.

MATERIAL AND METHODS

Study area

The study area extends over 2,100 km^2 (centered on 39°47'N, 4°04'W) and is located in the province of Toledo, central Spain. The climate is meso-mediterranean with mean temperatures ranging from 26°C in July to 5°C in January and 300-400 mm of rainfall concentrated in spring and autumn. The area is extensively cultivated, with irrigated maize *Zea mays* fields close to the Tajus river and non-irrigated barley *Hordeum vulgare* and wheat *Triticum* spp. fields, as well as scattered olive groves *Olea europaea* and vineyards *Vitis vinifera*, elsewhere. Holm oaks *Quercus ilex* dominate the less intensively used areas, whereas the most altered zones are dominated by esparto grass *Stipa tenacissima* or Mediterranean scrubland mainly composed by *Quercus ilex* shrubs, *Cistus ladanifer* and *Retama sphaerocarpa*. Other minor habitats include streams with riparian vegetation and recent pine *Pinus* spp. plantations. Rabbit densities in this study area are within the highest reported, whereas Martínez *et al.* (2003a) worked in an area of lower prey availability (Villafuerte *et al.*, 1995).

Territory location and habitat characterization

Eagle Owl pairs nesting in the study area between 1999 and 2003 were located by means of a combination of direct and indirect methods: intensive nest searching in suitable areas, listening to spontaneous vocalizations, visiting the area around potential nest or perch sites to look for molted feathers, fresh pellets and prey remains, and eliciting territorial calls by means of playbacks of conspecific vocalizations (Marchesi *et al.*, 2002; Martínez *et al.*, 2003a). Only pairs with clear evidence of reproduction (occupied or old nests, fledged chicks) in at least one of the study years were included in the analyses.

Both the habitat available and used by Eagle Owls for nesting were characterized by means of 17 environmental variables related to degree of humanization, land uses, physiography and local owl population density (Appendix). We determined distances, the index of topographic irregularity and the number of buildings by the

use of 1:25000 topographic maps of Spain (I.G.N.). Nest sites were incorporated into a Geographic Information System (GIS) and afterwards cover of land uses and the number of ecotones between land uses were measured in the digitalized 1:100000 Corine Land Cover maps using the Arc-View software. The 20 land use types provided by Corine Land Cover maps were grouped into nine categories in order to facilitate statistical analyses (Appendix). Random points used to estimate habitat availability were obtained by contingent generation of a number of pairs of UTM coordinates that was the same as the number of nests located. It was not checked whether random points were actually occupied or not, so a comparison was carried out between occupied and available habitat which is considered to be more informative than comparisons between occupied and unoccupied sites and allows making more proper inferences about habitat choice (Jones, 2001; but see Jones & Robertson, 2001).

Habitat variables were measured in circles of 250 (0.20 km^2), 500 (0.78 km^2), 1000 (3.14 km^2) and 1500 (7.07 km^2) meters of radius around nest locations and random points. No information was available on the foraging behaviour and home range size of nesting Eagle Owls in the study area. Hence, the spatial scales selected were inspired on the observed high nest density, expecting that the smaller scales (higher resolutions) would be related to selection of suitable nest sites while the larger (lower resolutions) would be related to selection of foraging territories. A total of 100 breeding pairs of Eagle Owls were found in the study area. The average nearest neighbour distance (NND) was 1450 ± 1719 m (range: 150-7275 m), that is among the lowest reported for Europe (reviewed in Marchesi et al., 2002), with only one denser breeding population recently reported in northern Seville, SW Spain (Penteriani & Delgado, 2004). Hence, the studied population is very dense, so that the home range size of nesting pairs should be much smaller than previously established (reviewed in Martínez et al., 2003a). Further, most owl nests tended to be located along seasonal brooks, so that modal NND (425 m) was much smaller than the average NND. This clumped and dense distribution was the basis for the range of scales selected (see Martínez et al., 2003a for a similar procedure).

Clumped distributions may bias results of empirical comparisons between habitat use and availability due to spatial autocorrelation of use data (Legendre, 1993). Such biases were assessed and removed, using as additional predictors for the models all terms of the cubic equation $Z' = b_1X + b_2Y + b_3X^2 + b_4XY + b_5Y^2 + b_6X^3 + b_7X^2Y + b_8XY^2 + b_9Y^3$, where X and Y are the longitude and latitude, respectively, for each nest and random point (Legendre, 1990, 1993; Bocard et al., 1992). X and Y were previously centred to mean zero (ranges of the longest axis from –1 to +1, Neter et al., 1985; Burrough, 1995). Alternatively, nonrandom distribution of nest sites could arise from intraspecific interactions such as competition or conspecific attraction, so that the NND of each nest and random point were included as a potential predictor of habitat preferences (Martínez et al., 2003a).

A forward stepwise logistic regression approach based on the Wald statistic was used to identify the set of variables that best separated nest from random sites (Hosmer & Lemeshow, 1989). Variables were arc-sin, root-square or log-transformed before analyses. There was no attempt to validate the models obtained by either resampling the database or using cases not employed to build up the models (Seoane & Bustamante, 2001) since we were mostly interested in whether model parameters changed with scale, instead on the predictive performance of such models. Predictive performance is overestimated by this modeling approach, but this positive bias was not likely to change with spatial scale (Pearce & Ferrier, 2000). Model performance was computed as the percentage of cases correctly classified as either occupied or random, using 0.5 as the threshold value for such classification. This balanced design allows to test simultaneously whether proportion of correct classifications differ from random expectations and whether such proportions changed with spatial scale using the fit of log-linear models to the three-way contingency table generated by the factors scale*model classification (occupied or random)*real classification (occupied or random) (Sokal & Rohlf, 1981). No such explicit and comprehensive test is currently possible with other estimates of model performance such as the kappa or AUC statistics (Pearce & Ferrier, 2000; Seoane & Bustamante, 2001).

RESULTS

The habitat around nests differed significantly from the habitat around random points. The habitat preference models at the scales of 250 (0.20 km^2), 1000 (3.14 km^2) and 1500 (7.07 km^2) meters of radius showed that the probability of finding an occupied nest increased with the irregularity of topography while it decreased with the distance to the nearest stream. The model for the 500 m (0.78 km^2) scale included the same variables than the models from the previous scales plus the cover of dehesas, which increased the probability of occupancy (Table 1). Two terms (X and Y^2) of the cubic equation witch defined the spatial distribution of the nest and random points entered into all the models as significant factors. Nevertheless, the predictors selected by the modeling approach barely differ from those selected without taking into account spatial autocorrelation (data not shown). The proportion of cases correctly classified by the models differed significantly from random expectations ($G^2_3 = 608.31$, $P < 0.001$; interaction model classification*real classification of cases), but such proportions did not differ across spatial scales ($G^2_3 = 3.08$, $P = 0.380$; scale*model classification*real classification interaction).

DISCUSSION

Multiscale analyses of habitat preferences to study habitat selection: advantages and pitfalls

Proper measurement of habitat availability is a key problem in habitat preference studies (Jones, 2001). Random sampling of habitat availability can lead to biased results if the studied species has a very specialized habitat selection behavior or if it requires particular places for nesting (Jones, 2001; Jones & Robertson, 2001). For this reason, Martínez *et al*. (2003a) consider as available habitat for nesting Eagle Owls in Alicante cliffs higher than 4 m and with suitable cavities only, and they compared habitat characteristics around occupied and unoccupied cliffs. Donázar (1988), Sánchez-Zapata *et al*. (1996) and Martínez & Calvo (2000) followed a similar criterion, while Penteriani *et al*. (2001b) used comparisons with both random points and unoccupied cliffs in the same study. In the present case, however, Eagle Owls show a high adaptability to occupy nesting places that may be considered as marginal in other studied populations, a result that can be related to the high abundance of suitable prey. In the present study area, Eagle Owls nest in a great variety of substrates apart from cliffs, such as abandoned buildings, in nests of other raptors or on the ground under trees or even under sparto grass clumps (*unpubl. data*). In this way, it was not sensible to limit the available nest sites to cliffs since this approach would have biased the observed habitat preference in the study area.

In the absence of independent data on the home range size of the studied species, the definition of the spatial scale of measurement is another key issue in studies of habitat preference, since the process of habitat selection is scale-dependent (Johnson, 1980; Jones & Robertson, 2001). Besides, processes different from habitat selection such as the effect of density-dependence on population or metapopulation regulation may be also scale-dependent, starting to influence nest distribution at some undefined spatial scale (Schneider, 1994). One way of tackling this is to select increasingly larger areas within a range seemingly relevant biologically for the species or population under study (Kevin, 1999). Martínez *et al*. (2003a) used areas of 7 (nest site), 25 (home range) and 100 (landscape) km^2 in a recent multiscale study of habitat preference by Eagle Owls in Spain. The size of the nest site scale was established according to the frequency of sightings of adult owls around nest sites before egg laying, the size of the home range scale according to results of radio-tracking studies of nesting individuals in central European populations, and the size of the landscape scale according to regional patterns of change in landscape structure (Martínez *et al*., 2003a). Here much smaller scales were used since the size of foraging areas are expected to vary among habitats according to prey availability (Dill, 1978), so that it would not have been sensible to use estimates of home range size obtained for populations experiencing contrasting levels of food supply. In this study area it seems unlikely that Eagle Owls would move further away from 1500 meters of the nest places because of the high density of both rabbits (Villafuerte *et al*., 1995) and owl te-

TABLE 1

Forward stepwise logistic regression models for the probability of finding occupied Eagle Owl *Bubo bubo* nests at four spatial scales.
[Modelos obtenidos mediante regresiones logísticas por pasos que estiman la probabilidad de presencia de nidos ocupados de Búho Real Bubo bubo *a cuatro escalas espaciales.]*

Variable	b	SE	Wald	P
250 meters of radius *[radio de 250 m]*				
Index of topographic irregularity	2.689	0.443	36.912	0.000
[Índice de irregularidad topográfica]				
Distance to the nearest stream	−3.150	0.701	20.214	0.000
[Distancia al arroyo más próximo]				
Y	−5.012	2.085	5.777	0.016
X^2	−3.924	1.428	7.552	0.006
Constant	−2.013	1.745	1.331	0.249

Overall correct classification rate *[porcentaje de clasificación correcta total]* = 93.5%
Random points correctly classified *[puntos al azar clasificados correctamente]* = 92.0%
Nest points correctly classified by the model *[nidos clasificados correctamente]* = 95.0%

500 meters of radius				
Index of topographic irregularity	1.885	0.296	40.437	0.000
Distance to the nearest stream	−3.220	0.640	25.312	0.000
Cover of dehesa	2.568	1.452	3.129	0.077
[Cobertura de dehesas]				
Y	−4.965	1.828	7.378	0.007
X^2	−3.124	1.225	6.506	0.011
Constant	−1.277	1.536	0.691	0.406

Overall correct classification rate = 91.0%
Random points correctly classified = 89.0%
Nest points correctly classified = 93.0%

1000 meters of radius				
Index of topographic irregularity	1.460	0.233	39.254	0.000
Distance to the nearest stream	−2.866	0.554	26.804	0.000
Y	−5.360	1.765	9.225	0.002
X^2	−3.477	1.218	8.146	0.004
Constant	−1.937	1.561	1.539	0.215

Overall correct classification rate = 89.5%
Random points correctly classified = 89.0%
Nest points correctly classified = 90.0%

1500 meters of radius				
Index of topographic irregularity	1.381	0.221	39.115	0.000
Distance to the nearest stream	−2.908	0.548	28.194	0.000
Y	−4.854	1.707	8.086	0.004
X^2	−3.459	1.189	8.472	0.004
Constant	−2.860	1.660	2.970	0.085

Overall correct classification rate = 89.0%
Random points correctly classified = 88.0%
Nest points correctly classified = 90.0%

rritories (Ortego & Calvo, 2003). Including larger scales would have thus lead to problems of lack of independence between data points, as well as to the risk of including effects of population regulation processes on the observed patterns of nest distribution.

*Habitat preferences and habitat selection
by Eagle Owls in central Spain*

The models obtained at the four selected scales had very high correct classification rates, a result that indicates that the independent variables selected were relevant for nesting Eagle Owls (Seoane & Bustamante, 2001). Model performance did not change across scales, and all models included the same variables as the most significant predictors, the irregularity of topography and the distance to the nearest stream. Thus, habitat preferences by Eagle Owls in the current study area were not dependent on the spatial scale analyzed.

The preference of Eagle Owls for places with irregular topography has been reported in most previous studies (Donázar, 1988; Martínez & Calvo, 2000; Sánchez-Zapata, *et al*. 1996; Martínez *et al*., 2003a; Ortego & Díaz, 2004). The usual interpretation of this result is that nests located in rocky areas and/or steep slopes would be less accessible to both predators and man. The observed preference for nesting closer to streams when available would be interpreted in the same way, as rocky outcrops and steep slopes characterize the surroundings of brooks and streams in the study area. On the other hand, the surroundings of streams might supply a higher abundance of prey because rabbits found in watercourses encounter greater amounts of food and softer soils to dig permanent refuges (Villafuerte *et al*., 1995; Virgós *et al*., 2003). Cover of dehesa positively influenced the probability of finding a nest of Eagle Owls at the scale of 500 meters. Again, this variable may be related to a higher protection of nests due to low levels of human use of this kind of habitat or to higher prey availability due to greater chances of prey capture in open areas.

All the models included as relevant factors two terms (X and Y^2) of the cubic equation used to define the spatial characteristics both of the nest and random points. This result indicates that distribution of owl nests in the study area is clumped. Statistical removal of the lack of independence due to spatial distribution (Legendre, 1990, 1993; Bocard *et al*., 1992; Liebhold & Gurevitch, 2002) did not affect the observed patterns of habitat preference as the predictors selected by the models did not change. In this case, at least, spatial dependence among the sampling points did not affect the reliability of habitat preference models (Lennon, 1999; Vaughan & Ormerod 2003).

Patterns of habitat preference of nesting Eagle Owls in central Spain did not appear to arise from a hierarchical process of habitat selection, as the main predictor variables (irregularity of topography and distance to streams) were the same for all scales. These results contrast sharply with those obtained by Martínez *et al*. (2003a) in eastern Spain, where Eagle Owls selected areas of presumably high food availability at the larger spatial scales and cliffs protected against both man and predators at the lower scales. Differences between the two studies might be attributed to the very high abundance of rabbits in central as compared to eastern Spain (Villafuerte *et al*., 1995; Blanco, 1998), which would lead to a coincidence in the size of nesting and foraging areas. In the area studied, Eagle Owls may select good nesting points as almost any good nesting place will have a high density of prey. Alternatively, differences between the two studies would be related to differences in the ranges of spatial scales covered. It is assumed, according to the knowledge on the distribution of Eagle Owls in the study area, that the spatial scales considered reflected the same basic biological processes than those considered by Martínez *et al*. (2003a), in spite of the differences in absolute values. It seems clear that independent data on the sizes of home ranges and foraging areas as related to levels of food availability in Eagle Owls are needed to choose between these alternatives.

General lack of data on the spatial scales biologically relevant in the habitat selection process of most species raise doubts about the adequacy of multiscale approaches to habitat preferences based on scales selected on the basis of incomplete knowledge of relevant biological traits of the populations under study. Inadequate scales, especially if too large, are expected to lead to unclear or erroneous conclusions on the behavioral responses involved in the habitat selection process (Martínez *et al*., 2003a). Independent data on the local behavior of the selected species, or on the fitness consequences of habitat selection, are thus urgently needed to ascertain whether results from multiscale studies truly reflect underlying biological processes (and what processes) or are biased by the parameter values of the modeling approach.

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<div align="center">APPENDIX</div>

Variables used to analyze habitat preference by Eagle Owls in central Spain. Distances, number of buildings and the index of topographic irregularity were measured on 1:25000 topographic maps. Land uses and number of ecotones were measured in digitalized 1:100000 Corine Land Cover maps, and the 20 land use types provided by such maps were grouped into nine cover categories.
[Variables empleadas para analizar las preferencias de hábitat del Búho Real en el centro de España. Las distancias, número de edificaciones y el índice de irregularidad topográfica se midieron en mapas topográficos de escala 1:25000. Los usos del suelo y el número de ecotonos se midieron en los mapas digitalizados 1:100000 del sistema Corine Land Cover. Los 20 usos diferenciados en estos mapas se agruparon en nueve categorías de uso]

Variable

Distance to the nearest village (m) *[Distancia al pueblo más próximo (m)]*

Number of buildings *[Número de edificaciones]*

Distance to the nearest paved road (m) *[Distancia a la carretera más próxima (m)]*

Distance to the nearest unpaved road (m) *[Distancia al camino más próximo (m)]*

Distance to the nearest stream (m) *[Distancia al arroyo más próximo (m)]*

Index of topographic irregularity (number of altitude curves crossed by two lines running N-S and E-W from the plot centre) *[Índice de irregularidad topográfica (número de curvas de nivel cortadas por dos líneas de dirección N-S y E-O que pasan por el centro del círculo de muestreo]*

Cover of non-irrigated herbaceous crops (%); sum of the covers of 1) non-irrigated arable land; and 2) land occupied mainly by agricultural uses with some areas of natural vegetation *[Cobertura de cultivos herbáceos de secano (%); suma de las coberturas de 1) tierras de labor en secano; y 2) terrenos agrícolas con espacios de vegetación natural]*

Cover of irrigated crops (%); sum of the covers of 1) permanently irrigated lands; and 2) other irrigated lands *[Cobertura de cultivos de regadío (%); suma de las coberturas de 1) cultivos herbáceos en regadío; y 2) otras zonas con irrigación]*

Cover of perennial crops (%); sum of the covers of 1) vineyards; 2) olive groves; 3) mixtures of perennial crops; 4) irrigated orchards; and 5) mixtures of annual and perennial crops *[Cobertura de cultivos leñosos (%); suma de las coberturas de 1) viñedos; 2) olivares; 3) mosaico de cultivos permanentes; 4) otros frutales de regadío; y 5) mosaico de cultivos anuales con cultivos permanentes]*

Cover of tree plantations (%); sum of the covers of 1) coniferous forest; and 2) other broad-leaved tree plantations *[Cultivos forestales (%); suma de las coberturas de 1) pináceas; y 2) otras frondosas de plantación]*

Cover of dehesa (%); cover of agro-forestry areas *[Cobertura de dehesa (%); cobertura de sistemas agroforestales]*

Cover of pastures (%); sum of the covers of 1) other pastures; and 2) salines *[Cobertura de pastizales (%); suma de las coberturas de 1) otros pastizales; y 2) salinas]*

Cover of scrublands (%); sum of the covers of 1) Low-density scrub and shrubland; and 2) High shrubland formations of medium to high density *[Cobertura de matorrales (%); suma de las coberturas de 1) matorral subarbustivo o arbustivo poco denso; y 2) grandes formaciones de matorral denso o medianamente denso]*

Cover of Mediterranean forests (%); sum of the covers of 1) forests of evergreen sclerophyllous and Lusitanian oaks; and 2) transitional woodland-shrubland *[Cobertura de bosque mediterráneo (%); suma de las coberturas de 1) perennifolios esclerófilos y quejigares; y 2) matorral boscoso de transición]*

Cover of water bodies (%); sum of the covers of 1) rivers and natural water courses; and 2) reservoirs *[Cobertura de medios acuáticos (%); suma de las coberturas de 1) ríos y cauces naturales; y 2) embalses]*

Number of ecotones (number of changes of land uses crossed by two lines running N-S and E-W from the plot centre) *[Number of ecotones (número de cambios de uso de la tierra cortados por dos líneas de dirección N-S y E-O que pasan por el centro del círculo de muestreo]*

Distance to the nearest occupied nest of Eagle Owl (m) *[Distancia al nido ocupado más próximo de Búho Real (m)]*