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Rocks and trees: habitat response of Tawny Owls *Strix aluco* in semiarid landscapes

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Breeding territories of Tawny Owls *Strix aluco* were surveyed in Murcia, SE Spain, in 1992 using imitating calls. In all, 178 territories were detected and although regional density was low, local breeding densities were as high as 17 pairs/100 km^2. The response of Tawny Owls to habitat characteristics in this semiarid region was related to the scale of the study. The slope followed by the forest cover were the best predictor variables for the Tawny Owl's breeding density at a 9 km^2 scale, whereas forest cover and the size of the forests were the best predictor variables when the scale was increased to 100 km^2. Owls seemed to select rugged rocky areas for breeding owing to the lack of suitable holes for nesting in the pine forest, but also required a certain amount of forest for hunting. Our results suggest that Tawny Owls might be very flexible with respect to habitat selection, even at the limits of its distribution range.

1. Introduction

Habitat fragmentation, and specially forest fragmentation, is another topic related to habitat selection that has been central in conservation biology and landscape ecology (Wilcove 1985, McGarigal & McComb 1995). Forest fragmentation has been documented as a major cause of biodiversity loss and the decline of endangered forest and shrubsteppe birds (Saunders et al. 1991, Hansson 1992, Knick & Rotenberry 1996). However, in semiarid mediterranean regions, forest fragmentation can be considered as a long-term process associated with human activities (Le Honerou 1981) and major climate constrictions resulting in patchy and changeable forest landscapes (Chaparro 1996).

The Tawny Owl *Strix aluco* is a forest owl whose breeding range reaches Mediterranean countries at its southern limits (Cramp 1985). Here, studies on the habitat of the species are lacking although the response and habitat tolerance of animals throughout their distribution ranges may provide valuable information for conservation (Lawton 1993).

Most studies concerning habitat relationships of raptors and owls focus on "microhabitat" variables such as tree characteristics, ground cover or perches, often measured at small detailed scales (Fuller 1979, Andrew & Mosher 1982, Cody 1985, Verner et al. 1986, Belthoff & Ritchison 1990, LaHaye, Gutiérrez & Call 1997). This has been a common approach to analysing the distribution and densities of numerous species (Wiens 1989), although multiscale studies have proved that species-habitat associations may differ at each scale (Wiens 1989, Rotenberry & Van Horne 1987, Kotliar & Wiens 1990, Jokimäki & Huhta 1996). In spite of this, large-scale studies on birds of prey habitat are scarce (Sánchez-Zapata et al. 1994, Donázar, Hiraldo & Bustamante 1993, Solonen 1994).

The objectives of this paper are: (1) to analyse the distribution and density of breeding Tawny Owls *Strix aluco* in semiarid regions at the limits of its distribution range; and (2) to discuss the role of habitat structure and scale.

2. Material and methods

2.1. Study area

The study area covered the Murcia Region, an 11 317 km^2 area located in SE Spain with a mediterranean arid and semiarid climate and mean annual rainfall ranging between 200 mm and 500 mm. Forests covered 2182 km^2 (19.28% of the region). Most forest patches (N = 248) were between 30–300 ha and only a few were larger than 1000 ha. The minimum patch area considered was 15 ha and the largest patch was 23 842 ha. The main tree species in Murcia's forests is, by far, *Pinus halepensis* Mill., other species like *Quercus rotundifolia* L., *Pinus pinaster* Aiton and *Pinus nigra* Arnold, are much less common.

2.2. Census

The presence of owls was determined by visiting all forest patches at the beginning of the 1992 breeding season (November–February) and imitating calls (Redpath 1994). Four imitating calls, lasting approximately 1 min., were given at 5 min. intervals for up to 30 min. in each forest patch. In a similar work with this method, Redpath (1994) indicated that 94% of all owls responded to imitation calls within the first 30 min. In forest patches larger than 100 ha imitating calls were played at least once in each 100 ha cell. When there was more than one pair of owls, territory boundaries were determined by imitating responses from neighbours simultaneously (Redpath 1995a). Our data can be considered as an estimate of the number of territories since the highest breeding densities in the study area are around 2 territories/100 ha (J. E. Martínez & M. Carrete, unpublished data). The censuses were conducted under favourable weather conditions (Fuller & Mosher 1981).

2.3. Habitat data

The location of recorded territories was incorporated into a Geographic Information System (GIS) using the Universal Transverse Mercator (UTM) grid of 1 km^2 cells. For the first landscape approach, the 1 km^2 cells map was transformed into a 9 km^2 cells map, so the regional map of 11 317 km^2 cells was transformed into 1381 cells of a 9 km^2 map.

The second landscape approach focused on 100 km^2 cells. As a result of increasing the size of the cells, a good proportion of them included large tracks of sea and neighbourg regions that were not surveyed. Thus, these cells were excluded from data analysis, so the study at the 100 km^2 scale included fewer breeding territories for the species in 88 cells of 100 km^2 (see results).

The same GIS was used to characterise the breeding sites, including the following groups of variables (Table 1):

1. Land-use variables. Different land-use categories were obtained from the maps of the Ministry of Agriculture (1:200.000). New categories were formed by combining related land-use cover categories (e.g., lemon, orange and other fruit trees were combined to give a single arboreous intensive agriculture category). The slope (degrees from horizontal) was calculated from the digitalised land model (Spanish Cartographic Service), by comparing the altitude of each point on the grid (200 × 200 m) with that of the surrounding points. An average value for the different cells was calculated from the data of each point. These values ranged from 0 to 24.2 at the 9 km^2 scale and from 0.2 to 13.5 at the 100 km^2 scale.
2. Edge variables were measured as the length (km) of the edges between different land uses using the digitalised land-use map.
3. Landscape structure variables. We used several variables to describe landscape structure further. These variables were measured as the number, size (ha) and shape (MSI) (McGarigal & Marks 1994) of the different patches of natural vegetation. The mean shape index (MSI) (Eq. 1) increases with the irregularity of the patch-shape and the minimum value

(MSI = 1) indicates a circular patch.

$$\mathrm{MSI} = \left(\sum\left[p_i / 2\sqrt{\pi} \times a_i\right]\right) / n \qquad (1)$$

where p_i = perimeter of patch i (m), a_i = area of patch i (m^2) and n is the total number of patches.

2.4. Genelarized linear models

We used Generalized Linear Models (GLMs) (Dobson 1983, McCullagh & Nelder 1989) for a mathematical description of breeding sites. GLMs permit a wider range of relationships between the response and the explanatory variables and the use of other error formulations, when the normal error for the traditional regression is not applicable. Three components have to be defined for a GLM: a linear predictor, an error function and a link function. A linear predictor (LP) is defined as the sum of the effects of the predictor variables as follows:

$$\mathrm{LP} = a + b \times 1 + c \times 2 + \ldots$$

where a, b, c ... are parameters to be estimated from the observed data and × 1, × 2,... the ex-

Table 1. Variables used to characterise the breeding areas

Land uses
PATCH: number of land-use patches per cell.
RICHNESS: number of different land-use patches per cell.
DIVERSITY: diversity (Shanon-Weaner) of land-uses.
AINTA: % of cell covered by arboreous intensive agriculture (i.e. lemon and orange trees).
HINTA: % of cell covered by herbaceous intensive agriculture (vegetables).
AEXTA: % of cell covered by arboreous extensive agriculture (i.e. olive and almond trees).
HEXTA: % of cell covered by herbaceous extensive agriculture (cereals).
SHRUB: % of cell covered by shrubland.
FOREST: % of cell covered by forest (mainly *Pinus halepensis*).
SHF: % of cell covered by mixed shrub-forest.
SLOPE: topographic irregularity index.

Edges
IAEA: length (km) of edges between intensive and extensive agriculture.
FOIA: length (km) of edges between intensive agriculture and forest.
IASH: length (km) of edges between intensive agriculture and shrubland.
IASF: length (km) of edges between intensive agriculture and mixed shrub-forest.
FOEA: length (km) of edges between forest and extensive agriculture.
EASH: length (km) of edges between extensive agriculture and shrubland.
EASF: length (km) of edges between extensive agriculture and mixed shrub-forest.
FOSH: length (km) of edges between forest and shrubland.
FOSF: length (km) of edges between forest and mixed shrub-forest.
SHSF: length (km) of edges between shrubland and mixed shrub-forest.

Structure
NFOREST: Number of forest patches per cell.
SFOREST: Mean size (ha) of forest patches per cell.
MSIFOREST: Mean shape index (irregularity) of forest patches per cell.
NSHRUB: Number of shrubland patches per cell.
SSHRUB: Mean size (ha) of shrubland patches per cell.
MSISHRUB: Mean shape index (irregularity) of shrubland patches per cell.
NSHF: Number of mixed shrub-forest patches per cell.
SSHF: Mean size (ha) of mixed shrub-forest patches per cell.
MSISHF: Mean shape index (irregularity) of mixed shrub-forest patches per cell.
NNAT: Number of natural vegetation patches per cell.
SNAT: Mean size (ha) of natural vegetation patches per cell.
MSINAT: Mean shape index (irregularity) of natural vegetation patches per cell.

planatory variables. The error function will depend on the nature of the data. For density response variables (number of territories), the Poisson distribution is an adequate error function (Vincent & Haworth 1983). One appropiate link function for a Poisson distribution is the discrete Poisson function. This means that the number of breeding pairs of an area being selected as a nest site is a discrete, s-shaped function when the linear predictor is a first-order polynomial, or a bell-shaped function for second order polynomials.

Univariative regressions of the number of territories on each of the environmental variables were calculated. In addition. quadratic terms were fitted to each model and retained if they improved the fit (Gibbons et al. 1994). Univariative regressions were used only as a guide to which variables were likely to be useful in subsequent modelling procedures and no ecological inferences were made (Austin et al. 1996).

For multiple regression models of forest and slope, we fitted each explanatory variable to the observed data using the "forward stepwise" procedure (Nicholls 1989) and chose a 1% level of significance to include a variable in a model (Donázar et al. 1993, Gibbons et al. 1994). For regression analysis, we used the program STATISTIX (Analytical Software 1992).

3. Results

3.1. Census

We detected 178 territories of Tawny Owls in 19 forest patches. Only 7.6% of forest patches within the study area held territories. The population was concentrated in clumps and in 94.7% of the 9 km^2 cells and 73.9% of the 100 km^2 cells the species was not detected. Overall regional density was low (1.57 territories/100 km^2), but densities in the 100 km^2 cells were as high as 17 territories/100 km^2. If only forest is considered, the mean regional density was 8.15 territories/100 km^2 of forest.

3.2. Response to land uses

The slope was the best predictor variable at the 9 km^2 scale, decreasing by 46.8% the deviance of the null model. A similar, but smaller decrease, was obtained with the forest (44.4%). The response to different agricultural land-uses was negative, and so was the response for other descriptors of land-use characteristics (patches and richness), except diversity (Table 2).

When the scale was increased, the proportion of land covered by forest was the best predictor variable, decreasing by up to 61.3% the deviance of the null model. The response was a bell-shaped function that included the quadratic term. At this scale, the slope accounted for only 16% of the change in the deviance. The responses to intensive agriculture uses and shrubland were negative, but the response to extensive agriculture uses, mixed shrub-forest and the other land-use categories were positive (Table 2).

3.3. Response to edges

The percentage of deviance explained by edge variables at the 9 km^2 scale was much smaller than that of land use variables. The length of edges between extensive agriculture and shrubland (EASH) decreased by 15% the deviance of the null model with a negative response. The responses were negative for most variables except edges between forest and extensive agriculture uses (FOEA), shrub (FOSH) and mixed shrub-forest (FOSF). At the 100 km^2 scale, edge variables performed better. The best fitting variables were the edges between forest and extensive agriculture (FOEA) and mixed shrub-forest (FOSF), which accounted for 27.7% and 26.5% of the decrease in the deviance of the null model respectively. The responses were negative for most of the edges among non-forested land uses (Table 2).

3.4. Response to landscape structure

The percentage of deviance explained by landscape structure variables at both scales was intermediate between edge and land use variables. The mean size of forest (SFOREST) was the best fitting structure variable in the 9 km^2 cells and accounted for a 33.5% decrease in the deviance of the null model. The mean size of forest (SFOREST) and the number of mixed shrub-forest patches

(NSHF) in the 100 km^2 cells decreased by 38.1% and 34.8% the deviance of the null model, respectively, with a positive bell-shaped function response in both cases. The response to non-wooded vegetation structures was negative (NSHRUB, MSISHRUB) or not signficant (SSHRUB) (Table 2).

3.5. Multivariative models

The GLM model of breeding density included the slope (SLOPE) and its quadratic term ($SLOPE^2$) as the first variable followed by the forest cover (FOREST) at the 9 km^2 scale. This model reduced by 58.4% the deviance of the null model (Table 3, Fig. 1).

Table 2. Response of the Tawny Owl *Strix aluco* to the different habitat variables. % dev = % deviance explained; ns, no significant; $P > 0.01$; *, $P < 0.01$; **, $P < 0.001$. Responses: (–) s-shaped negative function, (+) s-shaped positive function, (++) bell-shaped positive function. Df = 1379 for s-shaped functions; df = 1378 for bell-shaped functions.

	Scale			
	9 km^2		100 km^2	
	% dev.	Response	% dev.	Response
Land use				
PATCH	7.74**	–	3.87*	++
RICHNESS	1.87**	–	4.18*	++
DIVERSITY	6.48*	++	10.66**	++
AINTA	3.52*	–	3.92*	–
HINTA	9.16**	–	20.89**	–
AEXTA	3.72**	–	13.18**	++
HEXTA	10.77**	–	11.53*	++
SHRUB	12.13**	–	19.41**	–
FOREST	44.41**	+	61.31**	++
SHF	1.99**	+	13.31*	+
SLOPE	46.77**	++	16.01*	++
Edges				
IAEA	9.48*	–	16.01**	–
FOIA	ns		ns	
IASH	5.37**	–	7.10**	–
IASF	ns		7.54**	++
FOEA	6.22**	++	27.68**	++
EASH	15.02**	–	20.06**	–
EASF	0.85*	–	4.46**	++
FOSH	0.96**	+	3.47*	++
FOSF	8.90**	++	26.49**	+
SHSF	ns		ns	
Structure				
NFOREST	8.52*	++	7.98**	+
SFOREST	33.53**	++	38.08**	++
MSIFOREST	18.71**	++	18.95*	++
NSHRUB	ns		13.41**	–
SSHRUB	10.34**	–	ns	
MSISHRUB	ns		17.65**	–
NSHF	3.59**	++	34.75**	++
SSHF	2.06**	+	ns	
MSISHF	4.05*	++	7.28**	+
NNAT	0.57**	+	12.35**	++
SNAT	16.07**	++	27.50**	++
MSINAT	3.72**	++	7.95**	++

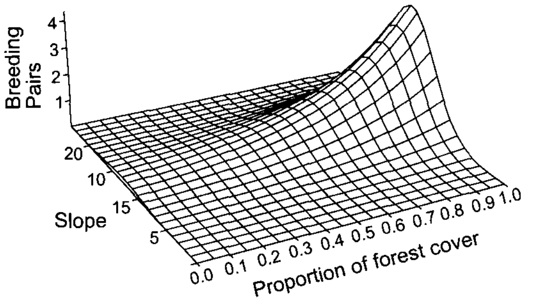

Fig. 1. Number of breeding pairs of Tawny Owl's in relation to slope and proportion of forest cover at the 9 km^2 scale.

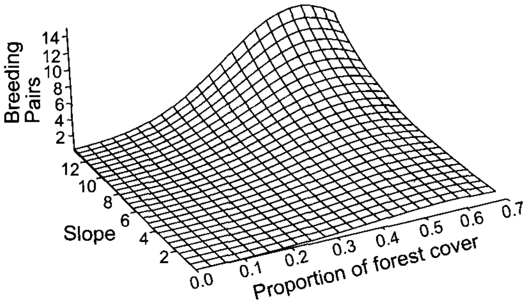

Fig. 2. Number of breeding pairs of Tawny Owl's in relation to slope and proportion of forest cover at the 100 km^2 scale.

When the scale was increased (100 km^2) the model performed slightly better (66.2% of deviance explained), but the order of the variables was the opposite. The forest cover (FOREST) and its quadratic term (FOREST^2) were entered first in the model, followed by the slope (SLOPE) (Table 4, Fig. 2).

4. Discussion

The Tawny Owl is a hole nesting bird of Paleartic distribution, which depends on trees for roosting, nesting and hunting (Mikkola 1983, Cramp 1985), though it can also survive in small woods, when the matrix surrounding the woods contains numerous perches (Hardy 1992). In semiarid landscapes, forest growth is poor and thus, holes in trees are rarely found. Our 9 km^2 landscape approach to the Tawny Owl's habitat showed that the slope was the best predictor variable, even slightly better than forest cover.

The slope can be considered a good descriptor of rugged terrain with rocks and cliffs, where the species can breed when tree-holes are lacking. However, it is possible that the response was also related to mature forest stands usually found on north-facing mountain slopes (Sánchez et al. 1995), providing both rocky holes for nesting and mature pine stands for perching and hunting (Petty & Peace 1992). Nevertheless, the response to slope followed a bell-shaped function, so that in highly rugged terrain the lower density of the owl may be due to the lack of trees in large rocky outcrops.

Forest fragmentation has been shown to influence breeding density (Hardy 1992) and behaviour of this species by either increasing home-range size (Redpath 1995a), interperch distances or both (Redpath 1995b). At the 9 km^2 scale, the response to variables related to fragmentation (e.g., edges) was negative, indicating a similar effect of fragmentation on the breeding density of owls in semiarid landscapes. When the scale was increased, the response to forest cover followed a bell-shaped function and the density of owls was lower with more forest cover. This pattern may be related to the negative relationship between small mammals density and forest size

Table 3. GLM model for the Tawny Owl *Strix aluco* breeding density. Scale 3 × 3 km; df = 1377; model deviance = 464.87; null model deviance = 1116.97; % change = 58.38.

	Coeff.	SE	P
constant	– 8.62879	0.67438	0.0000
SLOPE	1.06623	0.12874	0.0000
SLOPE^2	– 0.04134	0.00574	0.0000
FOREST	3.22507	0.30425	0.0000

Table 4. GLM model for the Tawny Owl *Strix aluco* breeding density. Scale 10 × 10 km; df = 84; model deviance = 113.49; null model deviance = 335.3; % change = 66.15.

	Coeff.	SE	P
constant	– 3.83264	0.54002	0.0000
FOREST	14.3734	2.89029	0.0000
FOREST^2	– 12.6665	3.68095	0.0000
SLOPE	0.17964	0.04325	0.0000

as has been found in some other studies (Tellería, Santos & Alcantara 1991, Redpath 1995a). This relationship may be even more relevant in mediterranean semiarid landscapes where small mammals are scarce (Herrera & Hiraldo 1976, Sánchez-Zapata et al. 1995, Sánchez-Zapata & Calvo 1998). Breeding numbers of Tawny Owls may also be constrained by the Eagle Owl *Bubo bubo*. The study area contains one of the most dense populations of Eagle Owls known in the world; these birds prefer rocky outcrops and cliffs for breeding (Martínez et al. 1992, Sánchez-Zapata et al. 1995). The Eagle Owl often preys on Tawny Owls and other raptor species and may affect their distributions (Mikkola 1983, Solonen 1993, Tella & Mañosa 1993).

Although breeding densities were generally low, the species seemed adaptable. Tawny Owls breed in almost any suitable habitat within the limit of its distribution range. Here small mammals are scarce, competitors and predators are commom and the Owl must shift between rocks and trees for breeding, hunting and roosting. Since rocky stands do not change (except a few destroyed by mining) and afforestation is increasing with the support of European Union agricultural regulations (R. 797/85/CEE, 1094/88/CEE & 1765/92/CEE), an increase in the population and distribution range of the species may be expected, as seems to be happening elsewhere in Spain (Fajardo & Babiloni 1994).

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Selostus: **Lehtopöllön reviirien sijoittuminen kaakkoisespanjalaisissa maisemissa**

Kirjoittajat tutkivat lehtopöllön pesimähabitaattien sijoittumista Kaakkois-Espanjassa 1992. Reviirit kartoitettiin tutkimalla vasteita nauhalta soitettuun soidinhuhuiluun. Tällä menetelmällä löydettiin 178 reviiriä 11317 km^2 kokoiselta tutkimusalueelta. Vaikka pesimätiehys oli keskimäärin hyvin alhainen, paikoin havaittiin jopa 17 pesivää paria 100 km^2:lla. Reviirit sijoitettiin paikkatietojärjestelmään ja niiden elinympäristöjen rakennetta tutkittiin perustuen alueen karttapohjaiseen maankäyttöluokitukseen eri mittakaavoissa. Maiseman topografinen vaihtelu (SLOPE) ja metsäpinta-ala selittivät parhaiten reviirien sijoittumista pienemmässä, 9 km^2:n mittakaavassa. Suuremmassa, 100 km^2:n mittakaavassa lehtopöllön esiintymistä selittivät parhaiten metsäpinta-ala ja metsälaikkujen koko. Lehtopöllö näyttää siis valikoivan mäkisiä, runsasmetsäisiä maastoja. Alueella sopivia pesäkoloja puissa on niukasti saatavilla, ja pöllöt enimmäkseen pesivät maaonkaloissa, joita on runsaammin saatavilla mäkisissä (kivikkoisissa) maastoissa. Metsän merkitys on lehtopöllölle suuri nimenomaan saalistusympäristöinä. Kirjoittajat kuitenkin toteavat, että lehtopöllö on sangen joustava elinympäristövaatimuksissaan, vaikka tutkimusalue sijaitsee lajin levinneisyysalueen eteläreunalla.

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Appendix. Mean and SE of the different variables used to characterize the habitat.

	Scale			
	9 km^2		100 km^2	
	MEAN	SE	MEAN	SE
Land use				
PATCH	10.30	0.12	60.44	1.71
RICHNESS	4.25	0.04	9.53	0.21
DIVERSITY	1.35	0.01	2.27	2.27
AINTA	4.43	0.33	5.63	0.86
HINTA	6.46	0.43	7.91	1.35
AEXTA	10.69	0.45	12.93	1.37
HEXTA	34.88	0.84	27.44	2.18
SHRUB	19.00	0.59	19.89	1.54
FOREST	14.74	0.64	16.74	1.81
SHF	5.98	0.34	6.22	0.74
SLOPE	4.43	0.09	4.39	0.26
Edges				
IAEA	1.29	0.07	16.90	1.59
FOIA	0.18	0.02	2.58	0.51
IASH	0.70	0.05	10.05	1.40
IASF	0.07	0.01	0.84	0.21
FOEA	1.84	0.09	21.61	2.52
EASH	4.27	1.35	51.18	3.76
EASF	1.00	0.06	11.22	1.50
FOSH	0.84	0.05	10.31	1.05
FOSF	0.79	0.06	10.38	1.68
SHSF	0.27	0.03	3.18	0.51
Structure				
NFOREST	1.11	0.04	5.09	0.38
SFOREST	87.03	4.45	371.20	57.65
MSIFOREST	0.87	0.02	1.65	0.07
NSHRUB	2.04	0.05	11.93	0.63
SSHRUB	84.72	3.68	180.10	16.41
MSISHRUB	1.24	0.02	1.74	0.02
NSHF	0.68	0.03	4.19	0.43
SSHF	34.91	2.26	136.40	17.36
MSISHF	0.61	0.02	1.37	0.08
NNAT	3.82	0.07	21.22	0.92
SNAT	112.70	37.21	220.20	13.78
MSINAT	1.46	0.01	1.76	0.02