Snake species richness and shrubland correlate with the short-toed eagle (*Circaetus gallicus*) distribution in south-eastern Spain

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The short-toed eagle (*Circaetus gallicus*) is a trophic specialist with a diet based almost exclusively on ophidians. In this work, the distribution of this eagle in south-eastern Spain taken from national atlases, is analysed in relation to environmental variables. The results show that the short-toed eagle is distributed primarily in shrublands, probably because there it can easily locate and capture its prey. It also prefers an intermediate cover of forest, because it needs trees for nesting. Lastly, there was a correlation, after statistically controlling for other variables, between snake species richness and eagle presence. It is possible that snake species richness favours the presence of this raptor, as it preys on different species. Alternatively, because this raptor preys preferentially on dominant ophidians in the study area, it is also possible that the presence of this eagle favours snake diversity by a top-down regulation on the ophidian community.

Introduction

The distribution of organisms in space is not aleatory, but rather is determined by their ecological niche, especially by resources needed to survive and reproduce (Brown 1995, Pulliam 2000, Wiens & Donoghue 2004). Therefore, specialist feeders should have a distribution strongly coinciding with that of the prey, as population size is limited by prey availability (Newton 1998). For this reason, prey availability strongly affects the reproduction and the distribution of raptors having trophic specialization (Newton 1979). However, prey accessibility, but not only prey availability, is important in determining the predator distribution (Janes 1985). For example, Bonelli's eagle (*Hieraaetus fasciatus*) preys primarily on rabbits (*Oryctolagus cuniculus*), but the capture rate for this prey is higher in territories with open vegetation, where detection and capture is easier (Ontiveros *et al.* 2005). In zones where accessibility to rabbits is lower, the capture rate for secondary prey (for example, pigeons, *Columba* sp.) was higher, showing adaptive flexibility in its diet (Ontiveros *et al.* 2005). Nevertheless, the more specialist the predator, the lower its flexibility, and aspects such as presence and accessibility of preys may
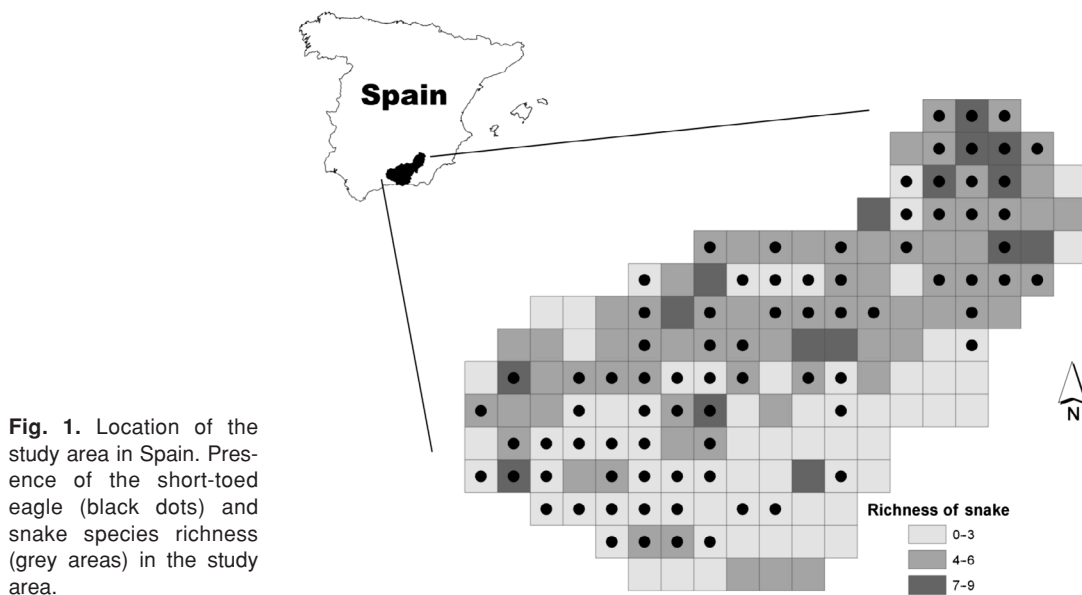
Fig. 1. Location of the study area in Spain. Presence of the short-toed eagle (black dots) and snake species richness (grey areas) in the study area.

be the primary factor limiting its distribution.

A raptor with a highly specialized diet is the short-toed eagle (*Circaetus gallicus*), which preys almost exclusively on ophidians (95% of its diet, Gil-Sánchez & Pleguezuelos 2001). Snakes are usually very elusive animals, and therefore factors determining the distribution of this eagle probably are related to the accessibility to its primary prey. For example, this raptor forages primarily among crops and pastureland searching for snakes, avoiding forest during foraging, probably because snake detection is easier in open lands (Bakaloudis *et al.* 1998). On the other hand, the presence of more snake species might favour the distribution of this eagle for different reasons (*see* Discussion), primarily because alternative prey may be available when the primary one is scarce, as occurs for the Bonelli's eagle (Ontiveros *et al.* 2005).

In this study, we seek to find the ecological factors that determine the distribution of the short-toed eagle in southeastern Spain. We predict that factors increasing snake accessibility should favour the eagle's presence. We test the effect of different habitats (land uses), with different coverage, and therefore, with different presumable effects on the access to snakes. Also, we analyse the effect of topographic (altitude, altitudinal range, kilometres of river) and climatic variables (temperature, thermal range,

precipitation) on the presence of the short-toed eagle. Moreover, we study the effect of human population, which is predicted to be negative, because there is direct persecution of this raptor (Sánchez-Zapata *et al.* 1995), and its snake prey (Pleguezuelos 2001). Finally, we also considered the relationship between prey (ophidians) species richness and eagle presence. The conservation of the short-toed eagle may be problematic, as ophidians are decreasing globally (Gibbons *et al.* 2000). Moreover, the short-toed eagle might be an indicator of snake species abundance.

Material and methods

This study concentrates on the province of Granada (Fig. 1) because the diet of the short-toed eagle is well known there (Gil-Sánchez & Pleguezuelos 2001). The study area has a broad variability of Mediterranean environments and the greatest altitudinal gradient in the Iberian Peninsula (0–3482 m). Short-toed eagles nest in this area during spring, but many migrate to Africa in autumn (Mañosa 2003). The province was divided into 158 squares of 10 × 10 km, which were the statistical units analysed. For each square, we considered whether the eagle was present or absent according to records in the Vertebrate Dataset of Spain (Ministerio de Medio

Ambiente 2003). Although these data may have sampling errors (Bustamante & Seoane 2004), these mistakes would diminish the statistical power, making analyses more conservative.

As predictor variables of eagle presence, three topographic variables were used: mean altitude, altitudinal range, and river length in each square. Three climatic variables were also used: total annual precipitation, mean annual temperature, and thermal range (range of annual mean temperature). For land uses, we used five variables: the percentage of the surface covered by pastures (grassland and other soils with scarce vegetation), cultivated, covered by forest, and by shrubland (shrubby vegetation); habitat heterogeneity (an index of environmental heterogeneity, measured as the sum of the different land uses in the square, with values between 1 and 11; *see* for example Atauri & de Lucio [2001]). The density of the human population was also included. All these variables were taken from maps of the Environmental Information Web of Andalusia (Junta de Andalucía 2001) by means of a geographic information system (SAGA; Conrad 2005). We also included the geographic coordinates of the square centre (longitude and latitude, in UTM), as well as their square and their interaction, in order to control for spatial autocorrelation (Legendre 1993). We did not introduce factorial interactions with polynomial terms or three-order terms because this destabilized the matrix, and the model could not be calculated. The last variable was ophidian species diversity for each square, which was determined from data in the Vertebrate Dataset of Spain (Ministerio de Medio Ambiente 2003).

All variables used in this study had a normal distribution according to a Kolmogorov-Smirnov test, or their errors were normalized by means of logarithms (Sokal & Rohlf 1995). In a first step, we tested whether the 13 variables differed in mean or variance between squares where the eagle was present and those where it was absent. Values of p were corrected with sequential Bonferroni. In a second step, we used a Generalized Linear Model with a binomial distribution of errors and linked it to a Probit function. In this model, we introduced those variables that could explain the distribution of the eagle (Guisan & Zimmermann 2000). We did not include altitude simultaneously with temperature, as they were highly correlated ($r = -0.83$; $p < 0.001$; $n = 158$ squares) and this might have provoked multicollinearity. We also used only a variable of land use, because these variables are proportions of the same squares and therefore are not independent of each other. To eliminate variables without significant effects on the presence of the eagle, we used a forward stepwise model, with $p = 0.10$. Results are given as mean ± SD.

Results

In the study area, the short-toed eagle was present in 80 out of 158 squares (50.6% of presences; Fig. 1). The squares with eagle did not statistically differ from those without eagle in any variable except for shrubland surface area, which was greater where the eagle was present (Table 1). This difference remained significant after Bonferroni correction. There was an almost significant difference in ophidian species richness, which was higher in squares were the eagle was present (Table 1 and Fig. 1). Temperature, altitude and forest surface means did not significantly differ, but the variances did, being higher for the three variables in squares where the eagle was not present (F-ratio > 3.0, $p < 0.001$; Levene test: $F_{1,156} > 10.0$, $p \leq 0.001$). This suggests that the eagle preferred zones with intermediate temperatures, altitudes, and forest cover, rejecting zones where these variables had extreme values. This did not occur for any other variable (F-ratio < 3.0, $p > 0.05$).

To test the effects of independent variables on the presence/absence of the short-toed eagle in a multivariate analysis, we used a forward stepwise Generalized Linear Model. We introduced temperature, but not altitude in the model (*see* Material and methods), because it had higher F values in Levene tests than did the altitude ($F = 19.9$ *vs*. $F = 17.5$, respectively). The only land-use category we introduced was shrubland surface area as, according to the t-test, it was the only factor significantly affecting the distribution of the eagle. The final model included 3 variables. The most important variable, according to the Wald statistic, was shrubland surface area, which positively affected the presence of

Table 1. Differences in characteristics (mean ± SD) between the squares where the short-toed eagle was present (*n* = 80) and those where it was absent (*n* = 78). Mean values are not transformed, but tests were performed with log-transformed values when necessary. The last column shows the correlation coefficient between ophidian species richness and variables. Asterisks indicate significant correlations after Bonferroni correction.

	Present	Absent	*t*	*p*	*r*
Altitude (m)	1399 ± 256	1470 ± 484	1.17	0.25	0.10
Altitudinal range (m)	106 ± 38	113 ± 37	1.21	0.23	0.37*
Rivers (km)	52.8 ± 18.2	52.6 ± 18.7	0.07	0.95	0.05
Precipitation (mm)	632 ± 193	614 ± 184	0.60	0.55	0.56*
Temperature (°C)	12.8 ± 1.1	12.5 ± 1.9	0.88	0.38	−0.09
Thermal range (°C)	18.48 ± 1.35	18.00 ± 1.81	1.89	0.06	−0.26*
Pastures (km^2)	19.1 ± 18.9	22.0 ± 20.1	0.94	0.35	0.01
Forests (km^2)	4.4 ± 5.6	6.1 ± 9.5	1.37	0.17	0.04
Cultivated area (km^2)	51.2 ± 28.2	48.3 ± 31.1	0.61	0.55	−0.21
Shrubland (km^2)	23.8 ± 18.5	15.6 ± 13.5	3.15	0.002	0.24*
Habitat heterogeneity	6.9 ± 1.5	6.7 ± 1.6	0.67	0.50	0.35*
Population (inhabitants km^{-2})	6754 ± 31784	3986 ± 7702	0.37	0.71	0.20
Snake species richness	4.21 ± 2.09	3.60 ± 1.92	1.91	0.058	

the eagle, following altitudinal range, which had a negative estimate (Table 2). The third most important variable was the ophidian species richness (Table 2). The remaining variables had non-significant effects on the eagle distribution (Table 2).

Discussion

The results of this study suggest a relationship between the distribution of the short-toed eagle and the shrubland surface area, having the most consistent effect on the eagle distribution. We found no significant effects of pastureland or cultivation, although in Greece Bakaloudis *et al.* (1998) found that this raptor forages primarily in such habitats. In our study area, it is possible that the short-toed eagle forages primarily in shrubland because ophidian abundance is higher there. In fact, snake species richness increased significantly with shrubland surface area, but not with cultivated area or area of pastures (Table 1). Bakaloudis *et al.* (1998) found that the major prey of the short-toed eagle in their study area (*Natrix natrix*) was distributed primarily in cultivated areas and pastures, where the eagle foraged. This raptor hunts by hovering to detect a prey, and then plunging down onto it (Grande & Hiraldo 1987). Evidently, ophidians are easier to detect in open areas with thin tree cover, which explains our findings and also those of Baka-

loudis *et al.* (1998). Therefore, this raptor needs open areas to hunt, although the characteristics of those zones vary geographically.

Alternatively, Sánchez-Zapata *et al.* (1999) found an effect of forest availability on the abundance of this raptor. This is probably because this eagle nests in trees (Grande & Hiraldo 1987, Bakaloudis *et al.* 2001). Therefore, at least during the breeding season, this raptor inhabits heterogeneous zones with availability of forests for nesting and open areas for hunting. In concordance with this, we found that squares

Table 2. Results of the Generalized Linear Model, showing the estimate, the Wald statistic and the probability. Variables included in the final model are indicated with boldface.

Variable	Wald statistic	*p*	Estimate
Shrubland	10.59	0.001	< 0.01
Altitudinal range	8.53	0.003	−2.72
Snake richness	4.69	0.03	0.20
$(Latitude)^2$	1.30	0.25	
Long. × Lat.	0.26	0.61	
Latitude	1.29	0.26	
Length of rivers	0.49	0.48	
Precipitation	0.44	0.51	
Temperature	2.17	0.14	
Thermal range	1.77	0.18	
Longitude	0.40	0.53	
Population	1.57	0.21	
Heterogeneity	0.01	0.94	
$(Longitude)^2$	0.43	0.51	

where this eagle was present had an intermediate presence of forests. In its winter quarters, by contrast, this eagle inhabits primarily treeless steppes and savannas (Alerstam 1997), where it might easily detect its prey (above) but does not need trees for nesting.

Moreover, the presence of the short-toed eagle was negatively correlated with altitudinal range, implying that it prefers flat zones. However, we failed to find an effect of human population on the presence of this eagle. The third variable explaining the distribution of the eagle was snake species richness. Why ophidian species richness is correlated with the presence of this eagle is intriguing. A possibility, common to all correlative studies, is that the ophidian species richness is correlated with other variables not considered that certainly affect the distribution of this raptor, without any causal correlation between snake richness and the short-toed eagle presence. A possibility is that the abundance of snake individuals correlates with ophidian species richness, and the abundance of individuals determines the presence of the raptor. For example, more productive zones may have higher population sizes for each species, and this would increase species richness as a consequence of a diminished risk of extinction (Evans *et al.* 2005).

The possibility of a direct influence of snake species richness on the presence of the short-toed eagle is improbable because the eagle preys on only four out of nine snake species present in the study area, and three of them (*Malpolon monspessulanus, Coluber hippocrepis* and *Elaphe scalaris*) comprise almost the 95% of the raptor's diet in the study area (Gil-Sánchez & Pleguezuelos 2001). Repeating the GLM with only these three species, we found no significant effect of snake species richness on the distribution of the short-toed eagle (Wald = 5.46, p = 0.14). This indicates that the effect of ophidian species richness was not due to the presence of these species consumed by the eagle. On the other hand, the diet of this eagle, although based on snakes, varies considerably among study zones, suggesting that this raptor is a trophic generalist within the order ophidians (Gil-Sánchez & Pleguezuelos 2001), and this might explain why the three key species in its diet did not affect its distribution,

but all species of snakes in the study area did. Therefore, according to this trophic generalism, the snake species diversity might affect the distribution of the short-toed eagle through different mechanisms:

1. A possibility is that different species of snakes are distributed structurally in time (throughout the day or throughout the year). If this is correct, higher snake species richness would favour more time available for hunting. However, this is unknown.

2. Similarly to other predators, individual eagles specialize on different prey (Werner & Sherry 1987). For example, Gil-Sánchez (1998) showed that different pairs of Bonelli's eagle selected different types of prey in the same study area. If the same occurs in the short-toed eagle, higher snake species richness would favour the presence of more pairs of this raptor.

3. It is possible that the short-toed eagle derives different nutrients from different prey, needing different snake species to cover nutritional necessities. However, this seems improbable as, in each study area, this eagle eats only a small set of the snakes that are available (Bakaloudis *et al.* 1998, Gil-Sánchez & Pleguezuelos 2001).

4. Another proposal is that the raptor needs a variety of snake species because nestlings are fed with different species than those consumed by adults, but this idea may be discarded as in the study area adult and nestling short-toed eagles have the same diet (Gil-Sánchez & Pleguezuelos 2001).

5. It is possible that in zones with low availability of the preferable snake species, eagles prey on alternative snakes. For example, both the red kite (*Milvus milvus*) and the Bonelli's eagle increase the trophic diversity in their diets when the availability of their primary food is low (Blanco *et al.* 1990, Ontiveros *et al.* 2005).

An alternative explanation for these results is that the presence of the short-toed eagle favours more snake species richness (not the reverse). If this eagle preys primarily on the most dominant snakes in the study area (*Malpolon monspessula-*

nus, *Coluber hippocrepis* and *Elaphe scalaris*), it may control their population sizes and reduce competition intensity with the other snakes. In this situation, the other snakes might have larger population sizes and more stable populations, provoking a larger diversity of snake species by a top-down regulation process (Pianka 2000). Moreover, *Malpolon monspessulanus*, the primary prey for the short-toed eagle, is an ophidiophagous snake (Pleguezuelos 1997). An example of such top-down regulation process involves the starfish *Pisaster ochraceus,* which favours larger prey diversity because this predator controls for the population size of the most efficient competitor, *Mytilus californianus*, which competitively displaces other species of marine invertebrates (Paine 1966).

Some authors have suggested that the conservation of reptile-rich habitats is important for the conservation of the short-toed eagle (Rocamora 1994, Malafosse & Rocamora 1999, Mañosa 2003). The reptile populations, in turn, are decreasing (Gibbons *et al.* 2000). In fact, four of the nine snakes in the study area are included in the Red Book of the Vertebrates in Andalusia (Franco Ruiz & Rodríguez de los Santos 2001). Nevertheless, if the presence of this raptor favours the diversity of snake species, the protection of the short-toed eagle would be positive for the ophidians. Moreover, this study, as others previously (Bakadoulis *et al.* 1998), highlights the importance of open areas for the conservation of this raptor, especially the shrubland in southeastern Spain, because these zones appear to favour the accessibility to prey.

In conclusion, raptor distribution is affected not only by prey abundance, but also by prey accessibility, which is mediated by the habitat structure (open lands favours prey availability). Moreover, the distribution of trophic specialists may be favoured by prey species richness, as alternative species of prey may be used when the primary one is scarce.

Acknowledgements

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