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ORIGINAL ARTICLE

Habitat partitioning in endangered Cantabrian capercaillie *Tetrao urogallus cantabricus*

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Abstract The endangered Cantabrian capercaillie (*Tetrao urogallus cantabricus*) lives at the southern edge of tetraonids' distribution range, in entirely deciduous forests. Its conservation planning has been always lek-centred. There is very little information about the specific habitat requirements of hens and broods, even though reproductive success appears to be a limiting factor. We analysed summer surveys from 1997 to 2004, carried out to estimate the reproductive success of the population. We compared the habitat characteristics at different spatial scales of hens with broods, broodless hens, and cocks in summer, with the better known spring habitat in display areas. Summer habitat showed higher proportion of open areas and was associated with more rugged zones at moderate spatial scales (78 ha) than spring habitat at display areas. Cocks and hens showed summer habitat partitioning; hens were associated with higher proportions of open and shrubby habitats. Furthermore, broodless hens preferred areas with higher slope variability than the display and summer areas preferred by cocks. These differences may reflect the sexual dimorphism of the species in reproductive role, energetic demands and conspicuousness. At larger spatial scales a previously developed habitat suitability model performed well to predict good brood-rearing areas. Hens with broods were located in the best-preserved areas in the range, mainly characterized by higher proportion of forest cover at a large (50 km^2) scale. We suggest that these characteristics indicate refuge habitats where Cantabrian capercaillie can still breed successfully.

Keywords Cantabrian capercaillie · Brooding hens · Habitat partitioning · Habitat suitability · Edge populations · Deciduous forests

Introduction

Intraspecific differences in habitat use by animals are often caused by sex-specific selection pressures and competitive exclusion (e.g., Selander 1966; Bleich et al. 1997; Ardia and Bildstein 2001). Even within sexes, the reproductive status may impose differences in habitat use due to differential resource acquisition, shelter requirements or role in reproduction. Such variability should be taken into account to develop sound conservation measures; otherwise actions could neglect or even harm parts of a population, thus hampering the conservation of the whole (Durell 2000; Bolnick et al. 2003). Habitat partitioning is often evaluated in relation to small-scale habitat features (such as the importance of understorey cover or insect availability for grouse species). However, the understanding of large-scale spatial patterns of suitable habitats and how populations partition their use provides valuable information for the development of management strategies (Collinge 2001).

This study is about Cantabrian capercaillie (*Tetrao urogallus cantabricus*), a subspecies listed as endangered according to IUCN criteria (Storch et al. 2006). Cantabrian capercaillie occupies a very southerly range within the grouse family (Quevedo et al. 2006b), and has recently been identified as an Evolutionarily Significant Unit because of its unique ecological and genetic characteristics (Rodríguez-Muñoz et al. 2007). The population appears to show low recruitment, with

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values as low as 0.54 juveniles per hen at the end of the summer and 74% of broodless hens in an 8-year period (Bañuelos et al. this study, see "Methods" for details). However, there is no information available about the habitat requirements of hens with broods, and this is compromising the design and enforcement of protected areas (Quevedo et al. 2006a, b). Diverse habitat characteristics are important for brooding hens in other populations: presence of moist areas (Wegge et al. 2005), presence of anthills (Storch 1993), diverse vegetation structure (Klaus et al. 1986), treeline meadows (Menoni 1990) or forest gaps (Saniga 1996). There is, however, a unifying feature: a relatively high cover of ericaceous shrubs, particularly *Vaccinium myrtillus*. This has been attributed to the high abundance of invertebrates in these habitats, which constitute the main diet of chicks during the first weeks, and to the refuge against predators provided by these plants (Jacob 1987; Atlegrim and Sjöberg 1995; Picozzi et al. 1999).

Grouse are, overall, a sexually dimorphic family, and habitat partitioning exists throughout the seasonal cycle (Bergerud and Gratson 1988). However, most information about habitat use in capercaillie is biased towards cocks and often corresponds to their conspicuous behaviour at display areas and their surroundings in spring (e.g., Rolstad and Wegge 1987; Picozzi et al. 1992). The Cantabrian capercaillie is no exception to this (Quevedo et al. 2006b). A habitat suitability map, aimed as a conservation tool, was developed for this population from data corresponding to occupied and abandoned leks (Quevedo et al. 2006a). However, the validity of this map to predict suitable habitat for hens with broods remained to be tested. The aim of our study was to analyse habitat use by Cantabrian capercaillie during the brood rearing season for a broad range of spatial scales, helping to fill the gaps in the understanding of this population. Although small-scale features are, indeed, related to many aspects of habitat selection, we focused on the landscape scale often required by managers.

The specific aims were as follows:

1. To determine whether habitat partitioning exists in relation to sex and reproductive status.
2. To assess how much the summer habitat differs from the much better known spring habitat of cocks attending leks.
3. To evaluate the performance of a lek-based habitat suitability map as a decision-support tool to identify brood-rearing habitats.

Methods

Capercaillie dataset and study area

This study was carried out in the northern watershed of the Cantabrian Range (Asturias, NW Spain, Fig. 1), where the Cantabrian capercaillie inhabits a rugged montane landscape of beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and birch (*Betula pubescens*) forests. A detailed description of the area and habitat characteristics can be found elsewhere (Quevedo et al. 2006a, b). The study is based on eight summer surveys (1997–2004) of capercaillie reproductive success, carried out by the Asturian Environmental Agency. These surveys consisted of drives with trained dogs, conducted between late July and early September. Note that in the Cantabrian Mountains, as in the Pyrenees and the Alps (Menoni 1990; Martínez 1993; Storch 1994), capercaillie reproduction appears to occur 3–4 weeks later than in northern populations (Moss et al. 2001; Wegge et al. 2005). More precisely, the information available from observation of nests and of the size of juveniles in the summer surveys suggests that hatching takes place in June and early July.

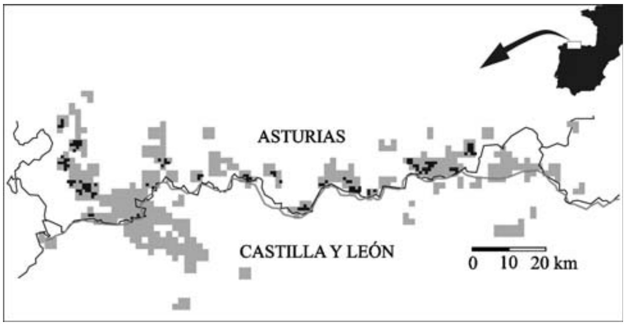

Fig. 1 Area of occupancy of Cantabrian capercaillie (*grey areas*) according to the last complete census in 2000, and study sites (*black zones*). The *grey line* shows the approximate division between the northern and southern watersheds of the Cantabrian Range

Forests in the northern watershed of the Cantabrian Range are highly fragmented (about 22% of the montane area above 700 m), dominated by beech and oak (Quevedo et al. 2006b). Beech forests are more frequent in the central and eastern parts of the range, whereas oak dominates in the western areas. Birch patches are widespread, often forming the tree line of those oak and beech forests (Díaz-González and Vázquez 2004). Thus, forest patches frame a patchy landscape of habitat matrix. In this context, the surveys were typically performed over continuous areas that included a diverse mosaic of beech and oak forest, treeline birch, brooms (*Citysus* spp., *Genista* spp.), heaths (*Erica* spp., *Calluna vulgaris*) and open areas (mostly pastures and scree).

We compiled a list of all the sightings of hens with broods, broodless hens and cocks collected during those summer surveys, which totalled 100 field-days and were carried out in 31 different areas where rangers had previously reported the presence of capercaillie. The surveyed areas are among the best capercaillie spots in the Cantabrian Mountains (Fig. 1). Nevertheless, even in these areas, densities are low and the terrain is rough, often yielding only one hen (or none) per field-day. The area covered in one field-day was, on average, 64 ha (range 15–165 ha), and the average area surveyed per year was 8.5 km^2. The location of each sighting was recorded with a global positioning system (GPS) device, and the information on flushed capercaillies was noted, including sex, age (juvenile or adult) and number of juveniles with the hen. We selected observations where sex could be determined ($n = 173$) and added 15 additional chance observations registered in the same years by other researchers, forest rangers and ourselves for a total of 188 summer sightings. Observations tagged in the field as potentially belonging to the same bird were discarded from the analyses. So that the habitat in those summer locations could be compared with cock spring habitat, the database was completed with the locations corresponding to all known display grounds occupied at least at some point during the past 10 years and located closer than 2 km from the summer observation sites ($N = 100$). See Quevedo et al. (2006b) for details on the characteristics of display grounds in the Cantabrian Mountains.

Habitat dataset

Information on habitat variables was extracted from a high-resolution geographic information system (GIS) database (Quevedo et al. 2006a, b). The information on land cover was summarized into four major habitat types to check for habitat partitioning: (1) beech and oak forest, (2) birch forest, (3) woody shrubs, and (4) meadows and open areas (Table 1). Note that this scheme does not in any way imply forest monospecificity, only dominance. The stands thus classified in our study also included varying amounts of several other species, such as hazelnut (*Corylus avellana*), holly (*Ilex aquifolium*) and mountain ash (*Sorbus aucuparia*), to name a few of the most common.

To characterize the habitat on local scales we defined circular plots of 50 m, 100 m, 200 m, 300 m, 400 m and 500 m radius around each capercaillie observed, which roughly corresponded to 1–78 ha, i.e., within the size range of forest patches occupied by Cantabrian capercaillie (Quevedo et al. 2006b). The circular plots contained varying proportions of the different types of habitat. This presented analytical difficulties due to the fact that the proportion of a given habitat was not independent of the other habitats in the plot, and the sum was 1. Let x_i be the proportion of the plot area occupied by a given habitat type i. To avoid the unit-sum constraint, we transformed the proportion of each habitat type x_i by using the centred log-ratio transformation $y_i = \ln (x_i/x_{\mathrm{mean}})$, being x_{mean} the mean value of the proportions of the different habitat types in each plot. These transformed variables are linearly independent of each other, and are commonly used to analyse compositional data like ours (Aebischer et al. 1993). Thus, for each capercaillie observation, we derived four independent habitat variables scaled to the area of the plots: bok_s (proportion of beech or oak forest), bir_s (birch forest), shr_s (shrubs), open_s (pastures and open areas), where the s subscript indicated the area of the plot in hectares.

To obtain topographic information for capercaillie locations we built a digital elevation model (DEM), of cell size 0.01 ha, from 1:5,000 digital elevation contours (5 m elevation interval). We derived slope and aspect from that DEM and calculated the average values of slope and northern exposure in a 0.09 ha neighbourhood (3 × 3 DEM cells) centred in each observation point. The elevation values of the observations in each discrete survey area were standardized to avoid introducing an area effect into the comparison among groups (hereafter std elevation). To estimate northern exposure, we transformed aspect into an index (north) ranging from 0 (maximum southern exposure) to 1 (maximum northern exposure). Terrain ruggedness (rug) was estimated by means of the standard

Table 1 Description of the four habitat types considered in this study, summarized from a high-resolution GIS database, to assess habitat partitioning in Cantabrian capercaillie: (1) beech and oak forest, (2) birch forest, (3) woody shrubs, and (4) open areas (*a.s.l.* above sea level)

Habitat type (abbreviation)	Description
Beech and oak forest (bok)	Mostly old-growth forest dominated by beech and oak, with interspersed patches of secondary growth, from about 700–1,300 m a.s.l. Understorey sparse and patchy, including great wood-rush (*Luzula sylvatica*), bilberry and tree heath (*Erica arborea*)
Birch forest (bir)	Birch-dominated forest, mostly forming the tree line and located on fresher exposures. These are mainly thicket-like patches with thin, twisted and multi-stemmed birch trees and a well-developed layer of bilberry and tree heath
Woody shrubs (shr)	Areas dominated by shrubs of variable heights up to 3 m, mainly brooms (*Cytisus* sp., *Genista* sp.) and heaths (*Erica arborea* and *Calluna vulgaris*) sometimes mixed with patches of bilberry, in well-preserved upland areas. *E. aragonensis* might be replacing the former species in a few burned areas at lower altitudes
Open areas (open)	Mountain pastures and scree slopes mostly situated above the tree line but also interspersed within forest patches at lower altitude

Table 2 Description of the variables considered in the analysis of habitat partitioning in Cantabrian capercaillie

Abbreviation	Description
$\mathrm{bok}_{s(1–78)}$	Centred log-ratio transformation of beech or oak forest cover (%) in plots of area *s* around observations
$\mathrm{bir}_{s(1–78)}$	Centred log-ratio transformation of birch forest cover (%) in plots of area *s* around observations
$\mathrm{shr}_{s(1–78)}$	Centred log-ratio transformation of shrub cover (%) in plots of area *s* around observations
$\mathrm{open}_{s(1–78)}$	Centred log-ratio transformation of open areas and meadow cover (%) in plots of area *s* around observations
std elevation	Mean elevation in a 9 ha neighbourhood centred in each observation, standardized to the mean altitude
rug	SD elevation (m a.s.l.) in a 9 ha neighbourhood centred in each observation
slope	Mean slope (%) in a 9 ha neighbourhood centred in each observation
north	Mean northern exposure (index ranging 0–1) in a 9 ha neighbourhood centred in each observation

deviations of the elevation in the 0.09 ha neighbourhood around each observation (Table 2).

Habitat partitioning

To analyse habitat characteristics and to assess capercaillie habitat partitioning, we used multinomial logistic regressions (logit link, *nnet* package, R Development Core Team 2006), an iterative method based on maximum likelihood estimation (Agresti 2002). This analysis handles continuous or discrete explanatory variables and categorical response variables with more than two levels or categories. We assimilated the type of observation [(1) hens with broods in summer, (2) broodless hens in summer, (3) cocks in summer and (4) cocks in display sites in spring] to a categorical response variable with four categories. The explanatory variables were topographic (std elevation, north, rug) and vegetation characteristics of the habitat (bok_s, bir_s, shr_s, open_s).

Variables were considered explanatory a priori according to the following criteria: (1) significant relationship with capercaillie habitat partitioning ($P < 0.1$) in univariate multinomial logistic regressions; (2) Pearson's correlation coefficient with the other explanatory variables lower than 0.6. To build the minimal adequate model, we followed a step-up procedure by fitting univariate models that were retained at $\alpha < 0.1$. We retained the univariate model with the lowest Akaike information criterion (AIC, Burnham and Anderson 1998), which trades-off goodness of fit of the model against its complexity. We then proceeded to test bivariate models, retaining the one that yielded the lowest AIC. The process ended when addition of new variables did not reduce the AIC any further. Thereafter, we tested for non-linearity and interaction effects by adding quadratic and product terms to the minimal adequate model. In multinomial logistic regression, one category of the response variable is chosen as the comparison category. We performed a series of multinomial logistic regressions, alternating the response category until all comparisons had been completed.

Habitat suitability

We used an existing habitat suitability map for capercaillie in the area (Quevedo et al. 2006a) to compare the predicted habitat suitability corresponding to sightings of hens with broods, cocks and broodless hens at the landscape scale. This habitat suitability map was developed from a logistic model, using the information of display grounds, so that the characteristics of presence areas (i.e., occupied leks) and absence areas (i.e., abandoned leks) were compared in a grid of 25 ha habitat units. See Quevedo et al. (2006a) for details on model construction and suitability maps. The model merged both natural and anthropogenic factors as relevant in determining the probability of capercaillie occurrence and identified the spatial scale of their effects. The proportion of forest cover in a local 25 ha habitat unit, the proportion of forest cover in a 50 km^2 neighbourhood, and the degree of northern exposure of the local habitat unit had positive effects on the probability of capercaillie presence, whereas the number of human settlements had a negative effect, most significant in a 28 km^2 neighbourhood. From a combination of those variables and their relative effects, a map of habitat suitability was derived as a conservation tool so that areas classified as highly suitable for capercaillie indicate areas of special interest. Since the model and the subsequent suitability map were built on the basis of display grounds, the question remains whether other sectors of the population are properly represented. Should brooding hens be located in areas predicted as highly suitable for capercaillie in the map, protection measures on such areas would also benefit this important group of the population. To check this, we compared the values of predicted habitat suitability and the values of the explanatory variables from the model for the locations of hens with broods, cocks, broodless hens and display

Table 3 Average values of main habitat features for Cantabrian capercaillie at spring and summer locations. For land cover variables, only the most relevant scale (78 ha) is shown. See Tables 1, 2 and Methods for a comprehensive explanation of each variable

Explanatory variables	Spring	Summer		
	Display areas (115)	Hens with broods (24)	Cocks (95)	Broodless hens (69)
bok_{78}	1.13 ± 0.03	1.05 ± 0.07	1.19 ± 0.03	1.05 ± 0.05
bir_{78}	0.31 ± 0.03	0.40 ± 0.08	0.21 ± 0.03	0.29 ± 0.04
shr_{78}	0.65 ± 0.04	0.64 ± 0.07	0.57 ± 0.03	0.65 ± 0.04
$open_{78}$	0.19 ± 0.02	0.28 ± 0.06	0.34 ± 0.03	0.35 ± 0.03
elevation	1,308 ± 16	1,378 ± 30	1,377 ± 30	1,402 ± 19
std elevation	−0.13 ± 0.11	0.39 ± 0.50	0.005 ± 0.11	0.12 ± 0.15
rug	3.9 ± 0.1	4.1 ± 0.2	4.2 ± 0.1	4.6 ± 0.2
slope	25.6 ± 0.7	26.3 ± 1.2	26.5 ± 0.6	28.6 ± 0.8
north	0.71 ± 0.02	0.77 ± 0.03	0.76 ± 0.02	0.78 ± 0.02

grounds using pairwise *t*-tests or Mann–Whitney tests, depending on the distribution of the variables.

Results

Summer sightings of capercaillies along the study period corresponded to 95 cocks and 93 hens. Only 24 (26%) of those hens were accompanied by one or more juveniles. There was an average of 0.54 juveniles per hen, a mean brood size of 2.2 (range 1–7), and 69 (74%) broodless hens.

Three vegetation and two topographical variables emerged as a priori explanatory variables for the habitat partitioning model: $open_{78}$, bok_{78}, bir_{78}, rug, and north. Although other variables showed higher values in summer (Table 3), the differences were not significant. The proportion of open areas in a 78 ha neighbourhood ($open_{78}$) showed the best fit to habitat partitioning and, thus, was entered first into the multinomial logistic model (Table 4). All summer groups showed higher $open_{78}$ values than did spring display areas (Tables 3, 5). The second variable to be entered into the final model was ruggedness (rug, Table 4). Broodless hens were located in more rugged terrain than cocks and spring display areas (Tables 3, 5). The third and last variable to be entered into the final model was the proportion of beech and oak forest (bok_{78}, Table 4). bok_{78} showed that cocks preferred sites with a higher proportion of beech and oak forest than the sites preferred by hens with or without broods. Adding aspect (north) and the proportion of birch forest (bir_{78}) did not further improve the performance of the model, although these variables yielded significant results in univariate tests: hens with broods and spring display areas were more closely associated with birch forest than cocks in summer, and broodless hens were located in areas with a more pronounced northern orientation than spring display areas (Tables 3, 6).

Table 4 Summary of the step-up model selection procedure for the multinomial logistic model of habitat partitioning between hens with broods, broodless hens, cocks and spring display areas of Cantabrian capercaillie (*RD* residual deviance, *AIC* Akaike information criterion, *df* degrees of freedom)

Parameter	RD	AIC	χ^2	*df*	*P*
Null model	739	744	–	–	–
$open_{78}$	711	723	28.0	3	<0.001
$open_{78}$ + rug	693	711	46.0	6	<0.001
$open_{78}$ + rug + bok_{78}	684	708	55.1	9	<0.001

Hens with broods were located in areas with higher habitat suitability than cocks or broodless hens according to the suitability map (pairwise *t*-tests, $P < 0.05$, Fig. 2). The main explanatory variable driving the habitat suitability model was the proportion of forest cover in a 50 km^2 neighbourhood. At this landscape scale, hens with broods and cocks both showed preference for a significantly higher proportion of forest cover than broodless hens (pairwise *t*-test, $P = 0.009$ and $P = 0.011$, respectively).

Discussion

The summer habitat of Cantabrian capercaillie differed from the much better known habitat in spring display areas, showing the increased importance of open areas. We found habitat partitioning among groups of birds, indicating that habitat partition in capercaillie might be found at broad spatial scales and in highly fragmented, patchy habitats. Hens with broods showed a clearer association with treeline birch forests, whereas cocks were preferentially located in beech or oak forests. Some topographic features also differed among groups: broodless hens were located in summer in more northern and rugged exposures than were cocks. Shifting up the spatial scale of analysis, we found that hens with broods were located in the most suitable areas for the species according to a previous habitat suitability map, mainly characterized by high proportion of forest cover at large spatial scales (Quevedo et al. 2006a).

Table 5 Coefficients of the three explanatory variables entering the minimal multinomial regression model of habitat partitioning for Cantabrian capercaillie. The *sign* of the coefficients refers to the group in the left column (e.g., values for $open_{78}$ are significantly lower for display areas than for hens with broods)

$open_{78}$	Hens w. broods	Broodless hens	Cocks	Display areas
Hens w. broods	–			
Broodless hens	1.31 ± 0.97	–		
Cocks	1.03 ± 0.94	−0.28 ± 0.61	–	
Display areas	−2.20 ± 1.01*	−3.50 ± 0.76***	−3.23 ± 0.70***	–
rug	Hens w. broods	Broodless hens	Cocks	Display areas
Hens w. broods	–			
Broodless hens	0.37 ± 0.21	–		
Cocks	0.09 ± 0.20	−0.28 ± 0.14*	–	
Display areas	−0.22 ± 0.20	−0.58 ± 0.15***	−0.30 ± 0.13*	–
bok_{78}	Hens w. broods	Broodless hens	Cocks	Display areas
Hens w. broods	–			
Broodless hens	0.10 ± 0.66	–		
Cocks	1.53 ± 0.69*	1.43 ± 0.54**	–	
Display areas	0.56 ± 0.88	0.46 ± 0.48	−0.97 ± 0.51	–

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

Table 6 Coefficients of bir_{78} and north in univariate multinomial regression models of habitat partitioning for Cantabrian capercaillie. The *sign* of the coefficients refers to the group in the left column (e.g., values for bir_{78} are significantly lower for cocks than for hens with broods)

bir_{78}	Hens w. broods	Broodless hens	Cocks	Display areas
Hens w. broods	–			
Broodless hens	−0.82 ± 0.64	–		
Cocks	−1.66 ± 0.65*	0.84 ± 0.50	–	
Display areas	−0.66 ± 0.61	0.16 ± 0.46	1.00 ± 0.46*	–
north	Hens w. broods	Broodless hens	Cocks	Display areas
Hens w. broods	–			
Broodless hens	0.55 ± 1.31	–		
Cocks	−0.23 ± 1.23	−0.78 ± 0.90	–	
Display areas	−1.47 ± 1.20	−2.02 ± 0.85*	−1.23 ± 0.71	–

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

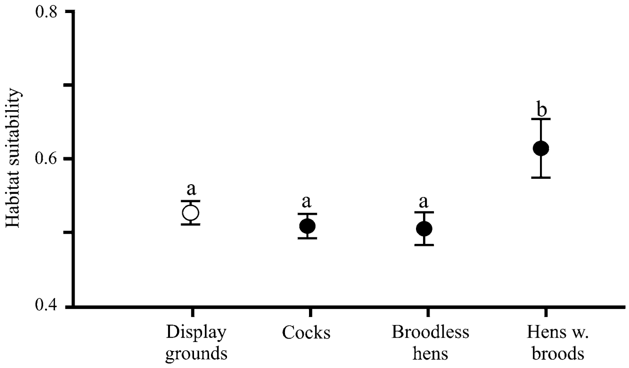

Fig. 2 Habitat suitability values (mean ± 2 SE) in the 25 ha habitat units containing display grounds in spring, and summer locations of cocks, broodless hens, and hens with broods, according to a habitat model developed for Cantabrian capercaillie (Quevedo et al. 2006a). *Different letters* above the *symbols* indicate significant differences in pairwise *t*-tests ($P < 0.05$)

Overall, in summer, capercaillie were sighted closer to forest edges than to spring display grounds, as evidenced by the increased importance of open areas in their surroundings. These open areas corresponded mainly to upland habitats, but also to smaller patches of scree and herbaceous gaps within the forest. Although the forest was still the most relevant habitat for all groups during the summer, the association was stronger for cocks, resembling the habitat partitioning found in Scandinavian capercaillies (Rolstad et al. 1988). That is also the case in the Pyrenees, where cocks are mostly associated with the forest in summer whereas hens are found in treeline habitats, near upland meadows and subalpine moors (Menoni 1990).

Differences in requirements and habitat use are not surprising in capercaillie, the largest and most dimorphic grouse, and should be incorporated into conservation plans. The mechanism for this habitat partitioning may be connected to differences in life history. Although females are less conspicuous than cocks, in terms of both appearance and behaviour, they are potential prey for a wider range of predators because of their smaller size and their reproductive behaviour during the nesting and chick-rearing periods. Together with the high demands of energy of chicks, this suggests that brood-rearing hens, which need good refuges and optimal food resources, would have the most restrictive habitat requirements. In our study, hens with broods showed a stronger association with birch forest than did cocks. In the Cantabrian Mountains, this habitat is usually characterized by a rich understorey of ericaceous shrubs, such as tree heath and bilberry, which provide abundant food and refuge. In addition, bilberry plants are taller and grow faster in birch-dominated tree lines than within denser and shadier oak and, especially, beech forests (Fernandez-Calvo and Obeso 2004).

The combination of results at local and regional scales highlights the importance of preserving tracts of intact ecosystems, and generalizes a previous habitat suitability model to predict good brood-rearing areas. The relatively high values of habitat suitability found for brooding hens were mainly due to higher proportion of forest cover in a neighbourhood of 50 km^2. This suggests that high suitability areas pinpoint the last locations where capercaillie reproduction can effectively take place within the ongoing process of population decline. These areas would constitute refuges, broadly understood as including better choices in terms of feeding, competition, predation and shelter, among several other relevant aspects for the survival of a population (Berryman et al. 2006). This idea is consistent with previous results that indicated an indirect relationship between the habitat configuration in the Cantabrian Mountains and the ongoing process of capercaillie decline (Quevedo et al. 2006a).

This unique capercaillie population has been studied and managed largely from a lek-centred perspective. This has somewhat neglected the importance of habitats other than old forest, such as gaps or treeline habitats with rich heath cover, which could be important in other stages of the capercaillie's life cycle (Quevedo et al. 2006b). Our results help to fill the gap, and we hope they will sustain better-informed habitat management and aid the enforcement of habitat protection. Our results also provide further evidence that treeline and generally upland habitats should not be forgotten in the conservation of the Cantabrian Mountains (Naves et al. 2006), a region where both forest fragmentation and anthropogenic pressure are very high (García et al. 2005; Quevedo et al. 2006a). From a more general perspective, these results highlight the need to consider different sectors of a population and different spatial scales in conservation practices.

This study does not include hard data about nesting and early brooding periods, which may have different requirements. However, obtaining significant information on these aspects of capercaillie life cycle in the Cantabrian Mountains seems difficult, both due to the ruggedness of the terrain and the low density of birds. Also, the disturbance associated with any study involving breeding hens might be detrimental to a highly endangered population such as this one, and its potential advantages and drawbacks should be carefully considered.

Zusammenfassung

Habitataufteilung beim bedrohten Kantabrischen
Auerhuhn *Tetrao urogallus cantabricus*

Das bedrohte Kantabrische Auerhuhn lebt am südlichen Rand des Verbreitungsgebiets der Raufußhühner in sommergrünen Laubwäldern. Die Planungen für die Erhaltung dieser Art haben sich immer auf die Arenabalz konzentriert. Es gibt nur wenig Information über die spezifischen Habitatbedürfnisse von Hennen und Bruten, und das obwohl der Fortpflanzungserfolg ein limitierender Faktor zu sein scheint. Wir haben Sommererfassungen von 1997 bis 2004 analysiert, die durchgeführt worden waren, um den Fortpflanzungserfolg der Population abzuschätzen. Wir haben die Habitatkennzeichen bei unterschiedlichen Raumgrößen für Hennen mit Bruten, Hennen ohne Bruten und Hähne im Sommer mit dem besser bekannten Frühlingshabitat in Balzarenen verglichen. Das Sommerhabitat wies einen höheren Anteil offener Flächen auf und war mit stärker zerklüfteten Zonen mittlerer Raumgröße (78 ha) assoziiert als das Frühlingshabitat in Balzarenen. Hähne und Hennen zeigten im Sommer Habitataufteilung; Hennen waren mit höheren Anteilen offenen und buschigen Habitats assoziiert. Außerdem bevorzugten Hennen ohne Bruten Flächen mit höherer Hangneigungsvariabilität als Balzarenen und von Hähnen bevorzugte Sommerflächen. Diese Unterschiede könnten den Sexualdimorphismus in Fortpflanzung, Energiebedarf und Auffälligkeit bei dieser Art widerspiegeln. Bei ausgedehnteren Raumgrößen funktionierte ein zuvor entwickeltes Habitateignungsmodell gut, um günstige Brutaufzuchtsplätze vorherzusagen. Hennen mit Bruten waren in den am besten geschützten Flächen des Gebiets zu finden, die hauptsächlich durch höhere Anteile an Waldbedeckung in großem Maßstab (50 km^2) charakterisiert waren. Wir schlagen vor, dass diese Eigenschaften Refugienhabitate anzeigen, in denen Kantabrische Auerhühner noch erfolgreich brüten können.

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References

Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325

Agresti A (2002) Categorical data analysis. Wiley, New York

Ardia DR, Bildstein KL (2001) Sex-related differences in habitat use in wintering American kestrels. Auk 118:746–750

Atlegrim O, Sjöberg K (1995) Lepidoptera larva as food for capercaillie chicks (*Tetrao urogallus*). Scand J For Res 10:278–283

Bergerud AT, Gratson MW (1988) Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis

Berryman AA, Hawkins BA, Hawkins BA (2006) The refuge as an integrating concept in ecology and evolution. Oikos 115:192–196

Bleich VC, Bowyer RT, Wehausen JD (1997) Sexual segregation in mountain sheep: resources or predation? Wildl Monogr 134:1–50

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, New York

Collinge SK (2001) Spatial ecology and biological conservation. Biol Conserv 100:1–2

Díaz-González TE, Vázquez A (2004) Guía de los bosques de Asturias. Trea, Gijón

Durell S (2000) Individual feeding specialisation in shorebirds: population consequences and conservation implications. Biol Rev 75:503–518

Fernandez-Calvo IC, Obeso JR (2004) Growth, nutrient content, fruit production and herbivory in bilberry *Vaccinium myrtillus* L. along an altitudinal gradient. Forestry 77:213–223

García D, Quevedo M, Obeso J, Abajo A (2005) Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain). For Ecol Manag 208:29–43

Jacob L (1987) Le régime alimentaire du Grand Tétras (*Tetrao urogallus* L.): synthèse bibliographique. Gibier Faune Sauvage 4:429–448

Klaus S, Andreev AV, Bergmann H-H, Müller F, Porkert J, Weisner J (1986) Die Auerhühner. Die neue Brehm-Bücherei. Ziemsen, Wittenberg

Martínez AM (1993) Contribución al conocimiento de la eco-etología del urogallo cantábrico. PhD thesis, Universidad de León, Spain

Menoni E (1990) Caquetements et territorialité des poules de grand tétras au printemps dans les Pyrenees. Acta Biol Mont 10:63–82

Moss R, Oswald J, Baines D (2001) Climate change and breeding success: decline of the capercaillie in Scotland. J Anim Ecol 70:47–61

Naves J, Fernandez-Gil A, Rodríguez C, Delibes M (2006) Brown bear food habits at the border of its range: a long-term study. J Mammal 87:899–908

Picozzi N, Catt D, Moss R (1992) Evaluation of capercaillie habitat. J Appl Ecol 29:751–762

Picozzi N, Moss R, Kortland K (1999) Diet and survival of capercaillie *Tetrao urogallus* chicks in Scotland. Wildl Biol 5:11–23

Quevedo M, Bañuelos MJ, Obeso JR (2006a) The decline of Cantabrian capercaillie: how much does habitat configuration matter? Biol Conserv 127:190–200

Quevedo M, Bañuelos MJ, Sáez O, Obeso JR (2006b) Habitat selection by Cantabrian capercaillie at the edge of the species distribution. Wildl Biol 12:267–276

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rodríguez-Muñoz R, Mirol PM, Segelbacher G, Fernández A, Tregenza T (2007) Genetic differentiation of an endangered capercaillie (*Tetrao urogallus*) population at the Southern edge of the species range. Conserv Genet 8:659–670

Rolstad J, Wegge P (1987) Habitat characteristics of capercaillie *Tetrao urogallus* display grounds in southeastern Norway. Holarct Ecol 10:219–229

Rolstad J, Wegge P, Larsen BB (1988) Spacing and habitat use of capercaillie during summer. Can J Zool 66:670–679

Saniga M (1996) Distribution, habitat preferences and breeding biology of the capercaillie (*Tetrao urogallus*) population in the Velká Fatra mountains (West Carpathians). Biol Bratisl 51:201–211

Selander RK (1966) Sexual dimorphism and differential niche utilization in birds. Condor 68:113–151

Storch I (1993) Habitat selection by capercaillie in summer and autumn: is bilberry important? Oecologia 93:257–265

Storch I (1994) Habitat and survival of capercaillie *Tetrao urogallus* nests and broods in the Bavarian Alps. Biol Conserv 70:237–243

Storch I, Bañuelos MJ, Fernández-Gil A, Obeso JR, Quevedo M, Rodríguez Muñoz R (2006) Subspecies Cantabrian capercaillie *Tetrao urogallus cantabricus* endangered according to IUCN criteria. J Ornithol 147:653–655

Wegge P, Olstad T, Gregersen H, Hjeljord O, Sivkov AV (2005) Capercaillie broods in pristine boreal forest in northwestern Russia: the importance of insects and cover in habitat selection. Can J Zool 83:1547–1555