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Habitat selection by Cantabrian capercaillie *Tetrao urogallus cantabricus* at the edge of the species' distribution

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We studied the patterns of habitat availability and use by the Cantabrian capercaillie *Tetrao urogallus cantabricus*, an isolated and endangered population at the southwestern edge of the species distribution. We combined field surveys and GIS analyses to show that this population differs from its conifer-specialist conspecifics in that it inhabits beech *Fagus sylvatica* and oak *Quercus petraea* forests, without specialisation as regards the tree species as long as enough forest cover remains. The habitat of Cantabrian capercaillie is highly fragmented, and smaller forest patches have been abandoned during the last few decades; the display areas that remain occupied are now located farther from forest edges. Lower tree density and more widespread distribution of bilberry *Vaccinium myrtillus* characterised the occupied display grounds. However, even abandoned areas showed tree densities well within the optimum range for capercaillie and bilberry in other populations, a result that should be taken into account before any habitat management action is considered. We found that some non-forested habitats were also used by capercaillie, especially during the autumn and winter. We suggest that the protection of Cantabrian capercaillie should be tightly coupled with an effective, strict protection of the few remaining large forest fragments in the range, and that information about nesting and brood rearing habitat should be obtained. Conditions for understory development should be favoured, preventing overgrazing by ungulates. The natural, non-forested matrix should also be considered in management plans, as a direct source of food and shelter and an important feature determining connectivity among patches.

Key words: deciduous forest, fragmentation, grouse, habitat structure, matrix, Tetrao urogallus

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Knowledge of the habitat requirements of species is fundamental for effective conservation and management, especially in areas where species decline and the habitat is exposed to relatively intense human use (Luck 2002, Oppel et al. 2004). Environmental conditions and biological interactions are not the same throughout a species' range (Gaston 2003, Guo et al. 2005), thus it is advisable to assess the ecological requirements of species in the area where the conservation measures are required. More specifically, because populations at the edge of a species' distribution are often smaller and use ecologically marginal habitats (Brown 1984, Diamond 1984, Lawton 1993), observations made in one part of the range are not always applicable at the edge of a species' distribution.

Although not globally threatened, the Western capercaillie *Tetrao urogallus* has declined throughout its range (Storch 2000a). The case of the Cantabrian capercaillie *T. u. cantabricus* (Castroviejo 1967, del Hoyo et al. 1994) is particularly serious as bird numbers have declined by about 50% in the last two decades (Obeso & Bañuelos 2003). This population, located on the southwestern edge of the species' distribution, is isolated from its nearest neighbours by more than 300 km, constrained to an area of < 2,000 km^2 (Fig. 1). In spite of the urgent need for appropriate management measures, very few aspects of the ecology of Cantabrian capercaillies are known, apart from their diet and the incidence of intestinal parasites (Obeso et al. 2000, Rodríguez & Obeso 2000). There is no detailed knowledge of habitat availability and use, only some general information (Castroviejo 1975, Martínez 1993), even though both quantity and quality of the habitat are limiting factors for other capercaillie populations (Storch 1993b, Storch 1995). In this sense, there is an overall trend towards recovery among some western European forests in the last few decades (Tucker & Evans 1997), due to the reduction in traditional harvesting and abandonment of upland pastures. Whether this is the case for the habitat of Cantabrian capercaillie, is yet to be tested. This lack of knowledge obscures the discussion about the effects of habitat loss and research and management needs and constitutes a conservation problem that affects the majority of the montane landscape in the region.

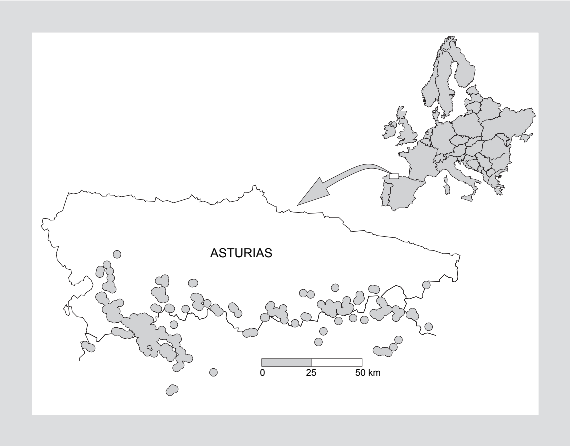

Figure 1. Approximate area of occupancy of Cantabrian capercaillie, mapped by plotting buffer areas of 2-km radius around display grounds occupied in 2000 (see Storch 2000b for criteria).

Most existing knowledge of capercaillie ecology comes from central and northern European populations, so the species is considered an old conifer forest specialist (Rolstad & Wegge 1987a, Picozzi et al. 1992). However, evergreen forests are almost absent from the Cantabrian Mountains, where this grouse species inhabits mainly deciduous forests of beech *Fagus sylvatica* and sessile oak *Quercus petraea* (Obeso & Bañuelos 2003, García et al. 2005), in one of the mildest climates within the species' distribution. These peculiarities certainly imply differences in preferred habitat structure, metabolic demands, quality and quantity of predators and competitors, and feeding habits, indicating a remarkable degree of phenotypic plasticity within the species (West-Eberhard 1989). Protection of the population implies the protection of both the evolutionary process of the species, and of the primeval features of Atlantic montane forest in southern Europe (Lesica & Allendorf 1995, Lundberg et al. 2000). The overall objective of our study was to analyse the habitat use and selection of this subspecies at different scales, so obtaining information relevant to its effective management. We aim to answer the following questions:

- Is there any large-scale preference among different forest types?
- Is there any trend in large-scale habitat use related to the recent decline?
- Which microhabitats are used within or near to the forest patches?
- What are the characteristics of forest structure in relation to occupancy by capercaillies?

Methods

Study area and regional context

The study area includes the entire landscape in the altitudinal range of the bird (700-1,700 m a.s.l.) within the boundaries of the province of Asturias (northwestern Spain; see Fig. 1). This covers about 60% of the extant range of the Cantabrian capercaillie.

The landscape combines both limestone and siliceous soils and is crisscrossed by steep cliffs, ravines and rocky peaks. The climate is humid and temperate. The average annual precipitation is 1,100 mm and the average temperature about 9°C, with irregular snow cover between December and March. The study area includes 764 km^2 of forest, which accounts for 22% of the landscape. Forests are highly fragmented, and the size dis-

Table 1. Forest availability and habitat use by Cantabrian capercaillie. For forest availability, % = contribution of the forest type to the total forested area, A_m = mean ±1 SE fragment size (in ha). N_{10} = number of forest fragments of > 10 ha, and A_{10} = mean ± 1 SE fragment size for fragments of > 10 ha. For occupied forest fragments and displaying grounds, N_f and N_d = numbers of occupied forest fragments and occupied display grounds in the different habitats, w_i = Manly selectivity index in which < 1 = avoidance, 1 = neutral and > 1 = positive selection.

	Forest fragment availability				Occupied forest fragments			Occupied display grounds		
Habitat	%	A_m	N_{10}	A_{10}	N_f	w_i	P	N_d	w_i	P
European beech	63	35.9 ± 6.3	299	154 ± 38	37	0.92	0.28	101	1.09	0.17
Sessile oak	21	11.1 ± 2.3	160	90 ± 28	16	1.18	0.37	24	0.77	0.17
Mountain birch	4	3.6 ± 0.6	53	34 ± 9	3	1.30	0.61	9	1.68	0.29
Pyrenean oak	5	3.9 ± 0.5	73	30 ± 7	2	0.66	0.34	2	0.28*	0.00
Conifers	3	17.5 ± 6.7	14	141 ± 15	3	1.69	0.35	4	0.99	0.99
Common oak	3	7.3 ± 1.5	34	50 ± 8	-	-		-	-	
Ash and maple	1	3.7 ± 1.2	12	40 ± 9	-	-		-	-	
Holly	<1	1.4 ± 0.2	7	13 ± 1	-	-		-	-	
Rowan	<1	2.3 ± 0.5	5	13 ± 1	-	-		-	-	

tribution is strongly skewed towards fragments of < 10 ha (García et al. 2005). These are mostly semi-natural forests with a long history of human use. Beech forests are the most abundant in the area and form the largest patches, followed by sessile oak forests with much lower mean fragment area (Table 1). Beech forests in the region are largely monospecific, whereas those dominated by sessile oak usually include some other species such as rowan *Sorbus aucuparia* and mountain birch *Betula pubescens*, the latter often forming the tree line above beech and oak. Finally there are a few conifer plantations, mainly Scots pine *Pinus sylvestris*, in the forested habitat in the region (see Table 1). Forest fragments are embedded in a matrix mainly composed of meadows and heaths (*Erica* spp.) or brooms (*Genista* spp.) Forest cover becomes scarce above 1,500 m, where heaths, brooms and subalpine meadows start to dominate the vegetation.

Trend in large-scale habitat availability

To evaluate potential shifts in large-scale habitat availability from the 19th century to the present, we used the earliest detailed vegetation cartography for the area, a mid-19th century land-use map of the province of Asturias (García-Martino 1862). We digitised the map with a grid cell size of 200 × 200 m, and extracted information on beech and sessile oak forest cover by identifying and reclassifying pixel colours. We generalised the contemporary GIS (Geographic Information System) data to a grid cell size of 200 × 200 m to enable comparison with the 19th century data set.

Capercaillie presence

We used capercaillie display areas as the unit for the analysis of capercaillie presence. Display areas and the surrounding habitat are central to capercaillie conservation because they sustain high capercaillie activity throughout the year (Picozzi et al. 1992, Storch 1995). These areas include the display ground itself, defined as the sites at which one or more cocks consistently display for hens (Picozzi et al. 1992) and the nearest surrounding habitat in the forest. The extent of the nearest surrounding habitat that was surveyed depended on the accessibility and the size of the forest fragments, but it was usually about 1 km^2. For simplicity we hereafter use the term display ground, with the broader meaning outlined above. All known capercaillie display grounds were repeatedly surveyed during spring (April-May) in 1997-2000, to coincide with the gathering and displaying of the cocks. The surveys were carried out by forest rangers, volunteers and the authors, with the same guidelines being followed throughout. Every display ground was visited at least twice, both at night and during the day. For night surveys, observers (2-3 per display area) were in the area close to the centre of activity before dawn and remained there until the display finished or until well past dawn when no capercaillie were seen or heard. Later in the day, the observers returned to the places where no direct sightings were made to look for signs of presence such as feathers, fresh droppings or footprints. When poor weather or disturbances prevented any conclusion as to whether or not a display ground was empty, return visits were made to the site 2-3 days later. We considered a display ground as occupied whenever signs of presence (direct sightings, feathers, fresh droppings or footprints) were recorded at least in one of the surveys performed. The display grounds were located on 1:10,000 digital maps, using a GPS and an altimeter.

We calculated the nearest neighbour distances (NND) between leks with a GIS, and checked the spatial distribution of display grounds in the study area using the index of aggregation R (Clark & Evans 1954). To test its significance, we used the standard normal deviate z.

Selection of forest fragments

We constructed up-to-date habitat maps from the high-resolution digital cartography (1:25,000) of the Asturian Environmental Council. We summarised the vegetation data into nine major habitat types: European beech, sessile oak, Pyrenean oak *Q. pyrenaica*, common oak *Q. robur*, mountain birch, holly tree *Ilex aquifolium*, conifer plantations (consisting mostly of Scots pine), rowan and mixed deciduous forests dominated by European ash *Fraxinus excelsior* and maple *Acer pseudoplatanus/ A. platanoides*. We considered a forest fragment as any isolated patch comprising the habitat types outlined above, calculated its area, and classified it according to the dominant tree species. This grouping scheme rendered a measuring resolution of about 0.01 ha. GIS data were combined with the display ground information to study selection of habitat at the landscape scale.

We compared the size of the fragments containing display grounds with a random selection of forest fragments of > 10 ha using ONEWAY analysis. Using a similar analysis, we compared the size of presently occupied forest fragments and those occupied in the early 1980s but deserted at the time of the present survey.

To estimate the selection of the type of forest fragments in the range we used Manly's selectivity index (Manly et al. 2002), which takes into account the proportion of occupied forest fragments or occupied display grounds in a given habitat, and the proportion of that habitat in the selected area. The index ranges from 0 (maximum avoidance) to infinite (maximum positive selection), where 1 indicates that the habitat is used according to availability. We corrected the significance of the w_i values for multiple comparisons using the false discovery rate method (Benjamini & Hochberg 1995).

Seasonal microhabitat use

We defined plots of 1,000 m radius around the display ground centre in the GIS to represent presumed core areas of capercaillie activity (Wegge & Rolstad 1986, Storch 1995). To assess habitat use in these areas, we selected four different locations throughout the range occupied by capercaillie in spring 2000, located at a minimum distance of 15 km from each other. In these zones, we designed four roughly circular transects with the help of digital vegetation maps in order to cover as many types of habitat as possible. Apart from the information about the forest fragments outlined above, we also extracted and summarised the data from the digital cartography regarding the non-forest matrix in which the forest patches are embedded using the following scheme: meadows, heaths, brooms (*Genista* spp. and *Cytisus* spp.), ferns and rocky or bare terrain.

Transects ranged in altitude within 1,060-1,650 m a.s.l., had an average length of 5.5 km, and were surveyed roughly every 10 days between October 2000 and October 2001, so that a total of 144 surveys were carried out (36 at each location). Signs of habitat use such as direct sightings, fresh droppings, feathers and footprints were assigned to the type of habitat where they were found. All signs were collected (droppings, feathers) or erased (footprints) in each survey to ensure that they were recorded only once. The minimum distance for considering a sign as an independent sample was 25 m. We estimated habitat use for two time-periods: autumn/winter (September-February) and spring/summer (March-August), corresponding to the dispersal and wintering period and to the reproductive season, respectively. We checked for habitat preference using the selectivity index described above (Manly et al. 2002), which relates the proportion of signs in a given habitat to the habitat availability along the transect. We corrected the significance of the w_i values for multiple comparisons using the false discovery rate method (Benjamini & Hochberg 1995). We compared the average abundance of signs of presence of capercaillie between the periods using a generalised linear model with a log link and a quasipoisson error distribution to control for overdispersion (Crawley 2002).

Forest structure of the display grounds

To assess habitat selection by capercaillie in terms of the structure of the forest in the display grounds, we used a sample of 58 display grounds homogeneously distributed throughout the range. They corresponded to 33 occupied and 25 empty display grounds according to the recent surveys. At each display ground, we analysed five circular plots each of 15 m radius, one at the centre and the others 125 m from the centre, to the left and to the right, downhill and uphill, following the elevation contour. We recorded the number of forested plots and the number of plots with a bilberry *Vaccinium myrtillus* cover of > 5% for each display ground. In each plot, we recorded tree density (trees ha^{-1}), size distribution (DBH, in cm) and bilberry cover. A comparison of all variables in occupied and empty display grounds was made. Tree density and size were analysed for all tree species together, and the subset of display grounds located in beech forest only (28 occupied and 22 empty) was analysed to control for results due to size-structure differences between species.

We used R Statistical Package (® Development Core Team 2004) for all the statistical and selectivity analyses.

Results

Trend in large-scale habitat availability

In the 19th century the main forest species in the Cantabrian capercaillie habitat, beech and sessile oak, covered 529 and 350 km^2, respectively, and accounted for 22.5% of the landscape. The present cover was 512 and 171 km^2 for beech and oak, respectively, accounting for 17.5% of the landscape. This is a reduction of 196 km^2, i.e. 22.2% of the beech and (mostly) oak forest has disappeared over the past 140 years.

Selection of forest fragments

In Asturias, the Cantabrian capercaillie lives mainly in beech and oak forests, corresponding to 60 and 26% of all the occupied fragments, and uses the forest according to availability (see Table 1). Similar results were obtained for the number of display grounds located in each type of forest, except that Pyrenean oaks were used less often than expected (see Table 1).

The presence of capercaillie was detected in 61 forest fragments in 2000. The fragments were significantly larger ($F_{1,120} = 49.5$, $P < 0.0001$, data $\log_{10}$-transformed) than a random selection of forest fragments (median size = 262 and 36 ha, interquartile range = 454 and 77 ha, respectively). Forest fragments containing display grounds in 2000 were also significantly larger than fragments containing display grounds in the 1980s but presently empty ($F_{1,\,120} = 11.5$; $P < 0.001$, data $\log_{10}$-transformed). Median sizes were 278 ha (interquartile range = 498 ha) and 94 ha (interquartile range = 204 ha) for occupied and deserted fragments, respectively.

In Asturias, the average distance between display grounds is 1,230 m (± 802 SD), and 75% of these are within an NND of 1,528 m. The display grounds occupied in 2000 showed shorter NND among them than among abandoned display grounds (Wilcoxon rank-test: $\chi^2 = 11.4$, $P < 0.001$), and this holds for the distance to the second and third nearest neighbour ($\chi^2 = 6.9$, $P = 0.009$ and $\chi^2 = 6.7$, $P = 0.009$, respectively). The average altitude (± 1 SD) of the display grounds occupied in 2000 (1,328 ± 158 m a.s.l., N = 151, corresponding to the 61 forest fragments reported above) was significantly higher than the altitude of those occupied in the 1980s but now empty (1,251 ± 185 m a.s.l., N = 193; $F_{1,\,342} = 16.4$, $P < 0.001$). Both occupied and empty display grounds showed regular spatial distribution within the forested areas ($R = 1.19$, $|z| = 4.51$ for occupied display grounds, and $R = 1.50$, $|z| = 13.25$ for empty grounds).

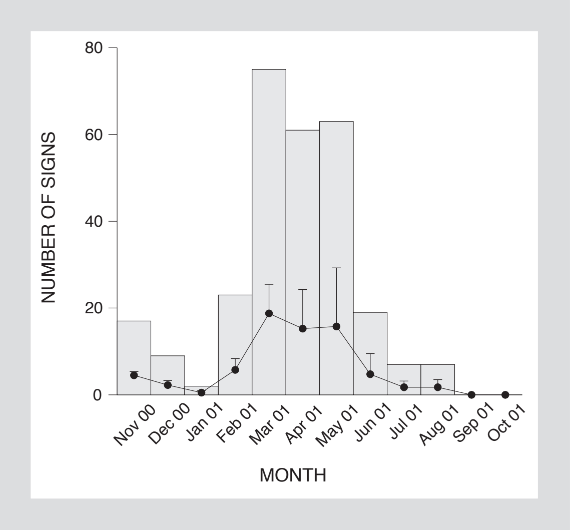

Figure 2. Monthly variation in number of signs along the transects for seasonal microhabitat use. Bars show the total number of capercaillie signs per month, whereas black dots show the mean monthly number (± 1 SE) of signs in each of the four zones.

Seasonal microhabitat use

The fixed transects in the core areas yielded 304 signs of presence, of which 80% were droppings, 11% roosting sites, 6% direct sightings, 2% footprints and 1% feathers. The number of signs found per transect changed substantially throughout the year, diminishing sharply in the autumn/winter period (Fig. 2). The mean values (± 1 SE) of signs per transect and date were 3.2 and 0.7 for the spring/summer and autumn/winter periods, respectively. These differences were significant ($t_{1,144} = -3.28$, $P = 0.0013$).

The availability of the different microhabitats and their variability among transects is shown in Fig. 3A. The signs collected along the transects showed that the Cantabrian capercaillie uses a variety of non-forest habitats throughout the year. During spring/summer capercaillie habitat selectivity was not significant, except for birch stands that were negatively selected (see Fig. 3B). During autumn/winter capercaillie showed significant negative selection of birch, heath and rocky terrain, and used the rest of the microhabitats according to availability (see Fig. 3B).

The number of signs that could be assigned to sex was 102 (out of 304); 76 and 26 signs for cocks and hens, respectively. Most of these signs, 65 and 21 respectively, were from the spring/summer period. The distribution of signs among habitats in that period differed significantly between sexes ($\chi^2_4 = 17.4$, $P = 0.0016$), whereas sex-assigned signs were too scarce in the autumn/winter period to permit further analysis. Cock signs in the

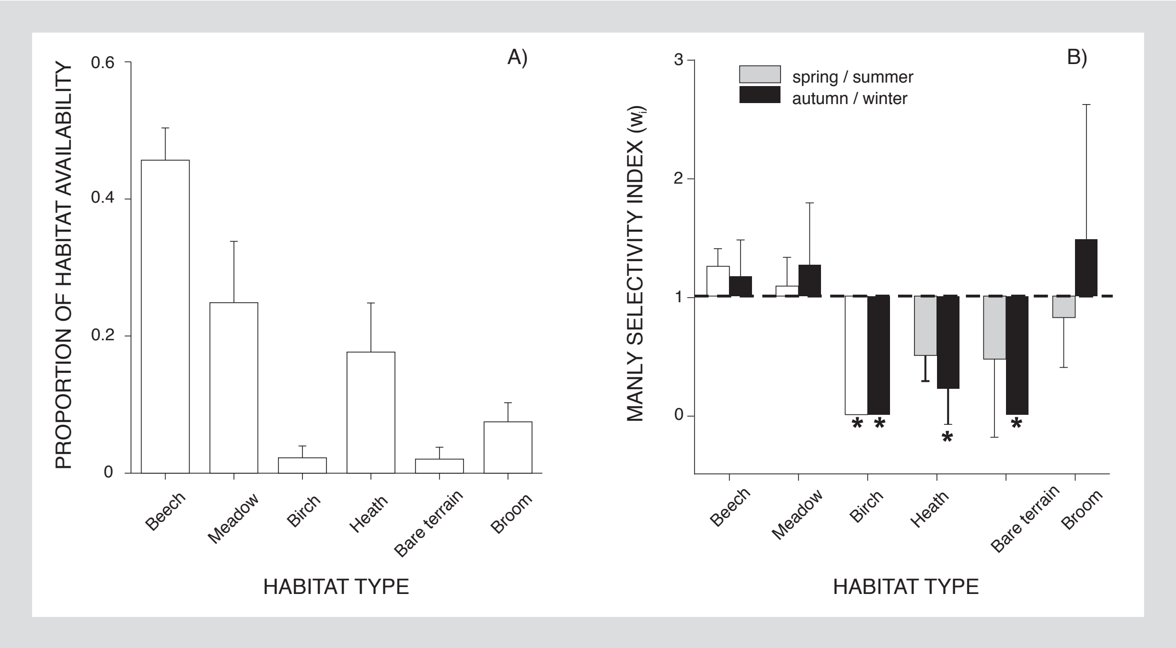

Figure 3. Microhabitat use by Cantabrian capercaillie in the display areas and their surroundings within about a 1-km radius expressed as availability of the different habitat types throughout the year (mean + 1 SE) along the four fixed transects (A). In B) the Manly selectivity index (w_i) calculated for the average use of each habitat between transects is given. Error bars indicate the standard error of the mean habitat use. The dashed line indicates neutral selectivity; $w_i > 1$ indicates positive selection and $w_i < 1$ indicates negative selection. * indicates that w_i values were significant after controlling for multiple comparisons.

spring/summer period were mainly found in beech forest (71%), followed by broom (11%), meadow (9%), heath (8%) and bare terrain (2%). Hen signs were more evenly spread, and were found in heath (38%), beech forest (33%), meadow (19%), broom (5%) and bare terrain (5%).

Forest structure of the display grounds

The amount of forested habitat in the occupied display grounds was greater than in empty grounds. Occupied display grounds showed a trend towards a more open forest structure, and this trend was significant when only beech trees were considered (Table 2). Beech trees accounted for > 75% of the trees both in occupied and empty display grounds. Empty display grounds showed significantly larger trees (see Table 2), although differences were not significant when only beech trees were considered.

We found more plots with bilberry in occupied display grounds (see Table 2). However, the bilberry cover was similar in occupied and empty display grounds when considering mean values for the five plots per location (see Table 2) and when considering bilberry cover only in plots with bilberry presence (19.9 ± 2.9% and 20.8 ± 6.4% for occupied and abandoned display grounds respectively; $t_{56} = 0.14$; $P > 0.05$).

Table 2. Forest structure in occupied (N = 33) and empty (N = 25) capercaillie display grounds in the Cantabrian range. Figures are mean ± 1 SE. ** indicates t-test significant at $\alpha = 0.01$, * indicates t-test significant at $\alpha = 0.05$. The number of display grounds used for beech analyses is given in parentheses. DBH = Tree diameter at breast height.

	Occupied	Empty	$t_{2, 56}$
Forested plots (max. 5)	3.5 ± 0.2	2.6 ± 0.2	3.5**
Plots with bilberry (max. 5)	1.8 ± 0.2	1.1 ± 0.2	2.03*
Bilberry cover (in %)	7.7 ± 1.6	5.1 ± 1.8	1.08
Tree density (number of trees × ha^{-1})	426 ± 62	503 ± 88	-0.7
Tree size (DBH, in cm)	20.3 ± 1.1	26.3 ± 2.5	-2.4*
Beech density (number of trees × ha^{-1})	377 ± 77 (28)	466 ± 85 (22)	-2.4*
Beech size (DBH, in cm)	23.4 ± 1.4 (28)	27.4 ± 2.9 (22)	-0.14

Discussion

We conducted a multi-scale study of habitat use and selection by an endangered population of capercaillie inhabiting the Cantabrian mountains (northwestern Spain), which has declined during the last decades to the point that only about 300 displaying males remain (Obeso & Bañuelos 2003).

Cantabrian capercaillies mainly dwell in beech and oak forests at the southwestern edge of the species' distribution. The size of forest fragments seems to be more important for them than tree species composition, which is in contrast with the classical view of capercaillie as a conifer specialist (Rolstad & Wegge 1987a, Picozzi et al. 1992). At the landscape scale, Cantabrian capercaillie used the forest according to availability, except for the negative selection of the less frequent, smaller patches of Pyrenean oak (see Table 1). The forest habitat in the Cantabrian range is severely limited (about 20% of the landscape) and likely has been so for centuries. There has been, however, an overall recovery of the forest cover throughout western Europe in the last decades (Tucker & Evans 1997). Some authors consider that forest cover in northern Spain reached a minimum in the 1970s (Manuel et al. 2003) and, since then, the forested area has increased by about 8% in some provinces, including Asturias (Manuel et al. 2003). These figures, however, are controversial since they include plantations of exotic tree species, such as eucalyptus *Eucalyptus* spp. and pine *Pinus* spp., and the changes in forest cover are not evenly distributed along the altitudinal gradient (Aedo et al. 1990). We showed that above 700 m a.s.l. in Asturias this recovery has not compensated for historical losses. Instead, we found that the present montane forest cover is about 22% less than it was in the middle of 19th century. This rough comparison does not necessarily mean that the general trend of recovery is not valid for this region, but instead may confirm the popular belief that the middle of the 20th century was the period with the heaviest deforestation, and that the slow recovery is still taking place.

Capercaillies inhabit mostly mature forests (Swenson & Angelstam 1993), and therefore these are the main and irreplaceable feature of their habitat. So, it is not too surprising that during a process of population decline, the remaining occupied territories were in the bigger forest fragments and at higher altitudes where anthropogenic disturbance is presumably lower. The Cantabrian mountains are a highly fragmented landscape (García et al. 2005), where the size of forest fragments is smaller than in other capercaillie populations, particularly in Scandinavia. The smallest size of an occupied forest patch for a Norwegian population was 48 ha, containing a solitary, displaying cock, and the minimum size for collective display grounds was 66 ha (Rolstad & Wegge 1987a). In Asturias 23% of the occupied fragments were smaller than 48 ha. The numbers are not immediately comparable, but they may help to explain why solitary, displaying cocks were recorded in 78% of display areas. Rolstad & Wegge (1987a) developed a predictive model about the effect of forest fragmentation on the density of leks and cocks, ranking forest habitat from coarse-grained to ultra fine-grained. According to this model, the habitat of the Cantabrian capercaillie would be between a medium-grained pattern where decrease in number of cocks per lek would be responsible for overall density decline, and a fine-grained pattern where patches become too small and isolated, and local extinctions occur.

In highly fragmented landscapes, forest patches are embedded in a matrix of other habitats, and forest dwellers like capercaillies frequently encounter open areas with diverse types of vegetation within their home ranges. These non-forest areas weave a complex mosaic of microhabitats that may differ greatly in their resistance to birds' movements, or in their quality as resources (e.g. food and shelter) affecting the response of organisms to habitat fragmentation at both individual and population levels (Vandermeer & Carvajal 2001, Jules & Shahani 2003). We showed that the small-scale habitat use of capercaillie throughout the year includes different microhabitats outside the forest cover, and some selection patterns suggest that the matrix plays a role in population dynamics (see Fig. 3B). During spring/summer we found no significant habitat selection; habitats were used according to availability. This is consistent with the dominance of beech forest along the transects (see Fig. 3A), and its role during the mating and chick-rearing seasons. Moreover, spring and summer bring about a peak in the production of beech buds and leaves, bilberry and understory herbs, which constitute an important food source for adults and chicks (Baines et al. 1996, Rodríguez & Obeso 2000). An exception to the lack of selectivity in the spring/summer period is the total avoidance of birch stands (see Fig. 3B). However these stands made up a very small proportion of the available habitat along the transects (see Fig. 3A), and their thicket-like nature made them particularly difficult to survey. This finding should therefore be interpreted with caution. In the autumn/winter period the Cantabrian capercaillie showed a wider, somewhat more generalist pattern. It used the forest according to availability and made greater use of meadow and broom, though with high variability among zones (see Fig. 3B). The wider habitat use in autumn and winter may be to supplement the diet of beech buds with resources outside the forest cover, consistent with the lower protein content and greater spatial scattering of beech buds than of pine needles (Rodríguez & Obeso 2000), and with the low winter productivity of the forest understory. It may also indicate refuge use because brooms are used beyond availability in some of the zones, but have not been found in the diet (Rodríguez & Obeso 2000). In the autumn/winter period we found significant negative selection of bare terrain, birch stands and heaths. However, the difference among microhabitats in the difficulty of tracking capercaillie signs, which has not been controlled for, and the overall low number of signs recorded along the transects impose caution when interpreting the results.

The composition of the matrix habitat influences the connectivity between patches of optimum habitat (Ricketts 2001). Therefore, in addition to the influence on the feeding behaviour, matrix composition may affect capercaillie perception of the landscape. Indeed, matrix affects the probability of patch colonisation and movement between patches in the hazel grouse *Bonasa bonasia*, another forest-dwelling grouse species (Åberg et al. 1995). Our analysis of matrix use by capercaillie may be affected by the unbalanced seasonal abundance of signs, which decreased notably during the autumn/winter period (see Fig. 2). Nevertheless, this in itself is interesting because it suggests lower activity, and also that the birds may move away substantially from the surroundings of display areas. Seasonal movements seem to be more common and wider in cocks (Storch 1995), although both sexes showed seasonal migrations between deciduous summer ranges and coniferous winter sites in some parts of the species range (Klaus et al. 1989). Such movements may be related to seasonal fluctuation in resource availability between habitats. The movements of Cantabrian capercaillie do not include changes between deciduous and conifer forest, but the seasonal habitat use may well be related to resource availability.

Forest structure plays an important role in determining occupancy, as occurs in northern populations (Picozzi et al. 1992, Swenson & Angelstam 1993). We found that occupied display grounds were surrounded by more forest plots than empty display grounds (see Table 2). We also found that tree density was similar in occupied and empty display grounds (see Table 2), but differences in the growth patterns of tree species may obscure the results: when analysing solely beech forests, we found a lower density of trees in occupied than in unoccupied display grounds. A preference for forest patches with an open structure has been related to better flight conditions in other European populations (Rolstad & Wegge 1987b, Gjerde 1991, Storch 1993a), and to the requirements for bilberry development. We found a more widespread distribution of bilberry in occupied than in unoccupied display grounds (see Table 2), which highlights the importance of this key resource that provides shelter and food for both adults and chicks (Storch 1993a, Baines et al. 1996, Selås 2000). However, both occupied and abandoned areas showed tree densities within the optimum range for capercaillie movements and bilberry development in other populations (Rolstad 1989, Rolstad & Wegge 1989), a result that should be carefully considered before any habitat-improving measure is taken in highly sensitive capercaillie areas.

Implications for conservation and future research

If the Cantabrian capercaillie is to be preserved, its habitat needs to be protected. Here we present the first up-to-date study of habitat selection by this endangered subspecies, suggesting that conservation measures should focus on the few remaining large forest fragments in the area independently of forest species composition. Conditions for understory development, particularly bilberry, should be favoured in these areas. This may be achieved by preserving the old-forest structure and avoiding overgrazing by ungulates (Klaus & Bergmann 1994, Menoni 1994, Côté et al. 2004). We suggest that the non-forest matrix should also be included in management plans, as a direct source of food and shelter, and an important feature that may increase the connectivity between forest patches in a historically modified landscape.

Our study was mainly concerned with capercaillie display areas and adjacent territories. The results therefore reflect the importance of these, specifically related to the remaining mature forest fragments in the area. However, this should not be confused with understating the importance of non-display habitats, such as dispersing habitats, possible foraging habitats not covered in the study, and especially nesting and brood habitat. The latter is particularly important not only because poor recruitment seems to be affecting the population (Obeso & Bañuelos 2003), but also because the spatial pattern of hen territories may determine lek settlement and spacing behaviour of cocks (Menoni 1997). This pattern may occur in the Cantabrian range, because it seems to appear in populations where brood habitats are restricted to certain areas, like in the Pyrenees (Menoni 1997), as opposed to some Scandinavian areas where brood habitats are available all over the forest, and the spacing behaviour of cocks determines hen territories (Wegge & Rolstad 1986). In addition, more information is needed about seasonal movements and dispersal abilities of this subspecies.

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