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ORIGINAL ARTICLE

Diet and habitat selection in Cantabrian Capercaillie (*Tetrao urogallus cantabricus*): ecological differentiation of a rear-edge population

Beatriz Blanco-Fontao · Alberto Fernández-Gil · José Ramón Obeso · Mario Quevedo

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Abstract Cantabrian capercaillie *Tetrao urogallus cantabricus* is a peripheral population with distinctive phenotypic, biogeographic, and genetic characteristics. Hence, the population may also show substantial ecological differentiation associated with its habitat in purely deciduous forests. We assessed seasonal diet selection, small-scale habitat selection, and patterns of trophic niche width in Cantabrian capercaillie over two years. Diet was found to be a driver of small-scale habitat selection, a result consistent with previous studies of stand-scale habitat selection. Diet and habitat selection showed the importance of beech *Fagus sylvatica*, holly *Ilex aquifolium*, bilberry *Vaccinium myrtillus*, and ferns in Cantabrian capercaillie's resource selection. Conversely, the abundant oaks *Quercus petraea*, birches *Betula pubescens*, and heaths *Erica sp.* were used below their availability. The reliance on bilberry appears as a unifying characteristic between central and peripheral capercaillie populations. Cantabrian capercaillie showed stronger reliance on understory resources than range-central populations. It also showed wider trophic niche and higher specialization of feeding events. Trophic niche patterns and reliance on ground resources indicated a marked ecological differentiation, which stresses the need for local data and specific conservation actions.

Keywords Rear-edge populations · Ecological differentiation · Diet selection · Trophic niche · Deciduous forests · *Tetrao urogallus cantabricus*

Introduction

The ecological niche of a species (sensu Hutchinson 1957) can be quite variable across distribution ranges, leading to different realized niches and variability in the demographic and behavioral characteristics of local populations (Chase and Leibold 2003). Peripheral populations, closer to the limits of tolerance of a species, are embedded in a set of community interactions that differs, both in quality and strength, from that at the central parts of their species range (Gaston 2003). In this regard, conservation measures based on information from the central part of a species' range may be of limited use, or even counterproductive, at the edges of the range (Hampe and Petit 2005).

Not only can the realized niche of a species vary among populations across geographic ranges—intrapopulation variability in features such as diet and habitat selection is another potentially important source of variation (Smith and Skúlason 1996; Bolnick et al. 2003). Conservation plans that protect an average population trait (for instance, a folivorous bird species said to obtain 60% of its diet from trees) might fail when a population is built up of substantially different sex, age-class, or individual components (Durell 2000; Bolnick et al. 2003). That said, both the conservation consequences of variation within populations and the ecological characteristics of populations at the rear

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B. Blanco-Fontao · J. R. Obeso · M. Quevedo (✉)
Instituto Cantábrico de Biodiversidad (UO-PA-CSIC)/Ecology Unit, Department of Biology of Organisms and Systems, Oviedo University, Campus del Cristo, 33006 Oviedo, Spain
e-mail: quevedomario@uniovi.es

B. Blanco-Fontao
e-mail: bbfontao.uo@uniovi.es

A. Fernández-Gil
Department of Conservation Biology, Estación Biológica de Doñana (CSIC), Avenida de Maria Luisa s/n, Pabellón del Perú, 41013 Seville, Spain

edge of distribution have been understudied (Durell 2000; Bolnick et al. 2003; Hampe and Petit 2005).

Capercaillie, *Tetrao urogallus* (Tetraonidae), in the Cantabrian Mountains of NW Spain is an endemic, rear edge population that lives at the southwestern edge of the species' range (Castroviejo 1975), and occupies a particularly southerly location within Palearctic grouse distribution (Storch 2007). Cantabrian capercaillie *Tetrao urogallus cantabricus* lives in purely deciduous forests in contrast with the vast majority of capercaillie populations that inhabit coniferous forests (Storch 2007). Hence, the population may be expected to show marked ecological and behavioral differentiation related to its distinct habitat. Although the population is known to be an evolutionary significant unit and may be part of a distinct southern capercaillie lineage (Duriez et al. 2007; Rodríguez-Muñoz et al. 2007), its potential ecological peculiarities remain largely unknown (e.g. Storch 2007). Unfortunately, the population has been declining sharply at least in the last three decades, and hence is also unique in terms of conservation status (Storch et al. 2006).

The trophic ecology of a population may provide an appropriate evaluation of divergence from central ecological and behavioral trends because resource selection is a key aspect of the ability of animals to cope with their environment. This is especially true in the case of herbivorous birds, which need to devote much time to foraging, because of their low intake rate and relatively small gut (Sedinger 1997; van Gils et al. 2007). Grouse specialize on different food resources depending on local conditions, although usually only a few plant species are important throughout the entire range (Sedinger 1997). Capercaillie are mostly folivores; however, diet and habitat selection probably vary substantially from the well-known habitat in boreal forests to the purely deciduous Atlantic montane forests. Bilberry may be a major exception to such differentiation (Storch 1993; Quevedo et al. 2006b). Hence, diet selection could be an important mechanism to explain patterns of habitat selection in birds like capercaillie on the scale of individual daily ranges.

Another biogeographic peculiarity is that capercaillie is the only extant grouse species in the Cantabrian Mountains; hence it does not compete for resources with any closely related species. Furthermore, in winter and early spring, deciduous forests lack the permanent food and shelter supplied by the needles of coniferous forests, which could be a key environmental constraint driving ecological differentiation. These peculiarities lead us to expect higher diversification in the diet of Cantabrian capercaillie and wider trophic niche than in conifer-dwelling populations. Previous studies have indeed shown that the diet of Cantabrian capercaillie might be varied (Castroviejo 1975; Martínez 1993; Rodríguez and Obeso 2000). However, these studies were based on opportunistic sampling schemes and did not address diet selection. Nonetheless, they have provided several hypotheses along the interface of diet and habitat selection for further investigation, for example the widely assumed importance of holly *Ilex aquifolium* for Cantabrian capercaillie (Castroviejo 1975) or the paradoxical minor importance in the diet of sessile oak *Quercus petraea* (Martínez 1993; Rodríguez and Obeso 2000), a canopy species that dominates large forest patches with capercaillie presence in the Cantabrian Mountains (Quevedo et al. 2006b).

In this study, we evaluated year-round diet selection, small-scale (daily-range) habitat selection, and trophic niche width in an area of presumed good habitat quality for Cantabrian capercaillie (Quevedo et al. 2006a). Our specific objectives were to assess the potential relationship between diet and small-scale habitat selection in the population, and to see how this related to previous stand-scale studies (Quevedo et al. 2006b). We also evaluated the extent of diet-related ecological differentiation of this peripheral population compared with other range-central capercaillie populations.

Methods

Study area and survey design

The fieldwork was conducted over a 10-km^2 tract of forested habitat on the northern slope of the western Cantabrian Mountains (NW Spain), centered at 42.94°N–6.48°W, between August 2002 and April 2004. Altitude in the study area ranges from 900 to 1,900 m a.s.l., and the average slope is 21%, resulting in a rugged landscape. Siliceous soils are the substrate of a mixed forest mostly composed of mountain birch *Betula pubescens* (39%), sessile oak *Quercus petraea* (30%), and beech *Fagus sylvatica* (14%). Isolated trees or small groups of holly *Ilex aquifolium* and rowan *Sorbus aucuparia* also occur scattered through the forest. The treeline lies at about 1,600 m a.s.l., and is a fine-grained mixture of birch thicket, tree heaths *Erica arborea*, common heather *Calluna vulgaris* and bilberry *Vaccinium myrtillus*, broom formations (*Genista florida*, *Cytisus scoparius*), grazing meadows, and talus.

The study area held at least three display areas occupied in 2001. Previous observations by forest rangers and the authors showed that the area also included capercaillie brooding, molting, and wintering areas. The study area was also chosen because of its relatively stable occupancy of display grounds compared with the overall population (M. Quevedo unpublished. data), its overall habitat quality for capercaillie in a previous model (habitat suitability values >0.60, Quevedo et al. 2006a), and the negligible presence of domestic ungulates (cattle and horses).

Sampling units were ten plots of 1 km^2 each, based on the UTM grid, which covered the complete surface of the study area. All plots were surveyed bimonthly, from August 2002 to April 2004. The same observer surveyed all the plots, devoting a sampling effort of 3 h per plot and zigzagging within its boundaries. Signs of capercaillie presence, such as direct sightings, fresh droppings, feathers, and footprints, were used to determine habitat use by recording vegetation composition and cover (to the nearest 5%). These variables were visually estimated for both canopy and understory within a circle of 25 m radius (2,000 m^2) centered on the sign of capercaillie presence. The minimum distance for considering signs as independent samples was 50 m. All signs were collected (droppings, feathers) or erased (footprints) in each survey to ensure they were recorded once only. Droppings were stored for posterior diet analysis. Additionally, to collect identical information on resource and habitat availability, control spots were selected randomly by taking one every 30 min of survey in each of the ten sampling plots.

Diet analyses

We used microhistological methods to identify plant remains in the droppings of capercaillie; these were then compared with reference material in a library. Although these methods may lead to some bias (reviewed in Holechek et al. 1982), they are non-intrusive, thus allowing study of diet in secretive and endangered populations (Holechek et al. 1982). Moreover, fecal analysis has been widely and successfully applied in the study of diet selection in herbivorous birds (Owen 1975; Madsen and Mortensen 1987). The technique relies on the resistance of plant epidermis to herbivore digestion, which leaves plant fragments undigested and identifiable in the droppings (Holechek 1982; Alipayo et al. 1992). The reference material was prepared from 28 potential food sources, determined from previous studies of capercaillie diet in the Cantabrian Mountains (Castroviejo 1975; Martínez 1993; Rodríguez and Obeso 2000) and plant availability in the particular study area. To do this, samples were dried at 60°C for 48 h, ground with a Retsch MM200 ball mill, and rinsed with NaOCl to improve clarity (Holechek 1982). Samples were then centrifuged to eliminate the supernatant fluid, and subsequently rinsed and centrifuged twice with distilled water. The resulting material was sieved through 1 and 0.2 mm pore-size filters, and the intermediate fraction was kept for analysis. Approximately 30 mg of the sieved material was mounted on a slide with a hydrophilic mounting medium (Jung tissue freezing medium). These reference slides were studied carefully before proceeding with diet slides, and the specific features of the epidermis (cells shape, hairs and trichomes, stomas) were digitally photographed under a 100× microscope.

Previous tests had been carried out to determine the asymptote of the relationship between the diversity of plant remains and fragments counted. As a result the number of plant remains identified per sample was fixed at 50 along two transects, i.e. the first 25 non-overlapping fragments intercepted per transect/scale line under a 100× microscope. Samples were classified into spring (March–June), summer–autumn (July–October), and winter (November–February), on the basis of capercaillie life cycle and plant phenology. Diet composition was used to calculate the proportion of understory resources in the diet and to compare it with that of other capercaillie populations.

Diet and habitat selection

Diet selection was analyzed on the basis of 11 plant categories, split into canopy and understory. Canopy categories consisted of the main tree species in the study area: beech, sessile oak, birch, holly, and rowan. Diet selection on understory plants was analyzed using the following categories: broom, bilberry leaves, berries and shoots, heaths, heather, ferns, and grasses. These categories were chosen to represent microhabitats that were to some extent different, and to maintain a balance between a too coarse-grained scheme that would underestimate selection, and a too fine-grained one that would merely reflect the natural patchiness of resources.

Diet and habitat selection were determined using *design I* (population level) selection ratios (Manly et al. 2002). These ratios are proportional to the probability of each category being used, assuming unrestricted access to available resources. Selection ratios range from 0 (null selection) to infinite (maximum positive selection), where 1 indicates that resources are used according to availability. Vegetation composition and cover data, in both used and control spots, was pooled, and the mean over the whole study area was used as an estimate of habitat and food availability (Sutherland and Green 2004) of perennial resources. Availability of ferns and grasses was estimated on a seasonal basis.

Niche width

Total trophic niche width and specialization of feeding events were estimated by following metrics that use the total diet of the population to define resource availability. These metrics have been reviewed and updated by Bolnick et al. (2002), who provided the companion software *IndSpec1* that facilitates metric calculations and provides resampling routines. To estimate total niche width (TNW) we used an index adapted to discrete data (Bolnick et al. 2002):

$$\mathrm{TNW} = -\sum_j q_j \ln q_j$$

where q_j is the proportion of the jth food category in the population's niche. The degree of specialization in feeding events for the population was estimated by means of the mean proportional similarity index (IS, Bolnick et al. 2002):

$$\mathrm{IS} = \frac{\sum_i^n \sum_j \min\left(p_{ij}, q_j\right)}{n}$$

where p_{ij} is the proportion of the jth food category in each dropping or feeding event i, and q_j are the same as above. Then, proportions of the different categories in the diet of the population are calculated as the average proportion of each food category. This similarity index estimates the degree of overlap between a given sample and the population. It approaches 0 for fully specialized feeding events (monodiet), and 1 for those with a generalist pattern. The main advantages of this metric over others available are that it estimates specialization for each sample, it is not too sensitive to artifacts resulting from the presence of purely monophagous samples, and it makes no assumption about particular distributions of resources (Bolnick et al. 2002). *IndSpec1* provides a Monte Carlo routine to test the significance of the IS index against a null model of a fully generalized diet. We compared overall, generalized, and seasonal IS values by means of one-way ANOVA and post-hoc Tukey tests. All analyses were performed with freeware (R Development Core Team 2008).

Last, we calculated TNW (as described above) and the proportion of understory resource use for other published studies on capercaillie diet (Jacob 1988; Storch et al. 1991; Picozzi et al. 1996; Saniga 1998; Summers et al. 2004). To enable comparison with our population, we only considered the studies that:

1. showed year-round quantitative data for adult animals; and
2. at least had the same taxonomic resolution as our data.

Additionally, diet categories in these studies were grouped according to categories from our data, that is: all tree and shrub species appearing in the diet, animal material, ferns, grasses, mosses, and unidentified plant remains.

Results

Sampling surveys over the two-year period yielded 146 signs of capercaillie presence in the 10 km^2 study area. Most of these signs were droppings (122), although feathers, footprints, and direct sightings were also included in the analyses of habitat selection. Signs of presence were balanced across seasons (spring 46, summer–autumn 57, winter 43).

Diet and habitat selection

The 122 diet samples analyzed yielded only two monodiets, both consisting of holly leaves in winter and early spring. In spring, diet was dominated by beech buds, bilberry shoots, and fern fronds, at 28, 19 and 16%, respectively ($n = 43$). In summer–autumn, major diet items were 54% bilberry and 10% fern fronds ($n = 49$). Most bilberry consumption in this period consisted of berries (63%). In winter ($n = 30$), holly leaves accounted for 33% of the diet, and beech buds, bilberry shoots, and fern fronds accounted for 13% each. Details of proportional use and availability are given in Appendix 1.

The diet selection index for tree species showed that beech and holly were preferred, whereas birch, oak, and rowan were consumed below availability. Results in spring and winter mirrored the overall trend except for beech in winter, which was consumed according to its availability (Fig. 1a). In summer–autumn, only rowan, which was not consumed at all, departed from availability (Fig. 1a). Among understory species, bilberry and ferns were important in diet selection. Bilberry was strongly selected in summer–autumn, whereas ferns were strongly selected in spring and winter (Fig. 1a). Heaths and brooms, the former a particularly abundant resource, were always used below availability (Fig. 1a). Cantabrian capercaillie obtained much higher percentages of understory or ground-based resources than other populations, averaging 65%, with maximum in summer–autumn (83%) and minimum in winter (50%, Table 1).

Habitat selection for tree species did not show a clear pattern. In spring, beech-dominated areas were used above availability whereas oak-dominated areas were used below availability. In summer–autumn, holly was used below availability (Fig. 1b). Habitat selection for understory vegetation showed that areas rich in bilberry and grasses were preferred in winter and spring, whereas areas rich in ferns were used below availability in spring, and brooms or common heather were used below availability all year round (Fig. 1b).

Niche width and diet similarity index

We found that TNW in Cantabrian capercaillie was wider than for any other capercaillie population analyzed (Table 1). Both overall and seasonal values of the similarity index (IS) for our study population were significantly different from those for generalized resource use (Table 2). In addition IS varied between seasons ($F_{2,119} = 11.3$,

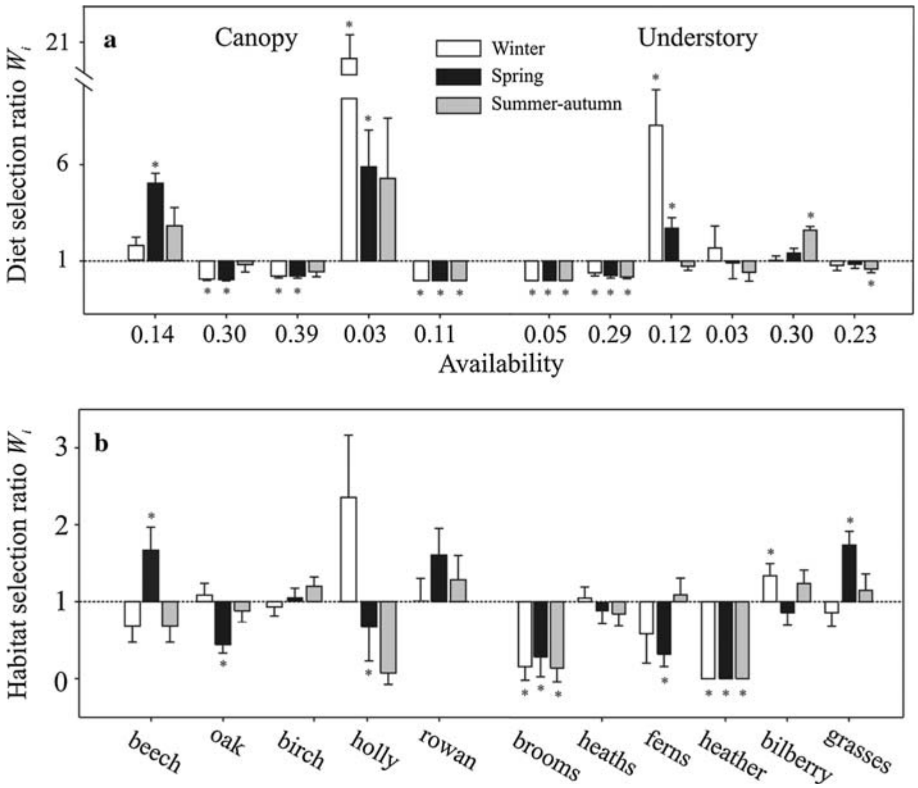

Fig. 1 Diet and habitat selectivity indexes for canopy and understory species, calculated from the average use of each resource category, and resource availability. **a** Diet selection ratio W_i. This equals 1 when resources are used according to availability. The *dashed line* at 1 separates a resource used above or below availability. *Asterisks* indicates W_i was significant after controlling for multiple comparisons (note that the significance of W_i is calculated on a seasonal basis). *Error bars* indicate the standard error of W_i. The numbers on the *X* axis correspond to the mean proportional abundance of the canopy and understory species written below them in the *X* axis of Fig. 1b. Canopy and understory proportions do not add up to 1 as species with less than 1% cover were not included in the analysis. For seasonal resources such as ferns and grasses, we show the seasonal average. **b** Habitat selection ratio *Wi*. Notation and interpretation as above

Table 1 Total trophic niche width (TNW) and average proportion of understory-based diet (UD) for different capercaillie populations

	TNW	$UD_{overall}$	UD_{spring}	UD_{summer}	UD_{winter}
This study	2.11	0.65	0.62	0.83	0.50
Scotland 1[a]	1.36	0.14	0.02	0.29	0
Scotland 2[b]	0.73	0.21	0.14	0.47	0.08
Slovakia[c]	1.50	0.43	0.44	0.78	0.08
Jura Mountains[d]	1.69	0.43	0.10	0.85	0.35
Bavarian Alps[e]	1.63	0.36	0.14	0.81	0.07

[a] Picozzi et al. 1996

[b] Summers et al. 2004

[c] Saniga 1998

[d] Jacob 1988

[e] Storch et al. 1991

$p < 0.0001$, Fig. 2) indicating that specialization of feeding events was higher in winter than in spring and summer–autumn ($p = 0.016$ and $p < 0.001$ in Tukey HSD tests, respectively).

Table 2 Total niche width (TNW) and mean proportional similarity index (IS ± standard error) for this study

	n	TNW	IS	p_{IS}
Pooled dataset	122	2.11	0.47 ± 0.01	<0.0001
Winter	30	2.08	0.45 ± 0.02	<0.0001
Spring	43	2.10	0.54 ± 0.02	<0.0001
Summer/autumn	49	1.74	0.61 ± 0.02	<0.0001

IS varies between 0 and 1, where diets departing strongly from the population overall approach 0 whereas diets similar to the population average approach 1. p_{IS} indicates the probability of IS being equal to that of a fully generalized overall diet

Discussion

Ecological singularity

In this study we confirmed that living in purely deciduous forests has trophic and possibly behavioral consequences for capercaillie. Cantabrian birds obtained, annually, 65% of their resources on the ground, whereas for other populations this ranged between 14 and 43%, averaging 34%.

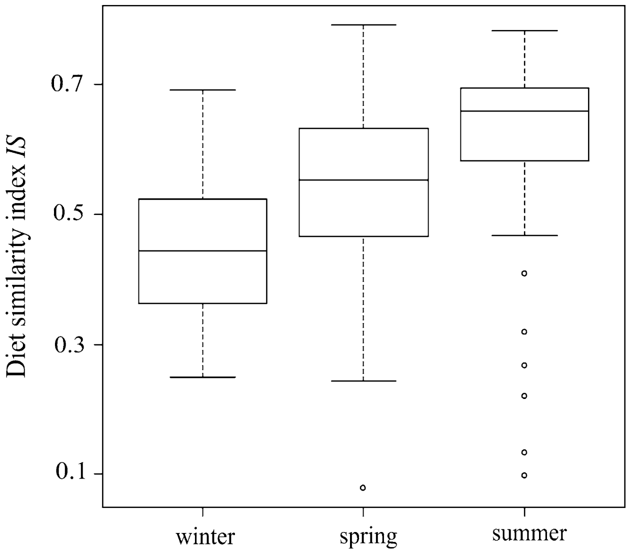

Fig. 2 Box plots showing the seasonal distribution of the proportional similarity index IS. This is an index of specialization of feeding events that approaches 0 for fully specialized feeding events (monodiet), and 1 for those with a generalist pattern. *Boxes* indicate the interquartile range of the data and the position of the median; *error bars* extend to non-outlier data within 1.5 times the interquartile range

This contrast appears particularly marked in winter, arguably the season with more pronounced structural differences between deciduous and conifer forests. The differences may be because of the lack of foliage in winter and early spring in deciduous forests, together with the rugged terrain where plants protrude above the snow in ridges, whereas the availability of conifer needles in most populations allows the birds to use trees as their primary food source. This result is a mechanistic example of differential interactions with both biotic and abiotic components of the environment, predicted for peripheral populations (Gaston 2003). Several consequences could result from this behavioral peculiarity. For instance, we speculate that higher reliance on understory resources may imply that Cantabrian birds are more susceptible than boreal birds to the overall unfavorable competition with large mammalian herbivores (van Gils et al. 2007).

In other capercaillie populations and forest grouse species, foraging is often concentrated on individual food items, and includes perching in individual trees for days or even weeks (Bergerud and Gratson 1988; Sedinger 1997). We found almost no such monodiet feeding events. In addition, diet and habitat preference showed several contrasting results, especially for holly and ferns, which were preferred as winter diet but were not especially common as part of winter habitat. All in all, we interpret this as a markedly distinct foraging behavior in which Cantabrian capercaillie moved more often and farther while foraging, departing from the usual overlap between food and cover found in other capercaillie populations and forest grouse species (reviewed by Bergerud and Gratson 1988).

Mechanisms of habitat selection

The high proportion of understory resources in the diet of capercaillie may partially explain the results of previous, larger-scale studies, which showed that stand-scale forest composition was not a key factor for habitat selection in Cantabrian capercaillie (Quevedo et al. 2006b). In addition, previous studies of stand-scale habitat selection also suggested a preference for areas richer in bilberry (Quevedo et al. 2006b), a trend which our diet analyses confirmed. Bilberry appears in high proportion in the diet all year round, and the birds positively selected it in summer–autumn. Leaves, shoots, and, mostly, berries were consumed. Therefore, bilberry reliance seems to be a general characteristic of both central and peripheral capercaillie populations (Martínez 1993; Storch 1993; Rodríguez and Obeso 2000, Selås 2000). It also seems that bilberry, a major source of food and shelter for adults and chicks (Storch 1994; Wegge et al. 2005), is the only major diet resource shared with birds from the conifer domain.

Diet selection and trophic niche width

The phenology of deciduous forests determines the availability of resources for herbivores. This may explain the highly positive selection of holly and ferns in winter and spring. Holly is the only evergreen tree species in the study area, although it appears highly scattered within the forest; it was present only in 82 of 429 surveyed plots, averaging 3% availability. Hence, as suggested in previous studies (Castroviejo 1975; Martínez 1993; Rodríguez and Obeso 2000), holly is a key winter food resource for Cantabrian capercaillie that may also provide shelter. Also important in the winter diet were beech buds, the first to appear in the season in these forests (B. Blanco-Fontao, personal observation). Diet preferences shifted markedly in summer–autumn, when Cantabrian capercaillie converged with other populations and selected bilberry. Conversely, the abundant oak and birch (taken together, representing a total of 69% of the canopy) and heaths (29% of understory), were consumed below availability. The low consumption of oak and birch may be related to the phenology of beech and bilberry, because the former is the first tree species to produce buds in winter, and the latter provides widespread supply of fresh leaves before oak and birch unfold theirs. This idea is supported by the use of beech as both a diet and habitat resource beyond its availability (Fig. 1). Nonetheless, accurately explaining such diet shifts would require higher sampling frequency than in this study, and chemical determinations. Overall, we found stronger patterns of diet and habitat selection in spring (Fig. 1), perhaps reflecting the fact that resources are still scarce in early spring, the season that marks the onset of the energy-demanding reproductive period for capercaillie.

We found that Cantabrian capercaillie showed a broader TNW than the other capercaillie populations studied. This result confirms our expectations based on both the strong seasonality of resource availability in deciduous forests and the lack of interspecific competition with other grouse species that may lead to niche expansion (Van Valen 1965; MacArthur et al. 1972; Costa et al. 2008). Interestingly, TNW of Cantabrian capercaillie was closest to that of those capercaillie populations living in montane habitats, for example the Jura Mountains and Bavarian Alps.

There were substantial seasonal differences in niche patterns. Niche width was narrower and the specialization of feeding events was lower in summer–autumn, as the population foraged on the preferred bilberry fruits. In winter we found the opposite: more food items were included in the diet, but single feeding events were less similar to those for the population overall. We interpret this as a consequence of the lack of an abundant, widespread resource for folivores in winter and early spring in deciduous forests, compensated for by a broader niche than for other capercaillie populations. This result is also consistent with previous, larger scale results indicating more varied winter habitat use in Cantabrian capercaillie (Quevedo et al. 2006b).

Final remarks

Our study revealed substantial ecological differences between Cantabrian and range-central capercaillie populations, and strong reliance on bilberry as a common feature among them. Our results stress the need for specific, local data to develop sound conservation plans, and suggest that bilberry, an important ground resource for Cantabrian capercaillie, should be specifically protected in capercaillie recovery plans. Most extant capercaillie areas in the Cantabrian range are protected (Quevedo et al. 2006a), but such protection does not prevent overgrazing on bilberry and other resources. Free-ranging livestock, though extensive and considered "traditional", attain densities up to an order of magnitude larger than those of wild ungulates in some areas. Moreover, they double the highest densities of native ungulates in protected areas where overgrazing has long been discussed, for example the Northern Range of Yellowstone National Park (Rodríguez et al. 2007). Reducing the season and range over which cattle herds graze and trample freely within sensitive areas has already been suggested for protecting the habitat of brown bears *Ursus arctos* in the Cantabrian range (Naves et al. 2006). We suggest that limiting overgrazing by livestock may also help capercaillie directly by reducing competition, and indirectly by improving bilberry productivity (Tolvanen 1994).

In this study we did not attempt to discriminate between hen and cock droppings because the overlap between them may be sometimes substantial, adding too much uncertainty to our quantitative approach. We considered that visual discrimination of sex from capercaillie droppings may be hampered by individual diet variation and seasonal diet shifts, which may be particularly important in our fine-grained study area. Nonetheless, sexual dimorphism and individual variation are potential sources of variability that could affect understanding of capercaillie ecology and management plans (Bañuelos et al. 2008). Intrapopulation variability in the use of resources should be addressed by specific studies that assign diet unequivocally to individuals, perhaps combining microhistological and molecular techniques.

Zusammenfassung

Ernährung und Habitatwahl des Kantabrischen Auerhuhn (*Tetrao urogallus cantabricus*): ökologische Unterscheidung einer randständigen Population

Das Kantabrischen Auerhuhn ist geographisch randständig verbreitet und hat phänotypisch, biogeographisch und genetisch eindeutige Merkmale. Deshalb sind substanzielle ökologische Unterschiede assoziiert mit dem Habitat, reinem Laubwald, relativ zu zentralen Auerhuhnpopulationen, zu erwarten. Wir haben die saisonale Nahrungswahl, die kleinräumige Habitatnutzung und die Verteilung der trophischen Nische des Kantabrischen Auerhuhns über zwei Jahre erfasst. Übereinstimmend mit vorherigen Studien war die Ernährung ein wichtiger Faktor bei der kleinräumigen Habitatwahl. Nahrungs- und Habitatwahl zeigte die Bedeutung von Buchen (*Fagus sysvatica*), Stechpalmen (*Ilex aquifolium*), Heidelbeeren (*Vaccinium myrtillus*) und Farnen für Ressourcenwahl Kantabrischer Auerhuhner auf. Umgekehrt wurden die reichlich vorhandenen Eichen (*Quercus petraca*), Birken (*Betula pubescens*) und Heidekraut (*Erica* sp.) weniger genutzt als ihre Verfügbarkeit es zulassen würde. Die Abhängigkeit von Heidelbeeren scheint ein gemeinsames Merkmal der zentralen und randständigen Populationen der Auerhühner zu sein. Kantabrische Auherhühner zeigten eine stärkere Abhängigkeit von Unterholzressourcen als Populationen im Zentrum des Verbreitungsgebietes. Sie zeigten ebenfalls eine größere Nischenbreite und einen höhere Spezialisierungsgrad von Nahrungsereignissen. Die Verteilung der trophischen Nische und die Abhängigkeit von Unterholzressourcen weisen auf eine ausgeprägte

ökologische Differenzierung hin; dies betont die Erfordernis und den Belang lokaler Daten für spezifische Naturschutzmassnahmen.

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Appendix 1

Table 3 Proportional abundance of resources and proportional use in the diet (mean ± 1 SD) of main canopy and understory species

Species	Availability	Proportional diet use		
		Spring	Summer–autumn	Winter
Fagus sylvatica	13.6 ± 23.6	28.1 ± 20.8	5.3 ± 11.4	12.7 ± 20.2
Quercus petraea	29.7 ± 29.8	0.6 ± 1.0	3.5 ± 7.8	1.3 ± 2.4
Betula pubescens	39.3 ± 26.1	3.9 ± 5.2	2.5 ± 8.4	4.8 ± 11.8
Ilex aquifolium	3.2 ± 6.6	7.8 ± 21.0	2.4 ± 13.1	33.0 ± 37.8
Sorbus aucuparia	10.6 ± 10.4	0	0	0
Vaccinium myrtillus	27.8 ± 16.1	19.1 ± 16.0	53.6 ± 27.7	13.3 ± 14.7
Erica spp.	29.2 ± 19.5	3.7 ± 5.5	4.0 ± 6.4	5.4 ± 5.4
Calluna vulgaris	2.7 ± 11.9	1.2 ± 2.7	0.9 ± 1.7	2.1 ± 3.8
Cytisus/ Genista spp.	4.5 ± 8.9	0	0	0
Ferns	11.6 ± 18.6	16.3 ± 20.8	10.3 ± 18.1	13.0 ± 20.4
Grasses	22.8 ± 20.4	4.1 ± 8.9	3.0 ± 5.1	2.3 ± 8.1
Mosses	–	6.0 ± 13.4	5.5 ± 8.8	4.2 ± 10.6
Unidentified	–	1.1 ± 1.95	2.6 ± 3.1	2.9 ± 5.7

For seasonal resources, for example ferns and grasses, the average availability value is shown

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