Habitat partitioning and molting site fidelity in *Tetrao urogallus cantabricus* revealed through stable isotopes analysis

---

Beatriz Blanco-Fontao[1]*, José Ramón Obeso[1], María-José Bañuelos[1], Mario Quevedo[1]

[1] Research Unit of Biodiversity (UO-PA-CSIC); Dpt. Biology of Organisms and Systems, Oviedo University.

Campus del Cristo, 33006 Oviedo, Spain.

*Corresponding author. Email: bbfontao.uo@uniovi.es

Phone: +34 98 510 48 30

Fax: +34 98 510 47 77

ABSTRACT

Sexual dimorphism is often associated with different feeding strategies between sexes because of distinct nutritional demands or intake rates. Capercaillie is the most sexually dimorphic grouse, thus sexual segregation in resource use is likely. This study assessed intrapopulation variation in the diet related to habitat use, focusing on differential feeding behaviors between Capercaillie females and males. We used stable isotopes analyses in feathers of Cantabrian Capercaillie, a population living at the southern edge of the range in purely deciduous forests. We analyzed feathers of females and males, and sorted them according to the dominant tree species in the patch where they were found. Mean isotopic values differed both between sexes and among forest types. The latter explained most of the isotopic variance, suggesting that birds consistently selected certain forest types to molt. Capercaillie females showed wider trophic niche and seemingly more intra-gender diversity in resource use than males. The differences between sexes in the trophic variability support the sexual segregation reported in previous studies which is associated with females using the more micro-habitat diverse treeline areas, while males mainly use the inner areas of the forests. Stable isotope analysis proved very useful to assess intersexual niche partitioning in rare species living in rugged terrains where it is logistically difficult to rely on direct approaches (i.e. direct observation, capture and radio-tracking).

KEY WORDS: sexual dimorphism, stable isotope analysis, trophic niche, habitat segregation, *Tetrao urogallus cantabricus*

Introduction

Adaptations to local resources at the population level are widely acknowledged in wildlife ecology. However, at a finer level of organization individuals or sectors within a population (i.e. age or sex-classes) might specialize on different food resources, depending on differences in habitat use and feeding behaviors (Durell 2000; Catry et al. 2005; Bearhop et al. 2006). Males and females are often subjected to different ecological constraints, and in turn, likely to show distinct feeding behaviors (Mysterud 2000; Bolnick et al. 2003; Ruckstuhl 2007). Differential ecological constraints can be driven by distinct nutritional demands (Isaac 2005; Bulte et al. 2008), and are frequently related to sexual segregation, i.e. seasonal, distinct habitat use by males and females. This is especially true in highly sexually dimorphic species as the degree of sexual size dimorphism and the level of inter-sex niche segregation are positively correlated (Mysterud 2000; Phillips et al. 2009).

Capercaillie (*Tetrao urogallus*) is the most sexually dimorphic grouse species. Males may almost double females in weight (i.e. males: 3.3-6.5 Kg, females: 1.5-2.5 Kg; Madge et al. 2002), and sexes differ in various other morphological, physiological and ecological aspects (e.g. Rintamaki et al. 1984; Borchtchevski 1987). Moreover, Capercaillie is a large, herbivorous bird, with a relatively simple digestive tract, and low intake rates (Sedinger 1997; Van Gils et al. 2007); as such, diet is an environmental constraint, likely to be reflected in sexual dimorphism. Diet differences between sexes can be either the result of differences in mean diet composition and preferences, or otherwise related to the diet variance, i.e. generalist or specialist character of each sex, or degree of intra-gender diversity in resource use. Regarding the latter aspect and following the predictions of the niche variation hypothesis, more generalized populations are likely to exhibit more intrapopulation niche variation (Van Valen 1965; Bolnick et al. 2007). We studied the Cantabrian population of Western Capercaillie (*Tetrao urogallus cantabricus*), the only population that inhabits all year round purely deciduous forests (Quevedo et al. 2006a, b). Previous studies on Cantabrian Capercaillie showed that habitat partitioning exists during summer in this population, related to sex and reproductive status, and associated with the females’ stronger reliance on more heterogeneous treeline habitats while males remain in more homogeneous inner areas of the forests (Bañuelos et al. 2008). These previous studies on the Cantabrian range, altogether with studies on northern Capercaillie populations that report more generalized diets for females (Storch et al. 1991; Odden et al. 2003; Borchtchevski 2009) are hinting possible sexual dimorphism in the diet and feeding behaviors. In addition, molting is a period of the annual cycle that determines reduced home ranges and high site fidelity in other Capercaillie populations (Rolstad et al. 1988; Martínez 1993). In the highly fragmented and heterogeneous Cantabrian landscape - result of a long-term process of both natural fragmentation and historical deforestation by humans (García et al. 2005) - molting site fidelity may be related to the selection of specific forest patches and, thus, it could be studied through analysis of habitat-related diet differentiation.

Stable isotope analysis can provide estimates of resource use over longer time periods than conventional diet analyses, which are often based on single feeding events (West et al. 2006; Inger and Bearhop 2008). For instance, the isotopic values in feathers, which are metabolically inert, reflect the resources assimilated by birds during feather formation (Hobson and Clark 1992; Bearhop et al. 2002). Hence, feathers provide valuable information on resource use during the cryptic, molting period, when energy demands are highest for Capercaillie (Lindén et al. 1984). Stable isotope analysis of molted feathers of Cantabrian Capercaillie is an indirect approach that allows evaluation of sex-related trophic ecology in a sparse population living in a rugged landscape. Specifically, we used stable isotope analysis to, 1) assess intra-specific dietary variation between females and males and, 2) evaluate fidelity to microhabitats during the molting. Our hypothesis is that Capercaillie’s marked sexual dimorphism would imply distinct dietary variation of each sex. Therefore, based on previous studies on habitat partitioning for this population (Bañuelos et al. 2008), we predict broader trophic niche in females.

Material and methods

Study area and sample collection

Our study area includes the entire Cantabrian Capercaillie (*Tetrao urogallus cantabricus)* range in the Cantabrian Mountains (provinces of Asturies and León, NW Spain, Fig.1). This rugged landscape contains the largest portion of the remnant Atlantic deciduous forest on the Iberian Peninsula, at the southernmost boundaries of this vegetation type (Polunin and Walters 1985; García et al. 2005). These are mostly semi-natural forests with a long history of human use that resulted in a highly fragmented pattern, with highly interspersed patches dominated by different tree species (García et al. 2005). Beech *Fagus sylvatica,* mountain birch *Betula pubescens* and sessile oak *Quercus petraea* are the dominant canopy species in the Cantabrian forests. The treeline lies at about 1600 m a.s.l., and is a mixture of forest, tree heaths *Erica arborea*, common heather *Calluna vulgaris* and bilberry *Vaccinium myrtillus*, broom formations (*Genista florida, Cytisus scoparius*), grazing meadows, and scree slopes.

A total of 125 different areas of aprox. 1 Km^2 in the vicinity of leks and known molting sites were surveyed during three consecutive molting seasons (2005-2007). These surveys consisted of drives conducted from 15th July to 15th September, in areas where Capercaillie was present according to spring surveys of lek occupancy, and summer survey of reproductive success. In the Cantabrian Mountains, Capercaillie reproduction appears to occur 3–4 weeks later than in northern populations (Martínez 1993; Moss et al. 2001; Wegge et al. 2005), and thus, molting is also delayed. See Bañuelos et al. (2008) for details on those surveys.

The feathers of Capercaillie females and males are easily differentiated by color and pattern. All feathers found in these surveys were positioned with a GPS and stored in paper envelopes. We collected Capercaillie feathers in 533 different points. We arbitrarily set a minimum distance of 500 m between feathers of the same sex to minimize the use of feathers from the same individuals, up to a total of 126 analyzed feathers (Fig. 1).

To evaluate microhabitat fidelity during the molt, we grouped feathers according to the dominant tree species in the patch were they were found - birch, beech or sessile oak - in a 500 m radius buffer around each feather. Each major canopy species roughly defines an array of accompanying plants. Thus, we used them as proxies to distinguish forest patches. Information on canopy species was extracted from a 1:25.000 GIS database (see Quevedo et al. 2006a, b, for details).

Feathers were split into six subsets for analysis: female feathers in birch (n = 18), beech (n = 21) and oak patches (n = 13) and male feathers in birch (n = 15), beech (n = 37) and oak patches (n = 22).

Stable isotope analysis

We measured $\delta^{13}C$ and $\delta^{15}N$ ratios in feathers to evaluate sexual- and habitat-mediated differences in trophic variability of the Cantabrian Capercaille population. The $\delta^{13}C$ ratio traces the importance of different carbon pools to a consumer, whilst $\delta^{15}N$ is an effective tracer of the origin of nitrogen in plants (Kelly 2000; Inger and Bearhop 2008). Therefore, the combination of both isotopes, together with the application of quantitative metrics (Layman et al. 2007) is a powerful approach to assess both the origin of resources and the trophic variability of populations (Newsome et al. 2007; Inger and Bearhop 2008). Only body-covert feathers were analysed to ensure that all feathers had a similar growing period. Feather samples were cleaned to remove oils and debris by rinsing in a 2:1 chloroform-methanol solution for 24 hours, then dried in an oven at 60ºC to constant weight (e.g. Hobson and Bairlein 2003; Symes and Woodborne 2009). Subsequently, feathers were frozen in liquid nitrogen and immediately ground to fine powder using a MM200 ball mill. Subsamples of 1 mg (± 0.2 mg) were packed into 6 × 4 mm tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analyses, which were performed using a continuous-flow isotope ratio mass spectrometer at UC Davis Stable Isotope Facility (USA). Stable isotopes ratios are expressed in δ notation, as part per thousand deviation from standard material, Pee Dee belemnite limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$ according to the equation:

$\delta X = [(Rsample / Rstandard) - 1] \times 1000$ where X is ^{15}N or ^{13}C and R is the corresponding ratio ^{15}N:^{14}N or ^{13}C:^{12}C.

To discard a spatial structure of the isotopic values in feathers we compared the standardized Euclidian geographical distance and isotopic distance matrices. We standardized the geographical and isotopic values by subtracting the mean of all elements in the matrix from each observation and then dividing by the SD (Fortin and Gurevitch 2001). The significance of the relationship was assessed using a simple Mantel test with 1000 randomizations with the software *zt* provided by Bonnet and Van de Peer (2002).

Trophic niche breadth and population specialization

To calculate trophic niche breadth and trophic variability we used quantitative metrics based on the position of individuals in the $\delta^{13}C$-$\delta^{15}N$ space, and Euclidean distances (Layman et al. 2007) We applied those metrics to the six subsets of the population (see above), using individuals as measurement units. The individuals of each subset were plotted in a $\delta^{13}C$-$\delta^{15}N$ niche space. To estimate the total niche of each subset we measured the total area of the convex hull (TA) that included the isotopic values of all individuals. To obtain null distributions of TA and test the significance of differences between subsets, we randomized the empirical data set of isotopic signatures 1000 times and calculated TA in each resampled data set. P values were approximated as the proportion of resampled data sets that exceeded the observed differences; for forest patch comparisons, false discovery rate was controlled using the FDR adjustment (Benjamini and Hochberg 1995).

To estimate the trophic variability within each subset of the population we calculated Euclidean distances among individuals in the $\delta^{13}C$-$\delta^{15}N$ bi-plot. First, we calculated the distance of each individual to the isotopic centroid of its subset (CD), providing an index of the trophic diversity in females and males. Then we calculated the coefficient of variation of the distances from each individual to its same-sex neighbors in the isotopic space (CVND), which gives a measure of the clustering of values and trophic redundancy (Quevedo et al. 2009).

Two-way ANOVAs and post hoc Tukey tests were used to test for differences among forest patches and between sexes regarding mean $\delta^{13}C$ and $\delta^{15}N$ values, CD (square root transformed to achieve normality) and CVND.

CD and CVND were calculated in a GIS. Convex hulls and TA were calculated using package Adehabitat (Calenge 2006), an extension to R statistical environment (R Development Core Team 2010), which we used for all the statistical analyses.

Results

Mean $\delta^{13}C$ and $\delta^{15}N$ isotopic values significantly differed between males and females and among forest patches (Table 1, Fig. 2). Forest patch explained the majority of $\delta^{13}C$ (75 %) and $\delta^{15}N$ variance (40%; the rest of $\delta^{15}N$ variance was equally distributed between sex and residual variance). Capercaillie feathers in oak patches showed higher values of $\delta^{13}C$ than in birch and beech patches whereas birch patches showed higher values of $\delta^{15}N$ than beech and oak ones (Tukey HSD tests, Table 2, Fig. 2). Males showed higher values for both isotopes (Tukey HSD tests, Table 2, Fig. 2).

Capercaillie total niche space (TA) varied among forest patches and between sexes. TA was significantly bigger in beech and birch patches than in oak ones (Table 3). Females showed significantly larger values than males (Table 3).

CD and CVND were significantly different among forest patches and CD was marginally larger for females (Table 3). Neither CVND between sexes nor both interactions significantly differed. CD was significantly shorter in oak patches than in birch ones ($p = 0.013$ in Tukey HSD tests) whereas the significant differences in CVND among forest patches were determined by lower values for oak patches than for birch and beech patches ($p = 0.006$ and $p = 0.002$ in Tukey HSD tests, respectively, Table 3).

There was no spatial structure in the isotopic values, i.e. no significant correlation was found between the standardized Euclidian geographical distance and the isotopic distance matrices (Mantel test: $r = 0.004$, $p = 0.42$).

Discussion

Trophic sexual dimorphism

A stable isotope analysis of molted feathers is a valuable, unintrusive tool to study the trophic ecology of an endangered, elusive bird, the Cantabrian Capercaillie. We found that females and males of this Capercaillie population showed differences in their average isotopic signatures, which could be related to distinct habitat use; females and males also showed distinct trophic variability, both results consistent with a sexually dimorphic species with marked separation of reproductive roles. Such differences suggest relevant dietary segregation within the population among individuals from different sexes, likely related to spatial segregation of females and males during the molt.

Using stable isotopes to study resource selection by herbivores has difficulties because of the wide variability of isotopic signatures in primary producers; intrinsic variances in plant signatures in pure C3 environments could have been expected to yield statistically undetectable differences between herbivore individuals, whereas carnivores in a similar system should render simpler interpretations because the variability of primary producers is averaged up the successive trophic levels (e.g. Fry 2008). Despite to the presumed difficulties, we found marked differences between sexes within the different microhabitats. Males and females differed in average isotopic values, with males showing higher δ^{13}C and δ^{15}N isotopic signatures (Fig. 2); they also differed in the trophic niche breadth and variability, reflecting distinct dietary variation of each sex. Regardless of the smaller sample size for females, their overall trophic niche (TA) was wider (Table 3) suggesting a more generalized diet (Storch et al. 1991; Odden et al. 2003; Borchtchevski 2009). In addition, longer distances to the isotopic centroid (CD; Table 3) indicated higher trophic diversity, i.e., females showed greater variability in resource use. Overall, differential trophic variability for each sex is apparent; females show a wider niche, with a higher level of intra-gender diversity compared to males that had more specialized diets with less intra-gender variability in resource use. These results thus lend support to the niche variation hypothesis (Van Valen 1965; Bolnick et al. 2007).

Our results suggest distinct trophic variability for each gender, which may be related to spatial separation in foraging; females use the more diverse and less homogeneous treeline forests, while males mainly use the inner areas of the forests during molting (Rolstad et al. 1988; Ménoni 1990; Bañuelos et al. 2008). Our main contribution to previous knowledge of Capercaillie feeding ecology (Storch et al. 1991; Odden et al. 2003; Borchtchevski 2009) is to reveal sex-related trophic variability in Capercaillie by means of stable isotope analysis, and trophic differences likely driven by habitat segregation. Using radio-tracking data, summer spatial sexual segregation is also found in Scandinavian Capercaillie populations related to differential sexual constraints of both predation and nutritional requirements (Rolstad et al. 1988), but not in the Alps where both sexes were reported to overlap in habitat use, converging in old forests with a well developed understory (Storch 1993).

From the viewpoint of conservation biology, results indicated sex-biased vulnerability to habitat change and likely differential responsiveness to habitat management. Thus, it should be again stressed that conservation measures should take into account for sex-related variation, (e.g. Durell 2000; Bolnick et al. 2003).

Site fidelity during the molting season

The kind of forest patch explained most variance for both isotopes. This is a very interesting result considering (i) the montane forest structure in the Cantabrian Mountains, (ii) our sampling design and (iii) the ecology of Capercaillie. First, our study area included the montane forests within the entire Cantabrian Capercaillie distribution range (Fig. 1). These forests show a highly fragmented pattern, where different canopy species often build small, interspersed patches (García et al. 2005). Second, feathers sampled in a given year and sorted to the dominant patch type where they were found, were actually formed during the previous molting season, i.e. one year before collection. Third, Capercaillie is an herbivorous bird that needs to devote extra-time to foraging (Sedinger 1997; Van Gils et al. 2007), and it is likely to use income resources to grow feathers (Thomas 1988; Meijer and Drent 1999). On the basis of these previous studies, Capercaillie molting and foraging activities are likely to overlap in time and space, and hence feathers are likely to reflect the trophic resources used in the forest patches where molt and growth occur. Thus, the striking differences found among average isotopic signatures of feathers collected in patches dominated by distinct tree species suggest that birds consistently selected certain forest types to molt. These differences might also indicate reduced home ranges during this period of the annual cycle due to fragmentation and small patch size. These findings agree with the smaller summer home ranges and with the observed return to summer molting places in consecutive years in other Capercaillie populations (Rolstad et al. 1988; Storch 1993). It is worth noting that the high site fidelity suggested here is microhabitat-related, i.e. individuals are seemingly returning to the same kind of forest patch during the molting period.

The isotopic approach in terrestrial systems has been widely used to assess predator diets or to evaluate the relative contribution of C3 and C4 plants to herbivore diets in tropical areas (reviewed in Kelly 2000, for birds and mammals). However, its application to study the feeding ecology of terrestrial herbivores inhabiting pure C3 plant environments is quite challenging (Herrera et al. 2003; Stewart et al. 2003; Feranec 2007; Symes and Woodborne 2009). In this study, we have found distinct average isotopic values in the feathers found in each forest type, which might be a consequence of the set of particular conditions that determine the dominance of one species or the other in the canopy of the forest patches. For instance, $\delta^{13}C$ indicates differences in moisture regimes; hence the higher $\delta^{13}C$ values in oak patches may reflect more xeric conditions in this kind of forest (Heaton 1999). However, this study was not designed to find a mechanistic proximate explanation for the isotopic signature of each subset of the population and further research on fractionation and isotopic routing for exclusively C3-plant consumers would greatly improve the possibilities of this approach and, therefore, the knowledge of the feeding ecology of terrestrial herbivores inhabiting these environments.

Isotopic applications and caveats

Stable isotope analyses do have several advantages over traditional techniques (reviewed in West et al. 2006; Inger and Bearhop 2008). However, the approach is indirect; it does not have the resolution required to capture subtle, yet meaningful, differences in resource use that could be derived from analyses of stomach content or droppings, approaches more directly related to birds' natural history. Hence, future research combining both isotopic and microhistological analysis of inert tissues and droppings, respectively, may provide more robust dietary information spanning different time-scales (e.g. Hobson and Clark 1992; Bearhop et al. 2002). This would be particularly useful to study the trophic ecology of elusive species (i.e. sexual or age-class trophic partitioning, population trophic structure; Post 2003; Newsome et al. 2007). Furthermore, unintrusive studies using droppings to obtain data on population structure and stress levels (e.g. Thiel et al. 2005; Jacob et al. 2010), combined with isotopic information may provide mechanistic insights into the feeding ecology of animals and open new research paths in trophic ecology.

Other caveats that could affect our results are related to the intrinsic isotopic variance in resources, and to different metabolic routing of distinct diet components (Matthews and Mazumder 2004; Araújo et al. 2007; Martínez del Rio and Anderson-Sprecher 2008). In our study we minimized potential biases due to intrinsic resource variance by including microhabitat (patch type) as a variable in the analyses. In addition, our goal was mainly to get comparative measures of trophic niche, rather than estimating the proportion of diet items; although the lack of baseline suggests a cautious interpretation of the results, we considered that baseline isotopic variance is unlikely to obscure the clear patterns identified here.

Acknowledgements

We thank the Asturian Environmental Agency (Consejería de Medio Ambiente del Principado de Asturias) for providing access to part of the feather that were analyzed. We also thank José Luis Benito, the coordinator of the summer drives and author of corresponding technical reports. We are especially grateful to Manuel A. González, Luis Robles, Maria Cano, Fernando Rodríguez, Andrés Gómez Merillas, Oscar Fernández Otero, José Carral and Alberto Fernández-Gil whose help was key in the field surveys. Amalia Segura participated in the laborious work of processing the samples. Jörg Müller, and two anonymous referees improved with their comments an early version of the manuscript. The study was funded by a PFPU-MEC fellowship to BBF, grant CN-07-174, from the Asturian Environmental Agency to JRO, grant UNOV-08-MB-2 from Oviedo University to MQ and grants IB08-158 from FICYT and CGL2010-15990 from MICINN to MJB.

References

Araújo MS, Bolnick DI, Machado G, Giaretta AA, dos Reis SF (2007) Using delta C-13 stable isotopes to quantify individual-level diet variation. Oecologia 152 (4):643-654

Bañuelos MJ, Quevedo M, Obeso JR (2008) Habitat partitioning in endangered Cantabrian capercaillie *Tetrao urogallus cantabricus*. J Ornithol 149 (2):245-252

Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiol Biochem Zool 75 (5):451-458

Bearhop S, Phillips RA, McGill R, Cherel Y, Dawson DA, Croxall JP (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Mar Ecol-Prog Ser 311:157-164

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J Royal Stat Soc Ser B (Methodological) 57:289-300

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):1-28

Bolnick DI, Svanback R, Araújo MS, Persson L (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proc Natl Acad Sci U S A 104 (24):10075-10079

Bonnet E, Van de Peer Y (2002) zt: a software tool for simple and partial Mantel tests. J Stat Softw 7 (10):1

Borchtchevski VG (1987) On the gut size of common capercaillie. In: Gabuzov OS (ed) Rearing of the valuable and rare animals. Moscow, pp 61–68

Borchtchevski VG (2009) The May diet of Capercaillie (*Tetrao urogallus*) in an extensively logged area of NW Russia. Ornis Fenn 86 (1):18-29

Bulte G, Gravel MA, Blouin-Demers G (2008) Intersexual niche divergence in northern map turtles (*Graptemys geographica*): the roles of diet and habitat. Can J Zool 86 (11):1235-1243

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Catry P, Phillips R, Croxall JP (2005) Sexual segregation in birds: patterns, processes and implications for conservation. In: Ruckstuhl KE, Neuhaus P (eds) Sexual segregation in vertebrates. Cambridge University Press, Cambridge,

Durell S (2000) Individual feeding specialisation in shorebirds: population consequences and conservation implications. Biol Rev 75 (4):503-518

Feranec RS (2007) Stable carbon isotope values reveal evidence of resource partitioning among ungulates from modem C-3-dominated ecosystems in North America. Palaeogeogr Palaeoclimatol Palaeoecol 252 (3-4):575-585

Fortin MJ, Gurevitch J (2001) Mantel tests: spatial structure in field experiments. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Oxford University Press, New York, pp 308–326

Fry B (2008) Stable Isotope Ecology. Springer Science, Baton Rouge, LA

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

Heaton THE (1999) Spatial, species, and temporal variations in the C-13/C-12 ratios of C-3 plants: Implications for palaeodiet studies. J Archaeol Sci 26 (6):637-649

Herrera LG, Hobson KA, Rodríguez M, Hernandez P (2003) Trophic partitioning in tropical rain forest birds: insights from stable isotope analysis. Oecologia 136 (3):439-444

Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. The Condor 94:181-188

Hobson KA, Bairlein F (2003) Isotopic fractionation and turnover in captive Garden Warblers (*Sylvia borin*): implications for delineating dietary and migratory associations in wild passerines. Can J Zool 81 (9):1630-1635

Inger R, Bearhop S (2008) Applications of stable isotope analyses to avian ecology. Ibis 150 (3):447-461

Isaac JL (2005) Potential causes and life-history consequences of sexual size dimorphism in mammals. Mammal Rev 35 (1):101-115

Jacob G, Debrunner R, Gugerli F, Schmid B, Bollmann K (2010) Field surveys of capercaillie (Tetrao urogallus) in the Swiss Alps underestimated local abundance of the species as revealed by genetic analyses of non-invasive samples. Conserv Genet 11 (1):33-44

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78 (1):1-27

Layman CA, Arrington DA, Montana CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88 (1):42-48

Lindén H, Milonoff M, Wikman M (1984) Sexual differences in growth strategies of capercaillie, *Tetrao urogallus*. Finn Game Res 42:29-35

Madge S, McGowan P, Kirwan GM (2002) Pheasants, partridges and grouse: a guide to the pheasants, partridges, quails, grouse, guineafowl, buttonquails and sandgrouse of the world. Princeton University Press, Princeton, New Jersey

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

Martínez del Rio C, Anderson-Sprecher R (2008) Beyond the reaction progress variable: the meaning and significance of isotopic incorporation data. Oecologia 156 (4):765-772

Matthews B, Mazumder A (2004) A critical evaluation of intrapopulation variation of delta C-13 and isotopic evidence of individual specialization. Oecologia 140 (2):361-371

Ménoni E (1990) Caquetements et territorialite des poules de Grand Tetras 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

Mysterud A (2000) The relationship between ecological segregation and sexual body size dimorphism in large herbivores. Oecologia 124 (1):40-54

Newsome SD, Martínez del Rio M, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429-436

Odden M, Wegge P, Eliassen S, Finne MH (2003) The influence of sexual size dimorphism on the dietary shifts of Capercaillie *Tetrao urogallus* during spring. Ornis Fenn 80 (3):130-136

Phillips RA, Bearhop S, McGill RAR, Dawson DA (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. Oecologia 160 (4):795-806

Polunin O, Walters M (1985) A guide to the vegetation of Britain and Europe. Oxford University Press, Oxford, United Kingdom

Post DM (2003) Individual variation in the timing of ontogenetic niche shifts in largemouth bass. Ecology 84 (5):1298-1310

Quevedo M, Bañuelos MJ, Obeso JR (2006a) The decline of Cantabrian capercaillie: How much does habitat configuration matter? Biol Conserv 127 (2):190-200

Quevedo M, Bañuelos MJ, Saez O, Obeso JR (2006b) Habitat selection by Cantabrian capercaillie *Tetrao urogallus cantabricus* at the edge of the species' distribution. Wildl Biol 12 (3):267-276

Quevedo M, Svanbäck R, Eklöv P (2009) Intrapopulation niche partitioning in a generalist predator limits food web connectivity. Ecology 90 (8):2263-2274

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rintamaki H, Karplund L, Linden H, Hissa R (1984) Sexual differences in temperature regulation and energetics in the capercaillie *Tetrao urogallus*. Ornis Fenn 61:69-74

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

Ruckstuhl KE (2007) Sexual segregation in vertebrates: proximate and ultimate causes. Integr and Comp Biol 47 (2):245-257

Sedinger JS (1997) Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. The Condor 99:314-326

Stewart KM, Bowyer RT, Kie JG, Dick BL, Ben-David M (2003) Niche partitioning among mule deer, elk, and cattle: Do stable isotopes reflect dietary niche? Ecoscience 10 (3):297-302

Storch I, Schwarzmüller C, Von den Stemmen D The diet of capercaillie in the Alps: A comparison of hens and cocks (1991) In: Transactions Congress International Union of Game Biologists Gödöllö, Hungary, pp 630-635

Storch I (1993) Habitat selection by capercaillie in summer and autumn: Is bilberry important? Oecologia 95:257-265

Storch I (2007) Grouse: status survey and conservation action plan 2006–2010. IUCN, Gland, Switzerland and Cambridge, UK, and the World Pheasant Association, Fordingbridge, UK

Symes CT, Woodborne SM (2009) Trophic level delineation and resource partitioning in a South African afromontane forest bird community using carbon and nitrogen stable isotopes. Afr J Ecol 48: 984-993

Thiel D, Jenni Eiermann S, Palme R (2005) Measuring corticosterone metabolites in droppings of capercaillies (Tetrao urogallus). Ann N Y Acad Sci 1046 (1):96-108

Van Gils JA, Gyimesi A, Van Lith B (2007) Avian herbivory: An experiment, a field test, and an allometric comparison with mammals. Ecology 88 (11):2926-2935

Van Valen L (1965) Morphological variation and width of ecological niche. Am Nat 99:377-390

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 (12):1547-1555

West JB, Bowen GJ, Cerling TE, Ehleringer JR (2006) Stable isotopes as one of nature's ecological recorders. Trends Ecol Evol 21 (7):408-414

Tables

Table 1

ANOVA table comparing the effects of sex and forest patch on the isotopic signatures of Capercaillie feathers.

Variable	**δ^{13}C**	**δ^{15}N**
Sex	$F_{1,122} = 4.56$; $p = 0.034$	$F_{1,122} = 5.56$; $p = 0.019$
Forest	$F_{2,122} = 10.\ 30$; $p < 0.001$	$F_{2,122} = 3.49$; $p = 0.033$
Sex*Forest	$F_{2,122} = 3.03$; $p = 0.052$	$F_{2,122} = 0.79$; $p = 0.453$

Table 2

δ^{13}C and δ^{15}N isotopic values (mean ± SD) in feathers of Capercaillie for sex and forest patch . Different superscripts indicate significant differences among groups after Tukey tests ($p < 0.05$).

Sex	**δ^{13}C**	**δ^{15}N**
Male	-24.1 ± 0.6^{a}	1.5 ± 1.0^{a}
Female	-24.4 ± 0.5^{b}	1.1 ± 1.3^{b}
Forest		
Birch	-24.3 ± 0.5^{a}	1.9 ± 1.4^{a}
Beech	-24.5 ± 0.6^{a}	1.2 ± 1.1^{b}
Oak	-23.9 ± 0.5^{b}	1.1 ± 1.0^{b}

Table 3

Summary of trophic niche metrics (mean ± SD) and comparisons among birch, beech and oak forests and between males and females. TA represents the total area of the convex hulls that included δ^{13}C-δ^{15}N isotopic values of each of the subsets; CD shows the distance of each individual to the isotopic centroid of its subpopulation; CVND is the coefficient of variation of distances from each individual to its neighbors in the isotopic space. *P* values for TA were estimated as the proportion of resampled data sets that exceeded the observed difference; for the forest variable, *p* values correspond to birch-beech, birch-oak and beech-oak forest patch comparisons after controlling for false discovery rate (FDR). *F* values correspond to two-way ANOVAs.

	TA		**CD**		**CVND**	
Forest	Male	Female	Male	Female	Male	Female
Birch	4.37	8.38	1.30 ± 0.75	1.53 ± 0.78	0.54 ± 0.12	0.54 ± 0.09
Beech	7.36	7.82	1.03 ± 0.55	1.16 ± 0.82	0.52 ± 0.13	0.56 ± 0.12
Oak	3.48	4.08	0.88 ± 0.41	1.06 ± 0.47	0.46 ± 0.06	0.45 ± 0.11
Variable						
Sex	p = 0.012		$F_{1,122} = 3.84$; p = 0.052		$F_{1,122} = 1.09$; p = 0.29	
Forest	p = 0.22; p = 0.050; p = 0.012		$F_{2,122} = 4.88$; p = 0.013		$F_{2,122} = 7.09$; p < 0.001	
Sex*Forest	-		$F_{2,122} = 0.06$; p = 0.94		$F_{2,122} = 0.73$; p = 0.48	

Figure captions

Fig. 1

Study area and approximate area of occupancy of Cantabrian Capercaillie (in grey), mapped by plotting buffer areas of 2-km radius around display grounds occupied in 2007 (see Storch 2007, for criteria). Flags correspond to feather collection points for males (n = 74) and white dots for females.

Fig. 2

$\delta^{13}C$ and $\delta^{15}N$ isotopic values (mean ± SE) for males and females of Cantabrian Capercaillie in birch, beech and oak forest patches.

Fig. 1

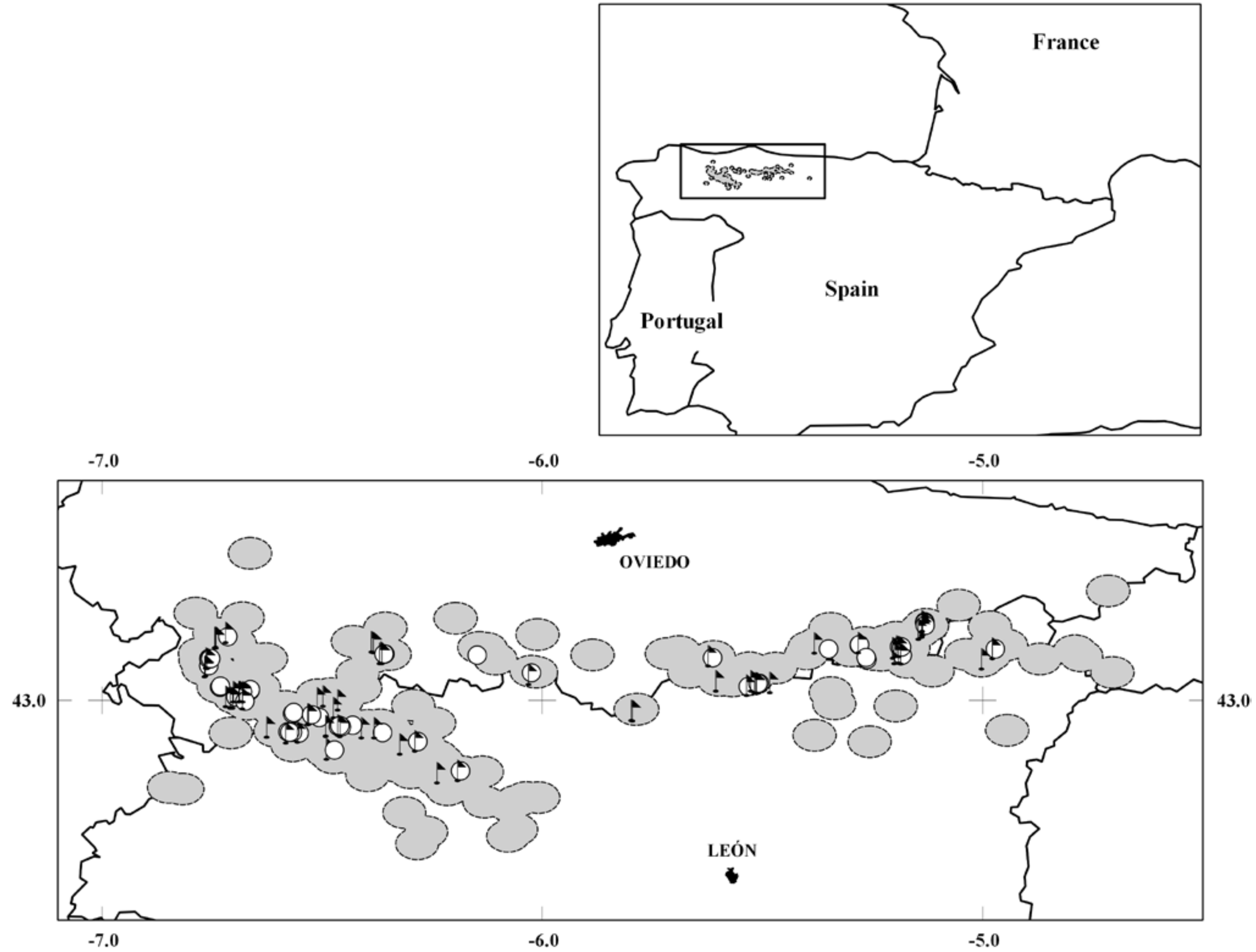
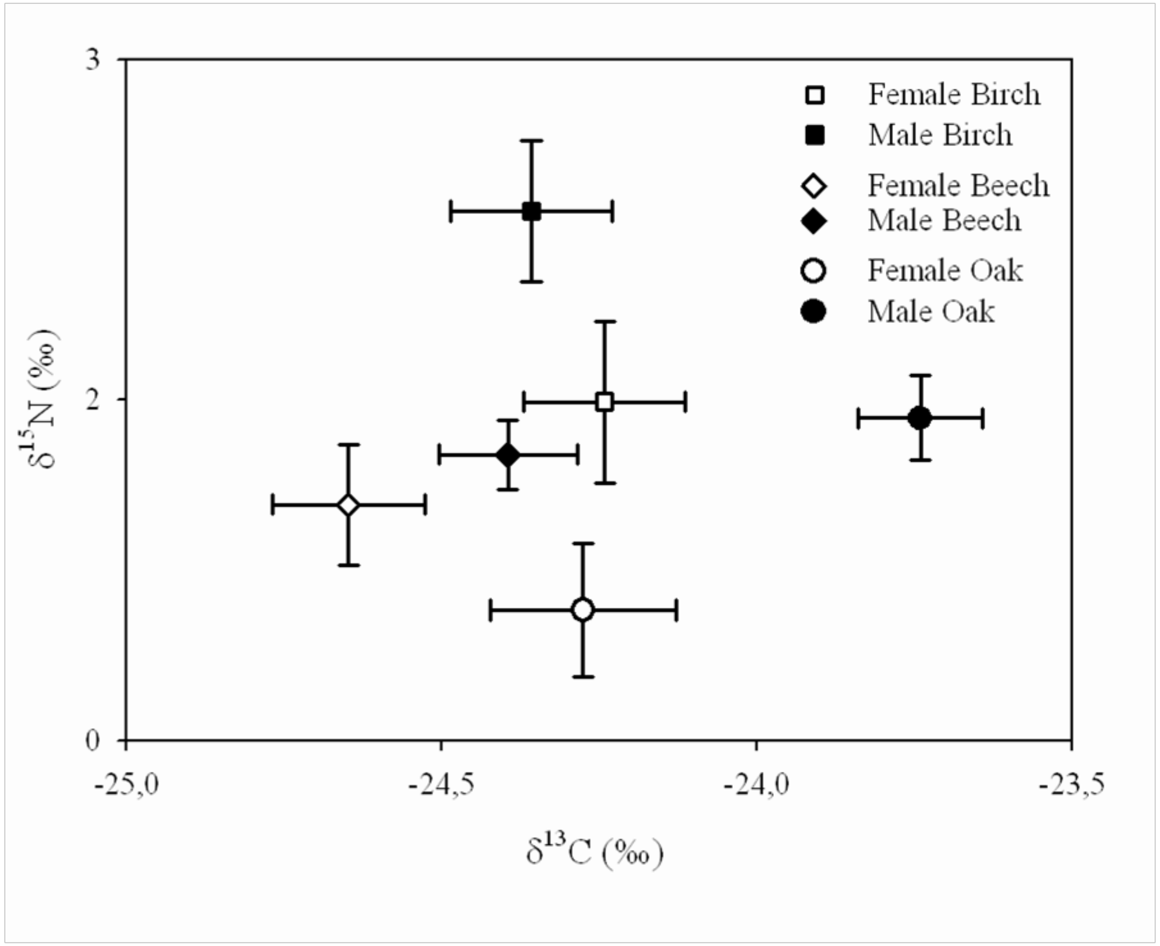


Fig. 2


3
2
0
-25,0
-24,5
-24,0
-23,5
δ15N (‰)
δ13C (‰)
□ Female Birch
■ Male Birch
◇ Female Beech
◆ Male Beech
○ Female Oak
● Male Oak