



## Habitat selection and diet of Western Capercaillie *Tetrao urogallus* in an atypical biogeographical region

MANUEL A. GONZÁLEZ,<sup>1\*</sup> PEDRO P. OLEA,<sup>2</sup> PATRICIA MATEO-TOMÁS,<sup>3</sup> SERGIO GARCÍA-TEJERO,<sup>1</sup>  
ÁNGEL DE FRUTOS,<sup>4</sup> LUIS ROBLES,<sup>5</sup> FRANCISCO J. PURROY<sup>1</sup> & VICENTE ENA<sup>1</sup>

<sup>1</sup>Department of Biodiversity and Environmental Management, University of León, Campus de Vegazana s/n,  
24071 León, Spain

<sup>2</sup>School of Biology, IE University, Campus Santa Cruz la Real, 40003 Segovia, Spain

<sup>3</sup>Instituto de Investigación en Recursos Cinegéticos, CSIC-UCLM-JCCM, Ronda de Toledo s/n, 13071,  
Ciudad Real, Spain

<sup>4</sup>Pyrenean Institute of Ecology (CSIC), Avda Montañana 1005, 50080, Zaragoza, Spain

<sup>5</sup>Asociación para la Conservación del Urogallo (ACU), C/San Roque 12, Boñar 24850, León, Spain

Ecological features and conservation requirements of populations at the latitudinal limits of a species' geographical range frequently differ from those in other parts of the range. Identifying such differences is key to implementing effective conservation strategies for threatened range-edge populations especially, in the context of rapid global warming, at the lower-latitude range edge. We studied habitat selection and diet of the endangered Cantabrian Capercaillie *Tetrao urogallus cantabricus* in a recently discovered population at the southernmost edge of the sub-species' range. This is the only Western Capercaillie population in the Mediterranean biogeographical region. We combined non-systematic surveys based on questionnaires, reports and field sampling with data from radiotracking to assess habitat selection. Diet was surveyed by micro-histological methods from droppings collected in the new population, which inhabits Pyrenean Oak *Quercus pyrenaica* forests and Scots Pine *Pinus sylvestris* plantations, and in two Cantabrian populations inhabiting Eurosiberian forests. Capercaillie preferred large (> 500 ha) and medium-sized (100–500 ha) Pyrenean Oak forest fragments and large Scots Pine plantations. Forest fragments smaller than 100 ha and non-forested habitats were always avoided. Diet differed markedly between Mediterranean and Eurosiberian populations. Bilberry *Vaccinium myrtillus* is common in the diet of most Capercaillie populations but was scarce in the study area and so was rare in the diet of the new population. Instead, Rockrose *Halimium lasianthum* was described for the first time as a major food resource for the Capercaillie and was consumed in autumn and winter. Pine needles were also heavily consumed in winter. We document for the first time the strong preference of Capercaillie for Pyrenean Oak forests and a moderately high consumption of the leaves, buds and acorns of this tree species throughout the year. Habitat selection and diet of this Mediterranean population differ from those of the core Cantabrian and other populations. Our results suggest a wider environmental tolerance (phenotypic plasticity) in the species than previously recognized. We advocate specific protection for this unique range-edge Capercaillie population and its Pyrenean Oak forest habitat.

**Keywords:** climate change, distribution edge, peripheral populations, Pyrenean Oak forest, Rockrose, *Tetrao urogallus cantabricus*.

\*Corresponding author.  
Email: magong@unileon.es

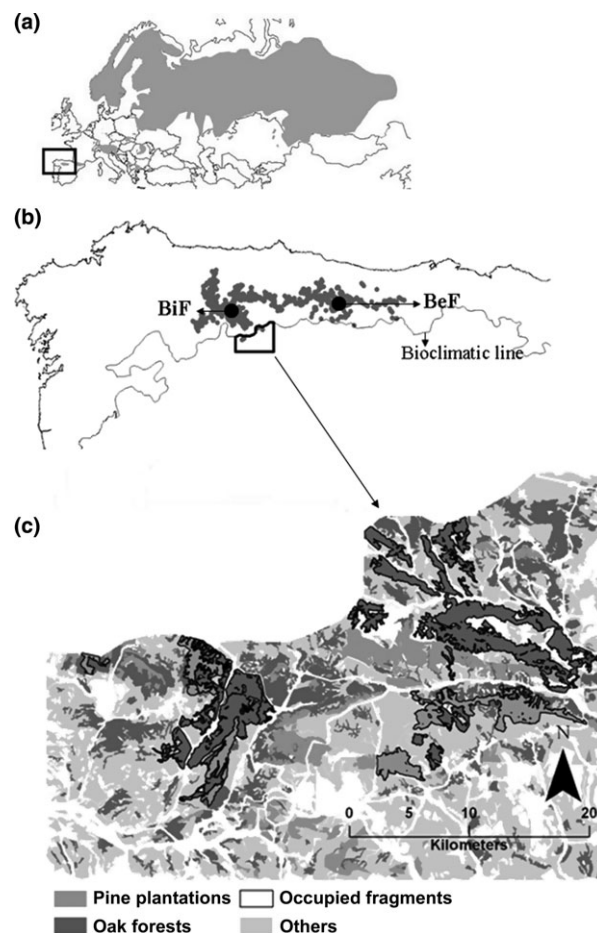
Populations at the periphery of species' distribution ranges generally experience less favourable environmental conditions than in the core of the

range and display lower and more variable densities (Brown 1984, Lawton 1993, Channel & Lomolino 2000). Peripheral populations therefore tend to be more fragmented, more isolated and smaller in size than populations in more central areas of the geographical range, making them more prone to extinction (Lesica & Allendorf 1995, Furlow & Armijo-Prewitt 1995, but see Channel & Lomolino 2000). Many populations at the edge of species' ranges occur in marginal and atypical habitats (Brown 1984, Lesica & Allendorf 1995), thereby promoting genetic differentiation (Lesica & Allendorf 1995). There is therefore particular interest in conservation of peripheral populations on both genetic and ecological grounds (e.g. Lesica & Allendorf 1995, Furlow & Armijo-Prewitt 1995, Hampe & Petit 2005). In addition, the edges of species' ranges are often where the last populations of species persist, so edge populations may become of overriding conservation value as refuges for species of high conservation concern (Furlow & Armijo-Prewitt 1995, Brook *et al.* 2000, Channel & Lomolino 2000).

In the face of expected future climate change, populations that inhabit the latitudinal boundaries of the distribution range have become the focus of attention, as they are expected to be the most sensitive to climate change and are the populations through which effects of climate change are manifested as range shifts (Thomas *et al.* 2004, Hampe & Petit 2005). In this context, populations occupying the low-latitude margins of species' ranges (hereafter rear-edge populations) may be of particular importance not only because of their possible role as centres of speciation and long-term reserves of genetic diversity but also because they are likely to be sensitive indicators of the effects of climate change (Hampe & Petit 2005). Climate change may wipe out rear-edge populations, resulting in range contraction (Davis & Shaw 2001, Hampe & Petit 2005, Huntley *et al.* 2006). Alternatively, evidence from past periods of climate change suggests that rear-edge populations might survive in areas with heterogeneous topography by tracking suitable conditions through small altitudinal shifts (Hampe & Petit 2005). Today, such responses may be impeded by anthropogenic landscape and habitat alterations that reduce suitable habitat and exacerbate the potential impacts of climate change (Davis & Shaw 2001). Where ecological requirements of rear-edge populations differ from those at the core of the range, the necessary conservation

measures may also differ (Lesica & Allendorf 1995, Hampe & Petit 2005), so that knowledge of population-specific requirements (Whittingham *et al.* 2007) is necessary to underpin effective strategies for the management and conservation of range-edge populations.

The Western Capercaillie *Tetrao urogallus* (henceforth Capercaillie) is a large forest grouse widely distributed in the Palearctic (Fig. 1a) with its core range in mature and continuous taiga forests (Storch 1993, 2001, Suter *et al.* 2002). In central and southern Europe, populations are fragmented and largely restricted to mountain coniferous forests (Storch 2007). The only Capercaillie population inhabiting purely deciduous forest is the



**Figure 1.** (a) Global Western Capercaillie distribution (adapted from Storch 2001). (b) Location of the study area (black contour) and of the beech (BeF) and birch (BiF) forests sampled within the Cantabrian Capercaillie distribution (grey area). (c) Detail of the study area, below the Eurosiberian–Mediterranean bioclimatic line, showing occurrence of forest fragments.

Cantabrian Capercaillie subspecies *T. urogallus cantabricus* (Castroviejo 1975), which occurs in the Cantabrian Mountains of northwestern Spain (Fig. 1b). It is an isolated rear-edge population at the southwestern margin of the species' range. This peripheral population displays distinctive phenotypic (Castroviejo 1975) and genetic characteristics, being considered an Evolutionary Significant Unit (ESU; Rodríguez-Muñoz *et al.* 2007). After a 60% population decline in the last three decades (Bañuelos & Quevedo 2008), the Cantabrian Capercaillie is classified as endangered according to the IUCN criteria (Storch *et al.* 2006). Historically, it has been considered to be closely associated with Bilberry *Vaccinium myrtillus* as a food source (Castroviejo 1975, Blanco-Fontao *et al.* 2010), and is found in Beech *Fagus sylvatica*, Birch *Betula pubescens* and Sessile Oak *Quercus petraea* montane forests in the Eurosiberian biogeographical region (Quevedo *et al.* 2006a,b).

Until recently, the Capercaillie was thought to be restricted to the Eurosiberian biogeographical region, but a remnant population of the Cantabrian Capercaillie has recently been found in the Mediterranean biogeographical region with a supra-Mediterranean bioclimate (González *et al.* 2010), south of the previously known range. This region experiences summer drought and Bilberry is very scarce (González *et al.* 2010). The remnant nucleus has an estimated population of at least 17 males (comprising at least 7% of all Cantabrian males) distributed in at least nine leks and occurs in Pyrenean Oak *Quercus pyrenaica* forests intermingled with Scots Pine *Pinus sylvestris* plantations (Quevedo *et al.* 2006a, González *et al.* 2010).

We studied habitat selection and diet of this recently discovered rear-edge Capercaillie population. We combined non-systematic surveys based on questionnaires, reports and field sampling with radiotracking data to study habitat selection. We also studied the diet of Capercaillie in this supra-Mediterranean bioclimate and compared it with that of birds in two Eurosiberian areas (mainly composed of beech and birch forests) within the range of Cantabrian Capercaillie (Fig. 1).

## METHODS

### Study area

The study was carried out over c. 1500 km<sup>2</sup> on the southern slopes of the Cantabrian Mountains

(Fig. 1). The area is located in the Mediterranean region close to the boundary with the Eurosiberian region (González *et al.* 2010). Average annual temperature ranges between 4 and 9 °C and the annual precipitation from 866 to 1100 mm. Precipitation is unevenly distributed throughout the year, with sporadic snowfalls in winter, rain mainly in spring and autumn, and a severe drought for 2 months during summer. The landscape is mountainous (elevation ranges from 800 to 1700 m asl). Dominant forests are supra-Mediterranean unburned (more than 50 years old) and post-fire Pyrenean Oak forests and monoculture Scots Pine plantations younger than 50 years old (Costa-Tenorio *et al.* 2005). Bilberry is completely absent or very scarce (< 0.5% of the forest ground cover; González *et al.* 2010). The remaining area is covered by semi-natural habitats mainly composed of *Populus nigra*, *Fraxinus excelsior* and *Alnus glutinosa* riparian lowland forests, meadows, heaths *Erica australis*, brooms *Genista* sp. and anthropogenic land cover such as crops, open mines, roads and villages. Human population density is very low (0.6 people/km<sup>2</sup>) and has declined by 85% since the 1950s (INE 2008), leading to the abandonment of pastures and the consequent increase of the forested landscape (Morán-Ordoñez *et al.* 2011). The main economic activity is livestock rearing, followed by coal mining, agriculture, forestry and hunting (Penas 1995).

### Forest map

A digital map of available habitat was created from the most recent national forest inventory (MARM 2009) using ARCGIS 9.3 (ESRI 2010). We validated this information with the most recent geo-referenced aerial photographs at 0.25-m pixel resolution (PNOA 2008) and with field observations made during the study. We identified three main types of habitat, classified according to the dominant species, namely oak forest, pine plantation and non-forested habitat (consisting of heaths and/or brooms and/or meadows). We defined a habitat fragment as a patch of habitat surrounded by other habitat types (García *et al.* 2005). The non-forested habitat category was included because previous studies showed them to be used by Cantabrian Capercaillie elsewhere (Quevedo *et al.* 2006b, Bañuelos *et al.* 2008). On the basis of the type and size of the fragment, we recognized seven habitat categories: small (< 100 ha), medium

(100–500 ha) and large (> 500 ha) Pyrenean Oak fragments; small (< 100 ha), medium (100–500 ha) and large (> 500 ha) Scots Pine plantations; and non-forested habitats.

### Species data from observations

We gathered information on the distribution of Capercaillie in the study area between 2002 and 2009 from questionnaires and reports sent by forest wardens, hunters and local people to the regional environmental agency (Consejería de Medio Ambiente of the Junta de Castilla y León). An experienced observer then validated these data through field surveys which consisted of 3–4-h systematic zig-zag transects in the fragment looking for signs of Capercaillie presence (direct sightings, display grounds, footprints, droppings or feathers), every 1–2 months up to six times throughout the year, or until signs were found. Some biases may exist in this non-systematic sampling, mainly due to different accessibility of observers to forest fragments and differences between habitats in detectability of Capercaillie. To minimize bias from this non-systematic sampling, we pooled the data on presence signs over all the study years (2002–2009). We considered a fragment to be occupied by Capercaillie when at least one presence sign was registered during 2002–2009 and unoccupied when no sign was observed in that period.

### Species data from radiotracking

In addition, we trapped four Capercaillie (two females and two males) using funnel trap boxes in the study area in May 2000, November 2006 and November 2007 (Robles 2007). Trapped birds were one adult male (> 2 years old), one sub-adult male (< 2 years old) and two sub-adult females. All birds were radio-collared with adjustable necklace transmitters (Biotrack-TW 3, 21 g weight with mortality sensor). The total weight of transmitter plus harness did not exceed the recommended limit of 3–5% of body weight (Kenward 2001). Tracking equipment comprised an Icom ICR-20 receiver, a directional three-element Yagi antenna (150–152 MHz; Biotrack Ltd, Wareham, UK) and a hand-held GPS (Garmin e-Legend HCx). We determined the location of the radiotagged Capercaillie using the standard triangulation technique (Millspaugh & Marzluff 2001). We tracked each bird over more than 18 months (range: 72–96 weeks)

and at least twice a week 2 days apart in order to reduce autocorrelation (Harris *et al.* 1990). For each triangulation point we recorded *x* and *y* coordinates, habitat type (i.e. Pyrenean Oak, Scots Pine or non-forested) and date. Following Kenward (2001), we estimated by an experimental trial our inherent error in determining the real position by triangulation of the transmitter, which resulted in an error estimate of  $35.56 \pm 3.75$  m (mean  $\pm$  se). We therefore buffered each location with a 35-m radius. A habitat patch (fragment) with at least one radio location of a tagged Capercaillie was considered occupied.

### Habitat selection analysis

We measured Capercaillie habitat selection at population and individual level using data from observations (presence signs) and radio locations, respectively. At the population level, we estimated available habitat as the proportion of each of the seven habitat types within a 5-km radius buffer of the most outlying occupied fragment. This radius was chosen to encompass mean dispersal distances of adult Capercaillie in fragmented landscapes (Storch 1995a, García *et al.* 2005, Bollmann *et al.* 2011). Habitat used by Capercaillie was estimated as the proportion of each habitat type recorded as occupied (see above). We only analysed a year-round measure of habitat selection because presence signs were impossible to assign to a precise date, thus preventing a seasonal analysis. Data were analysed with Manly's selectivity index using *design I*, appropriate to datasets where individual animals are not distinguished, and implemented using the *adehabitat* package in R software (Manly *et al.* 2002, Calenge 2006, R Development Core Team 2008). The Manly index ranges from infinity (all observations within the habitat type) to 0 (no observations within the habitat type; 1 = use according to availability) for each habitat and tests the selection/avoidance under the null hypothesis that animals use the habitat in proportion to availability, computing a Pearson's chi-square test for each habitat pair (Manly *et al.* 2002). Because there are seven habitat types, *P*-values were compared with a Bonferroni-corrected  $\alpha$  level of  $0.05/7 = 0.007$ .

Using data from the four radiotagged birds, we first estimated the utilization distribution (UD), a probability density function that quantifies each animal's relative use of space (Silverman 1986,

Millspaugh *et al.* 2006). UD is commonly estimated using the kernel technique (Worton 1989, Marzluff *et al.* 2004). For this, we performed computations using the B-RANGE software (Katajisto & Moilanen 2006), which yields a digital UD layer. Based on this layer, we calculated the smallest area associated with a 90% and 50% probability of use (HR90 and HR50, respectively) using ARCGIS 9.3 (ESRI 2010). HR90 and HR50 are generally considered robust estimators of the home-range of animals and the area of frequent use (i.e. core area), respectively (Samuel *et al.* 1985, Börger *et al.* 2006). We measured the available habitat in each of the seven categories for each tagged bird as the area delimited by a 5-km radius surrounding each HR90. Used habitat was estimated as the proportion of the UD value in each habitat considered. Space use at individual level was then analysed using Jacobs' preference index (Jacobs 1974), which estimates an absolute selection value for each habitat as  $J = (r - p) / [(r + p) - 2rp]$ , where  $r$  is the used proportion and  $p$  the available proportion of habitat fragments.  $J$  ranges between +1 for exclusive selection of a habitat type and -1 for complete avoidance. We analysed both annual and seasonal (spring: April–June, summer: July–September, autumn: October–December and winter: January–March) habitat selection. Because our sample size was only four tagged individuals, we did not undertake any formal statistical testing of these  $J$  values.

### Sampling and analysis of diet

To describe the diet of Cantabrian Capercaillie in Mediterranean forests, experienced observers searched for droppings bimonthly from December 2005 to December 2007. Observers used pre-established tracks in fragments where Capercaillie presence was previously confirmed. We regarded any dropping within a 50-m radius of the first one found as belonging to the same sample and season. Droppings were collected or destroyed to prevent finding them in the next field survey. We collected and analysed 76 dropping samples from all the forest fragments known to be occupied by Capercaillie in the study area. The total collection of dropping samples was roughly proportional to the distribution of occupied forest fragments by Capercaillie (see Results); 10 came from Scots Pine plantations and 66 from Pyrenean Oak fragments used by the species.

To identify plant remains in the droppings we used micro-histological methods. The technique relies on the resistance of plant epidermis to herbivore digestion, leaving plant fragments undigested and identifiable (Holeček 1982, Alipayo *et al.* 1992). We followed the protocol of Blanco-Fontao *et al.* (2010). Briefly, each dropping sample was dried at 60 °C for 48 h, ground with a Retsch MM200 ball mill to grind and homogenize, and rinsed with NaOCl to improve clarity. To eliminate the supernatant fluid, samples were centrifuged and then rinsed with distilled water and centrifuged again. We sieved the resulting material through 1- and 0.2-mm pore-size filters and the intermediate fraction was stored for analysis. A sub-sample of *c.* 30 mg of the sieved material was laid on a slide with hydrophilic mounting medium (Jung tissue freezing medium) under a 100× microscope. Plant fragments (i.e. plant remains) were searched for along two transects of the slide. We compared plant fragments in the droppings with reference material in a library (Holeček 1982). The asymptote of the relationship between the plant fragments counted and diversity of plant remains was reached from 50 fragments. Therefore we sampled 50 plant fragments in each dropping and expressed the frequency for each plant species as a percentage. Samples were classified by season into spring (April–June), summer (July–September), autumn (October–December) and winter (January–March) based on Capercaillie life cycle and plant phenology in the study area.

We considered 16 potential food sources based on previous studies in the Cantabrian Mountains (Castroviejo 1975, Martínez 1993, Rodríguez & Obeso 2000) and plant availability in the study area. These were Pyrenean Oak, Scots Pine, Hazel *Corylus avellana*, Birch, Holly *Ilex aquifolium*, Rowan *Sorbus aucuparia*, brooms (*Cytisus* and *Genista* spp.), Bilberry, heath *Erica australis* ssp. *aragonensis*, Blackberry *Rubus* sp., Rockrose *Halimium lasianthum* ssp. *alyssoides*, ferns, grasses, mosses and lichens. We included arthropods as an animal category and a last category grouped unidentified remains.

Preliminary analyses revealed no differences in Capercaillie diet between 2006 and 2007 in the study area, so we pooled data across years to test seasonal variation in diet composition across the five main species found in droppings collected from birds in the Eurosiberian area (Rodríguez & Obeso 2000, Blanco-Fontao *et al.* 2010) and in this

study; namely, Holly, Bilberry, Pyrenean Oak, Scots Pine and Rockrose, by means of one-way ANOVA of arcsine-transformed percentages and *post hoc* Tukey tests (SPSS Statistics 17.0; SPSS Inc., Chicago, IL, USA). We also calculated the annual percentage of plant resources obtained from canopy and understorey species.

Finally, to compare diet of Cantabrian Capercaillie in the Mediterranean and Eurosiberian biogeographical regions, in 2007 we collected dropping samples from three birch forests ( $n = 24$ ) and three beech forests ( $n = 24$ ) (BiF and BeF, respectively; Fig. 1b) within the Eurosiberian region. Sampling and analyses of droppings followed the same methods described above. We tested for differences in diet by season between our Mediterranean study area and Eurosiberian birch and beech forests with non-metric multidimensional scaling (NMDS). Dissimilarities among sites were calculated on the raw frequencies of the 16 categories of feeding remains found in the birds' droppings (see above) using Bray–Curtis distances. Results were obtained for two dimensions. These analyses were performed with library *vegan* (Oksanen *et al.* 2010) in the R statistical package (R Development Core Team 2008).

## RESULTS

Available habitat for Capercaillie in the Mediterranean ecoregion consisted of 1088 fragments (mean surface  $\pm$  sd:  $83 \pm 200$  ha; range: 10–3274 ha), of which 325 were forested ( $n = 256$  oak fragments and  $n = 69$  pine plantations) and 763 non-forested. Forested fragments comprised 46% (41 682 ha; 32% oak forests and 14% pine plantations) of the total available habitat and the remaining 54% was non-forested habitat. Of the 325 forested fragments, 77% were smaller than 100 ha.

Between 2002 and 2009, 52 questionnaires/reports were received and we observed 211 Capercaillie signs (dropping samples:  $n = 123$ ; footprints:  $n = 13$ ; feathers:  $n = 51$ ; and direct sightings:  $n = 24$ ), validating presence in 29 forested fragments: six Scots Pine (26% of the occupied area) and 23 Pyrenean Oak fragments (74%). Forested fragments occupied by Capercaillie (mean area  $\pm$  sd:  $706 \pm 977$  ha; range: 17–3274 ha) covered 13 919 ha, of which 72% (9956 ha) were Pyrenean Oak forests and 28% (3963 ha) Scots Pine plantations.

The four radiotagged Capercaillie provided 1138 locations, across 10 occupied fragments of

which two were Scots Pine plantations and eight were Pyrenean Oak fragments, all of them within the set of 29 fragments known to be occupied via non-systematic sampling.

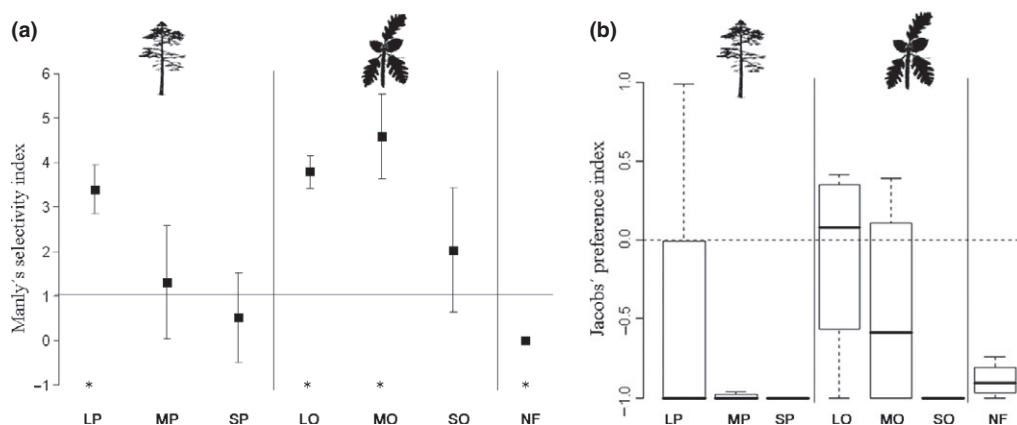
## Habitat selection

Capercaillie did not use different habitats in proportion to their availability ( $\chi^2 = 261.9$ ,  $df = 6$ ,  $P < 0.001$ ). Manly's selectivity index at population level showed that large Scots Pine fragments were positively selected ( $w_i = 3.40$ ;  $P < 0.001$ ), whereas use of medium Scots Pine fragments was not significantly different from their availability ( $w_i = 1.31$ ;  $P = 0.80$ ). Large and medium oak fragments were positively selected ( $w_i = 3.80$ ;  $P < 0.001$  and  $w_i = 4.59$ ;  $P < 0.001$ ). Use of both small oak ( $w_i = 2.04$ ;  $P = 0.46$ ) and small pine fragments ( $w_i = 0.51$ ;  $P = 0.63$ ) was not significantly different from availability, whereas non-forested habitats were never used ( $w_i = 0.00$ ;  $P < 0.001$ ) (Fig. 2a).

Results from Jacobs' preference indices for tagged Capercaillie were very similar for HR50 and HR90, so we only show the results for HR90 (Fig. 2b; results of HR50 are shown in Fig. S1). Seasonal and annual patterns of habitat selection were very similar (see Figs 2b and 3). There was strong variation among individuals in both the annual and the seasonal use of large pine and large and medium oak fragments, as shown by the wide error bars of these habitat types (Figs 2b and 3). Capercaillie selected large oak fragments both annually and seasonally (Figs 2b and 3). The remaining habitat types were used less than would be expected on the basis of availability, with the exception of large pine plantations, which were used according to their availability (Figs 2b and 3). Two of the four radiotracked Capercaillie never used Scots Pine plantations, although these were available to them.

## Diet

Mean annual consumption in the study area was similar for both canopy (48%) and understorey resources (46%). In winter, Capercaillie droppings were mainly composed of Scots Pine needles (40%), Pyrenean Oak (16%), grasses (15%) and Rockrose (12%; Table 1), and in five of the 17 dropping samples, the diet consisted wholly of Scots Pine needles. Spring diet was dominated by pine needles, grasses and Pyrenean Oak leaves,



**Figure 2.** (a) Manly's selectivity index (mean  $\pm$  1 se) calculated with the presence data. Values range from 0 (complete avoidance) to infinity (maximum preference) where 1 indicates that the habitat is used according to availability. \*Significant  $P$ -value ( $P \leq 0.05$ ). (b) Annual Jacobs' preference index for each fragment type and size used by Cantabrian Capercaillie within the 90% fixed Kernel isoline. Values range from  $-1$  (complete avoidance) to  $1$  (exclusive use). Boxes indicate the 25–75th percentile range and contain the median line. Bars represent the 10th and 90th percentile values. LP (large Scots Pine plantation fragment:  $> 500$  ha), MP (medium Scots Pine plantation fragment:  $> 100$ – $500$  ha), SP (small Scots Pine plantation fragment:  $0$ – $100$  ha), LO (large Pyrenean Oak fragment:  $> 500$  ha), MO (medium Pyrenean Oak fragment:  $> 100$ – $500$  ha), SO (small Pyrenean Oak fragment:  $0$ – $100$  ha) and NF (non-forested habitats: heathlands, brooms and meadows).

with 29, 22 and 20% occurrence of remains in droppings, respectively. In summer the major occurrences in droppings were fern fronds (30%), Pyrenean Oak leaves (19%) and grasses (17%). In autumn, Pyrenean Oak (25%), fern fronds (17%), grasses (16%), Scots Pine needles (9%) and Rockrose (8%) were dominant in the droppings. In the samples of droppings from the Eurosiberian area, two species occurred that were absent in the Mediterranean samples: Beech and Heather *Calluna vulgaris* (Supporting Information Tables S1 and S2).

Considering seasonal variation of the five main food species separately (i.e. Holly, Bilberry, Pyrenean Oak, Scots Pine and Rockrose) results from ANOVA revealed significant differences only in Scots Pine occurrence ( $F_{3,23} = 7.60$ ,  $P = 0.001$ ) between winter and summer ( $P = 0.003$ ) and nearly significant differences between winter and autumn ( $P = 0.07$ ), with the highest pine consumption in winter. For the other species, we found no significant seasonal variation: Holly ( $F_{3,23} = 0.373$ ,  $P = 0.774$ ), Bilberry ( $F_{3,23} = 0.153$ ,  $P = 0.927$ ), Pyrenean Oak ( $F_{3,23} = 0.553$ ,  $P = 0.652$ ) and Rockrose ( $F_{3,23} = 1.69$ ,  $P = 0.199$ ).

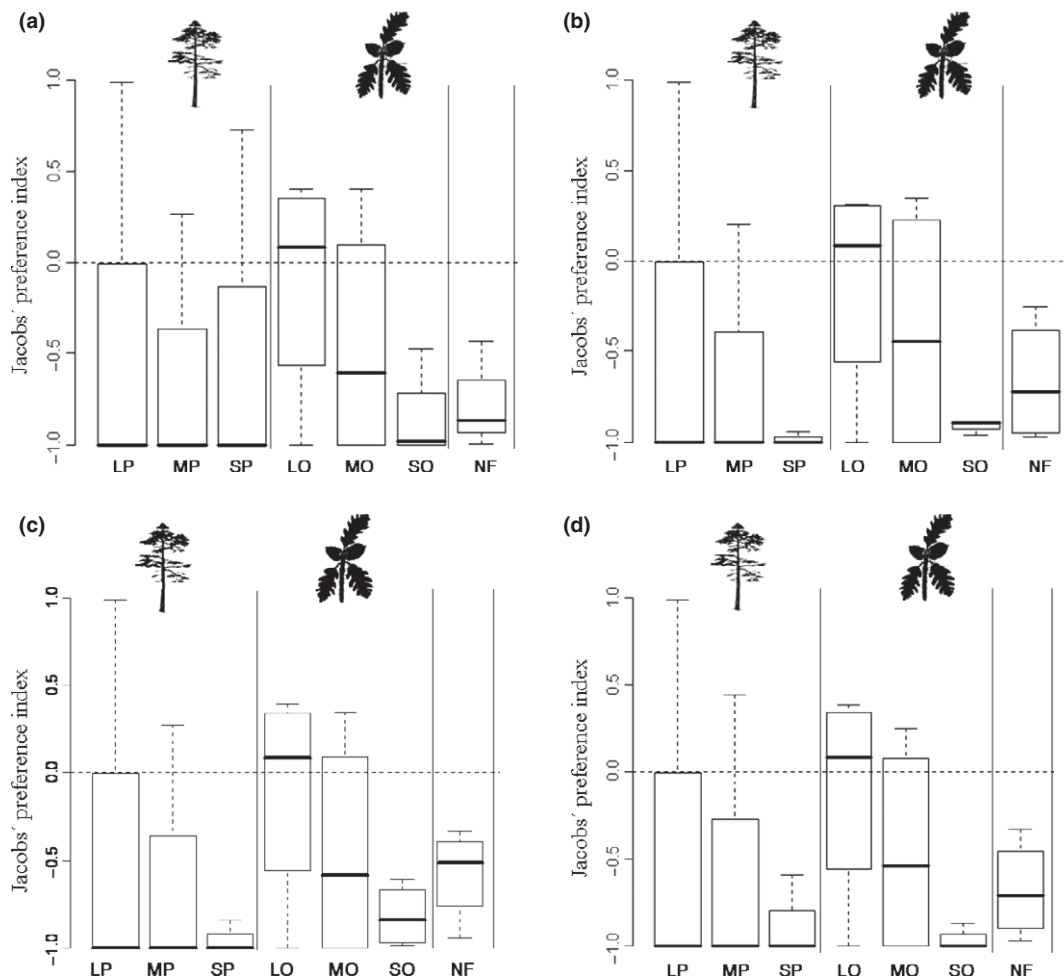
The NMDS analysis showed differences in the composition of the droppings collected in Mediterranean (i.e. Pyrenean Oak and Scots Pine) and Eurosiberian (i.e. beech and birch) forests (Fig. 4). Mediterranean habitat clustered apart from the beech and birch forests, which partially overlap.

Moreover, Capercaillie inhabiting birch forests apparently feed on quite diverse sources throughout the year (i.e. points lying more scattered in the plot). Birds in beech and Mediterranean habitats appeared to have a more homogeneous diet over time.

## DISCUSSION

The general pattern of habitat use by Capercaillie was similar whether data were based on signs or on radiotracking. Results from field signs showed a strong annual preference for large and medium Pyrenean Oak forest fragments and large Scots Pine plantations, whereas radiotracking data from four individuals showed a clear preference only for large Pyrenean Oak fragments. However, the occupation pattern inferred from the study of four radiotracked birds in only part of the study area was consistent with the wider survey based on field signs (i.e. all 10 forest patches used by the radiotagged Capercaillie had been identified previously as occupied by the field survey). This is consistent with a recent comparative study showing that data based on non-systematic surveys over large areas perform comparatively well and may be even preferable to systematically sampled data from a smaller area (Braunisch & Suchant 2010).

Both sampling approaches had clear limitations. Non-systematic sampling suffered from bias due to



**Figure 3.** Jacobs' preference index by seasons ((a) spring; (b) summer; (c) autumn; (d) winter) for each fragment type and size used by Cantabrian Capercaillie within the 90% fixed Kernel isoline. Values range from  $-1$  (complete avoidance) to  $1$  (exclusive use). Boxes indicate the 25–75th percentile range and contain the median line. Bars represent the 10th and 90th percentile values. Habitat codes as in Fig. 2.

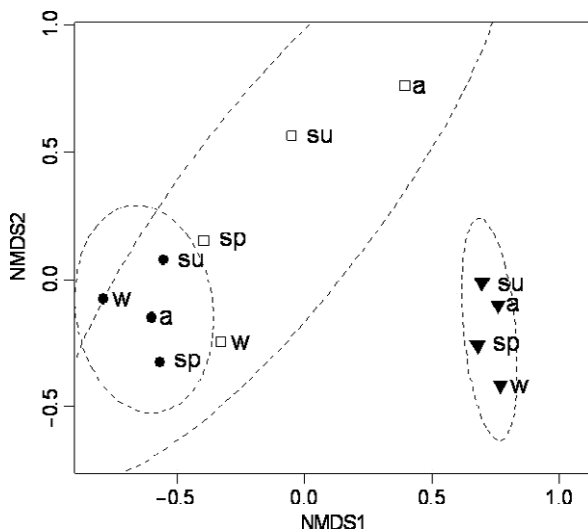
differences among habitats in both sampling effort and detectability of presence signs, while the study of radiotagged birds had a low sample size. Nonetheless, both approaches showed that Pyrenean Oak forests were in general used more than Scots Pine plantations year-round. Scots Pine plantations in the study area comprise young growth stages (between 30 and 50 years old), which probably offered lower habitat quality for Capercaillie than the older Pyrenean Oak forests. Diet data also suggested that Capercaillies fed on leaves, buds or acorns of Pyrenean Oak throughout the year (Table 1) and it is also known that Capercaillie use these forests as a breeding area, as indicated by leks and nests discovered in these forests (González *et al.* 2010). Our results support the idea that

Pyrenean Oak forests are an important habitat for Cantabrian Capercaillie (González *et al.* 2010), in contrast to the results of Quevedo *et al.* (2006b), who observed that Cantabrian Capercaillies avoided Pyrenean Oak forest on the northern slope of the Cantabrian range in the Eurosiberian biogeographical region. These contrasting results could be due to the fact that Pyrenean Oak fragments to the north are smaller and scarcer than those in our Mediterranean study area and/or due to other habitat alternatives in the Eurosiberian area such as beech, birch or sessile oak forests (Costa-Tenorio *et al.* 2005, García *et al.* 2005, Quevedo *et al.* 2006a,b). Large and medium forest fragments, regardless of the forest type, were more frequently used than small ones, which agrees with other studies that



**Table 1.** Percentage occurrence of plant remains in Capercaillie droppings in the study area (mean  $\pm$  1 sd) by season and globally ('Annual'). Main species (\*). Understorey resources: *Cytisus/Genista* spp., *Vaccinium myrtillus* (leaves, berries and shoots), *Erica* spp., *Rubus* spp., *Halimium lasianthum*, ferns, grasses, mosses and lichens. Canopy resources: *Ilex aquifolium*, *Betula pubescens*, *Sorbus aucuparia*, *Quercus pyrenaica*, *Corilus avellana* and *Pinus sylvestris*. The 16 individual categories plus the amount of unidentified remains by season are also shown.

	Percentage occurrence of remains in droppings (mean $\pm$ 1 sd)				
	Summer	Autumn	Winter	Spring	Annual
Main species	32.7 $\pm$ 7.7	47.7 $\pm$ 9.4	74.0 $\pm$ 15.5	55.0 $\pm$ 12.8	52.3 $\pm$ 9.4
Understorey resources	60.7 $\pm$ 9.7	52.3 $\pm$ 6.4	35.4 $\pm$ 5.3	34.3 $\pm$ 6.6	45.7 $\pm$ 6
Canopy resources	33.7 $\pm$ 7.7	42.7 $\pm$ 9.2	59.3 $\pm$ 15.2	59.0 $\pm$ 11.4	48.7 $\pm$ 9.9
* <i>Ilex aquifolium</i>	0	0.7 $\pm$ 1.6	0.7 $\pm$ 1.6	1.0 $\pm$ 2.4	0.6 $\pm$ 1.6
* <i>Vaccinium myrtillus</i>	7.3 $\pm$ 7.7	5.0 $\pm$ 8.5	4.7 $\pm$ 7.3	5.3 $\pm$ 6.4	5.6 $\pm$ 7.1
<i>Betula pubescens</i>	1.8 $\pm$ 2.4	0.7 $\pm$ 1	0	2.3 $\pm$ 5.7	1 $\pm$ 3.1
<i>Sorbus aucuparia</i>	7.3 $\pm$ 3.7	7.0 $\pm$ 5.3	2.0 $\pm$ 1.3	6.7 $\pm$ 5.3	5.8 $\pm$ 4.5
* <i>Quercus pyrenaica</i>	19.0 $\pm$ 8.6	25.2 $\pm$ 18.8	16.3 $\pm$ 10.2	19.7 $\pm$ 9.4	20.1 $\pm$ 12
<i>Corylus avellana</i>	0.3 $\pm$ 0.8	0	0	0.3 $\pm$ 0.8	0.2 $\pm$ 0.5
* <i>Pinus sylvestris</i>	6.0 $\pm$ 5.9	9.0 $\pm$ 11.1	40.3 $\pm$ 19.3	29.0 $\pm$ 17.9	21 $\pm$ 19.9
<i>Rubus</i> sp.	1.0 $\pm$ 2.4	4.7 $\pm$ 5.5	0	0	1.4 $\pm$ 3.4
<i>Erica</i> sp.	2.0 $\pm$ 2.2	1.7 $\pm$ 2.0	1.3 $\pm$ 1.6	1.7 $\pm$ 2.3	1.7 $\pm$ 1.9
* <i>Halimium lasianthum</i> ssp. <i>allyssoides</i>	0.3 $\pm$ 0.8	7.7 $\pm$ 9.0	12.0 $\pm$ 20.1	0	5.2 $\pm$ 11.7
<i>Cytisus/Genista</i> sp.	0.7 $\pm$ 1.6	0	0	0	0.2 $\pm$ 0.8
Ferns	30.0 $\pm$ 21.7	17.0 $\pm$ 14.3	2.7 $\pm$ 3.5	3.7 $\pm$ 5.6	13.3 $\pm$ 16.9
Mosses	1.3 $\pm$ 1.6	0.3 $\pm$ 0.8	0	1.3 $\pm$ 2.4	0.8 $\pm$ 1.5
Grasses	17.4 $\pm$ 12.4	16.0 $\pm$ 10.3	14.7 $\pm$ 12.8	22.3 $\pm$ 9.9	17.7 $\pm$ 11
Lichens	0	0	0	0	0
Arthropods	0.3 $\pm$ 0.8	0	0	0	0.1 $\pm$ 0.4
Unidentified	5.3 $\pm$ 3.5	5.0 $\pm$ 4.1	5.3 $\pm$ 3.5	6.7 $\pm$ 3.3	5.7 $\pm$ 3.3



**Figure 4.** NMDS ordination for diet samples at different collecting seasons (stress value = 4.7). Symbols represent forest types (● = beech forests, □ = birch forests, ▼ = study area, i.e. Scots Pine and Pyrenean Oak forests). Seasons are shown in lower case letters (su = summer, a = autumn, w = winter, sp = spring). The dotted lines correspond to the 95% confidence region of possible ordination values for each of the forest types.

show fragment size to be a more important factor than species composition explaining Capercaillie occurrence (Storch 1991, Quevedo *et al.* 2006b, Bollmann *et al.* 2011). Nonetheless, studies of structure and quality of forests should be addressed in this Mediterranean area to better understand patterns of Capercaillie occurrence.

Non-forested habitats (i.e. those above the tree line) have been shown to be important for breeding females both in the Cantabrian Mountains (Bañuelos *et al.* 2008) and in the Pyrenees (Menoni 1991) but were little used in our study. Here, the existence of a 2-month period of drought during the summer (Rivas-Martínez *et al.* 2004) and the traditional use of fire as a tool both to control these non-forested habitats and to increase grassland surface (Luis-Calabuig *et al.* 2000) might have increased the plant density after fire in heathlands and brooms, making them unavailable to Capercaillie. Nonetheless, more detailed research on habitat used by males and females in the study area would be needed to test this idea more formally.

As in previous Cantabrian studies, we detected heavy consumption of pine needles, especially in

winter (Rodríguez & Obeso 2000). The winter season is considered more critical for Cantabrian Capercaillie than for other subspecies due to the lower caloric content and the scattering of their food items in a deciduous forest, which may make winter survival difficult by increasing energy expenditure when the ground is snow-covered (Rodríguez & Obeso 2000, Quevedo *et al.* 2006b). However, in the warmer Mediterranean area, pine may not be as critical a resource in winter as in European populations, where a greater snow cover is present over space and time (Gjerde & Wegge 1989, Spidso & Korsmo 1994), and it is notable that two radiotagged individuals in our study did not use pine plantations at all, despite their availability.

Both in the main Mediterranean oak/pine study area and in the sampled Eurosiberian beech forests, the percentages of understorey food resources (46 and 48%, respectively) were slightly higher than the mean values found in other European populations (43% in France, 43% in Slovakia, 36% in Germany, and 14 and 21% in Scotland; Jacob 1988, Picozzi *et al.* 1996, Saniga 1998, Storch *et al.* 1991, Summers *et al.* 2004) but it was smaller than that recorded by Blanco-Fontao *et al.* (2010) in Eurosiberian birch and mixed forests of the Cantabrian range (65%) as well as in the birch forests studied by us (59%). These differences among areas may be related to the availability of pine, which balances the consumption of canopy-understorey resources by increasing the use of canopy food resources, especially during winter. However, the understorey is also relatively richer in plant species and covers a greater surface in birch than in beech forests (Costa-Tenorio *et al.* 2005). This seems also to be reflected in the somewhat higher diversity of food sources on which Capercaillie fed in birch forests (Fig. 4).

Although Bilberry is usually considered a key species for Capercaillie diet in the Eurosiberian region (Storch 1995b, Quevedo *et al.* 2006b, Blanco-Fontao *et al.* 2010, this study; Tables S1 and S2), some exceptions occur. In some areas in the southern Pyrenees, Bilberry is replaced in the diet by Bearberry *Arctostaphylos uva-ursi* due to the absence of the former in the area (Robles *et al.* 2006). In our study area, Bilberry is also nearly absent (González *et al.* 2010) and hence scarce in Capercaillie diet (Table 1); other species such as oak, ferns and grasses seem to replace the lower consumption of Bilberry. It is worth noting the consumption of Rockrose in the Mediterranean

forests, a species never described before as a food resource for Capercaillie that is consumed frequently in autumn and winter (Table 1). Our results show significant differences in the diet between Mediterranean (i.e. Pyrenean Oak and Scots Pine) and Eurosiberian (i.e. beech and birch) forests that are geographically close to each other (Fig. 4, Tables S1 and S2), suggesting that the same population of Capercaillie displays some trophic plasticity and potential tolerance to environmental change.

### Implications for conservation

The severe and rapid decline of Cantabrian Capercaillie in recent decades has renewed range-wide efforts to gather information on the ecology of this subspecies for application to conservation. We have documented for the first time the strong preference for medium and large Pyrenean Oak forest fragments and a moderately high consumption of Pyrenean Oak leaves, buds or acorns throughout the year, highlighting the importance of these native forests for the conservation of the species. Our data also show that Scots Pine plantations, especially large ones, may provide food resources, especially in winter and early spring, when food availability is lower in Pyrenean Oak forest. Conservation efforts should focus on preventing fragmentation of all natural deciduous forest where Capercaillie occur, with emphasis on the largest fragments, but recognizing the potential value of smaller fragments in providing for dispersal (Bollmann *et al.* 2011). We also recommend maintaining and managing some pine plantations for Capercaillie by creating structural heterogeneity in imitation of the heterogeneous and mature structure of the natural pine forests (Leclercq 1987, Rolstad & Wegge 1989, Sjöberg 1996), as they might eventually become higher quality habitats for Capercaillie in this Mediterranean area.

Our study shows that Capercaillie exhibit considerable plasticity in diet and habitat use within a limited geographical area at the edge of the global range, which may enable a greater tolerance to environmental change. Additionally, this very peripheral population might diverge ecologically and/or genetically from others as a result of natural selection in this Mediterranean environment, implying even higher conservation value (Lesica & Allendorf 1995, Furlow & Armijo-Prewitt 1995, Hampe & Petit 2005). This unique, small and quite

isolated rear-edge population of Capercaillie merits strong protection and further research. Immediate conservation actions should include protection of the study area, including it in the *Natura 2000* network and developing conservation measures of the habitat of Pyrenean Oak forests.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Annual (a) and seasonal (b: spring; c: summer; d: autumn and e: winter) Jacobs' prefer-

ence index for each fragment type and size used by Cantabrian Capercaillie within the 50% fixed Kernel isoline.

**Table S1.** Percentage of occurrence of plant remains in capercaillie droppings (mean  $\pm$  1SD) in beech Eurosiberian forests by season and globally ("Annual").

**Table S2.** Percentage of occurrence of plant remains in capercaillie droppings (mean  $\pm$  1SD) in birch Eurosiberian forests by season and globally ("Annual").

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