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Upland habitat use by Pyrenean grey partridges *Perdix perdix hispaniensis* during the breeding season

Claude Novoa, Nicholas J. Aebischer & Philippe Landry

Whereas in most of Europe the decline of the grey partridge *Perdix perdix* is due primarily to agricultural intensification, the Pyrenean grey partridge *P. p. hispaniensis* is believed to suffer from the opposite effect, namely the abandonment of agricultural practices which allows the encroachment of dense shrublands. We investigated habitat use by the Pyrenean grey partridge during the breeding season and its relationship with reproductive success and survival. The study was based on 22 radio-tagged grey partridges in a 5,800-ha upland area of the eastern Pyrenees. Habitat use was non-random, and shrubland with a shrub canopy cover higher than 40% was the most important requirement during the breeding season. In the spring, pairs that successfully reared a brood used shrublands (20-60% cover) twice as frequently as unsuccessful breeders, then in the summer halved their use of open habitats (montane grassland and shrubland with <40% cover), whereas failed breeders increased it sevenfold. Consequently, a good mixture of different cover types in the spring and summer is likely to provide the most suitable breeding habitat. There was no evidence linking the spring/summer survival of adult partridges to a particular habitat use. Current grazing practices, especially with the use of controlled burning to clear shrubby vegetation, reduce the amount of mature shrublands used by Pyrenean grey partridges. However, grazing management also delays the natural vegetation succession and hence contributes to the long-term persistence of partridge habitat. Grazing practices that prevent reafforestation and maintain a mosaic of dense and open shrublands should be encouraged in the Pyrenean uplands.

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The grey partridge *Perdix perdix* was once a common and widespread species throughout the temperate zone of western Eurasia, but numbers have declined marked- ly in most parts of its native range since the 1950s (Potts 1986, Del Hoyo, Elliott & Sargatal 1994). This is par- ticularly true of the southern parts of its distribution-

al range: the original stock is now probably extinct in Italy and in the French Alps (Matteucci & Toso 1985, Lescourret & Ellison 1987), and the Pyrenean race *P. p. hispaniensis* numbers fewer than 15,000 pairs restricted to three distinct nuclei in the Pyrenees, the northern Iberian Mountains and the Cantabrian Mountains (Lescourret 1988, Lucio & De Buruaga 1997).

Whereas in most of Europe the decline is due primarily to agricultural intensification (Aebischer & Potts 1994), it is thought that the Pyrenean grey partridge suffers from the opposite effect, namely the abandonment of agricultural practices in its upland habitats (Génard & Lescourret 1990, Lucio, Purroy, De Buruaga & Llamas 1996). In both cases, habitat restoration is one of the keys to reversing the partridge decline (Aebischer & Potts 1994), but successful conservation plans need to be built upon a sound knowledge of the habitat requirements of the species.

Most of the studies carried out on grey partridge ecology in open arable landscapes have addressed questions of habitat use and quality, especially during the breeding season. For nesting, vegetative cover in the form of hedgerows and grassy banks (Potts 1986, Rands 1988), idle uplands (Church & Porter 1990), or wheat crops (Bro, Reitz & Clobert 2000a) is required for concealment and protection against predators. After hatching, suitable brood-rearing cover combines a loose structure for ease of passage and abundance of insects for the chicks to eat, and an overhead canopy for protection against predators; cereal field margins were ideal before the advent of modern pesticides (Green 1984, Rands 1986, Potts 1986). Hence, the habitat suitability of agricultural lands for the grey partridge may be predicted by measuring the extent of one or more of these different habitat features. The relationship between breeding densities and hedgerow characteristics in Britain (Rands 1986) is one clear example.

In contrast, the Pyrenean grey partridge lives in upland habitats where the availability of cover for nesting or brood-rearing is rarely restrictive. Indeed, in Mediterranean upland areas, both the natural vegetation growth and the fall in grazing pressure may result in cover so dense that it is considered detrimental to all partridge species (Génard & Lescourret 1990, Bernard-Laurent & de Franceschi 1994). On the other hand, previous studies of the Pyrenean grey partridge have shown that it makes considerable use of dense shrublands that satisfy certain criteria for vegetation height and canopy cover (Lescourret & Génard 1993, Lucio et al. 1996, Novoa, Dumas & Prodon 1998). None of them, however, related use to availability. The effects of the spread of shrublands may thus be regarded in sev-

eral different ways, making difficult the evaluation of suitability of upland habitats for the Pyrenean grey partridge.

To address this issue, in the present study we investigated the cover requirements of the Pyrenean grey partridge during the breeding period. We evaluated the availability of different habitat types to grey partridges and measured their use by radio-telemetry, the most accurate method of evaluating resource usage (Porter & Church 1987, White & Garott 1990). We addressed the following questions: during the breeding season, do Pyrenean grey partridges use the available habitat at random? If not, how does the amount of cover affect relative use? Does habitat use vary with respect to reproductive stage, reproductive success and survival?

Material and methods

Study area
The study was conducted during 1992-1997 in the eastern French Pyrenees on the 'Soulane du Carlit' (42°31'N, 1°54'E), an extensive south-facing hillside where the average slope does not exceed 30%. Within this montane area of almost 30,000 ha, the altitudinal range varies between 1,300 m and 2,800 m a.s.l. The climate of the area is continental (Izard, Casanova, Devau & Pautou 1985). At 1,960 m a.s.l., the long-term daily mean temperature is 4.8°C (averaged over a year), and the mean annual precipitation is 820 mm. Winters are relatively dry, with only 28% of annual precipitation on average falling from December to March. Vegetation is dominated by a mosaic of shrubs (*Cytisus purgans*, *Juniperus communis*, *Arctostaphylos uva-ursi*), grassland (*Festuca rubra*, *F. eskia*, *F. paniculata*) and pine woodland (*Pinus uncinata*). Cultivated areas amount to less than 1% of the study area. The main agricultural activity is cattle grazing, which takes place from June to October. The cowherds practise controlled burning during November-March to prevent the invasion of grassland by shrubs. Vehicular access within the study area was very limited, so all the fieldwork was undertaken on foot.

Habitat data
Habitats were classified into eight categories based mainly on the height and canopy cover of the woody plants (Table 1). Montane grassland, shrublands and woodlands represented successive stages of the *Pinus uncinata*, *Juniperus nana* and *Arctostaphylos uva-ursi* vegetation series (Dupias 1985). We distinguished between three types of shrubland according to the degree

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Table 1. Classification of the upland habitat types used in the study of habitat use by grey partridges during the breeding season in the eastern Pyrenees.

Habitat types	Code	Percentage cover and height of main habitat components
Bare ground	BG	Bare ground & stones > 80 %; vegetation < 20 %
Montane grassland	MG	Shrubs <20%; grasses and forbs > 60 %
Sparse shrubland	SS	20% < shrubs < 40%
Open shrubland	OS	40% < shrubs < 60%
Dense shrubland	DS	Shrubs > 60%
Open woodland	OW	20% < pine trees < 40%
Mature woodland	MW	Pine trees > 40%
Controlled burn	CB	Area burnt within the last five years

of canopy cover of the shrubs *Cytisus purgans* and *Juniperus communis*; percent cover was estimated visually by comparing the projection of the foliage mass onto a horizontal plane with reference drawings representing cover of 10% intervals (Prodon & Lebreton 1981). Areas burnt within the last five years were considered as a distinct habitat type in order to assess their use by grey partridges. Habitat patches were first delimited from aerial photographs and mapped on a 1:10,000-scale map after checking in the field. Contours of each habitat patch were then digitised onto a Geographical Information System (ArcInfo 3.5; Environmental Systems Research Institute, Redlands, California, USA).

Partridge data

Within the study area, grey partridge density averaged two pairs/km^2 in spring (Novoa 1998). Between 1992 and 1997, 59 grey partridges were captured in late winter - early spring using decoy trapping (Smith, Hupp & Ratti 1981) or spotlight and hand-net trapping (Upgren 1968), and fitted with necklace 10-g radio-transmitters

(Holohil System Ltd.). The radio-tagged birds were located once a week during the winter season (November-February), and at least twice a week during the breeding season (March-October), using a portable receiver (Custom Electronics) and a hand-held Yagi antenna and by approaching the birds to within 50 m. The breeding status (paired or unpaired) of each bird was recorded, as was the outcome of any nesting attempt by the pair.

In terms of habitat availability, an accurate definition of the limits of the study area would have been the whole range of all the radio-locations (Litvaitis, Titus & Anderson 1996). However, logistically it was not feasible to map the habitats over this global range of almost 30,000 ha, so we confined our study to a 5,800-ha core area representing 80% of radio-locations and topographically delimited by mountain ridges (2,800 m) and valley bottoms (1,300 m). Many radio-tagged partridges spent at least some time outside this core area and thus could not be included in the analysis of habitat use. Taking losses and radio failures into account as well, this meant that only 22 radio-tagged birds provided valid data for analysis of habitat use during the breed-

Table 2. Data on radio-tagged grey partridges used in the study of habitat use in the eastern Pyrenees during 1992-1997 (N = 22 individuals).

Year	Sex	Age	Breeding status	Spring monitoring (no of radio-locations)	Summer monitoring (no of radio-locations)
1992	♂	Juv.	Paired	11/03 - 22/06 (55)	24/06 - 09/10 (59)
	♂	Juv.	Paired	18/03 - 22/06 (48)	24/06 - 01/10 (50)
	♂	Juv.	Paired	10/04 - 18/06 (30)	
	♂	Ad.	Paired	10/04 - 19/06 (36)	22/06 - 29/09 (50)
1993	♂	Ad.	Paired	04/03 - 24/06 (44)	28/06 - 02/10 (48)
	♂	Juv.	Paired	07/04 - 21/06 (33)	
	♀	Juv.	Paired		23/06 - 11/10 (62)
1994	♂	Juv.	Paired	16/03 - 21/06 (45)	
	♂	Juv.	Unpaired		05/08 - 30/09 (18)
	♂	Juv.	Unpaired		24/06 - 30/09 (41)
	♂	Juv.	Unpaired		20/06 - 30/09 (40)
1995	♂	Juv.	Unpaired		20/06 - 02/10 (33)
	♂	Ad.	Unpaired	03/03 - 25/05 (24)	
1996	♀	Ad.	Paired	04/03 - 24/06 (42)	27/06 - 03/10 (38)
	♂	Juv.	Paired	12/04 - 17/06 (27)	18/06 - 09/09 (39)
	♀	Juv.	Paired	16/04 - 20/06 (26)	21/06 - 04/10 (42)
	♂	Juv.	Unpaired	29/04 - 27/06 (18)	27/06 - 04/10 (35)
1997	♀	Juv.	Paired	27/02 - 11/06 (32)	
	♀	Juv.	Paired	27/02 - 26/05 (27)	
	♂	Juv.	Paired	06/03 - 09/06 (28)	
	♂	Juv.	Paired	10/03 - 19/06 (26)	23/06 - 03/10 (32)
	♂	Juv.	Paired	12/03 - 09/06 (28)	11/06 - 03/10 (44)

ing season (Table 2). Of these, one bird was monitored in two consecutive breeding seasons and was treated as two separate individuals in the statistical analysis. A tagged male and a tagged female that were paired were treated as a single pair, so the 22 individuals finally entered into the analysis represented 15 separate pairs and six unpaired birds. Bro, Sarrazin, Clobert & Reitz (2000b) showed that age does not affect demographic variables in female grey partridges, so we did not consider age in the analyses.

The breeding season was divided into two monitoring periods: (i) spring including the period from the end of pair formation (early March) to incubation (late June), and (ii) summer including hatching and brood rearing to the point where the chicks were fully grown (early October). Because of late catching dates or low survival rates, only 10 of the 21 birds under study were monitored over the two consecutive periods (see Table 2).

Invertebrate data

We carried out invertebrate surveys in four habitat types (MG, SS, OS and DS; see Table 1) previously known to be suitable breeding habitat (Novoa et al. 1998), to investigate variation in the biomass of chick-food items. A total of 10 sites, three in MG, four in SS, one in OS and two in DS, were sampled using two pit-falls and two yellow water-traps on each site. From 1992 to 1996, the 10 sites were sampled three days per year between July and mid-August. Traps were set at sunrise and emptied after sunset. For each site, the total catch per day (pitfall + water traps) was pooled, and invertebrates were separated into different taxonomic groups, dried in an oven and weighed to the nearest 0.001 g. The food-insect biomass at each site in each year was defined as the average daily dry weight of Formicidae, Orthoptera and Coleoptera, the most important insect food items for Pyrenean grey partridge chicks and adults during the breeding season (Moreby, Novoa & Dumas 1999, Novoa, Garcia Gonzalez & Aldezabal 1999). The relatively large size of the latter two taxa and the ground-dwelling habits of all three taxa justified the use of passive traps rather than the suction trapping or sweep netting often used to sample chick-food abundance in arable crops (e.g. Green 1984, Potts 1986).

Data analysis

Habitats were mapped exhaustively within the 5,800-ha core area between 1,300 and 2,800 m a.s.l., and the habitat changes resulting from winter burns were incorporated each year. Hence, the proportions of the different habitat types in the study area were calculated for each of the six study years.

Habitat use relative to availability was analysed at two levels corresponding to the different selection orders (Johnson 1980, Aebischer, Robertson & Kenward 1993b). First, we considered the selection of a home range from an arbitrarily defined study area. Availability was defined as the proportions of the eight habitat types over the 5,800-ha core area (AREA), and individual use as the proportions of the eight habitat types in the minimum convex polygon (MCP) home range calculated from the radio-locations of each tagged bird (LOC). Second, we considered local habitat use within each home range. At this second level, availability was defined as the proportions of the eight habitat types in the MCP, and use as the proportions of the eight habitat types contained within 1-ha circles centred on the radio-locations.

Proportional use and availability of the eight habitat types were compared by compositional analysis (Aebischer et al. 1993b). The eight proportions of utilised or available habitats summed to one, and so were linearly dependent. We rendered them independent and approximately normally distributed by using the proportion of bare ground as denominator in a log-ratio transformation of each of the other seven proportions. The choice of the habitat type as denominator does not affect the results (Aitchison 1986).

To test the null hypothesis of random use, we calculated the difference in log-ratios between matching pairs of utilised and available habitats for each partridge. With random use, the mean difference calculated over all partridges is expected to equal zero. This hypothesis was tested by a multivariate analysis of variance (MANOVA) using the Wilk's lambda statistic, for which an exact transformation to the F-statistic existed in all cases considered here (Aitchison 1986). If the hypothesis of random use was rejected, we then ranked the habitat types in order of relative use. For this, we calculated the mean log-ratio difference for all possible pairs of habitat types, compared them to zero using a t-test, and displayed the results in matrix form (Aebischer et al. 1993b). The relatively most used habitat type was the one for which the mean log-ratio differences were positive whichever habitat type was used as denominator, and vice versa for the relatively least used habitat type. The ranking matrix thus enabled us to rank habitat types in order of relative use, although in most cases sample sizes were too small to produce clear patterns of significant differences between ranks.

Differences in habitat use according to year, period of the breeding season, breeding status, nesting success and survival were examined using MANOVA applied to the log-ratios (Aebischer, Marcström, Kenward &

Karlbom 1993a). Comparisons of spring and summer habitat use were based on paired data from birds monitored in both periods, so the corresponding MANOVA analyses were carried out on the within-bird differences between matching log-ratios for spring and summer use. In all analyses, missing habitat types in the home ranges or radio-locations were replaced by 0.01%, following Aebischer et al. (1993a, 1993b).

Comparison of the seasonal altitudinal movements between partridges that bred successfully and partridges that bred unsuccessfully was carried out on the within-bird mean altitudinal differences between spring and summer using ANOVA. Comparison of mean food-insect biomass in the different habitat types was carried out using ANOVA with repeated measures (four habitat types over five years) applied to log-transformed data.

All statistical tests were carried out using Systat 7.0 (Wilkinson 1997), and means are expressed with one standard error.

Results

Effects of year, time period and breeding status on habitat use

Across all 22 individuals, there were no significant between-year differences neither for the choice of home range within the study area (MCP vs AREA: $F_{7,14} = 0.18$, $P = 0.98$) nor for habitat use within the home range (LOC vs MCP: $F_{7,14} = 1.33$, $P = 0.31$). For the 10 partridges monitored in both spring and summer, no significant between-period difference was detected at either level (MCP vs AREA: $F_{7,3} = 0.33$, $P = 0.90$; LOC vs MCP: $F_{7,3} = 2.30$, $P = 0.27$). There was also no significant difference in habitat use between six unpaired and 16 paired birds, neither in home-range selection (MCP vs AREA: $F_{7,14} = 1.21$, $P = 0.36$) nor in habitat use within the home range (LOC vs MCP: $F_{7,14} = 0.60$, $P = 0.75$). We therefore pooled all 22 partridges for an analysis of overall habitat use during the breeding season, using all available radio-locations on each individual.

Overall habitat use during the breeding season

MCP home-range size for the 22 partridges averaged 478 ± 124 ha. There was no correlation between home-range size and the number of radio-locations ($r_{20} = 0.07$, $P = 0.76$), implying that sufficient radio-locations had been obtained for the MCP estimates of home range to have stabilised.

All habitat types were regularly distributed both in the study area and in the MCP home ranges. The hypothesis of random habitat use by Pyrenean grey partridges was rejected both at the level of home-range selection (MCP vs AREA: $F_{7,15} = 10.15$, $P < 0.001$) and of habitat use within the home range (LOC vs MCP: $F_{7,15} = 8.23$, $P < 0.001$).

Based on the ranking matrices (Table 3), the order of the habitat types in terms of relative use, from most to least used, was: DS > OS > MW > MG > OW > SS > CB > BG at the level of the study area, and DS > OS > OW > MG > SS > CB > BG > MW at the level of the home range (see Table 3). At both levels, shrublands

Table 3. Simplified ranking matrices for relative habitat use of Pyrenean grey partridges during the breeding season, based on: A) comparison of the proportional habitat use within the MCP ranges with the proportions of total available habitat types, and B) comparison of the proportions of the radio-locations for each partridge in each habitat type with the proportion of each habitat type within the partridge's MCP range. A +/- sign indicates that the row habitat type is used more/less than expected from the availability relative to the column habitat; the sign is tripled when the difference is significant at the level of $P < 0.05$. The row with the most positive values corresponds to the relatively most used habitat (Rank 7), whereas the one with the most negative values is the relatively least used (Rank 0).

A) Home range MCP (use) vs study area (availability)

	BG	MG	SS	OS	DS	OW	MW	CB	Rank
BG		---	---	---	---	---	---	---	0
MG	+++		+	---	---	+	-	+	4
SS	+++	-		-	---	-	---	+	2
OS	+++	+++	+		-	+	+	+	6
DS	+++	+++	+++	+		+++	+	+++	7
OW	+++	-	+	-	---		-	+	3
MW	+++	+	+++	-	-	+		+	5
CB	+++	-	-	-	---	-	-		1

B) Radio-locations (use) vs home range MCP (availability)

	BG	MG	SS	OS	DS	OW	MW	CB	Rank
BG		---	-	---	---	---	+	-	1
MG	+++		+	-	---	-	+++	+	4
SS	+	-		---	---	-	+++	+	3
OS	+++	+	+++		-	+	+++	+++	6
DS	+++	+++	+++	+		+	+++	+++	7
OW	+++	+	+	-	-		+++	+	5
MW	-	---	---	---	---	---		---	0
CB	+	-	-	---	---	-	+++		2

with a shrub canopy cover higher than 40% (DS and OS) appeared to be the most important cover requirement for breeding grey partridges (Fig. 1).

Spring habitat use and breeding success

Of the 15 paired birds, four failed during incubation, four failed during the first week after hatching and seven successfully reared a brood. We investigated whether breeding success was linked with habitat use in the spring. There was no detectable difference in habitat composition of the spring home ranges between successful and unsuccessful birds ($F_{7,7} = 0.64$, $P = 0.71$). However, the proportions of the eight habitat types in the spring radio-locations differed significantly between the two groups ($F_{7,7} = 13.32$, $P = 0.001$). Based on a matrix of pairwise differences between the groups, the habitat types were ranked in the order: SS > OS > MG > OW > DS > BG > MW > CB, starting with habitat types most strongly related to success. The ranks of SS and OS were not significantly different and, in fact, the significant overall difference in habitat use between the groups was due to a difference in the use of shrublands with less than 60% cover (SS + OS); without these two habitat types, the difference vanished ($F_{5,9} = 1.12$, $P = 0.41$). The average utilisation of SS + OS was 30 and 13% for birds that successfully reared a brood and for birds that failed, respectively ($t_{13} = 2.68$, $P = 0.02$).

Seasonal change in habitat use according to breeding success

We also examined whether habitat use changed between spring and summer in relation to breeding success for the nine partridges that attempted to breed out of the 10 monitored over the two time periods. There were no significant effects at the level of the home range (difference between time periods: $F_{7,1} = 20.46$, $P = 0.16$; interaction with breeding success: $F_{7,1} = 19.70$, $P = 0.17$). At the level of the radio-locations, the habitat use changed significantly between spring and summer (difference between periods: $F_{7,1} = 352.32$, $P = 0.04$;
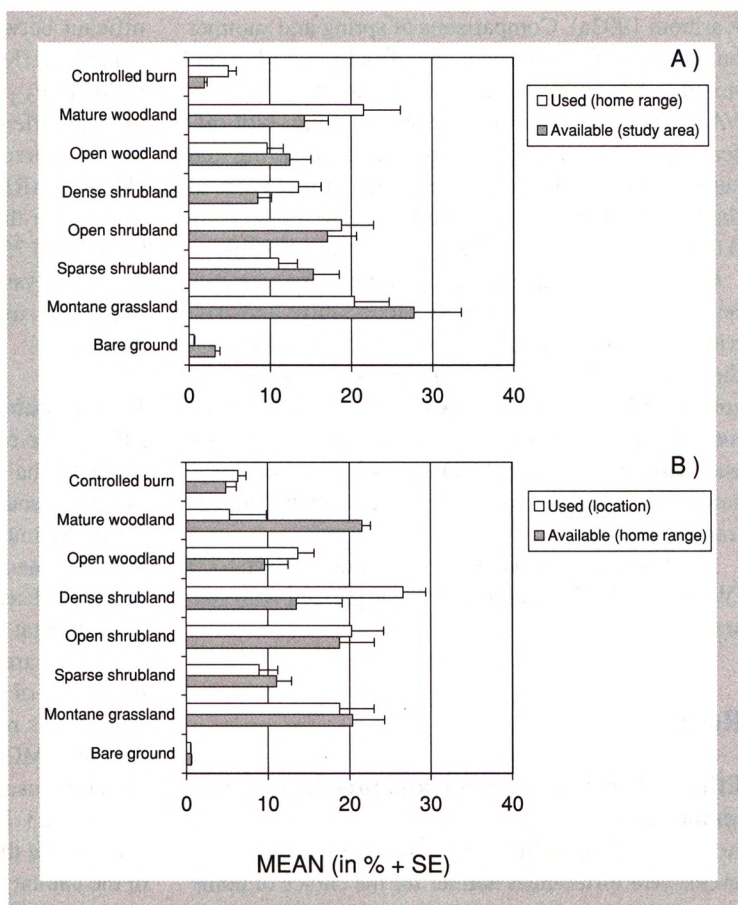

Figure 1. Two-level comparison of proportional availability and use of eight habitat types by 22 radio-marked grey partridges during the breeding season expressed as mean + SE. A) Minimum Convex Polygon home range (use) vs availability (study area); B) use (radio-locations) vs availability (home range). Availability in the study area is presented as mean (in % + SE) habitat proportions over the six years 1992-1997.

interaction with breeding success: $F_{7,1} = 179.19$, $P = 0.06$). Curiously, if the interaction term was dropped, the effect of time period disappeared ($F_{7,2} = 0.78$, $P = 0.66$). Given the small sample size, we interpreted this as indicating that the interaction term, borderline in terms of statistical significance, should not be ignored. The rank-order matrix resulting from testing the interaction coefficient associated with each pairwise combination of habitat types gave: SS > MG > BG > MW > OW > OS > DS > CB, suggesting that open habitats (sparse shrubland and montane grassland) played an important role. The ranks of SS and MG did not differ significantly, and a separate analysis of SS + MG confirmed that there was a strong interaction between spring/summer habitat use and breeding success ($F_{1,7} = 22.61$, $P = 0.002$). For successful birds, the proportionate use of SS + MG decreased from 29% before hatching to 15% after hatching, whereas for unsuccessful birds it increased

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from 7% in spring to 49% in summer. These differences were not associated with post-breeding movements of unsuccessful birds at higher altitudes into alpine habitats dominated by grassy open habitats. Indeed, the mean altitudinal differences between spring and summer did not differ between successful and unsuccessful birds ($F_{1,7} = 0.36$, $P = 0.57$).

Habitat use and survival

To determine if habitat use could influence the survival of adult grey partridges, we compared habitat use between 10 birds that were killed by predators during the breeding season and 11 that survived. Of the 10 cases of predation, mammalian predators were responsible for six, raptors for three and an unknown predator for one. We found no relationship between adult survival and habitat use, neither at the level of the home range ($F_{7,13} = 0.28$, $P = 0.95$) nor at the level of the radio-location ($F_{7,13} = 0.26$, $P = 0.96$).

Insect food availability and habitat type

There was no interaction between site and year in the repeated-measures ANOVA for food-insect biomass ($F_{4,12} = 0.53$, $P = 0.87$). The mean dry weight of Formicidae, Orthoptera and Coleoptera did not differ between the four habitat types ($F_{3,6} = 0.19$, $P = 0.90$; Fig. 2). Hence, the results of our insect surveys did not enable us to demonstrate a relationship between habi-
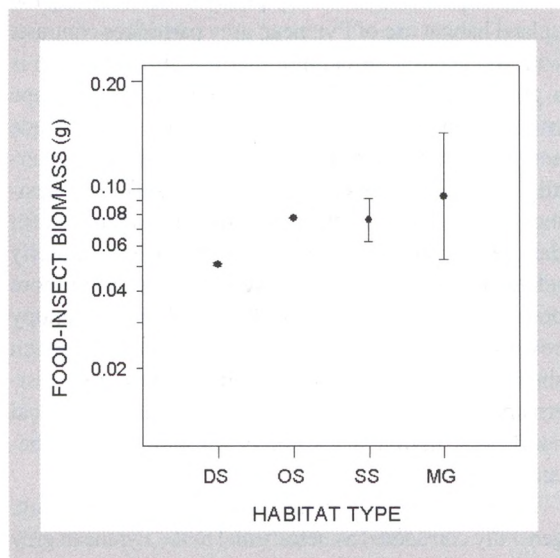

Figure 2. Food-insect biomass in four habitat types (DS: dense shrubland; OS: open shrubland; SS: sparse shrubland; MG: montane grassland) used by breeding Pyrenean grey partridges. Food-insect biomass is expressed as mean (± SE) daily dry weight (in g) of Formicidae, Orthoptera and Coleoptera (for details see Material and methods - invertebrate data).

tat types and availability of insect food items preferred by Pyrenean grey partridge. However, given the small sampling effort, this lack of relationship should be interpreted with care.

Discussion

In this study we examined the requirement of the Pyrenean grey partridge in terms of vegetation cover in the eastern Pyrenean uplands. Out of eight cover types, representing the main stages of the natural vegetation succession, we found that Pyrenean partridges used open and dense shrublands, i.e. areas of *Cytisus purgans* and *Juniperus communis* with a canopy cover greater than 40%, more frequently than expected by chance. Previous studies on the habitat relationships of this subspecies also noted the importance of woody plants in mountainous habitat, either in the Cantabrian Range (Llamas & Lucio 1988, Lucio et al. 1996, Junco Ruiz & Reque Kilchenmann 1998) or in the Pyrenees (Lescourret & Génard 1993, Novoa et al. 1998). All these studies reported preferential use of shrublands with medium (30-60%) and high (>60%) cover of woody plants such as *Genista* sp., *Cytisus* sp., *Vaccinium* sp. and *Rhododendron ferrugineum*. As a general rule, shrublands with canopy cover less than 25% or higher than 80% were avoided. The height of selected shrublands was more variable, from 0.25 to 1.2 m. Unlike the aforementioned studies, our use of radio-telemetry enabled us to quantify the use of different habitat types more accurately. Moreover, we showed that these habitat preferences occurred at two levels (the selection-orders of Johnson 1980), in the location of the home range in a given area and in the habitat utilisation within the home range.

Among the factors determining habitat selection, predation has been shown to influence the habitat requirements of birds (Lack 1968, Cody 1985), and this may be particularly true of the grey partridge. Indeed, like many other ground-nesting birds, the grey partridge suffers high predation on nests and incubating hens (Potts 1980, Reynolds, Dowell, Brockless, Blake & Boatman 1991), and also on broods (Putaala & Hissa 1998). Although in upland habitats cover may also be related to protection against adverse meteorological conditions such as hailstorms, nesting cover is usually associated with the reduction of predation risk on nests. In agricultural landscapes, the availability of suitable cover reduces nest losses (Potts 1980, Rands 1988, Panek & Kamieniarz 2000). In the Pyrenees, the use of dense shrublands seems to be as beneficial to nest

fate as to brood protection. Out of 15 nests monitored in the present study, 11 hatched successfully and resulted in seven fully-fledged broods. In contrast, Putaala & Hissa (1998) found a higher proportion of losses for broods in the Finnish margin of its range. Hence, other factors such as abundance and distribution of predators may be as important for brood survival as habitat characteristics, as suggested in farmland by Tapper, Potts & Brockless (1996).

Pairs that successfully reared a brood used sparse (20-40%) and open (40-60%) shrublands in the spring more frequently than unsuccessful breeders. The link between spring habitat use and reproductive success may be due to pre-hatching influences on reproduction. Such influences, well documented for some grouse species (Moss, Watson & Parr 1975, Moss & Watson 1984) have also been discussed for the grey partridge (Southwood 1967, Dahlgren 1990). From experimental data, Dahlgren (1990) showed that the amount of insects in the diet of pre-laying hens could influence positively both egg production and chick survival. The insect surveys carried out in our study area do not enable us to demonstrate a higher abundance of protein-rich food resources in sparse and open shrublands than in dense ones. Hence, we cannot verify the hypothesis according to which greater use in spring of the former may improve the pre-nesting body condition of females. Alternatively or in addition, the spring habitat use may reflect breeding habitat quality. Since the use of various types of cover in spring is associated with breeding success, good interspersion of different cover types in the pre-nesting home range is likely to provide the most suitable breeding habitat. Other authors have documented differences in grey partridge reproductive success according to habitat type (Rands 1988, Birkan, Serre, Skibnienski & Pelard 1992, Panek 1997, Panek & Kamieniarz 2000). Some of these differences have been associated with the influence on chick survival of certain post-hatching factors such as insect abundance or meteorological conditions (Potts 1986, Panek 1992), but others, as with our own, suggest that as well as these environmental factors coming into play mainly after hatching, the reproductive success of the grey partridge also depends on spring habitat use.

In the summer, failed breeders made much more use of open habitats than successful breeders. This difference could have been explained by the failed breeders moving to higher altitudes, where grassland, bare ground and sparse shrubland prevailed. However, our results show that altitudinal movements in early summer did not differ between successful and failed breeders. The difference could also have been explained

by successful breeders leading their broods to the most invertebrate-rich habitats, except that we could not detect a significant difference in the abundance of invertebrates between habitat types. We therefore suggest that the difference may arise because once a breeding attempt fails, the adults are no longer confined to habitats that confer cover for the nest or chicks.

Although, for many galliform species, adult survival has been related to habitat use (Bergerud 1988, Aebischer et al. 1993a), we found no such relationship in this study. Contrary to our expectation, there was no evidence that use of dense shrublands influenced the survival of adult partridges during the breeding season. Because dense cover was not limited in the study area, all the birds extensively used this habitat type. It is likely that any benefit in terms of survival will be more marked when the availability of dense cover is reduced, for instance in winter after heavy snowfalls. In addition, the fact that birds were killed by a range of predators may also explain the lack of relationship between survival and habitat use. The degree of safety afforded to adult grey partridges by the different cover types will vary according to the type of predator. Habitats such as open grassy areas offer little protection against raptors, while cover that is too dense (>80%) may hamper attempts to escape from mammalian predators. Hence in terms of survival, medium cover, i.e. shrub canopy cover between 40 and 80%, probably represents the best compromise for the partridges.

The importance of woody plants in determining the upland habitat use of Pyrenean grey partridges contrasts with the general perception that the grey partridge is a grassland bird that originally evolved in a steppe environment (Potts 1986). Because of the high altitude and dry climate of our study area, grasses are generally not tall or thick enough to supply sufficient nesting cover. As a result, the suitability of a given area for the grey partridge in the eastern Pyrenees is directly related to the availability of evergreen shrubs, or more precisely with the amount of shrublands with a canopy cover of more than 40%. This presence of evergreen shrub cover is likely to be less important in the western and central Pyrenees, where wetter meteorological conditions favour a greater development of herbaceous cover.

The effects of the decline in upland cattle grazing, generally considered as detrimental to the Pyrenean grey partridge (Génard & Lescourret 1990), should be reconsidered in the light of these latest results. The subspecies appears to rely heavily on mature shrublands, so that the spread of the broom *Cytisus purgans* caused by the reduction in grazing pressure should be consid-

ered as beneficial - at least in the short term. Current grazing practices, especially with the use of controlled burning to clear shrubby vegetation, reduces the nesting cover available to the grey partridge. However, this negative short-term effect is more than compensated for by the fact that, in the long term, grazing management also delays the natural replacement of shrubland by pine woodland and consequently contributes to the long-term persistence of partridge habitat. In terms of land management, an ideal scheme would therefore be a system of rotational burning and grazing which would punctually slow down the natural succession of shrublands, in order not only to prevent the reafforestation of grey partridge habitat but also maintain a mosaic of dense and open shrublands.

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