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Home-range size of Pyrenean grey partridges *Perdix perdix hispaniensis* during the breeding season

Claude Novoa, Samuel Dumas & Jean Resseguier

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We investigated spacing patterns of Pyrenean grey partridges *Perdix perdix hispaniensis* during the breeding season (March-September) to refine our recommendations concerning restoration of nesting and brood rearing habitats. The study was based on 30 grey partridges, 24 yearlings (19 males, five females) and six adults (five males, one female) radio-monitored in two study areas of the eastern Pyrenees. Movements and home ranges were analysed for the pre- and post-hatching periods. For each bird and period, we used cluster analysis to identify core areas within home ranges. Throughout the breeding season, 24 of the 30 birds were paired and six yearling males remained unpaired. The latter used larger home ranges than paired birds, at least before hatching. The home-range size (Minimum Convex Polygon) of the 24 pairs averaged 118 ha in spring (from pair formation to hatching) and 126 ha in summer (brood-rearing period). Pairs tended to use larger core areas after hatching (mean = 10.8 ha) than before (mean = 6.2 ha). After hatching, broodless pairs used larger core areas (mean = 14.4 ha) than those with broods (mean = 8.7 ha). For both groups, we found little overlap between core areas used before and after hatching. For unsuccessful breeders, the small overlap was associated with post-breeding movements to higher altitudes. For successful breeders, it was related to movements to brood rearing habitat. Daily inter-fix distances of broods averaged 126 m during the first three weeks after hatching, then regularly increased up to 249 m as chicks exceeded the age of six weeks. The size of core areas used by broods indicates that treatment plots should cover 5-10 ha to restore breeding habitats with a diversity of shrubland vegetation types.

Key words: core area, French Pyrenees, grey partridge, habitat management, home range, Perdix perdix hispaniensis, radio-tracking

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Analysis of animal space use including seasonal movements and size and shape of their home ranges, is essential not only for formulating management guidelines (Gullion 1972, Peek 1986, Payne & Bryant 1994) but also for understanding population persistence in fragmented habitats (Temple 1991, Fahrig & Merriam 1994). Movements and spatial requirements of the grey partridge *Perdix perdix* have been widely studied in the context of open arable landscapes both in North America (Weigand 1980, Church et al. 1980, Smith et al. 1982, Church

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& Porter 1990, Carroll et al. 1990) and in northern Europe (Birkan & Serre 1988, Montagna et al. 1991, Birkan et al. 1992, O'Gorman et al. 2000, Reitz & Mayot 2000, Salek et al. 2002). Because of variations in season definitions, sampling regimes and analytical techniques, results of different radio-tracking studies cannot be easily synthesised and generalised (Harris et al. 1990). Although these grey partridge studies contribute to effective habitat management in most parts of the species' distribution range, they do not address the particular vegetation types and high degree of habitat fragmentation found in the mountainous habitats of the Pyrenees and the Cantabrian range.

The habitat preferences of the Pyrenean grey partridge *P. p. hispaniensis* are rather well known during the breeding season, and include a dense cover of shrubs interspersed with herbaceous cover (Lucio et al. 1992, Lescourret & Génard 1993, Junco Ruiz & Reque Kilchenmann 1998, Novoa et al. 2002). However, without fire or grazing, shrublands are invaded by forests. Restoration or maintenance of breeding habitats therefore requires active management, usually by burning (Novoa & Landry 1998), sometimes by mechanical means. The appropriate size and configuration of burns or mechanical clearings to favour partridges depend largely on the birds' spatial requirements in the different seasons.

The aim of our study was therefore to investigate the spatial use of Pyrenean grey partridges from pairing to the end of brood rearing. We paid particular attention to the core part of home ranges to translate the results into guidelines for managing habitats.

Material and methods

Study areas

We radio-tagged grey partridges in the eastern French Pyrenees in two study areas approximately 45 km apart. Partridges were marked from 1990 to 1991 in the first study area, Barbet (42°31'N, 2°29'E) and from 1992 to 2000 in the second area, Carlit (42°30'N, 1°55'E; Fig. 1). In both areas, reproductive habitat of grey partridges occurred mainly on south-facing hillsides in the subalpine zone (1,750-2,300 m a.s.l.), where there was a mosaic of shrublands (broom *Cytisus purgans*, juniper *Juniperus communis*, bearberry *Arctostaphylos uva-ursi*), grasslands of fescues (*Festuca rubra, F. eskia* and *F. paniculata*) and woodlands of mountain pine *Pinus uncinata*. Cultivated areas covered less than 1% of the study areas. The main agricultural activity was cattle grazing, which took place from June to October. Stockmen practised controlled burning from November to March to prevent the invasion of grassland by shrubs. From 1989 to 1995, a total of 240 ha of broom shrublands were burned on the two study areas, with an average burn size of 10 ha.

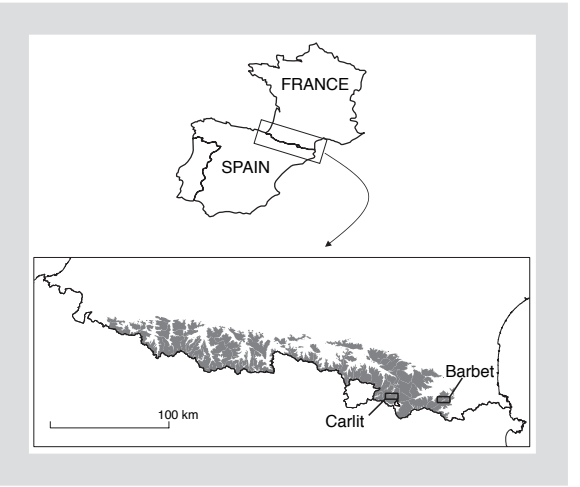


Figure 1. Location of the study areas, Carlit and Barbet, within the distribution range of the Pyrenean grey partridge in France.

Partridge data

Between years and study areas, grey partridge densities ranged within 1-6 pairs/km^2 in spring (Novoa 1998). Partridges were captured using two methods. We used decoy trapping in late winter and early spring (Smith et al. 1981), and spotlight and hand-net trapping at roost sites (Upgren 1968) in spring and autumn. According to season, birds were classified as juveniles (3 months old), yearlings (< 12 months old) or adults (≥ 12 months old) based on the shape of their primary flight feathers (Birkan 1977). We captured and radio-monitored 84 grey partridges, 10 at Barbet during 1990-1991 and 74 at Carlit during 1992-2000. At Barbet, birds were fitted with 9.5-g necklace radio-transmitters (Biotrack) with an expected lifespan of eight months. At Carlit, the necklace radio-transmitters weighed 7 or 10.5 g (Holohil System Ltd.) and had an expected lifespan of 12 months. Birds were located from the ground to within 50 m using a portable receiver (Custom Electronics) and a handheld Yagi antenna at least twice a week during the breeding season (early March - late September). Radio locations were plotted in grid cells (50 × 50 m) superimposed on a 1:10,000 scale map of the study area. For various reasons some birds did not provide sufficient data for analysis (e.g. due to early predation, radio failure or location in inaccessible sites). We obtained enough data on 30 birds, 24 yearlings (19 males, five females) and six adults (five males, one female), to analyse home ranges during the breeding period. Of these, one male

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was monitored during two consecutive breeding seasons, mated with a different hen each year, and was therefore treated as two separate individuals. We recorded the breeding status (paired or unpaired) of each bird and the outcome of any nesting attempt by the pair. As in grey partridge pairs, male and female always stay close together throughout the breeding season, the space use of a pair may be estimated by radio-tracking only one of the mates.

Movement and home-range analysis

The breeding season was divided into two monitoring periods. Spring extended from the end of pair formation (March-April) to hatching (median date 13 July; range: 4 July - 3 August). Summer covered the brood rearing period up to the date when chicks were fully grown (late September). Because of low survival rates or radio failures, only 25 of the 30 birds under study were monitored during both spring and summer.

We initially estimated size of home ranges using the minimum convex polygon (MCP) method, including all fixes. We termed this estimation the 'maximum area' (Johnstone 1998). We also measured the home-range length as the distance between the two most widely separated fixes (Church et al. 1980, Birkan & Serre 1988, Bernard-Laurent 1991). Because of their wide use, these two home-range measurements provided comparability with previous studies (Harris et al. 1990). To assess whether sufficient radio locations had been obtained for stabilising home-range estimates, we tested the relationship between home-range size (maximum area) and the number of radio locations, on paired and unpaired birds separately. Although the minimum convex polygon method allows direct comparisons to be made between studies, this home-range estimation is strongly influenced by outliers and does not allow one to define the 'core area' (Harris et al. 1990, White & Garrott 1990). As grey partridge space use appeared to be mostly multinuclear, we also defined home ranges using cluster analysis (Harris et al. 1990, Kenward 1992, Kenward et al. 2001). To determine the percentage of locations that best defined core areas, we used multi-range utilisation plots, following the approach of Kenward (1992). For each season and breeding status, we plotted the coefficient of variation of home-range size as a function of the percentage of radio fixes and looked for the percentage of fixes lowering the variation in home-range size. Except for unpaired males in spring, the variation in home-range size increased when the most dispersed 15-20% of radio fixes were included in home-range estimations (Fig. 2). Because long excursions were frequent for unpaired males in spring, their home-range size varied greatly, especially when considering the low percentages of radio fixes (see Fig. 2). For this category, we needed at least 80% of radio fixes to stabilise the variation in home-range size. Hence, for all seasons and social status, the threshold of 80% appeared to be the best compromise to define core areas, although plots of home-range size variation sometimes indicated a minimum with 85% of fixes (see Fig. 2). Core areas were therefore calculated by cluster analysis using 80% of fixes.

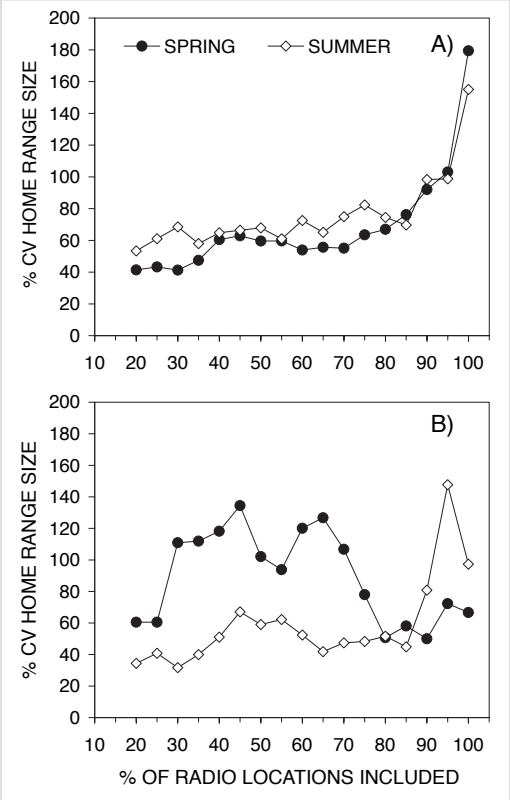


Figure 2. Variation in home-range size (i.e. core area) of 24 paired birds (A) and six unpaired males (B) as a function of the number of fixes (% of radio locations) included in the cluster analysis. The data are given for spring (●) and summer (◇) on two study areas of the French Pyrenees. CV = coefficient of variation.

Each core area consisted of one or several nuclei of radio fixes, termed 'activity centres'. The size of core areas equalled the summed area of the different activity centres (Johnstone 1998). We also calculated the overlap between seasonal core areas, for each of the 19 pairs monitored over the whole breeding season. We determined difference in altitudes occupied from spring to summer by comparing the mean elevation of all radio locations made during the two seasons.

Daily movements can be used as another index of the

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Table 1. Size (in ha) of grey partridge home ranges in the eastern Pyrenees, according to breeding status and season expressed as mean and range (in parentheses). Maximum area = MCP and core area = cluster analysis with 80% of fixes and is the total area of one or more activity centres.

Breeding status	Season	Maximum area size (ha)		Maximum length (km)[a]		Core area size (ha)	
Paired (N = 24)	Spring	118	(5 - 763)	1.9	(0.3 - 5.8)	6.2	(1.3 - 17.9)
Paired (N = 19)	Summer	126	(11 - 524)	1.7	(0.5 - 4.1)	10.8	(0.3 - 30.9)
Unpaired (N = 6)	Spring	1743	(337 - 2890)	8.2	(4.1 - 11.6)	80.2	(26 - 148)
Unpaired (N = 6)	Summer	185	(38 - 391)	3.6	(1.0 - 5.9)	14.3	(6 - 28)

[a] Distance between most widely separated fixes.

area required by an individual to meet its needs (Carroll et al. 1990, Samuel & Fuller 1996). Therefore, we measured inter-fix distances travelled by radio-tagged birds from one day to the next. For this, we considered only fixes recorded on consecutive days, without disturbances on the first day. We calculated the mean distance travelled from one day to the next for the successive weeks following hatching using the brood as the statistical unit to avoid concerns over pseudoreplication.

All home-range calculations were performed using Ranges V (Kenward & Hodder 1995). As distributions of home-range sizes and daily movements showed strong evidence that data were not normally distributed, differences in core area size according to breeding status, season and breeding success were therefore examined using non-parametric tests (Wilcoxon-Mann-Whitney test). Comparisons of size of spring and summer ranges were based on paired data from birds monitored in both periods (Wilcoxon signed-rank test). Altitudes of radio locations were normally distributed. Using ANOVA on within-bird mean altitudinal differences, we also compared the altitudinal movements of pairs between seasons. We performed two-tailed tests using npSTAT (Ratsira 1994) and Systat 7.0 (Wilkinson 1997) software.

Results

Home-range estimations

The number of radio locations collected for each bird and season averaged 32 (SE = 1 location). For the 24 pairs, we found no correlation between home-range size (maximum areas) and the number of radio locations per pair, neither in spring (before hatching) nor in summer (after hatching) implying that sufficient radio locations had been obtained to stabilise these estimations of home-range size (spring: N = 24 pairs, $r_s = 0.11$, P = 0.61, and summer: N = 19 pairs, $r_s = 0.13$, P = 0.62). For the six unpaired birds, we found no evidence that size of maximum area increased with number of radio locations (spring: N = 6, $r_s = -0.70$, P = 0.14, and summer: N = 6, $r_s = -0.20$, P > 0.71). Similarly, the number of radio locations did not appear to affect the size of core areas in neither spring nor summer (spring: N = 24, $r_s = 0.39$, P = 0.06, and summer: N = 19, $r_s = 0.01$, P = 0.96).

Seasonal home ranges and breeding status

Breeding status greatly influenced size of both maximum and core areas (Table 1). The spring core areas of the six unpaired birds, all juvenile males, were much larger than those of the 24 paired birds (U < 0.001; P < 0.001), but this difference did not persist during summer (U = 36; P = 0.18; see Table 1). In fact, isolated males stopped their nomadic movements in June and joined unsuccessful breeders or neighbouring broods after young hatched in July. Most grey partridge pairs found all their breeding requirements within core areas representing < 10% of the maximum areas (see Table 1). Among the 24 paired birds, mean size of core areas did not vary according to sex, neither in spring (males: 6.1 vs females: 6.3 ha; U = 50; P = 0.82) nor in summer

Table 2. Size (in ha), overlap (in %) and altitude (in m a.s.l.) of grey partridge home ranges in the eastern Pyrenees, according to breeding success and season. Overlap between seasonal core areas (in %) is calculated for each of the 19 pairs. All values are expressed as mean and range (in parentheses).

Breeders	Season	Core area size		Overlap between core areas		Altitude
Successful	Spring	7.1	(1.3 - 17.9)	23.5	(0 - 50)[a]	1940 (1520 - 2150)
(N = 12)	Summer	8.7	(0.3 - 18.6)	20.7	(0 - 47)[b]	1960 (1530 - 2180)
Unsuccessful	Spring	6.6	(2.8 - 12.4)	20.7	(0 - 58)[a]	2000 (1750 - 2190)
(N = 7)	Summer	14.4	(4.8 - 30.9)	10.2	(0 - 29.3)[b]	2200 (2030 - 2310)

[a] Spring core areas overlapped with summer core areas;
[b] Summer core areas overlapped with spring core areas.

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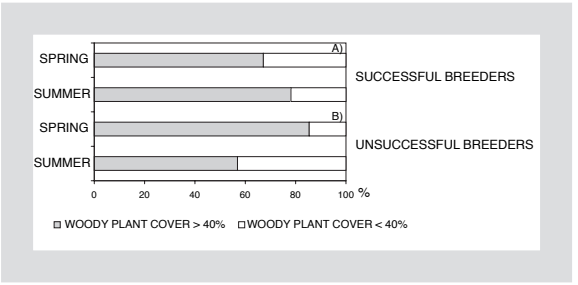


Figure 3. Variations in habitat use during spring and summer for seven successful (A) and three unsuccessful (B) grey partridge breeders in the Carlit study area. For each bird, the percentages of two categories of plant cover were calculated within a 1-ha circle centred on the radio locations. The habitat map originated from a previous study (Novoa et al. 2002).

(11.1 vs 10.1 ha; U = 29; P = 0.73). This result supports the statement that for the grey partridge the radio-tracking of one mate represents the space use for the pair. Pairs tended to use larger core areas after hatching than before hatching (see Table 1), but this difference was not significant (Wilcoxon signed-rank test: N = 19, Z = 1.43; P = 0.15). Of these core areas, 90% were < 14 ha and multinuclear because 2-6 activity centres (nuclei of fixes) could usually be distinguished. For the 24 pairs, the mean size of 94 activity centres in spring was 1.6 ha, whereas 42 activity centres of 12 broods averaged 2.5 ha.

Seasonal home ranges and breeding success

For the 12 successful breeders, the size of spring and summer core areas did not differ (Wilcoxon signed-rank test: Z = 0.79; P = 0.43). The summer core areas, equivalent to the brood home range, varied in size from 0.3 to 18.6 ha (Table 2). For seven unsuccessful breeders monitored during both spring and summer, mean size of core areas tended to be larger in summer than in spring (Wilcoxon signed rank test: Z = 1.35; one-tailed P = 0.18), suggesting a greater mobility of pairs after failure of the nest or brood (see Table 2).

The core areas of pairs, whether successful or not, showed little overlap before and after hatching (see Table 2), suggesting a change in grey partridge space use during the breeding season. Among unsuccessful breeders, this low overlap was associated with post-breeding movements uphill to altitudes about 200 m higher (see Table 2). But the low overlap between spring and summer core areas among the 12 successful breeders was not due to birds moving uphill, but rather to a change in habitat use related to brood rearing (cf. Novoa et al. 2002). For seven pairs with broods, the proportion of open habitat at the level of radio locations decreased from 33% in spring to 22% in summer, whereas for the three unsuccessful birds it increased from 15 to 43% (Fig. 3). In other words, broods moved into dense shrublands, whereas in summer broodless pairs preferred more open alpine habitats. The mean difference in altitude between spring and summer home ranges of unsuccessful breeders was greater than that of successful breeders ($F_{1,17} = 15.3$; P = 0.001; see Table 2).

Daily mobility of birds

In total, we measured 454 inter-fix distances from one day to the next among the 24 pairs; 204 in spring and 250 in summer. As expected, we found a good relationship between mean inter-fix distance and core area size in both periods (spring: N = 14 pairs, $r_s = 0.75$, P < 0.005, and summer: N = 16 pairs, $r_s = 0.65$, P < 0.005). The daily mobility of birds was greater in summer than in spring, both for successful and unsuccessful breeders. However, this seasonal difference was more marked in unsuccessful breeders (Table 3). Nevertheless, the daily mobility of successful vs unsuccessful breeders did not differ neither in spring (U = 22, P = 0.52) nor in summer (U = 13, P = 0.42).

During the first and the eleventh week after hatching we recorded 165 daily inter-fix distances among the 12 pairs rearing a brood. The distance travelled from one day to the next by the broods averaged 126 m ± 12 (SE) during the first three weeks following hatching, then regularly increased up to a mean of 249 m ± 47 (SE) as chicks exceeded the age of six weeks (Fig. 4).

Discussion

Breeding status of birds significantly influences their use of space (Bernard-Laurent 1991, Orlando 2002). In

Table 3. Daily mobility (inter-fix distances; in m) of grey partridge in the eastern Pyrenees according to breeding success and season expressed as mean and range (in parentheses). Straight-line distance was measured between fixes recorded on two successive days without disturbance the first day.

Breeders	Season	Inter-fix distances	Wilcoxon signed-rank test
Successful (N = 6)	Spring	128 (65 - 231)	Z = 1.78; P = 0.08
	Summer	151 (80 - 214)	
Unsuccessful (N = 6)	Spring	105 (58 - 146)	Z = 2.20; P = 0.03
	Summer	250 (96 - 633)	

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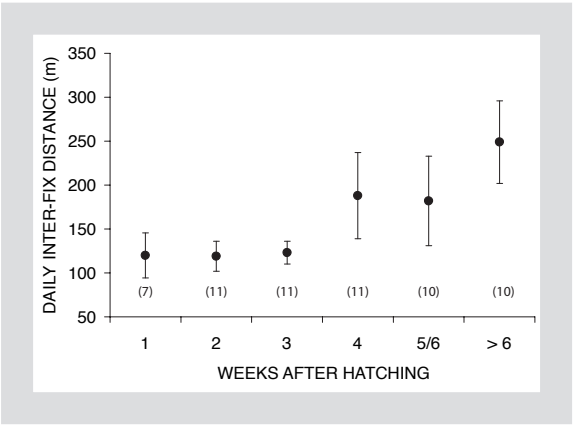


Figure 4. Mobility index expressed as daily inter-fix distances (in m) of grey partridge broods in the eastern Pyrenees according to chick age (in weeks after hatching). Mean distance ± SE between fixes was recorded on two consecutive days, and the number of broods is given in parentheses.

our study, 11% of birds were unpaired males, a proportion similar to that found in other studies (Jenkins 1961, Weigand 1980, Potts 1986, O'Gorman & Kavanagh 2002). Unpaired males moved more extensively than paired males, at least up to the time of hatching. The high mobility of single birds was probably due to searching for a mate.

Home-range length represents a common index of the shape of home range and is often the only technique strictly comparable between studies. Length of spring home ranges of pairs found in our study (0.3-5.8 km; see Table 1) differed little from those reported by Birkan & Serre (1988) in northern France (0.4-4.1 km) and Church et al. (1980) in Wisconsin (0.9-9.6 km), despite noticeable differences in ecological conditions, i.e. type and distribution of habitats. Spacing behaviour of pairs before hatching greatly influenced the length of spring home ranges. Fourteen pairs stayed on the same area from pairing to hatching without noticeable movements. In contrast, the other 10 pairs moved to nesting areas far from the ranges occupied in early spring. Previous investigators have reported such spring movements of pairs (Potts 1986, Birkan & Serre 1988). Potts (*op. cit.*) termed these movements 'spring pair dispersal' and showed that they were positively related to grey partridge hen densities in late winter and negatively to nesting cover availability. In contrast, we observed important movements of pairs even though spring densities were low and nesting cover abundant. Further investigations are needed to understand why some pairs move in spring.

Like most animals, grey partridges tend to concentrate their activities in preferred areas. The fact that maximum home-range areas of pairs averaged 118 ha in spring and 126 ha in summer and were up to ten-fold larger than core areas confirms this point. This huge difference between maximum and core areas was probably due to the fragmented nature of mountain habitats. Indeed, Pyrenean grey partridge breeding habitats are rarely distributed in a continuous pattern, suitable patches of dense shrublands being regularly interrupted by large blocks of unsuitable habitat like dense woodland or open grassland. In contrast, in more homogeneous farmland habitats the size of maximum areas used by grey partridge pairs averaged only 3.7 ha in spring and 8.7 ha in summer (Salek et al. 2002).

In our study, cluster analysis showed that from pairing to hatching, i.e. during 3-4 months, the 24 grey partridge pairs concentrated their activities on fairly small core areas (mean = 6.2 ha, SE = 0.8 ha). Likewise, 12 broods used core areas averaging 8.7 ha (SE = 1.4 ha) during 2-3 months after hatching. Moreover, cluster analysis revealed that core areas were subdivided into several nuclei or activity centres whose mean size varied from 1.5 to 3 ha, but we could not determine the time spent in each activity centre. These estimations are quite similar to the 3.5 ha reported by Birkan & Serre (1988) for size of daily home ranges in northern France, and to the 4 ha used by pairs in Wisconsin during a 2-week period in March (Church et al. 1980).

Inter-fix distance from day to day might be a simple index of space use that could be compared among studies, but this approach has rarely been used. In Northern France, Birkan et al. (1992) reported a mean distance between two successive days of 173 m (SE = 13.5 m) for 20 grey partridges radio-monitored from May to August. Distances travelled per day by broods in North Dakota ranged from 85 m (SE = 21 m, N = 5 broods < 2 weeks) to 141 m (SE = 34 m, N = 3 broods 2-4 weeks; Carroll et al. 1990). Surprisingly, our estimations of straight-line distances travelled between days (see Table 3) agreed with these previous results, despite probable differences in abundance and distribution of resources between study areas.

Management implications

As space use may be analysed at a variety of scales, including landscape or regional level, home range and activity centre (Litvaitis et al. 1996), guidelines for habitat managing may be also proposed following the same hierarchical scheme. At the regional scale, results from home-range studies are helpful for establishing the boundaries of game management units (Edge et al. 1986). In our study, the 25 grey partridges (19 pairs and six un-

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paired birds) radio-monitored at Carlit used a maximum area of 20,000 ha (MCP of the 1,289 radio locations) that was 33.7 km long. Although space requirements of individuals during the breeding period are fairly small, the persistence of a population could depend on suitable habitat, i.e. subalpine shrublands and grasslands, lying within such a large region. We therefore believe that management units for populations and their habitats in the Pyrenees should cover 15,000-25,000 ha, or more if heavy snows force the birds to move far from their breeding range. Home-range studies are also helpful for specifying the size of treatment plots in habitat restoration plans (Peek 1986, Payne & Bryant 1994). For instance, in his guidelines for improving ruffed grouse *Bonasa umbellus* habitat, Gullion (1972) proposed that aspen *Populus tremula* forests be cut in blocks with an area equal to the home range of a brood, i.e. 2 - 4 ha. The same approach may be applied to preserve or even improve the Pyrenean grey partridge habitat. Although previous studies on Pyrenean grey partridge habitat use have shown a preference for a mosaic of dense shrublands interspersed with grassy openings (Lescourret & Génard 1993, Novoa et al 2002), none has provided information on the graininess of this mosaic. Our results on space use suggest that the ideal scheme would be to aim for the highest diversity of habitat structure within areas of about 5-10 ha, a treatment plot corresponding to the mean size of core areas of broods. If we assume that a fine-grained mosaic would the most suitable brood rearing habitat, then the width of habitat patches within this core area should be < 150 m (mean daily inter-fix distance), i.e. habitat patches smaller than 1-2 ha in size.

In the Pyrenees, controlled burnings or mechanical clearings carried out to improve the carrying capacity for livestock by reducing shrub cover should take into account such guidelines in order to preserve suitable reproductive habitats for the Pyrenean grey partridge at different levels. Only a system of rotational burning conducted under wet conditions (ground partly covered by snow and/or damp atmosphere) with a long periodicity (> 10 years) will enable managers to obtain such a habitat pattern (Novoa et al. 1998).

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