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In the French Pyrenees, lek habitats of capercaillie *Tetrao urogallus* are spatially separated from brood-rearing habitats, which are defended by hens before laying. Spring territories of hens thus determine the placement of leks, which are as near to the geometric centre of the locations of one or more territorial hens as lek habitat allows. The number of cocks on leks on a small and large study area was proportional to the number of territorial hens. Locations of leks were systematically influenced by proximity of brood habitats, and the number of cocks on leks was positively correlated with the total area of brood habitats. Establishment of a lek may depend on the prior presence of one or more territorial hens. Because hens influence establishment and size of leks, territoriality in hens may limit numbers of both cocks and hens. These findings support recent models emphasising the effects of hens on lek formation, and contrast with those from Norway, where behaviour and habitat requirements of cocks determine size and location of leks. This may result from brood habitats in the Pyrenees being in localised patches, whereas those in Norway are available throughout the forest. However, the regular distribution pattern of leks in both the Pyrenees and Norway, supports the aspect of the Norwegian model which attributes lek location to the spacing behaviour of cocks.

Key words: hens, lek, territories, Tetrao urogallus

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In capercaillie *Tetrao urogallus*, matings take place only during a few days in spring on traditional display sites of cocks (Hjorth 1982, Sjöberg 1990, Winqvist 1990, Rolstad & Wegge 1987, Castroviejo 1975, Roth & Nievergelt 1975, Devau & Catusse 1988, de Franceschi & Bottazzo 1988). In the Pyrenees, 2-25 cocks come together to display within 10-200 m from each other.

Several authors imply that the location of leks is determined by habitat preferences of the cocks (Catusse 1988, Wegge & Larsen 1987, Roth & Nievergelt 1975). Others have concluded that capercaillie leks are situated at the junction of the spring home ranges of cocks (Larsen, Wegge & Storaas 1981, Hjorth 1981, 1985, Wegge & Rolstad 1986, Leclercq 1987). Forest structure and fragmentation affect the choice of spring home ranges, and therefore the location of leks (Wegge & Rolstad 1986, Lindén & Pasanen 1987, Rolstad & Wegge 1987). Rolstad & Wegge (1987) developed a model to predict the number of lekking cocks from forest age and graininess. According to most of the above studies, the location and the number of cocks on a lek should depend only on the spring habitat requirements of cocks, and not on the spacing behaviour of hens. However, recent work on several other lekking species supports the

idea that habitat selection in females has influenced the evolution of collective courtship behaviour of males, including the number of males that will display on a lek (Queller 1987) and the spatial distribution of leks (Bradbury 1981, Bradbury, Gibson & Tsai 1986).

There have been numerous attempts to explain the size and spacing of leks. In some studies no evidence was found that females influenced the spacing of leks. In contrast, two hypotheses suggest an important role of the hens: in the 'hotspot model', leks were preferentially located in areas through which females travelled between their wintering and nesting ranges before mating, and the distribution of males among leks was related proximately to variation in the number of females visiting each lek (Gibson 1996). Leks should be evenly distributed at distances approximating the diameter of female home ranges.

In the 'black hole model' developed for ungulates, leks arise because clusters of male territories retain mobile females. This model predicts that leks will be evenly spaced at distances of approximately one female home range diameter, as in the previous model, and that lek size will increase with increasing male density (Stillman, Deutsch, Clutton-Brock & Sutherland 1996).

In the central French Pyrenees, in spring and summer, capercaillie mainly live in the higher part of the forests, near the timberline. But in many cases cocks and hens are largely separated; cocks use old fir *Abies alba* and beech *Fagus silvatica* forests, whereas hens use treeline habitats near high pastures and subalpine moors (Devau & Catusse 1988, Ménoni 1990).

I examined, in this particular situation, the effects the location of breeding habitats chosen by hens, and the number of hens may have on the distribution of leks and the number of displaying cocks. I analysed these relationships first on a small study area, then at a larger scale. Finally, I propose a model for the Pyrenees to explain the size and the location of the leks that considers the contrasting ideas of Wegge & Rolstad (1986), Rolstad & Wegge (1987) and Bradbury et al. (1986), regarding the influence of the respective spacing behaviour of the two sexes.

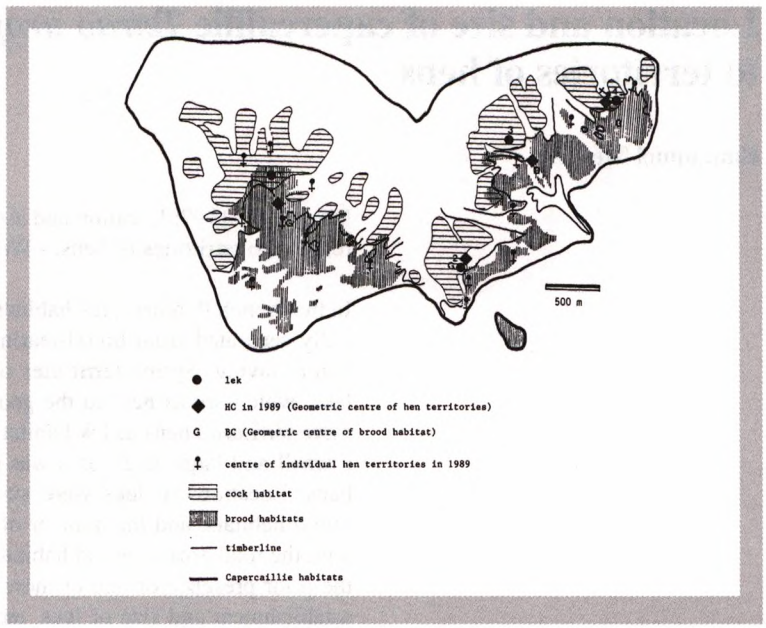

Figure 1. Capercaillie habitat in 1989, in the Esbas-Sajust area, Pyrenees, France.

Study areas

The study was conducted in the southern part of the Department de Haute-Garonne (central French Pyrenees), located between 42°42'N - 42°58'N and 0°27'E - 0°50'E. Within this area 300-500 capercaillies live on mountain slopes often steeper than 100%, at altitudes of 1,000-2,000 m a.s.l. The study was carried out at two different scales. Detailed studies were done in an area of 720 ha south of Luchon (Esbas-Sajust) (Fig. 1), in old largely unmanaged forests dominated by fir and beech. Following a landslide in 1865 (Abt 1989), pine *Pinus montana*, spruce *Picea abies* and larch *Larix decidua* were planted on 200 ha to control erosion. In the late 1800s, grazing was prohibited on half the study area, allowing 80 ha of overgrazed meadows to develop into favourable capercaillie habitat (Ménoni & Novoa 1987). Thus, as a consequence of plantations and reduced grazing pressure, the treeline has moved upward nearly 400 m in altitude over the last hundred years. Some data used in this detailed study come from a 400-ha fir/beech forest neighbouring Esbas-Sajust.

I also carried out studies at a larger scale, in an area of 520 km^2 in the department de Haute-Garonne. The area included 20,650 ha of old forest, composed principally of two vegetation associations, mountain beech/fir and subalpine fir (Dupias 1985) (Fig. 2). Half of these forests have been logged by selective

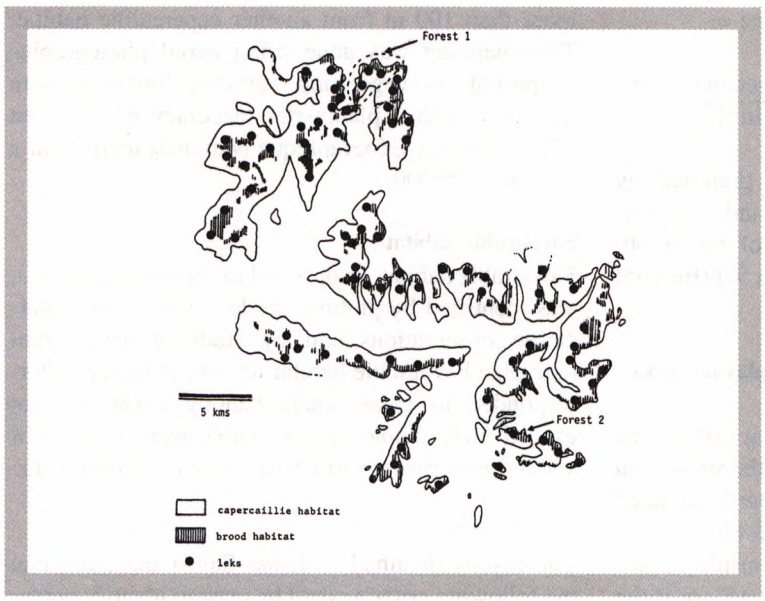

Figure 2. Cartography of capercaillie habitat on the extensive study area.

cutting. The forest was fragmented into 38 patches, ranging in size from 6 to 6,900 ha. In accordance with Rolstad & Wegge (1987), I define a suitable patch as an area of habitat separated by more than 100 m from any other area of the same type. The capercaillie habitats include all types of vegetation used by the species around a year (e.g. forest with canopy cover of <80%, treeline habitats near high pastures and subalpine moors).

Fragmentation was the result of topographic relief and old land clearings by neolithic human populations dating back to 4,000 B.C. (Jalut, Aubert, Galop, Fontugne & Belet 1996). Most of the current brood habitats are heathlands and subalpine meadows, situated adjacent to, and just above, the timberline. Habitats potentially favourable to broods cover only 4,200 ha of 20,650 ha.

Methods

I defined a lek as a site where one or more cocks displayed in spring on the same area of 1-10 ha during at least two consecutive years.

Local scale study at Esbas-Sajust

Counts of territorial cocks

Four leks were present. The cocks were counted at least twice each spring during 1979-1991, following the method of Catusse & Novoa (1983), during the period when hens frequented the leks. I distinguished territorial cocks displaying on the ground from non-territorial cocks, which remained perched in trees.

Counts of territorial hens

During 2-3 weeks before the copulations, hens in the Pyrenees are markedly territorial; they live alone near their future nesting site, and show their territoriality by cackle calls, and other aggressive behaviour including fight. Cackle calls may occur during day and night, and most frequently during two hours after daybreak (Ménoni 1990). Cackle calls were recorded along transects during the two hours following daybreak, on the whole study area, on 15 different mornings in spring 1988 and 1989. The transects were sketched so that every point of the study area was in a distance of ≤400 m from a transect. Calls were either spontaneous or elicited by use of recorded calls emitted from stations 200-500 m apart (Ménoni 1990). Thus, individual hens could be identified by plotting the locations of their cackle calls on the different mornings. Data of one radio-tagged hen supported the notion that hens are very site tenacious in spring (Ménoni 1990).

Construction of hen territories from recorded cackle calls

The maps of the localisations of the hens counted on the successive transects were very similar and their superposition resulted in groups of points within radii of <200 m. Each different group of points was assumed to be from the same bird. The home range of each hen was therefore constructed as the convex polygon joining the outer points of each group.

Determination of brood habitat

Vegetation types, defined by vegetation structure and species composition, were mapped at a scale of 1:5000 m, resulting in 32 different vegetation types on the 720-ha study area. Broods were counted each year from 1984 to 1990 by a complete survey of the study area using pointers, and brood locations were plotted on the vegetation map. A frequentation index was calculated for each vegetation type, as follows:

Frequentation index for a vegetation type =

$$\frac{\text{number of broods observed in the vegetation type}}{\text{surface of the vegetation type in \%}}$$

A vegetation type was described as preferred by broods if the index was greater than an index expected for random use (= total number of brood observed/total surface of the study area in %) (Bernard 1981).

Determination of potential habitat for displaying cocks (= cock habitat)

I used the criteria established by Devau (1986) and Devau & Catusse (1988) to identify on the vegetation map potential display sites. These criteria included old forests with a canopy cover of 25-80%, and a shrub cover of <50%. Areas were considered unfavourable if mountain slopes exceeded 45°, or if the forest patch was smaller than 5 ha.

Comparison of the spatial distribution of territorial hens and brood habitats

I defined the geometric centre of the localisations of territorial hens in spring (HC), and that of the brood habitat (BC), within each home range area (see definition below). HC is the centre of gravity of all the localisations of territorial hens obtained from the recorded cackle calls during the transect counts. I compared the distances lek-HC and lek-BC to the distances of 152 random points within the 'cock habitat', selected by a grid laid over the habitat map.

Definition of 'home range area'

The home range area of a lek is defined as the surface surrounding a lek containing the spring home ranges of the territorial cocks displaying on this lek; generally, the home range area of a lek is limited at the mid-distance between this lek and the surrounding leks. Here, the width of the home range areas varied from 1 to 2.5 km.

Regional scale study

Capercaillie habitat

I considered all forests belonging to the montane and subalpine vegetation associations to be potential habitat for capercaillie, including heaths and meadows within 250 m of the timberline. Following Rolstad & Wegge (1987), I considered a capercaillie habitat patch to be isolated if it was separated by more than 100 m from another capercaillie habitat. This mapping was done using aerial photographs, supported by vegetation surveys. Surfaces were measured with a planimeter (accuracy of 10%) on I.G.N. (Institut Géographique National) maps with a scale of 1:25,000.

Favourable habitat

Favourable habitat, as opposed to capercaillie habitat, was identified by plotting the locations of all capercaillie observations and by studying aerial photographs. Favourable habitat on the photographs corresponded to areas where canopy cover did not exceed 80%. Some denser stands were retained if small scale openings of <1 ha occurred within them.

Brood habitat

The results obtained at Esbas-Sajust indicated that the following criteria could be used to identify potential brood habitat, without any consideration of the tree layer: presence of a field layer >25 cm tall with ground cover of >80% (very wet areas excluded). The mapping of brood habitats was done using aerial photographs, supported by vegetation surveys run on test sites selected at random, and covering more than 50% of the patches found potentially favourable. I verified the resulting map by locating 180 broods in the field.

Localisation and mapping of leks

Leks were located by searching for displaying cocks, and signs such as tracks or faeces in the snow, by interviewing local inhabitants and by plotting the observations in Bugnicourt & Laurent (1982). Leks were then classified into four categories:

- verified lek (with displaying cocks);
- probable lek (cocks were regularly present during the display period, but displaying was not confirmed);
- possible lek (vague report not confirmed by field work);
- abandoned lek (no longer frequented).

Spacing of leks

The distance between neighbouring leks was measured on the map. I calculated the average distance between leks, and the distribution of the inter-lek distances, by the Nearest Neighbour Method given by Clark & Evans (1954) to get an estimation of the divergence from a random distribution. I only used data from zones where the capercaillie habitat was

Table 1. Distances (m) between the four leks, the geometric centre of good brood habitat (BC) and the geometric centre of the localisation of territorials hens (HC) on the corresponding home range areas. The distances between the leks, and BC and HC, respectively, have been compared to the mean distances of random points in the potential lek habitat (99% Confidence Intervals are given in parentheses). The mean distances HC-BC, lek-BC, and lek-HC are shorter than distances to random points (Mann Whitney U-Test, U = 0, N = 4, P = 0.014; U = 2, N = 4, P = 0.057; U = 2, N = 4, P = 0.057).

Lek number	Distance between HC and BC	Distance between lek and BC	Mean distance of random points to BC	Distance between lek and HC	Mean distance of random points to HC	% of random points closer to HC than to the lek centre
1	230	470	835 (771 - 899)	230	710 (645 - 775)	2/82 = 2.4%
2	120	100	296 (229 - 363)	100	290 (242 - 338)	0/23 = 0%
3	100	370	570 (513 - 627)	300	500 (451 - 549)	2/29 = 6.9%
4	220	200	475 (393 - 557)	80	290 (205 - 375)	1/18 = 5.6%
Mean	170	285	544	177	448	5/152 = 3.3%

continuous or the distance between patches did not exceed 100 m.

Counts

The number of cocks on 33 leks was determined as accurately as possible at least once between 1984 and 1989. If counts were made on a lek during more than one year, the mean number was retained in the following analyses. On 16 other leks, the number of cocks was estimated either by searching for tracks in the snow (Leclercq 1977), or by retaining the maximum number reported by local inhabitants.

Results

Local scale study at Esbas-Sajust

Location of leks in relation to brood and nesting habitats

Four leks covering 18 ha were present at Esbas-Sajust, whereas 143 ha of potential lek habitat were available. The potential lek habitat was separated by the timberline from the brood habitat (175 ha) situated at higher elevations, with an overlap of only 11 ha between the two habitats.

Ménoni (1990) showed that the distribution of territorial hens before nesting coincided with the brood habitat (see Fig. 1). In this study area, more than 75% of the locations of 11 radio-marked broods were made in non-forested habitat (canopy cover ≤10%), i.e. a different habitat than that used by lekking males (Ménoni 1990). Moreover, the surface occupied by a territorial hen (9.7 ha) was similar to that of the home range of a brood (11.7 ha.) (Ménoni 1990). Within each home range area in the present study, the centre of gravity of the localisations of the territorial hens was near that of the brood habitats (mean separation of 170 m) (Table 1). Only during four days did a radio-tagged hen leave her territory to visit the nearest leks (Ménoni 1990).

Figure 1 and Table 1 suggest that the four leks were located near the habitat used by hens in spring. In particular, the four leks were not in the centre of the potential lek habitat but tended to be near the timberline and the brood habitats. Two leks (1 and 4) were situated in areas where the two habitats overlapped. Moreover, the distances between the leks and the centre of the territories of the territorial hens (HC), and the distances between the leks and the centre of the brood habitat (BC), were less than expected by choosing random points within the potential lek habitat (see Table 1). Only 5 and 3% of the 152 random points extracted from the potential lek-habitat were nearer to each other than the distances of 'lek-HC' and 'lek-BC'.

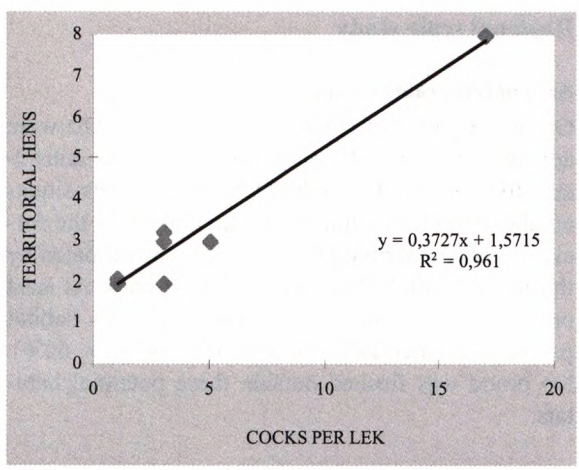

Figure 3. Relationship between the mean number of cocks per lek and the mean number of territorial hens on seven home range areas in 1988/1989 at Esbas-Sajust and in an adjacent forest (N = 7).

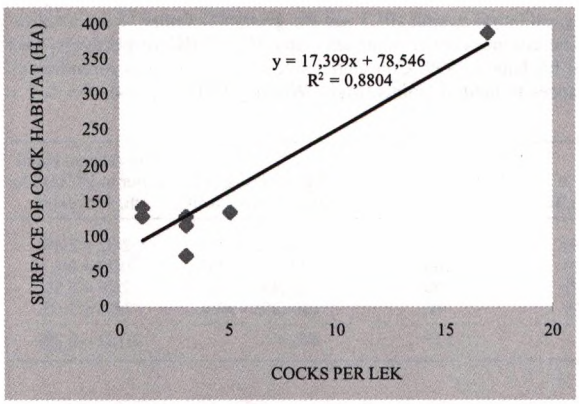

Figure 4. Relationship between the number of cocks per lek and the surface of cock habitat in seven home range areas (N = 7).

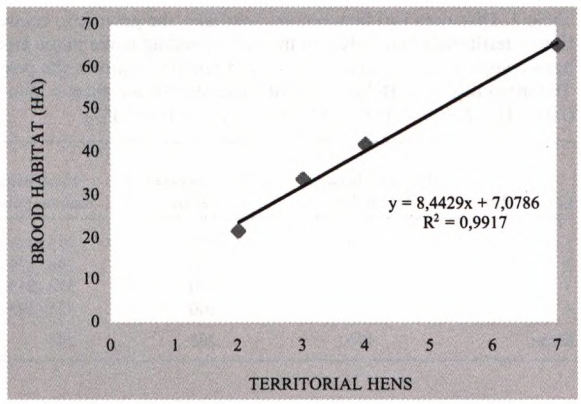

Figure 5. Relationship between the number of territorial hens and the surface of brood habitat in four home range areas.

Correlation between number of cocks on leks and number of territorial hens

The number of territorial cocks on seven leks (four at Esbas-Sajust and three on an adjacent mountain) was positively correlated with the number of territorial hens localised on the corresponding home range area ($r = + 0.99$, $N = 7$, $P < 0.001$) (Fig. 3). I also found a positive correlation between the number of cocks per lek and the corresponding surface of cock habitat (Fig. 4). But, if I exclude the very large lek from this analysis, only the first correlation remains (respectively: $r = + 0.73$, $N = 6$, $P < 0.1$, and $r = + 0.17$, $N = 6$, n.s.). At Esbas-Sajust, the number of territorial hens was correlated with the surface of brood habitat available per home range area ($r = + 0.996$, $N = 4$, $P < 0.01$); the number of cocks per lek was also correlated with the area of brood habitat (Fig. 5) ($r = + 0.929$, $N = 4$, $P < 0.005$).

Regional scale study

Area of favourable habitat

Of the 20,700 ha of potential habitat, 13,500 ha were actually frequented by capercaillie and thus considered to be favourable; only 4,050 ha, generally situated above the timberline but contiguous with the forest, are potential brood habitat. This was validated by the mapping of 180 observations of broods. At least one brood was flushed on 90 out of 145 habitat patches classified as favourable to broods (i.e. 62%). No brood was flushed outside these potential habitats.

Spacing of leks

The average distance between leks was 1,395 m (SD = 641 m, N = 65), based on the 65 leks in areas with continuous capercaillie habitat or distances between patches of <100 m. Analysis of the distribution of the inter-lek distances by the nearest neighbour method given by Clark & Evans (1954) suggested divergence from a random distribution ($P = 0.10$). Rather, leks tended to be uniformly spaced ($c = 20.1$, 65 intervals, $R = 2.3$), which implies that cocks tended to be searching for maximum spacing.

Position of the leks in relation to the capercaillie habitat

If lek placement is influenced by the location of brood habitat within the home range areas, as the data from Esbas-Sajust suggest, one should be able to validate this relationship on a larger area. On the other hand, the centre of gravity of a home range area (HRC) should be the ideal point for the establishment of a lek, according to the 'piece of pie' theory of the organisation of cock home ranges around the lek (Hjorth 1981, 1982, Leclercq 1987, Wegge & Larsen 1987).

I calculated the following two distances for 63 home range areas with a known lek; from lek centre to HRC, and from lek centre to centre of gravity of the brood habitat (BC). In the 12 cases where BC fell outside the forest, I considered it to lie in the nearest forested habitat.

The mean of the distances 'lek - HRC' was 319 m (SD = 173 m, N = 63) and that of 'lek- BC' was 187 m (SD = 133 m, N = 63) (unilateral paired t-test, $t = 4.94$, $N = 2$, $P < 0.001$). Figure 2 shows that leks tend to approach brood habitats. Only two out of 83 verified or abandoned leks were not within, or contiguous with, a brood habitat. Therefore, leks are not established near the theoretical centre of gravity of a home range area.

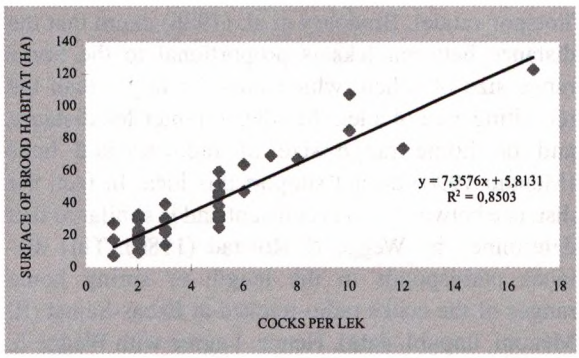

Figure 6. Relationship between the maximum number of cocks per lek and the surface of brood habitat in the home range area (N = 49).

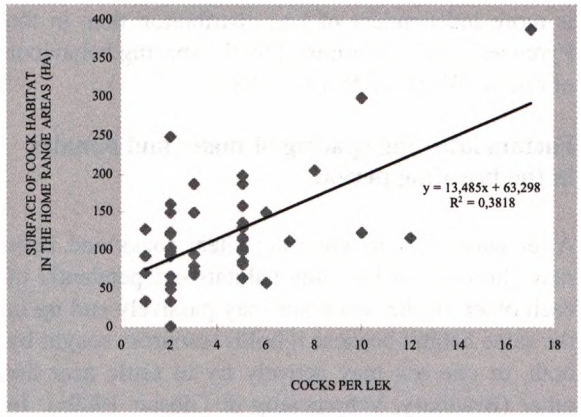

Figure 7. Relationship between the maximum number of cocks per lek and the surface of cock habitat in the home range area (N = 49).

A particular case supporting the hypothesis of a lek/brood habitat relation

Forests 1 and 2 in Figure 2, which are respectively an oak/beech forest on blueberry *Vaccinium myrtillus* and a grazed forest of birch/hazelnut *Corylus avellana*, offer no habitat for winter and early spring, but are very favourable to broods. Nevertheless, some cocks colonise them each spring in order to use them as display sites, and at the beginning of the display season, they have to fly long distances to feed themselves (minimum 2.8 km, case 2), as was visually observed.

Relationship between the number of displaying cocks and the area of brood habitat

I now asked if the correlation between the number of displaying cocks and the area of favourable brood habitat found at Esbas-Sajust holds on a larger scale. To eliminate the influence of human activities on the density of cocks, I excluded leks situated on ski stations or near recently constructed roads, and those located in areas with heavy shooting pressure on capercaillie. For the leks retained, the number of cocks per lek was positively correlated with the surface of brood habitat in its surrounding home range area ($r = + 0.92$, $N = 49$, $P < 0.001$) (Fig. 6).

The number of cocks on a lek was also correlated with the surface of cock habitat within its surrounding home range area ($r = + 0.62$, $N = 49$, $P < 0.01$) (Fig. 7).

However, at Esbas-Sajust, there was a correlation between the size of the home range area and the surface of brood habitat ($r = + 0.73$, $N = 4$, $P < 0.01$). The correlation between the number of cocks and the surface of brood habitat being stronger, it suggests that this is the parameter which explains most of the variation observed. Indeed, Figure 6 indicates that one territorial cock is added for each supplementary 7.5 ha of good brood habitat in the home range area, which is similar to the 9.7 ha occupied by a territorial hen.

Discussion

Influence of spring habitat of hens on the location of leks

The results obtained at Esbas-Sajust, and on a larger area, suggest that leks are established near brood habitats where hens defend a nesting territory in spring. Cocks thus appear to maximise their reproductive success by displaying near sites that are occupied by hens in the breeding season.

In Norway and in the Alps, radio-tracking of capercaillie indicated that there was no relationship between the position of a lek and the nesting sites of hens (Wegge & Rolstad 1986, Storch 1997). But the spatial arrangement of habitats in these areas differs from that in the Pyrenees. Here, the nesting and brood rearing habitats are quite distinct from those of cocks, and they are limited in surface and occupy a zone situated above the leks, near the timberline. In contrast, in Norway and in the Alps, habitats selected by hens in spring are scattered randomly throughout the forest (Fig. 5 in Wegge 1985 and Fig. 6 in Wegge & Rolstad 1986, Storch 1997). This random distribution of hens may mean that the choice of the lekking site

is more independent of hen distribution than in the Pyrenees, and is determined by the spacing behaviour of cocks (Wegge & Rolstad 1986).

Factors affecting spacing of males and females in the breeding period

After leaving their wintering sites, cocks and hens may choose their breeding habitats independently of each other, or the two sexes may passively end up in the same habitat because it holds resources sought by both, or one sex may actively try to settle near the other (Bradbury, Vehrencamp & Gibson 1989a). In the latter two cases, either sex may arrive first.

In the Pyrenees, the results show that cocks do not position their leks independently of habitats selected by hens. The second hypothesis of a common resource bringing one sex near the other may be eliminated because the habitats used by displaying cocks in late winter and spring (old forests containing conifers) differ from the open habitats selected by hens for nesting and brood rearing. Indeed, at this time of year, the hens are very often found in the ground cover near the timberline. I therefore retain the third hypothesis, namely that hens are attracting cocks.

Furthermore, I suggest that when an area is newly settled by capercaillie, hens arrive first, for the following reasons: 1) Wegge (1985) shows that, at the end of winter, a proportion of hens move out of the general area occupied during winter; 2) this movement to nesting areas from winter ranges was abrupt and direct, before the mating season; 3) recent studies based on radio-tracking suggest that, in capercaillie, hens are colonisers, whereas cocks disperse less and tend to establish their home ranges near their natal brood ranges (Rolstad 1989, Storch 1993).

This pattern agrees with the proposition of Parker (1978 in Queller 1987) that leks sites are chosen to increase the copulation opportunities of the cocks. Bradbury et al. (1986) refined this idea in their 'hotspot' model, which says that leks are established near points of maximum traffic of hens. The model apparently explains the distribution of sage grouse *Centrocercus urophasianus* leks (Bradbury et al. 1986). Bernard (1981) proposed an equivalent scheme for the black grouse *Tetrao tetrix*. My results also seem coherent with the 'hotspot' model. Schroeder & White (1993) also accept this model for the prairie-chicken *Tympanuchus cupido*.

Yet, capercaillie do not fit all aspects of the 'hotspot' model. Bradbury et al. (1986) claim that the distance between leks is proportional to the home range size of a hen, which must be larger than the recruiting area of a lek. My data on inter-lek distance and on home range size of radio-tracked hens (Ménoni 1990) do not support this idea. In fact, the distance between leks is constant and is similar to that determined by Wegge & Rolstad (1986). This distance corresponds to the length of spring home ranges of the cocks radio-tracked at Esbas-Sajust (E. Ménoni, unpubl. data). Hence, I agree with Wegge & Rolstad (1986) that spacing behaviour of cocks largely determines inter-lek distance in Norway, where brood habitats are available throughout the forest. Yet, the spatial behaviour of cocks is certainly not the primary determining factor: Indeed, cocks are able to move each day in early morning to poor male habitats, i.e. young forest without coniferous trees, to display on good brood habitats. Besides, Ménoni & Bougerol (1993) showed that a lek is established on a forest patch only if it possesses enough brood habitat. Thus, according to Storch (1997), finely grained fragmentation of good nesting habitats affects the range use of hens. Storch (1995) concluded that female potential of mobility may be a better cue to understanding the evolution of lek mating systems than actual home range size, and that spacing of capercaillie leks depends on the dispersion of hens.

Even though the size of hen territories observed in this study during spring is not in agreement with that foreseen by Bradbury et al. (1986), several characteristics of their behaviour still support the 'hotspot' hypothesis. Although their territories are small (<15 ha), they move over a much larger area (mean length of daily movements of a radio-tracked hen at this period is 790 m on 105 ha, Ménoni 1990) just before settling down. Moreover, they regularly fly over the lek and often cackle noisily. The nesting territory must therefore be attractive for cocks at the beginning of their display period.

Why is the lek not always near the theoretically ideal point?

In the analysis of a large area, the mean distance between leks and the centre of the brood habitat of the hens was 187 m, or less than the 319 m found between the lek and the centre of the home range area. I think that this displacement of the lek towards the hens without leaving the cock habitat, reflects the optimum solution to the problem of displaying as

closely as possible to the hens without becoming vulnerable to predation.

Why are leks generally spatially stable in the Pyrenees?

The explanation of Bradbury, Gibson, McCarthy & Vehrencamp (1989b) for sage grouse displaying over time on traditional sites is that the reproductive habitat of hens is fragmented and stable. Hens thus disperse over it each year in the same way, determining comparable lek places. In the Pyrenees, nesting and brood rearing habitats are also stable. For example, the development of *Ericaceous* heaths is naturally very slow, and is halted in many areas by grazing (Doche, Pommeyrol & Peltier 1991). Display on a traditional site, once established, also permits cocks to easily escape predators in a familiar environment, to reduce energy through prior knowledge of neighbours' territory borders and to decrease searching time for hens (Hjorth 1985).

Determinants of lek size

In two small areas containing seven leks, the number of cocks per lek was correlated with the number of territorial hens on the home range area around each lek, and with the surface of reproductive habitat available to the hens. The latter relationship tended to hold also over a larger area. Although some hens may nest far from the lek where they copulated, most nest are placed within the home range of this same lek (Wegge 1985, Wegge & Rolstad 1986). This suggests that in the Pyrenees, where the habitats of the two sexes are well separated, cocks might adjust their numbers to those of hens available in the surrounding area. This seems to be the case in sage grouse (Bradbury et al. 1989b). Hence regulation of local population density would be the result of an intrinsic mechanism based on the behaviour of hens. Experimental data on such a mechanism are scarce (Hannon 1988). Parker (1978 in Queller 1987) proposes an alternative model in which males of lek species adjust their numbers to maximise the opportunity to copulate. Queller (1987) suggests that numbers on a lek are the result of an optimisation between the search for reproductive success and the search for maximum security. Nevertheless, it is not known if cocks have better reproductive success on big or small leks (Hjorth 1970, 1985). According to Hjorth (1970, 1985), attractiveness of leks to hens may also vary with lek size and therefore have consequences for the evolution of lek size.

Rolstad & Wegge (1987) proposed a model to estimate the number of cocks per lek based only on the amount of old forest and its 'grain' (size of patches) in the home range area. My results suggest that in the Pyrenees the amount of brood habitat is the better predictor of the number of both territorial hens and cocks.

In conclusion, I propose that the genesis of a lek in the Pyrenees is as follows: the appearance of brood habitat attracts one or more hens, which in turn attract one or more cocks. The number of hens establishing territories is determined by the quantity of brood habitat, and the number of cocks on the lek will depend on the number of hens within a radius of 0.7 km of the lek. Whatever the density of hens, leks will be spaced at intervals of about 1.4 km. This regular spacing of leks, however, seems to result from the spacing behaviour of cocks.

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