Lek site defines annual spatial use of male Black Grouse (*Tetrao tetrix*)

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Adult male Black Grouse (Tetrao tetrix) are assumed to use the same lek throughout their life-span and juveniles are rarely observed settling far from their natal areas. Here we report results on a study of lek site fidelity in male Black Grouse using mark-recapture, radio-telemetry, and lek observations between 1984 and 1992. Data were collected at two sites in central Sweden with six and two leks, respectively. A total of 306 Black Grouse (230 full-grown adult and juvenile males, and 76 chicks) were captured and tagged. We found that all recaptured males tagged as chicks (n = 7) were caught on the lek closest to their initial capture site. Twenty-six percent (n = 59) of individuals ringed as full-grown were recaptured at least once in the subsequent springs. Fewer individuals attended leks during the mating period than the premating period ($t_{(15)} = 3.06, P = 0.008$). Juvenile males were closer to the lek in the premating period (95% confidence interval = 0.45-0.65 km) than in the mating period (0.73–1.13 km), in contrast to adults, which were closer to leks in the mating period (0.44–0.61 km) than the premating period (0.80–0.95 km). Inter-lek movement probability of the birds was 15% (n = 9) in the study area. Male Black Grouse remain close to their lek all year round and their recruitment is local. This indicates that leks consist of well-defined local populations, which have limited interactions with other leks.



1. Introduction

Dispersal in grouse has not been extensively studied, but there appears to be a marked sex difference in natal dispersal distances, where males are recruited more locally than females (Schroeder 1986, Martin & Hannon 1987, Small & Rusch 1989). This reduces the risk of inbreeding, especially if kin recognition is poor. Black Grouse (*Tetrao tetrix*) have a lek mating system (Bradbury & Gibson 1983), in which males contest to be selected by females during the mating period. The



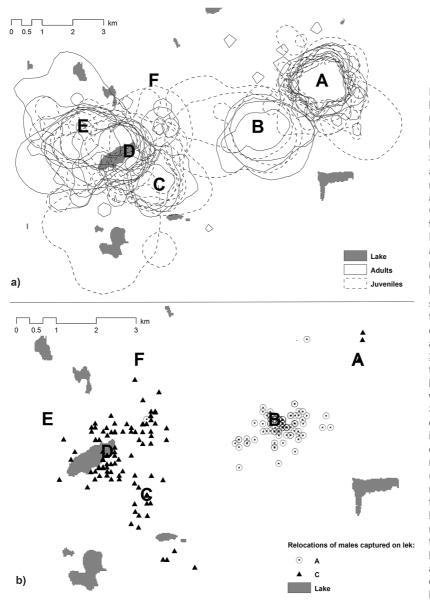


Fig. 1. Map showing home ranges and movements of male Black Grouse around lek A-F at study Site 1, Sweden, 1984-1987. a) Annual home ranges of 25 adults and 24 juveniles Black Grouse males captured at lek A-E. b) Relocations of one adult and five juvenile radio-collared Black Grouse males that have changed lek sites. One adult and two juveniles were recaptured at a new lek, and three juveniles had ≥ 50% of their relocations closer to another lek than where they were initially caught. Small open circle with dot and dark triangle indicate individuals' capture lek. One juvenile and one adult (both recaptured and radio-tracked) moved from lek-A to lek-B (2.6 km), one juvenile (both recaptured and radiotracked) moved from lek-C to lek-A (6.3 km), and three juveniles (radio-track only) from lek-C to lek-D (1.5 km).

males display in open forest habitats in spring and to a lesser extent in autumn (Rintamäki *et al.* 1999). The leks are commonly 1–2 km apart (Alatalo *et al.* 1992, Rolstad *et al.* 2009). Females visit the leks during a brief period in spring to mate and large leks attract relatively more females than small ones (Alatalo *et al.* 1992, Hovi *et al.* 1997, Isvaran & Ponkshe 2013). A high proportion of adult males appear to be faithful to a lek throughout their life (Alatalo *et al.* 1992), which is also common in sympatric Capercaillie (*T. urogallus*)

(Wegge & Larsen 1987) as well as Greater Sage-Grouse (*Centrocercus urophasianus*) (Schroeder & Robb 2003, Gibson *et al.* 2014) and Sharptailed Grouse (*Tympanuchus phasianellus*) (Drummer *et al.* 2011). Furthermore, leks of Black Grouse within a large study area hold genetically closely related males (Höglund *et al.* 1999); but see (Lebigre *et al.* 2008).

Juvenile male Black Grouse are rarely observed settling on leks further than 2 km from their natal areas (Caizergues & Ellison 2002, Warren &

Baines 2002). An observational study in Finland has shown that juvenile male Black Grouse sometimes visit leks other than their origin lek before settling, and can also permanently move to another lek (Alatalo *et al.* 1992). Similar lek exploratory behaviour of juvenile males has also been detected in Capercaillie (Wegge & Larsen 1987, Storch 1997, Gjerde *et al.* 2000), Sage-Grouse (Emmons & Braun 1984), and Ruff (*Philomachus pugnax*) (Widemo 1997). It has been suggested that young males are recruited to their father's lek in order to increase the lek's size, which would improve their indirect fitness despite their low chance of mating success (Kokko & Lindström 1996).

The aim of this study is to quantify lek site fidelity of male Black Grouse among neighbouring leks using data from 230 marked full-grown individuals and 76 chicks in two areas in Sweden. The overall question is whether male Black Grouse at a lek site can be considered as a separate group, or if there is a significant exchange of males between lek sites. We predict that male chicks, marked before fledging, should be recruited to the lek closest to the capture site. Adult males should not change lek sites and should remain close to their lek. We expect to see a maximum number of males displaying during the peak mating week.

2. Material and methods

2.1. Study area

We studied male Black Grouse in two areas in the boreal forest of central Sweden, specifically Boda (Site 1) between 1984 and 1987, and Länstersjön (Site 2) between 1990 and 1992. These sites were 200 km apart. Site 1 was an area of 32 km² located in Gävleborg County (approx. 61° N, 15° E) while Site 2 was an area of 19 km² located in Västernorrland County (approx. 62° N, 14° E). Both areas consisted of intensively managed Pine (*Pinus sylvestris* and *P. contorta*), and Norway Spruce (*Picea abies*) forests. Site 2 had substantially younger forest stands than Site 1.

At Site 1, five Black Grouse leks (A–E) were located in spring 1984 (Fig. 1). The average distance \pm SD between neighbouring leks was 2.40 \pm 0.80 km. One of those leks, lek-D, was on a frozen lake. A new lek (lek-F) was formed in spring 1985.

By spring 1987, lek-E showed no activity, most likely due to the increasing canopy closure of the Pine plantation on the lek site. Males that were displaying on lek-D were moving to lek-E, the nearest lek, whenever the lake ice melted. Every late winter-spring during the four-year study period, we were actively searching for new leks within and nearby the study site by listening for calling males and searching for display tracks on the snow. We did not find any other lek within 2.50 km radius outside these six leks. However, we observed one solitary displaying male. At Site 2, we studied two leks, both of which were located in late winter of 1990. These leks were 1.10 km apart, and no other leks were located within a 2.50 km radius during the study period.

2.2. Data

We collected data on movements of male Black Grouse using three methods: (1) capture-mark-recapture, (2) radio-telemetry, and (3) lek counts.

(1) Capture-mark-recapture These data were grouped in three categories:

(A) Males captured on leks. We captured 208 fullgrown (juvenile and adult) males in March-May over the study period on leks at both Site 1 and Site 2 using drop-traps covered with soft net. Seventy-four percent of these individuals (103 juveniles and 50 adults) were captured at Site 1, while the remaining 28% (27 juveniles and 28 adults) were caught at Site 2 (Table 1). A total of 55 males from Site 1 were captured on lek-A, the largest lek (Fig. 1). We captured the individuals by randomly scattering 10–15 numbers of drop-traps in a compact plastic net of circa 20 cm high fence that we installed around each lek. We made sure the traps were the only openings in the fence. These traps were designed to be triggered by a nylon string when the birds walked under it (Willebrand 1988, Willebrand 1992). Males were caught leaving or entering the leks by foot through these trap-gates. We set the traps and the fences each day before midnight and collected them after the display was over in the morning. The fence was placed well outside the lek to reduce disturbance. One to two persons stayed in hides adjacent to each lek until the next morning so that any trapped birds were tagged or checked and released as soon as possible.

(B) Males captured in snow-burrows. We captured 22 full-grown males (16 juveniles and 6 adults) in snow-burrows during winter outside the leks at Site 1. Captures in the snow-burrows were aided by locating radio-collared males that were previously captured on a lek. We used a snowmobile to approach the located snow-burrows, and placed a net (175×175 cm; a 7 cm mesh) over the snow-burrow. Males captured in snow-burrows were assigned to the same lek as the radio-located males from a known lek. The males that were not accompanied by known males were assigned to the lek closet to the capture site.

All captured males in categories A and B (n = 230; 66% juveniles) were tagged with aluminium leg rings. The captured individuals were aged according to the form and pigmentation of their primary feathers (Helminen 1963). We defined males ≤ 18 months (until end of December of their second year) of age as juveniles and > 18 months as adults. We performed the captures every year during the study period with the recaptures occurring when we carried out these captures.

(C) Chicks captured before the brood break up. At Site 1, 76 chicks of < 21 days old, of both sexes, were captured and wing-tagged between the 2nd-3rd weeks of June in 1984–85. The chicks were too young to determine sex or to fit leg rings.

(2) Radio-telemetry

Among the captured and ringed full-grown males of Site 1, we fitted 113 males with 15–17 gram radio collars from Biotrack, UK with a minimum battery lifetime of 10 months. Out of the 113 radio-collared males, we obtained ≥ 20 positions for 54 individuals (33 juveniles and 21 adults) and used that data to evaluate movements and home ranges. Of these 33 juveniles, seven were captured in January–February in snow-burrows. We did not have any radio-collared juveniles that were tagged be-

fore brood break up. A subset of 15 males (7 juveniles and 8 adults) was used to estimate short-term (intensive tracking) home ranges by relocating them at least three times a day for 7–11 days. We managed to change the collar of nine males \geq two times during the recaptures. Consequently, four males were tracked for four subsequent years, five for three years, 26 individuals for two years, and the rest of the 19 individuals for \leq one year. We recorded a position by triangulation every other week throughout a year. The coordinates of the positions were extracted to the closest 100 m. All radio tracking occurred during daylight hours, 06:00-18:15.

(3) Lek counts

The number of males on leks at Site 1 were systematically counted from a well-camouflaged hiding spot in late winter-spring (February until May), and in autumn, lekking activities were recorded from 16th September to 1st October. During the late winter-spring display period, we further distinguished between premating (1985: 1/2–6/5; 1986: 1/2-1/5; 1987: 1/2-28/4 day/month) and mating (1985: 7/5-20/5; 1986: 2/5-20/5; 1987: 29/4-20/5 day/month) periods. Here, the mating period was the time when females are observed mating on the leks. Throughout the study, we observed each leks 4-12 days per month during the winter-spring pre-mating period, and every day during the mating period for three years. Non-lekking periods were defined as 1st June–15th September, and 1st November-31st January.

2.3. Analysis

We calculated the shortest distance of all radio locations to all lek sites. For each individual, we used the proportion of spring relocations when closest to its capture lek as a measure of site fidelity. We considered that an individual had changed lek when it was recaptured in spring at a lek other than the initial capture lek and/or if it showed weak site tenacity *i.e.*, when $\geq 50\%$ of the spring relocations were nearer to another lek other than that of its first capture. Thus, both mark-recapture and radio tracking data were used to record how many leks an individual visited.

Table 1. Mark-recapture histories of male Black Grouse in successive springs after initial capture, Sweden,
1984–1992. The birds' age (juvenile & adult) are shown in the brackets.
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Location	Initial capture	1 st spring	2 nd spring	3 rd spring
Site 1	175 (117 & 58)	43 (17 & 26)	7 (2 & 5)	3 (1 & 2)
Site 2	55 (27 & 28)	16 (9 & 7)	1 (1 & –)	-

The maximum number of males observed (discrete, response) on each lek was used to test if more males were present during the mating period (categorical) than *premating period* (categorical). The difference between the two periods was tested in a pairwise t-test. We fitted a random intercept generalized linear mixed model with identity link normal distribution error to determine the effect of age (adult and juvenile; independent variable) and period (premating, mating, autumn lekking, and non-lekking; independent variable) on average distance (continuous, dependent variable) of each individual's relocations to its capture lek. We treated the individuals as a random effect (random intercept), and the *period* and *age* as fixed effects. We fitted all the models with Maximum Likelihood (ML) for model selections and then refitted the highest ranked model with Restricted Maximum Likelihood (REML). All models were compared using the corrected Akaike Information Criteria (AICc) (Akaike 1973, Burnham & Anderson 2002), and we selected the best model using the rule of a minimum difference in \triangle AICc of two.

Short-term, seasonal, and annual home ranges were calculated using kernel estimates with optimum bandwidth (Worton 1989, Seaman & Powell 1996, Kie et al. 2010), excluding the 5% most peripheral positions. Individuals used to calculate short-term home ranges had a median of 32 relocations (range = 21–47 relocations) obtained as explained above. For the seasonal home ranges, we included individuals that had at least 20 relocations (median = 25 relocations, range = 20-54 relocations) in a season, whereas for annual home ranges we included individuals with a minimum of 30 relocations during a year (median = 47 relocations, range = 30-85 relocations) (Seaman *et al.* 1999). We reported both area and median overlap (%) of the individuals' home ranges. We treated lek-D and lek-E as one (E/D) for annual home range overlap analysis due to the individuals' displacement as stated above. We evaluated the overlap of short-term home ranges of males of lek-A only since most of the intensively tracked individuals belonged to this lek (n = 8).

We carried out all analysis using R 3.2.0 (R Core Team 2015) and we used ArcGIS (ESRI 2010) to produce Fig. 1. For all three home range analyses, we used package adehabitatHR (Calenge 2006) with dependent data classes provided by package sp (Bivand *et al.* 2008). We used the package lme4 (Bates *et al.* 2014) for the mixed modelling. We used package AICcmodavg to get AICc estimate (Mazerolle 2016). We used 0.05 *P*-value for all statistical tests and interpretation, and presented the 95% confidence interval where applicable.

3. Results

3.1. Inter-lek movement

Seven males of 76 ringed chicks were recaptured the following spring on the lek closest to their natal area. Twenty-six percent of 230 full-grown males (33 juveniles and 26 adults) were recaptured at least once in the subsequent springs (Table 1). Nine of these males (7 juveniles and 2 adults) were recaptured on a lek other than where they were first caught. The rest were recaptured on the same lek where they were initially captured. All but one of those males that changed leks were originally captured on a lek in spring, the other being a juvenile male captured in a snow-burrow in January. Two juveniles moved from lek-A to lek-B (2.6 km), and one juvenile from lek-C to lek-A (6.3 km). From these observations, the inter-lek movement probability of males was 15% (95% confidence interval = 6-25%). More juveniles than adults changed lek but the difference was not statistically significant (prop.test: $\chi^2 = 1.14$, P =0.29).

Radio-locations from three of the seven recap-

Table 2. Annual and seasonal 95% kernel home range estimates of radio-collared Black Grouse males from Site 1 in Sweden, 1984–1987. The extensive estimates refer to the biweekly relocations while the intensive estimates to at least 3 daily relocations for 7–11 consecutive days. Results are presented as median (*minimum—maximum*; n) in km².

	Extensive	Extensive	Intensive	Intensive	
Season	Adult	Juvenile	Adult	Juvenile	
Spring Summer	2.4 (1.8–10.0; 12) 1.4 (1.2–2.6; 9)	6.1 (4.6–7.5; 2) 1.6 (1.0–4.0; 6)	3.4 (2.8–3.9; 2) 2.1 (0.5–2.5; 4)	8.1 (5.4–10.9; 2) 0.5 (0.4–2.0; 3)	
Fall Winter Annual	1.9 (0.9–8.3; 12) 4.4 (3.2–5.0; 5) 3.5 (1.5–9.2; 25)	2.3 (1.3–8.3; 5) - 4.9 (2.3–12.0; 24)	1.4 (0.5–6.2; 6) 2.1 (1.9–5.3; 3) –	0.8 (0.6–1.1; 3) – –	

tured juveniles that moved to a new lek site revealed that they were ≤ 100 m of the new lek's centre during the following spring (Fig. 1b). Combining both radio tracking and recapture data, one of the juveniles changed leks twice in the same spring. It was one of the juvenile males that were captured in a snow-burrow. This individual travelled 6.30 km to a second lek, after visiting another lek in between. Of the other six juveniles that changed lek, four moved 2.50 km, one moved 1.10 km, and the other one moved 1.50 km to the new lek. The two adults that moved to a new lek changed to the nearest lek (1.10 and 1.50 km, respectively).

Additional information on the inter-lek movement was also obtained from those males that were radio-collared but never recaptured. Three juveniles of the 54 radio tracked males (6%) had \geq 50% of their spring relocations closer to a neighbouring lek than to their initial capture lek (Fig. 1b). All of these males moved from lek-C to lek-D (1.5 km). These juveniles occasionally revisited their capture lek, lek-C. Four males, including one of these males, visited at least two leks other than their capture lek.

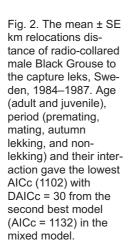
3.2. Home range and lek fidelity

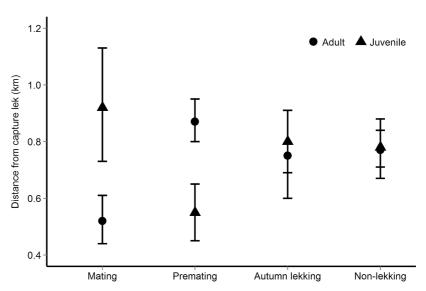
Home ranges of adults and juveniles were, to a large extent, similar in size, except during spring when the juveniles' home ranges were two times larger than the adults' both in the extensive and intensive tracking (Table 2). Note that the home ranges from the intensive tracking were not substantially smaller than the seasonal home ranges

that obtained during a three month period. Small sample size made it difficult to test for seasonal effect, but annual home ranges did not statistically differ between adults and juveniles ($t_{(41)} = -1.86$, P = 0.07, pairwise t-test; Table 2).

Males stayed close to their leks all year round, and annual home ranges of individuals from the same lek overlapped to a large extent (Fig. 1a). The median overlap among the home ranges of males from lek-A, B, C, and D/E was 71%, 64%, 71%, and 59%, respectively. Annual home ranges of two of the three radio-tracked emigrated juveniles showed a limited overlap with males of their first capture lek (median < 1%), but substantial overlap with males of their new lek site (median = 27%; 67%). The overlap of home ranges between males from different leks was small; the highest overlap was between males at lek-C and lek-D/E (median = 27%). For all the other combinations of lek sites, the median home range overlap was less than one percent. Short-term summer, autumn and winter home ranges of eight males at lek-A all overlapped and the median overlap was 45%.

Age (adult and juvenile), period (premating, mating, non-lekking, and autumn lekking), and their interaction, were important in explaining the individuals' relocation distance to the capture leks (Fig. 2). This full mixed model gave the lowest AICc (1102), with Δ AICc = 30 from the next best model (AICc = 1132), which was an additive of period and age. The model with age only had the highest (AICc = 1170). While the adults were closer to the leks during mating period, the juveniles were closer to the lek during premating. The two age groups had comparable distances from their leks during the autumn lekking and non-





lekking periods. Note that the juveniles in the autumn lekking refer to 1.5 year old males. Furthermore, counts of males on the leks showed that more males were observed on the leks during the early lekking period compared to when females arrived at the leks to mate in spring (mean difference = 4, $t_{(15)} = 3.06$, P = 0.008, pairwise t-test).

The maximum relocation distance from the centre of the capture lek was 5.60 km (March) for an adult and 6.80 km (June) for a juvenile. A juvenile captured in a snow-burrow and fitted with a radio-collar was never recorded attending a lek. It was observed displaying alone in a tree-top after dispersing about 6.5 km from the point of capture.

4. Discussion

This is the only study, to our knowledge, that has produced data on male Black Grouse movement dynamics in relation to neighbouring lek sites, across consecutive years. We have shown that males displaying at a lek site stay close to their lek throughout the year, and have substantial overlap with each other's home ranges. The overlap of males from neighbouring lek sites was small, and only a few males changed leks. All males tagged as chicks and recaptured the following spring were recaptured at the lek closest to their natal area, a result that indicates that most males are recruited locally. Few chicks survive until next spring as mor-

tality is high, *i.e.*, 70–80% (Willebrand 1992, Bowker *et al.* 2007, Ludwig *et al.* 2010). Assuming an even sex ratio of tagged chicks and a 30% survival, our seven recaptures correspond to more than 60% of the surviving male chicks.

High site tenacity of male Black Grouse has been reported in France (Caizergues & Ellison 2002), UK (Baines 1996, Warren & Baines 2002), and Norway (Gregersen & Gregersen 2014). Black Grouse males within a lek are somewhat more closely related than males among leks (Lebigre et al. 2008) and clusters of related males have been found on Capercaillie leks in Russia (Segelbacher et al. 2007), and on Lesser Prairie-Chicken (Tympanuchus pallidicinctus) leks in New Mexico, USA (Bouzat & Johnson 2004). This has also been observed in other lekking bird species such as White-Bearded Manakin (Manacus manacus) (Shorey et al. 2000), and Peacock (Pavo cristatus) (Petrie et al. 1999). Likewise, juvenile Red Grouse (Lagopus lagopus scotica) males are tolerated by their relatives when settling at a territory (Watson et al. 1994, MacColl et al. 2000).

Our results showed an unexpected, significant decline, rather than an increase, in the number of males observed on the leks from late winter-spring to the period of mating in early May. The reduction occurred at a time when juvenile males began to spend more time away from the lek centres, which resulted in larger home ranges. It is known that

yearling Black Grouse males avoid active lekking and hostility by staying on the edge of the lek (Koivisto 1965, Alatalo et al. 1996). High lek attendance and active lekking would enhance mating success (Alatalo et al. 1991, Rintamäki et al. 1995, Höglund et al. 1997). However, juvenile Black Grouse males have a minor chance of copulation even if they have established a territory on a lek (Kervinen et al. 2012). We propose that juvenile males have a better chance to mate by searching for females in the surroundings of the leks. We have observed a single displaying male with three females, and mating with at least one of them. It is also documented that, compared to adults, a lower percentage of juvenile Sage-Grouse males attended leks when the number of visiting females were the highest (Emmons & Braun 1984, Walsh et al. 2004), and that none of the juveniles affiliated with a lek were detected to mate (Bird et al. 2013). Likewise, Capercaillie (Wegge & Larsen 1987), and Little Bustard (Tetrax tetrax) (Ponjoan et al. 2012) yearlings and sub-adults have wider home ranges than adults during mating period.

The lek activity both in autumn and in spring occurs when juvenile females disperse, with limited dispersal movements in the intervening winter period (Willebrand 1988, Caizergues & Ellison 2002, Warren & Baines 2002). In Willow Ptarmigan (*Lagopus lagopus*), a large proportion of female recruits have their natal area more than 10 km away from where they settle to breed (Hörnell-Willebrand *et al.* 2014). We expect a similar pattern in Black Grouse (Warren & Baines 2002, Lebigre *et al.* 2008). At Site 1, four radio-collared juvenile Black Grouse females that survived from autumn to late spring dispersed 5.10–8.00 km from their natal area (Willebrand 1988), a distance that made them pass one-two leks.

One important function of the lek mating system is to provide cues for females in selection of males (Höglund & Alatalo 1995), but we suggest that leks also function to attract females that go through natal dispersal in autumn and spring. High site fidelity of males makes it possible for dispersing females to use lek size and activity as a cue of the area's quality for chick production and survival. Although juvenile males have little success in obtaining a central territory in their first spring, they could increase their indirect fitness through kin selection, by helping their adult relatives to at-

tract females by contributing to a high activity on their "natal" lek (Kokko & Lindström 1996). Attracting dispersing females would also increase the chance for juveniles to mate with females outside the lek. It is, therefore, advantageous for juvenile males to remain in the group of lekking males because females that have made a breeding attempt will return to breed the next year (Willebrand 1988, Marjakangas *et al.* 1997). Furthermore, an annual mortality of about 50% (Willebrand 1988, Bowker *et al.* 2007) will create several opportunities for juvenile male to fill up in vacant territories on the lek (Kokko *et al.* 1998).

5. Conclusions

Our findings suggest that the Black Grouse males at a lek consist of a well-defined local male population, and have a limited interaction with males from other leks. Displaying Black Grouse males can be audible for 2–3 km (personal observation) and males at one lek are probably aware of one or more neighbouring leks. Males appear to be recruited locally, and there is a high likelihood that they remain on the same lek until the following year. Adult males, in particular, remain close to their lek all year round. This is different from other lekking grouse males such as Sage Grouse (Bradbury et al. 1989, Leonard et al. 2000) and Capercaillie (Rolstad et al. 1988, Hjeljord et al. 2000) that stay away from lek sites during the non-breeding period, even though they too are faithful to a lek site in spring. For management purposes, counting Black Grouse males on leks in spring during the premating period instead of the mating week may give more reliable abundance estimates.

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Orrtuppars spelplats bestämmer deras rörelsemönster

Orrtuppar antas komma tillbaka till samma spelplats år efter år, medan juvenila tuppar antas etablera sig på den spelplats som ligger närmast det område där de kläcktes. Här presenterar vi resultat från en undersökning av orrtuppars ortstrohet till en och samma spelplats genom att analysera data från fångst/återfångst, orrtuppar märkta med sändare och direkta spelplatsobservationer under perioden 1984 till 1992. Vi samlade data från två områden i centrala Sverige med vardera sex och två spelplatser. Totalt fångades och märktes 306 orrar (230 vuxna orrtuppar och 76 kycklingar).

Alla vingmärkta kycklingar (n=7) återfångades på den spelplats som var närmast till märkningsplatsen. 26 % (n=59) av de vuxna tupparna återfångades minst en gång under efterföljande år. Färre tuppar observerades på spelplatser under de dagar när hönor kom för att para sig än tidigare under våren $(t_{(15)}=3.06, P=0.008)$. Under den tidiga perioden var juvenila tuppar närmare spelplatsen (95% C.I.=0.45–0.65 km) jämfört med perioden för parning (95% C.I.=0.73–1.13 km). I fråga om adulta tuppar var förhållandet det motsatta: de var närmare spelplatsen under dagarna för parning (95% C.I.=0.44–0.61 km) än under den tidigare perioden (95% C.I.=0.80–0.95 km).

Vi fann att endast 15 % (n = 9) av tupparna i den här studien bytte spelplats. Resultaten visar att orrtuppar på en spelplats utgör en väl definierad social grupp med begränsat utbyte med andra spelplatsgrupper och att rekryteringen av nya tuppar i huvudsak sker från den närmaste omgivningen.

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