

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

Degitu Endale Borecha\*, Tomas Willebrand & Olafur K. Nielsen

*D. E. Borecha, Department of Forestry and Wildlife Management, Faculty of Applied Ecology and Agricultural Sciences, Campus Evenstad, Inland Norway University of Applied Sciences, N-2480, Koppang, Norway. Corresponding author's e-mail: degitu.borecha@inn.no*

*T. Willebrand, Department of Forestry and Wildlife Management, Faculty of Applied Ecology and Agricultural Sciences, Campus Evenstad, Inland Norway University of Applied Sciences, N-2480, Koppang, Norway*

*O. K. Nielsen, The Icelandic Institute of Natural History, P.O. Box 125, 212 Garðabær, Reykjavík, Iceland*

*Received 13 June 2016, accepted 10 March 2017*

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 pre-mating period ( $t_{(15)} = 3.06, P = 0.008$ ). Juvenile males were closer to the lek in the pre-mating 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 pre-mating 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.



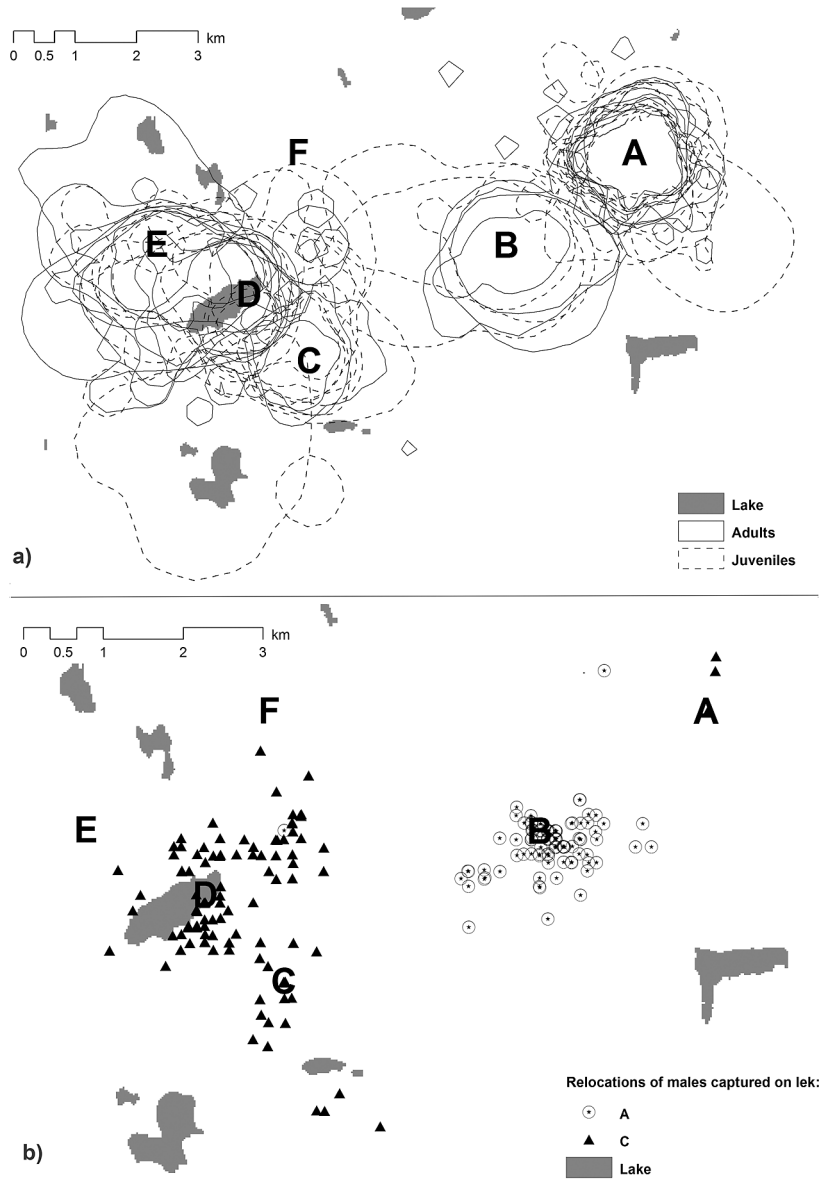
## 1. Introduction

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  $\geq 50\%$  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 radio-tracked) 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 & Ponskhe 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 Sharp-tailed 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 km<sup>2</sup> located in Gävleborg County (approx. 61° N, 15° E) while Site 2 was an area of 19 km<sup>2</sup> 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 full-grown (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 closest 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  $\leq 18$  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 2<sup>nd</sup>–3<sup>rd</sup> 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  $\geq 20$  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  $\geq 2$  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  $\leq 1$  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 16<sup>th</sup> September to 1<sup>st</sup> 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 1<sup>st</sup> June–15<sup>th</sup> September, and 1<sup>st</sup> November–31<sup>st</sup> 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.

Location	Initial capture	1 <sup>st</sup> spring	2 <sup>nd</sup> spring	3 <sup>rd</sup> 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 *pre-mating 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* (*pre-mating*, *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  $\Delta\text{AICc}$  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 over-

lap 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 km<sup>2</sup>.

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

tered juveniles that moved to a new lek site revealed that they were  $\leq 100$  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 (pre-mating, 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  $\Delta AICc = 30$  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 pre-mating. The two age groups had comparable distances from their leks during the autumn lekking and non-

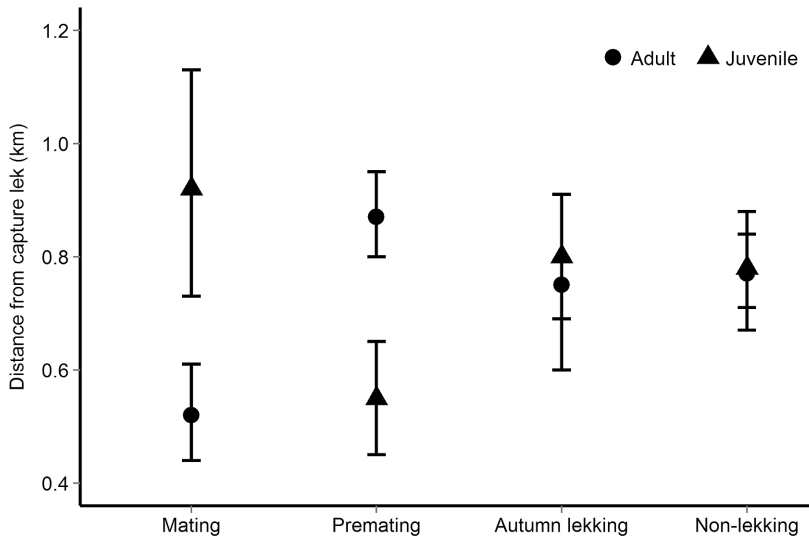


Fig. 2. The mean  $\pm$  SE km relocations distance of radio-collared male Black Grouse to the capture leks, Sweden, 1984–1987. Age (adult and juvenile), period (pre-mating, mating, autumn lekking, and non-lekking) and their interaction gave the lowest AICc (1102) with DAICc = 30 from the second best model (AICc = 1132) in the mixed model.

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.

*Acknowledgements.* We would like to extend our genuine gratitude for both The Swedish Environmental Protection Agency and Svenska Jägareförbundet for funding our research. We also owe a great deal to both Gert Olsson and Gert Mattsson for their gracious help during the data collection.

## Orrtuppars spelplats bestämmer deras rörelsemönster

Orrtuppar antas komma tillbaka till samma spelplats år efter år, medan juvenila tuppar antas eta-



blera sig på den spelplats som ligger närmast det område där de kläcktes. Här presenterar vi resultat från en undersökning av orrtupparns 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.

## References

- Akaike, H. 1973: Information theory as an extension of the maximum likelihood principle. — In second international symposium on information theory (ed. Petrov, B. N. & Csaki, F.): 267–281. Akademiai Kiado, Budapest.
- Alatalo, R. V., Hoglund, J. & Lundberg, A. 1991: Lekking in the Black Grouse: A test of male viability. — *Nature* 352: 155–156.
- Alatalo, R. V., Hoglund, J., Lundberg, A., Rintamäki, P. T. & Silverin, B. 1996: Testosterone and male mating success on the Black Grouse leks. — *Proceedings of the Royal Society B-Biological Sciences* 263: 1697–1702.
- Alatalo, R. V., Hoglund, J., Lundberg, A. & Sutherland, W. J. 1992: Evolution of Black Grouse leks: female preferences benefit males in larger leks. — *Behavioral Ecology* 3: 53–59.
- Baines, D. 1996: Seasonal variation in lek attendance and lekking behaviour by male Black Grouse (*Tetrao tetrix*). — *Ibis* 138: 177–180.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014: lme4: Linear mixed-effects models using Eigen and S4. — R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>.
- Bird, K. L., Aldridge, C. L., Carpenter, J. E., Paszkowski, C. A., Boyce, M. S. & Coltman, D. W. 2013: The secret sex lives of Sage-Grouse: multiple paternity and intraspecific nest parasitism revealed through genetic analysis. — *Behavioral Ecology* 24: 29–38.
- Bivand, R. S., Pebesma, E. J. & Gomez-Rubio, V. 2008: Applied spatial data analysis with R. — Springer, NY.
- Bouzat, J. L. & Johnson, K. 2004: Genetic structure among closely spaced leks in a peripheral population of Lesser Prairie-Chickens. — *Molecular Ecology* 13: 499–505.
- Bowker, G., Bowker, C. & Baines, D. 2007: Survival rates and causes of mortality in Black Grouse (*Tetrao tetrix*) at Lake Vyrnwy, North Wales, UK. — *Wildlife Biology* 13: 231–237.
- Bradbury, J. W. & Gibson, R. M. 1983: Leks and mate choice. — In *Mate Choice* (ed. Bateson, P): 109–138. Cambridge University Press, Cambridge.
- Bradbury, J. W., Vehrencamp, S. L. & Gibson, R. M. 1989: Dispersion of displaying male Sage Grouse: 1. Patterns of temporal variation. — *Behavioral Ecology and Sociobiology* 24: 1–14.
- Burnham, K. P., & Anderson, D. R. 2002: Model selection and inference: A practical information theoretic approach. 2<sup>nd</sup> edition. — Springer, New York.
- Caizergues, A. & Ellison, L. N. 2002: Natal dispersal and its consequences in Black Grouse (*Tetrao tetrix*). — *Ibis* 144: 478–487.
- Calenge, C. 2006: The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. — *Ecological Modelling* 197: 516–519.
- Drummer, T. D., Corace, R. G. & Sjogren, S. J. 2011: Sharp-Tailed Grouse lek attendance and fidelity in Upper Michigan. — *Journal of Wildlife Management* 75: 311–318.
- Emmons, S. R. & Braun, C. E. 1984: Lek attendance of male Sage Grouse. — *Journal of Wildlife Management* 48: 1023–1028.
- ESRI 2010: ArcGIS Desktop Version 10. — Environmental Systems Research Institute.
- Gibson, D., Blomberg, E. J., Atamian, M. T. & Sedinger, J. S. 2014: Lek fidelity and movement among leks by male Greater Sage-Grouse (*Centrocercus urophasianus*): A capture–mark–recapture approach. — *Ibis* 156: 729–740.
- Gjerde, I., Wegge, P. & Rolstad, J. 2000: Lost hotspots and passive female preference: the dynamic process of lek formation in Capercaillie (*Tetrao urogallus*). — *Wildlife Biology* 6: 291–298.
- Gregersen, H. & Gregersen, F. 2014: Wildlife cameras effectively survey Black Grouse (*Lyrurus tetrix*) leks. — *Ornis Norvegica* 37: 1–6.

- Helminen, M. 1963: Composition of the Finnish population of Capercaillie (*Tetrao urogallus*) and Black Grouse (*Lyrurus tetrix*) in the autumns of 1952–1961 as revealed by a study of wings. — *Papers on Game Research* 23: 1–124.
- Hjeljord, O., Wegge, P., Rolstad, J., Ivanova, M. & Beshkarev, A. B. 2000: Spring–summer movements of male Capercaillie (*Tetrao urogallus*): A test of the “landscape mosaic” hypothesis. — *Wildlife Biology* 6: 251–256.
- Hovi, M., Alatalo, R. V., Halonen, M. & Lundberg, A. 1997: Responses of male and female Black Grouse to male vocal display. — *Ethology* 103: 1032–1041.
- Höglund, J. & Alatalo, R. V. 1995: Leks. — Princeton University Press, Princeton.
- Höglund, J., Alatalo, R. V., Lundberg, A., Rintamäki, P. T. & Lindell, J. 1999: Microsatellite markers reveal the potential for kin selection on Black Grouse leks. — *Proceedings of the Royal Society of London Series B-Biological Sciences* 266: 813–816.
- Höglund, J., Johansson, T. & Pelabon, C. 1997: Behaviourally mediated sexual selection: Characteristics of successful male Black Grouse. — *Animal Behaviour* 54: 255–264.
- Hörnell-Willebrand, M., Willebrand, T. & Smith, A. A. 2014: Seasonal movements and dispersal patterns: Implications for recruitment and management of Willow Ptarmigan (*Lagopus lagopus*). — *Journal of Wildlife Management* 78: 194–201.
- Isvaran, K. & Ponskhe, A. 2013: How general is a female mating preference for clustered males in lekking species? A meta-analysis. — *Animal Behaviour* 86: 417–425.
- Kervinen, M., Alatalo, R. V., Lebigre, C., Siitari, H. & Soulsbury, C. D. 2012: Determinants of yearling male lekking effort and mating success in Black Grouse (*Tetrao tetrax*). — *Behavioral Ecology* 23: 1209–1217.
- Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J. M. & Moorcroft, P. R. 2010: The home-range concept: are traditional estimators still relevant with modern telemetry technology? — *Philosophical Transactions of the Royal Society B-Biological Sciences* 365: 2221–2231.
- Koivisto, I. 1965: Behavior of the Black Grouse (*Lyrurus tetrax* (L)) during the spring display. Volume 26. — *Finnish Game Research*, Helsinki.
- Kokko, H., Lindstrom, J., Alatalo, R. V. & Rintamäki, P. T. 1998: Queuing for territory positions in the lekking Black Grouse (*Tetrao tetrax*). — *Behavioral Ecology* 9: 376–383.
- Kokko, H. & Lindström, J. 1996: Kin selection and the evolution of leks: Whose success do young males maximize? — *Proceedings of the Royal Society of London Series B-Biological Sciences* 263: 919–923.
- Lebigre, C., Alatalo, R. V., Forss, H. E. & Siitari, H. 2008: Low levels of relatedness on Black Grouse leks despite male philopatry. — *Molecular Ecology* 17: 4512–4521.
- Leonard, K. M., Reese, K. P. & Connelly, J. W. 2000: Distribution, movements and habitats of Sage Grouse (*Centrocercus urophasianus*) on the Upper Snake River Plain of Idaho: changes from the 1950s to the 1990s. — *Wildlife Biology* 6: 265–270.
- Ludwig, G. X., Alatalo, R. V., Helle, P. & Siitari, H. 2010: Individual and environmental determinants of early brood survival in Black Grouse (*Tetrao tetrax*). — *Wildlife Biology* 16: 367–378.
- MacColl, A. D. C., Pieltney, S. B., Moss, R. & Lambin, X. 2000: Spatial arrangement of kin affects recruitment success in young male Red Grouse. — *Oikos* 90: 261–270.
- Marjakangas, A., Valkeajarvi, P. & Ijas, L. 1997: Female Black Grouse (*Tetrao tetrax*) shift nest site after nest loss. — *Journal Fur Ornithologie* 138: 111–116.
- Martin, K. & Hannon, S. J. 1987: Natal philopatry and recruitment of Willow Ptarmigan in north central and northwestern Canada. — *Oecologia* 71: 518–524.
- Mazerolle, M. J. 2016: AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). — R package version 2.1-0. <https://cran.r-project.org/package=AICcmodavg>.
- Petrie, M., Krupa, A. & Burke, T. 1999: Peacocks lek with relatives even in the absence of social and environmental cues. — *Nature* 401: 155–157.
- Ponjoan, A., Bota, G. & Manosa, S. 2012: Ranging behaviour of Little Bustard males (*Tetrax tetrax*) in the lekking grounds. — *Behavioural Processes* 91: 35–40.
- R Core Team 2015: R: A language and environment for statistical computing 3.2.0. — R Foundation for Statistical Computing Vienna, Austria. <http://www.R-project.org/>.
- Rintamäki, P. T., Alatalo, R. V., Höglund, J. & Lundberg, A. 1995: Mate sampling behavior of Black Grouse females (*Tetrao Tetrax*). — *Behavioral Ecology and Sociobiology* 37: 209–215.
- Rintamäki, P. T., Karvonen, E., Alatalo, R. V. & Lundberg, A. 1999: Why do Black Grouse males perform on lek sites outside the breeding season? — *Journal of Avian Biology* 30: 359–366.
- Rolstad, J., Wegge, P. & Larsen, B. B. 1988: Spacing and habitat use of Capercaillie during summer. — *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 66: 670–679.
- Rolstad, J., Wegge, P., Sivkov, A. V., Hjeljord, O. & Storaunet, K. O. 2009: Size and spacing of grouse leks: comparing Capercaillie (*Tetrao urogallus*) and Black Grouse (*Tetrao tetrax*) in two contrasting Eurasian boreal forest landscapes. — *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 87: 1032–1043.
- Schroeder, M. A. 1986: The fall phase of dispersal in juvenile Spruce Grouse. — *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 64: 16–20.
- Schroeder, M. A. & Robb, L. A. 2003: Fidelity of Greater Sage-Grouse (*Centrocercus urophasianus*) to breeding

- ding areas in a fragmented landscape. — *Wildlife Biology* 9: 291–299.
- Seaman, D. E., Millsbaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., & Gitzen, R. A. 1999: Effects of sample size on kernel home range estimates. — *Journal of Wildlife Management* 63:739–747.
- Seaman, D. E. & Powell, R. A. 1996: An evaluation of the accuracy of kernel density estimators for home range analysis. — *Ecology* 77: 2075–2085.
- Segelbacher, G., Wegge, P., Sivkov, A. V. & Hoglund, J. 2007: Kin groups in closely spaced Capercaillie leks. — *Journal of Ornithology* 148: 79–84.
- Shorey, L., Piertney, S., Stone, J. & Hoglund, J. 2000: Fine-scale genetic structuring on *Manacus manacus* leks. — *Nature* 408: 352–353.
- Small, R. J. & Rusch, D. H. 1989: The natal dispersal of Ruffed Grouse. — *Auk* 106: 72–79.
- Storch, I. 1997: Male territoriality, female range use, and spatial organisation of Capercaillie (*Tetrao urogallus*) leks. — *Wildlife Biology* 3: 149–161.
- Walsh, D. P., White, G. C., Remington, T. E. & Bowden, D. C. 2004: Evaluation of the lek-count index for Greater Sage-Grouse. — *Wildlife Society Bulletin* 32: 56–68.
- Warren, P. K. & Baines, D. 2002: Dispersal, survival and causes of mortality in Black Grouse (*Tetrao tetrix*) in northern England. — *Wildlife Biology* 8: 91–97.
- Watson, A., Moss, R., Parr, R., Mountford, M. D. & Rothery, P. 1994: Kin landownership, differential aggression between kin and non-kin, and population fluctuations in Red Grouse. — *Journal of Animal Ecology* 63: 39–50.
- Wegge, P. & Larsen, B. B. 1987: Spacing of adult and subadult male common Capercaillie during the breeding season. — *Auk* 104: 481–490.
- Widemo, F. 1997: The social implications of traditional use of lek sites in the Ruff (*Philomachus pugnax*). — *Behavioral Ecology* 8: 211–217.
- Willebrand, T. 1988: Demography and ecology of a Black Grouse (*Tetrao tetrix* L.) population. — Uppsala University Uppsala.
- Willebrand, T. 1992: Breeding and age in female Black Grouse (*Tetrao-Tetrix*). — *Ornis Scandinavica* 23: 29–32.
- Worton, B. J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. — *Ecology* 70: 164–168.