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Dispersal and migration of female Black Grouse *Tetrao tetrix* in eastern central Finland

Arto Marjakangas* & Satu Kiviniemi

Marjakangas, A., Department of Biology, P.O. Box 3000, FI-90014 University of Oulu, Finland. Present address: Savontie 1316, FI-84880 Ylivieska, Finland. arto.marjakangas@oulu.fi (Corresponding author)*
Kiviniemi, S., Saarijärven Keskuskoulu, Koulutie 4, FI-43100 Saarijärvi, Finland. satu.kiviniemi@saarijarvi.fi

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We studied the movement patterns of 209 female Black Grouse radio-marked during 1990–1993 in eastern central Finland. Females were captured for marking in late winter, and the transmitters had a life expectancy of 6–10 months. Adults tended to initiate spring movement to breeding range earlier than yearlings. The median net distance between the marking (winter) site and nest site was 2.6 km for adults and 9.2 km for yearlings, and the maximum distances recorded were 29.6 and 33.2 km, respectively. The spring dispersal directions of yearlings differed from a uniform distribution. Data from radio-tracking, recapturing and recoveries from the public revealed that females that moved less than the median distance in spring as yearlings tended to show fidelity to their first winter range. In contrast, those individuals that moved more than the median distance, mostly switched to using a new winter range. Females marked as adults tended to show fidelity to their winter range. The longest migratory movement recorded between breeding and winter range was 19 km. We conclude that female Black Grouse possess good dispersal abilities, and had no movement problems in our study area consisting of a managed forest landscape.

1. Introduction

Natal dispersal has been defined as the movement of a young animal from its birth site to the site of its first actual or potential reproduction (Greenwood 1980), while migration means round-trip travelling (Stenseth & Lidicker 1992), typically the seasonal movement between breeding site and winter site. Dispersal is a fundamental life-history trait among animals, and understanding dispersal and other movements is vital to advances in population and metapopulation biology, population genetics, conservation biology, wildlife management, and the study of fragmentation (Johnson & Gaines 1990, Stenseth & Lidicker 1992, Porter & Dooley 1993, Hanski & Simberloff 1997, Paradis *et al.* 1998). The human-induced fragmentation of natural habitats can affect animal populations by three major mechanisms, i.e. edge effects such as predation, and the degradation and isolation of remnant habitat patches (Cooper & Walters 2002). Edge effects and habitat degradation affect populations by altering fecundity and survival, while isolation may alter dispersal patterns (Cooper & Walters 2002).

Finnish populations of forest grouse (subfamily Tetraoninae) have shown cyclic dynamics with a periodicity of about 6 years and large-scale synchrony, and dispersal was considered an important factor in maintaining this synchrony (Lindström *et al*. 1996). However, the cyclicity seems to have disappeared since 1990s, and one reason for this might be habitat fragmentation due to modern forestry that might hinder dispersal (Anonymous 1999). The isolation of suitable habitat patches (because of fragmentation) may be a serious problem for resident grouse species with poor dispersal abilities (Swenson 1991). Indeed, there is experimental evidence that habitat fragmentation can hinder the movements both of resident and migrant forest birds (Bélisle *et al.* 2001, Cooper & Walters 2002). On the other hand, fragmentation might enhance dispersal due to more potential dispersers, although evidence for such effects are scarce. The dispersal distances of Nuthatches *Sitta europaea* tended to increase in a highly fragmented forest landscape (Matthysen *et al.* 1995).

Grouse are important game for hunters. Small *et al.* (1991) and Smith & Willebrand (1999) suggested that grouse numbers on heavily hunted areas are maintained by dispersal from adjacent areas with lower or no hunting mortality. Thus high hunting mortality could drastically decrease the density of grouse where dispersal is reduced by habitat fragmentation (Small *et al.* 1991).

In birds, juvenile females disperse typically longer distances than juvenile males (Greenwood 1980, Clarke *et al.* 1997). This pattern has also been observed in grouse (Dunn & Braun 1985, Schroeder 1985, 1986, Hines 1986, Willebrand 1988, Small & Rusch 1989, Giesen & Braun 1993, Caizergues & Ellison 2002, Warren & Baines 2002). In a given grouse population, net distances moved during natal dispersal vary considerably between individual juveniles, and birds can be classified as long- or short-distance dispersers, and sometimes also as non-dispersers (Schroeder 1985, Hines 1986, Beaudette & Keppie 1992). However, the distribution of distances is usually skewed to relatively short distances (Schroeder 1985, 1986, Hines 1986, Giesen & Braun 1993). In general, the magnitude of dispersal seems to be independent of population density (e.g. Hines 1986, Keppie & Towers 1992), and survival or reproductive success, or both, are mostly similar for individual grouse with differential dispersal or migration patterns (Herzog & Keppie 1980, Hines 1986, Beaudette & Keppie 1992, Small *et al.* 1993).

In Spruce Grouse *Dendragapus canadensis* (Herzog & Keppie 1980, Schroeder 1985) and Black Grouse *Tetrao tetrix* (Willebrand 1988, Caizergues & Ellison 2002, Warren & Baines 2002), natal dispersal is divided into an autumn phase, when a juvenile moves from its natal area to its first winter range, and a spring phase, when an individual moves to its first potential breeding range. In Spruce Grouse, subsequent migratory movements retrace the first spring dispersal movement (Herzog & Keppie 1980, Schroeder 1985).

While patterns of dispersal and migration among North American grouse are relatively well known (see literature cited above), data on Eurasian boreal forest grouse are scarce (Willebrand 1988, Rolstad & Wegge 1989, Swenson 1991). Our aim is here to present data on the timing, distances and directional orientation of dispersal and migratory movements among radio-marked female Black Grouse, in order to assess life-time movement patterns. Especially we test the hypothesis that the migratory movements of adults retrace their first spring dispersal movement made as yearlings (Herzog & Keppie 1980, Schroeder 1985).

2. Material and methods

2.1. Study area

The study was conducted during 1990–1994 in eastern central Finland (ca. 64°N, 27–28°E). Female Black Grouse were radio-marked in 1990–1993 at 2–4 sites, 5–10 km apart (Fig. 1). Each marking site was a supplemental winter feeding station installed on a lekking site on an open bog and supplied with oats for wild Black Grouse. The lekking sites and, consequently, the marking sites in our study were most likely within the natural winter range of each local flock. This is because adult males having territories at a given lek are highly sedentary throughout the year (Willebrand 1988), and they are social also during summer (Koskimies 1957). A local winter flock is probably formed when birds from adjacent areas join the

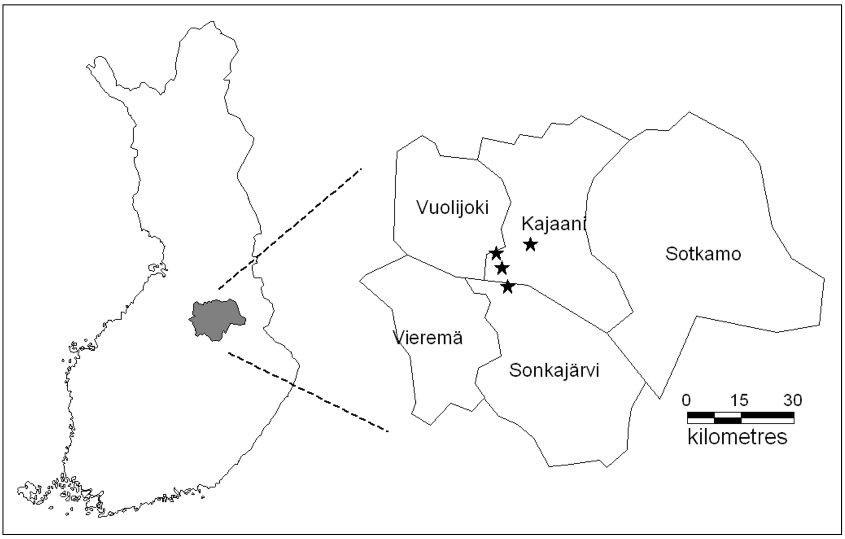

Fig. 1. Location of the study area and the sites (asterisks *) where female Black Grouse were radio-marked.

adult male assemblage in autumn (Koskimies 1957). The area where nests of radio-marked females were located, covered 1,000–1,500 km². The elevation of the study area ranges from 125 to 350 m above sea level, and the major habitat types were commercially managed coniferous forests, bogs and sapling stands. The major logging method was clear-cutting. Forested bogs had been mostly drained for forestry (Forest Statistics Information Service 1995).

2.2. Capture and radio tracking

Female Black Grouse were captured in traps baited with oats mostly during February to March. They were classified as yearlings (hatched the previous year) or adults (Helminen 1963). We marked females with a numbered aluminium leg band and a coloured plastic band using a given colour each year to be able to identify and recapture females marked during previous years. Females were fitted with a 17 g necklace radio-transmitter (1.6–2.2% of body weight) with a life expectancy of 6–10 months, and released immediately after marking.

Caizergues & Ellison (1998) found that in the French Alps the breeding success of female Black Grouse marked with necklace transmitters during or just before laying was lower than that of females marked several months before laying. In our study females were marked about two months before laying (Marjakangas & Törmälä 1997), and we believe this period was long enough for the birds to adjust with the transmitter. Studies addressing the possible impact of necklace transmitters on survival in gallinaceous birds have shown no effect (for a review, see Caizergues & Ellison 1998).

Female Black Grouse were located about once a week by flushing or by triangulation using portable receivers and yagi-antennas. The bearings for a triangulation were mostly taken within 30 min., hence we believe that possible bias in radio fixes caused by movements of birds was small. When consecutive locations indicated no movement, we approached birds until they either flushed or their remains were found. All locations were marked on maps of scale 1:20,000. Because we attempted to find all radio-marked females, missing birds were located from an aircraft, with a side-looking antenna under each wing, during late April to early June. First, the approximate locations of females were determined by flying a rectangular search pattern (Kenward 1987) over an area of 60 × 60 km. The parallel search transects were 7 (in 1990) or 10 km (1991–93) apart because transmitters with a known location were detected from the aircraft at a distance of 5 km or more. During the next flight each female was located more accurately by circling around its approximate location.

Nests were mostly located at the onset of incubation. During summer females were flushed twice to estimate brood size. During autumn and

Table 1. Dates of initiating spring movements in yearling and adult female Black Grouse during 1990–93.

	Yearlings			Adults		
Year	median	range	n	median	range	n
1990	14 April	8–25 April	21	12 April	19 March–26 April	18
1991	12 April	6–28 April	16	9 April	1–21 April	32
1992	26 April	7 April–9 May	23	25 April	26 March–3 May	12
1993	24 April	3–30 April	17	24 April	10 April–7 May	11
1990–93	22 April	3 April–9 May	77	12 April	19 March–7 May	73

early winter they were located at least twice a month, until the radio signals of all females were lost, in best case until the end of December. However, most transmitters were expected to expire during September to November. Marked females were recaptured during January 1993 and during January and March 1994 at the marking sites in order to collect transmitters. For a more detailed description of the study area and field methods, see Marjakangas & Törmälä (1997) and Marjakangas *et al.* (1997).

2.3. Analysis of data

The dates of initiating spring dispersal or migration were estimated for yearlings and adults, respectively, by calculating the median date between the last location of each bird at the marking site (winter range) and the first time when absent. The straight-line distances between the marking sites and nest sites for both yearlings and adults, and the directions of spring dispersal for yearlings were measured from maps. Straight-line measurements are commonly used in dispersal studies, and besides, the number of fixes per female was insufficient for assessing total distance travelled by each female. However, 31 females were killed by predators during laying or incubation period in May and early June before their nests were found. For these females, we measured the distance between the marking site and the kill site, because the kill sites of 12 females with a known nest were relatively close to their nests (median distance between kill site and nest = 298 m; A. Marjakangas, unpubl.). In addition, for ten females that survived over the breeding season no nest was found. We assume that they had laid eggs, but their nests had been robbed before they were located. In general, all female black grouse attempt to nest (Storaas & Wegge 1985, Willebrand 1992). For each of these females we calculated the mean location of all radio fixes and direct observations at flushing during nesting period to represent the location of the nest.

We used two-tailed Mann-Whitney U test or one-tailed Kruskal-Wallis test (both corrected for ties) to compare two or more independent data sets with continuous variables. Rao's spacing test (Batschelet 1981) was used to analyse whether the dispersal directions of yearlings were uniformly distributed, and two-tailed Fisher's exact test to compare categorial variables.

3. Results

3.1. Spring dispersal and migration

We radio-marked 258 female Black Grouse during 1990–1993. Of these, 29 females were killed by predators between 14 March and 30 April, before their spring movements were assessed. The radio signals of eight females could not be detected at all (probably because of tag failure), and 12 females were located several times on their winter ranges until their signals were lost during spring. Hence we were able to observe the spring movements of 209 females.

The median date of initiating spring dispersal or migration was estimated for 150 females (Table 1), while 59 females showed no distinct spring movement. The dates differed between years both for yearlings (Kruskal-Wallis test, $H = 41.24$, d.f. = 3, $P < 0.001$) and for adults ($H = 25.24$, d.f. = 3, $P < 0.001$). Adults tended to initiate spring movement earlier than yearlings (Mann-Whitney U test, z = –

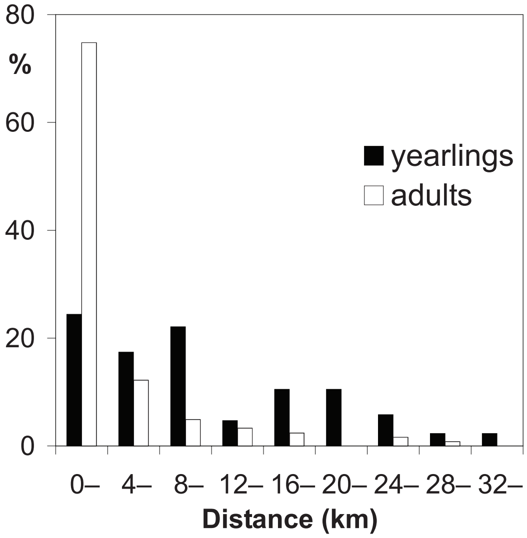

Fig. 2. Distribution of spring dispersal and migration distances of yearling (n = 86) and adult (n = 123) female Black Grouse, respectively, during 1990–93.

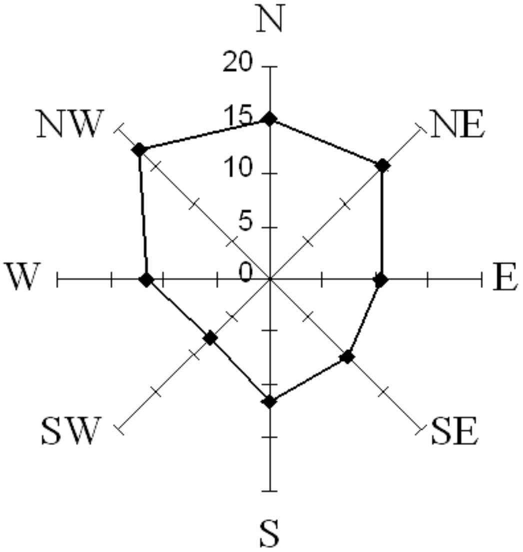

Fig. 3. Directional distribution (%) of spring dispersal in yearling female Black Grouse (n = 86) during 1990–93.

4.51, $p < 0.001$, years combined; Table 1). The difference between age classes was significant in 1990 ($z = –2.54$, $P < 0.02$) and 1991 ($z = –2.21$, $P < 0.05$) but not in 1992 or 1993 ($P > 0.05$ for both years).

Data on spring dispersal or migration distances were combined over years, because distances did not differ between years for yearlings (Kruskal-Wallis test, $H = 6.24$, d.f. = 3, $P > 0.1$) or for adults ($H = 1.09$, d.f. = 3, $P > 0.1$). However, the distances differed between marking sites for adults ($H = 8.63$, d.f. = 3, $P < 0.05$) but not for yearlings ($H = 4.45$, d.f. = 3, $P > 0.2$). The median distances for adults marked at the four sites were 2.7, 1.8, 2.4 and 2.8 km. The overall median straight-line distance between the marking site and nest site was 2.6 km for adult females (range 0.2–29.6 km), and 74.8% of adults moved 4 km or less (Fig. 2). For yearlings, the overall median dispersal distance was 9.2 km (0.7–33.2 km), and 24.4% of yearlings moved 4 km or less. The distances differed between age classes (Mann-Whitney U-test, $z = –7.16$, $P = 0.0001$).

Yearlings were classified as long- or short-distance dispersers according to whether they moved more or less than the median distance (9.2 km) in spring (see Hines 1986, Beaudette & Keppie 1992). The overall median date of initiating spring dispersal was 24 April both for short-distance ($n = 32$) and for long-distance dispersers ($n = 43$; Mann-Whitney U-test, $z = –1.37$, $P > 0.1$, years combined).

In spite of aerial searching efforts, the radio signals of 12 females were lost during late March through early May. The age ratio of the missing females (10 yearlings, 2 adults) matched the age ratio of females that moved more than 20 km (18 yearlings, 3 adults; Fisher's exact test, $p = 1.00$) during spring.

Data on the directions of spring dispersal in yearlings were pooled over years and marking sites, because the directions did not differ between years (Kruskal-Wallis test, $H = 3.58$, d.f. = 3, $P = 0.31$) or sites ($H = 4.40$, d.f. = 3, $P = 0.22$). The overall directional distribution (Fig. 3) differed from a uniform distribution (Rao's spacing test, $U = 148°$, $n = 86$, $P < 0.05$).

3.2. Subsequent migratory movements

The movements or fates of altogether 23 long-distance dispersers marked as yearlings were recorded after their first breeding season. Eighteen females were radio-tracked until October–December, and of these, 16 females stayed in their breeding ranges. In contrast, two females were probably returning to their first winter range, because one was shot by a hunter in September only 4.2 km apart from the site where she was marked, and the other was located during late October through early November in the midway between her nest site and marking site.

Five of the 23 long-distance dispersers marked as yearlings were either recaptured during January or March 1994, or their remains with the leg band were found by chance. Two of these had returned to their first winter range, while three females had stayed in their breeding ranges. In total, 19 out of 23 long-distance dispersers (82.6%) did not return to their first winter range. The spring dispersal distance was 9.9–10.8 km for three of the four females that returned or were probably returning, and 20.8 km for the one that was shot.

The movements of altogether nine short-distance dispersers marked as yearlings were recorded after their first breeding season. Five females were monitored until October–December, and four of these stayed at their breeding range (and close to their first winter range), while one female moved 8.5 km to another winter range. Furthermore, four of the nine females were recaptured one or two years later in January–March. Three of these were captured at the same capture site as where they were marked, while one was captured 5 km apart from her first capture site. In total, two of the nine short-distance dispersers (22.2%) appeared to have switched winter range.

Seventeen females marked as adults were recaptured at marking sites, 12 of them during next winter. Of the 17 females, 14 (82.4%) were recaptured at the same site as where they were marked, and three at a different site. One female was clearly a long-distance migrant; she was captured for marking in 1990 and 1993 at the same site, and moved 19 km in both years to breed in the same range. In the autumn of 1993 she was located on the breeding range on 12 October, but on the winter range on 26 October. Additionally, two adult females that moved 7.2 and 27.6 km in spring were located during October–November in the midway between the marking site and breeding range.

4. Discussion

4.1. Dispersal in the Black Grouse

We found that the dates of initiating spring movement differed between years and age classes. On average, yearlings moved much longer distances than adults, the longest distances recorded covering 30 km or more, and the directional distribution of spring dispersal differed from a uniform distribution. Whether a female showed fidelity to her first winter range after her first breeding season or not, tended to depend on the distance of her first spring dispersal.

Adult female Black Grouse moved much shorter distances than yearlings in spring in our study area. Unlike yearlings, adults do not have to search for a breeding range, because female Black Grouse show high fidelity to previous breeding site (Willebrand 1988, Ellison *et al.* 1989, Marjakangas *et al.* 1997). Nevertheless, adults tended to leave earlier than yearlings. This might be due to the fact that adults have experience in at least one breeding attempt. Female grouse feed on nutritious plant food during the prelaying period to produce viable eggs (Siivonen 1957). Willebrand (1992) suggested that adult female Black Grouse might be more efficient than yearlings in selecting nutritious spring food, since adults have better physical condition at egg-laying. Consequently, adult females lay larger eggs and clutches than yearlings (Willebrand 1992, Valkeajärvi & Ijäs 1994, Marjakangas & Törmälä 1997). Further, Bergerud & Gratson (1988) suggested that grouse females may assess potential nest sites and the abundance and distribution of nest predators on their breeding ranges during prelaying period. Adult females might be more apt than yearlings to this prospecting behaviour.

Temperatures were higher and snow melted 2–3 weeks earlier in 1990 and 1991 than in 1992 and 1993 in the study area (Marjakangas & Törmälä 1997), and females initiated spring movements earlier in 1990 and 1991. Thus the initiation of spring movements paralleled weather conditions in early spring. On average, females dispersed 2–4 weeks before the initiation of egg-laying (Marjakangas & Törmälä 1997). Since female Black Grouse mate only a few days before they start laying (Willebrand 1988), females that dispersed

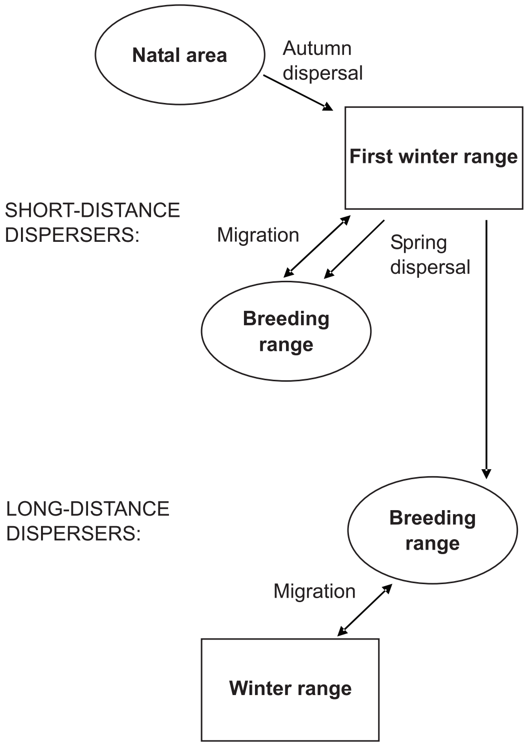

Fig. 4. A tentative model of lifetime movement patterns in female Black Grouse in the study area. For details, see text.

many kilometres probably mated at leks close to their breeding ranges rather than at their winter ranges.

Yearling female Black Grouse travelled maximally more than 30 km in spring. Because females that disappeared in spring were mostly yearlings, we believe that at least some of them had moved even longer distances, beyond our tracking system. Earlier observations on the dispersal distances of female Black Grouse are scarce. However, distances (max. 25–26 km) recorded for females wing-tagged as chicks in Finland and Sweden and recovered as juveniles or adults (Höglund 1957, Koskimies & Rajala 1959, Koivisto 1962, Vuolanto 1972) are in agreement with spring dispersal distances found here. Similarly, the mean natal dispersal distance of four female Black Grouse radio-marked as juveniles in Sweden was 6.2 km (Willebrand 1988). The mean spring and natal dispersal distances of female Black Grouse were 4.8 and 8.0 km, respectively, in the French Alps (Caizergues & Ellison 2002), and 5.8 and 9.3 km in northern England (Warren & Baines 2002). There are more observations on the dispersal distances of female Capercaillie *Tetrao urogallus* wing-tagged as chicks (Höglund 1957, Koskimies & Rajala 1959, Koivisto 1962, Vuolanto 1972), and they are strikingly similar to those found here for radio-marked female Black Grouse.

Our estimates of the spring dispersal distances of yearling Black Grouse were longer than spring or total natal dispersal distances reported earlier for radio-marked forest grouse in North America (e.g. Schroeder 1985, Hines 1986, Small & Rusch 1989, Whitcomb *et al.* 1996), but, interestingly, rather similar to those found for Sage Grouse *Centrocercus urophasianus*, a prairie species (Dunn & Braun 1985, 1986). Even though the habitat associations of Sage Grouse and boreal Black Grouse and Capercaillie are different (Johnsgard 1983), all these are lekking species, with neighbouring leks located a few to several kilometres apart (e.g. Koivisto 1965, Dunn & Braun 1985, 1986, Rolstad & Wegge 1987, Willebrand 1988). Hence, females' ability to disperse long distances is possibly related to mating system in these species. Our results support Willebrand's (1988) conclusion that yearling female Black Grouse may traverse several leks before they settle down to breed.

Our results on the directional orientation of dispersing yearling females suggest that yearlings tend to prefer (or avoid) certain directions. A possible explanation for this pattern is that the quality of breeding habitats varied between different parts of the study area. Further, the directions did not differ between the marking sites, suggesting that yearlings selected breeding habitats at a spatial scale as large as the whole study area, or even at a larger scale. However, testing these explanations would require a separate analysis with more detailed data.

The period of autumn migration in female Black Grouse obviously precedes winter flock formation and other behavioural changes characteristic of the species in autumn (Koskimies 1957). In Finland, more than 90% of individual Black Grouse were observed in flocks already in September (Koskimies 1957). Thus, most females radio-tracked in late autumn probably had completed their autumn migration before their transmitters expired.

4.2. Conclusions: A conceptual model of Black Grouse movements

Our data allow to reconstruct a tentative model of lifetime movement patterns in female Black Grouse in the study area (Fig. 4). We have no data on autumn dispersal distances between natal area and first winter range, but we believe that they cover many kilometres. The average autumn dispersal distance of juvenile females was 3 km in Sweden (Willebrand 1988), 6 km in the French Alps (Caizergues & Ellison 2002), and 10 km in northern England (Warren & Baines 2002), and in general the distances recorded here exceed those found in earlier studies. The spring dispersal distance, with the median distance as an approximate cut point, mostly determines whether a given female shows fidelity to her first winter range or not. Short-distance dispersers tend to return to their first winter range. Adult female Black Grouse show fidelity both to their breeding range (Willebrand 1988, Ellison *et al*. 1989, Marjakangas *et al.* 1997) and to their winter range (Willebrand 1988, Ellison *et al.* 1989, Caizergues & Ellison 2002, this study). Hence, the subsequent migratory movements of short-distance dispersers retrace their spring dispersal movements, as shown for Spruce Grouse (Herzog & Keppie 1980, Schroeder 1985). In contrast, long-distance dispersers tend to move their winter range. We expect on the basis of the distances recorded for adults in spring that their new winter ranges were mostly within 4 km of their breeding ranges. It is important to note in Fig. 4 that in many birds breeding and winter ranges may overlap at least partly, and hence they might be called residents.

We conclude that female Black Grouse possess good dispersal abilities, and had no movement problems in the study area with relatively fragmented managed forest landscapes. Thus the hypothesis that habitat fragmentation would disturb dispersal patterns and, consequently, would be at least partially responsible for the disappearance of large-scale population synchrony and cyclicity among grouse (Anonymous 1999) was not supported by our data. However, the proportion of total forestry land was relatively high in the study area, whereas that of non-forestry land, e.g. farmland and settlements, was low (Forest Statistics Information Service 1995). One might find different movement patterns for female Black Grouse in areas with higher proportion of non-forestry land. Furthermore, data from recent wildlife triangle censuses show that even though the density of Black Grouse was relatively low during 1990s and early 2000s, there were signs of a periodicity of 3–4 years, instead of the former 6-year periodicity (Helle & Wikman 2001).

Our results support Swenson's (1995) view that relatively long dispersal distances are expected in species adapted to early successional stages of forest, because they must be able to colonize new habitat patches that appear unpredictably for a relatively short time in the landscape. On the other hand, females showed various movement patterns, especially in terms of distance, within the same general area. This suggests that some unknown factors rather than e.g. the spatial arrangement of seasonal habitats (Rolstad & Wegge 1989) are more likely to cause differential movement patterns.

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Naarasteeren kevätdispersaali ja vuodenaikaisliikunnot

Naarasteerien liikkuvuutta tutkittiin Etelä-Kainuussa ja Pohjois-Savossa sijaitsevalla tutkimusalueella vuosina 1990–94. Yhteensä 258 naarasta pyydystettiin kevättalvisin 1990–93 talviruokintapaikoilla ja merkittiin kaulalähettimin, joiden odotettu toimintaikä oli 6–10 kk. Kaikkiaan 209 naarasteeren liikkuvuutta voitiin seurata sekä maasta että keväisin myös lentokoneesta käsin. Vuosina 1990 ja 1991, jolloin kevääntulo oli aikainen, naaraat aloittivat siirtymisen talvehtimispaikoilta pesimäpaikoille aiemmin kuin muina vuosina. Lisäksi aikuiset naaraat aloittivat siirtymisen aikaisemmin kuin nuoret eli edellisenä kesänä syntyneet naaraat. Yleensä siirtyminen pesimäpaikoille alkoi 2–4 viikkoa ennen muninnan alkua. Aikuisten naaraiden suoraviivainen mediaanimatka talvehtimispaikalta pesäpaikkaan oli 2.6 km (vaihteluväli 0.2–29.6 km), nuorten naaraiden puolestaan 9.2 km (0.7–33.2 km). Jotkin naaraat saattoivat siirtyä vielä kauemmaksi, sillä yhteys kaikkiaan 10 nuoren ja 2 aikuisen naaraan radiolähettimeen katkesi kevään aikana. Nuorten naaraiden dispersaalisuunnat poikkesivat tasaisesta jakaumasta, mikä viittaa siihen, että ne suosivat tai välttivät tiettyjä suuntia tutkimusalueella.

Naaraiden liikuntoja seurattiin pitkälle merkintävuoden syksyyn, jopa joulukuuhun saakka, ja aineistoa kartutettiin myös uudelleenpyyntien ja rengaslöytöjen avulla. Nuorina merkityt naaraat jaettiin kevätdispersaalimatkan perusteella lyhyen (< 9.2 km) ja pitkän matkan (> 9.2 km) siirtyjiin. Pitkän matkan siirtyjistä 82.6 % (n = 23) ei palannut ensimmäiselle talvehtimisalueelleen, kun taas lyhyen matkan siirtyjistä vain 22.2 % (n = 9) vaihtoi talvehtimisaluetta. Aikuisina merkityistä naaraista, jotka pyydystettiin uudelleen useimmiten seuraavana talvena (n = 17), 82.4 % pyydettiin samalta paikalta missä ne oli merkitty. Vuosina 1990 ja 1993 seurattu aikuinen naaras muutti keväisin ja syksyisin 19 kilometrin matkan talvehtimis- ja pesimäalueen välillä.

Vaikka tutkimusalue koostui pääasiassa melko pirstoutuneista talousmetsistä, naarasteerillä ei näyttänyt olevan liikkumisvaikeuksia. Tuloksemme tukevat Swensonin (1995) ajatusta, että metsän nuoriin sukkessiovaiheisiin sopeutuneen lajin kuten teeren yksilöt kykenevät dispersoimaan pitkiä matkoja. Toisaalta naaraat liikkuivat samalla alueella hyvin erilaisia matkoja, joidenkin ollessa ympäri vuoden aitoja paikkalintuja ja joidenkin liikkuessa jopa kymmeniä kilometrejä. Tämä viittaa siihen, että erilaiset liikkumismallit johtuvat enimmäkseen muista syistä kuin eri vuodenaikaisympäristöjen keskinäisestä sijainnista.

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