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Spring-summer movements of male capercaillie *Tetrao urogallus*: A test of the 'landscape mosaic' hypothesis

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The 'landscape mosaic' hypothesis predicts that adult male capercaillie *Tetrao urogallus* track available habitat when making distinct seasonal migrations. We tested this hypothesis by comparing movement from leks to summer range in three geographical regions, viz. northwest Russia (Pechora), southwest Russia (Tver) and southeast Norway (Varaldskogen). All radio-collared males dispersed out of their daytime lek territories to an average distance of 2.3 km (±0.37) from lek centres (N = 52). In Russia, three birds, which were not included in this estimate, moved beyond the 6-7 km detection distance, but returned the following year. Due to large variation among birds at each lek, the only significant difference in movement was found between the birds at the lek in Pechora ($\bar{x}$ = 1.3 km) and those at one of the two leks in Tver ($\bar{x}$ = 3.6 km) and at one of the three leks in Norway ($\bar{x}$ = 3.2 km). At all leks except the one in Tver, the amount of suitable summer habitat, e.g. old Norway spruce *Picea abies* forest on rich soil, was smaller within a 1-km radius of leks centres than in the outer two 1-km zones. Despite a large proportion of old spruce forest at and near the lek site in Tver, the males at this site moved >2 km from the lek centre in late May/early June. When data were pooled, the dispersal distance did not correlate with the amount of old spruce forest nor with the size of patches (e.g. grain size) with increasing distance from leks. However, at the Norwegian study area, which is highly fragmented with a fine-grained habitat mosaic due to commercial forestry, variation in topography and soil quality, birds tended to move farther away from the leks with increasing patch size and with increasing proportion of old spruce forest. When fitting a second polynomial regression function to the pooled data, there was only a weak relationship between dispersal distance and grain size for leks (P = 0.19). When including all birds, the relationship was highly significant (P = 0.002). The Pechora lek in northwest Russia contributed mainly to the lack of a clear relationship between movement pattern and distribution of old spruce forest. Here large, contiguous bands of old spruce forest were located along the main river courses in a coarse-grained fashion within 2 km of lek sites. Thus, local configuration of preferred summer habitat at the landscape scale probably affects both direction and movement to a larger extent than predicted from the 'landscape mosaic' hypothesis.

Key words: boreal forest, capercaillie, dispersal, lek, seasonal movement, summer habitat

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After spending more than one month on the lek, the physical condition of capercaillie *Tetrao urogallus* males is severely reduced in early summer (Lindén 1984). As this is also the start of the moult period, replacement of body reserves and growth of new feathers make summer the most energy requiring season of the year (Lindén 1984). During this period male capercaillie select home ranges with a high proportion of Norway spruce *Picea abies* forest on rich soils, and there is an increase in the use of old forest throughout the summer (Semenov-Tian-Shansky 1960, Rolstad, Wegge & Larsen 1988, Helle, Jokimäki & Lindén 1990, Storch 1993, Beshkarev, Blagovidov, Teplov & Hjeljord 1995). In these habitats males feed on a varied diet rich in proteins and easily digestible energy, e.g. berries of *Vaccinium* species, herbs and ferns from nutrient-rich sites (Semenov-Tian-Shansky 1960).

Studies of radio-collared capercaillie males show that they undertake seasonal movements of varying distance from the lek to their summer range of old spruce forest (Rolstad et al. 1988, Helle et al. 1990, Storch 1995, Beshkarev et al. 1995). Two general and not mutually exclusive hypotheses have been proposed to explain seasonal movement or local migration patterns in forest grouse. First, seasonal movements of adults may retrace the dispersal routes they made as juveniles. This seems to be the case in the North American spruce grouse *Dendragapus canadensis* (Ellison 1973, Herzog & Keppie 1980, Schroeder 1986) and ruffed grouse *Bonasa umbellus* (Small & Rush 1989, Small, Holzwart & Rush 1993). Secondly, local seasonal movement patterns may be determined by graininess, e.g. the mix of summer and winter habitats in the area surrounding the lek, as has been suggested for Fennoscandian capercaillie populations. According to this 'landscape mosaic' hypothesis (Rolstad & Wegge 1989), a high degree of habitat interspersion promotes resident populations, while a low degree triggers seasonal movements (Rolstad 1989).

We tested the latter hypothesis by comparing movements of radio-equipped male capercaillie from leks to summer range in three regions with different landscape composition, viz. in southeast Norway (Varaldskogen), in northwest Russia (upper Pechora basin) and in southwest Russia (upper Volga basin).

Material and methods

The study area in northwest Russia was a large lek within a 20,000-ha section of the Pechora-Illych Nature Reserve (62°N, 57°E; Beshkarev et al. 1995) which occurs as an island surrounded by logged forests. The area is typically flat, northern Russian taiga dominated by Scots pine *Pinus sylvestris*. Spruce occurs in bands along streams and fens (Table 1).

In southwest Russia we worked on two leks in the Central Russian Forest Reserve (56°N, 32°E); one in the main reserve (Sopki lek) and one in the buffer zone (Barsuchicha lek). Within the main reserve of approximately 25,000 ha, dense spruce forest on rich soil dominates while deciduous forest and pine occur on windfalls and on bogs, respectively (see Table 1). The buffer zone of approximately 35,000 ha is a mixture of large pine covered bogs, old spruce forests and clear-cuts (see Table 1).

In Norway we analysed data from three leks at Varaldskogen covering an area of ca 10,000 ha of mixed pine and spruce forest located in the southeastern part of the country (60°10'N, 12°30'E). As a result of commercial forestry operations with clear-cutting and replanting, the area is highly fragmented in terms of forest age classes with new planted forests covering >50% (see Table 1). The average stand size is <10 ha, resulting in habitats distributed in a highly fine-grained pattern.

During the springs of 1991 and 1992, 16 male capercaillie (11 adults and five two-year olds) were radio-collared on the Pechora lek. On the Barsuchicha lek seven males (six adults and one one-year old) and on the Sopki lek three adult males were radio-collared during 1997 and 1998. At Varaldskogen, the movement of 30 radio-collared males were monitored during 1980-

Table 1. Proportion of four different age classes of trees (%) within approximately 10 km of lek centres: P = Pechora in northwest Russia, B = Barsuchicha and S = Sopki in southwest Russia, and V = Varaldskogen in southeast Norway.

	Tree species											
	Pinus sylvestris				*Picea abies*				Deciduous			
Age class	P	B	S	V	P	B	S	V	P	B	S	V
<40 years	12	2	<1	30	<1	7	<1	23	<1	7	2	4
41-80 years	19	5	2	3	<1	4	5	7	2	16	19	<1
81-160 years	12	17	2	30	1	21	40	6	<1	11	19	<1
>160 years	35	4	2	0	9	4	6	0	<1	1	2	<1

1986 at the Tharoberget lek (N = 11), the Karpasuo lek (N = 6) and the Torstimäki lek (N = 13). These were the three largest leks within the study area (none with more than 10 resident males in any one year) and were located approximately 4 km apart (other smaller leks were located closer than this distance).

We analysed the influence of habitat graininess (e.g. caused by logging or natural forest mosaic) on dispersal distance to summer range by comparing the proportion of spruce forest and the size of spruce forest patches on forest maps within 0-1 km, 1.1-2.0 km and 2.1-3.0 km from lek centres. Although the dispersal distances of some males exceeded 3 km, we chose this as the largest radius. In Pechora, this was the approximate distance from the lek centre to areas beyond the border of the reserve, and for these areas no vegetation maps were available. No males, however, dispersed into unmapped areas. Graininess was also expressed as a 'grain index': using vegetation maps, eight equally spaced linear transects were aligned from lek centres (N, NW, W....), and the number of crossings of edges between spruce forest older than ca 50 years and above the size of 10 ha and all other habitat types, were averaged for each of the three zones on each lek.

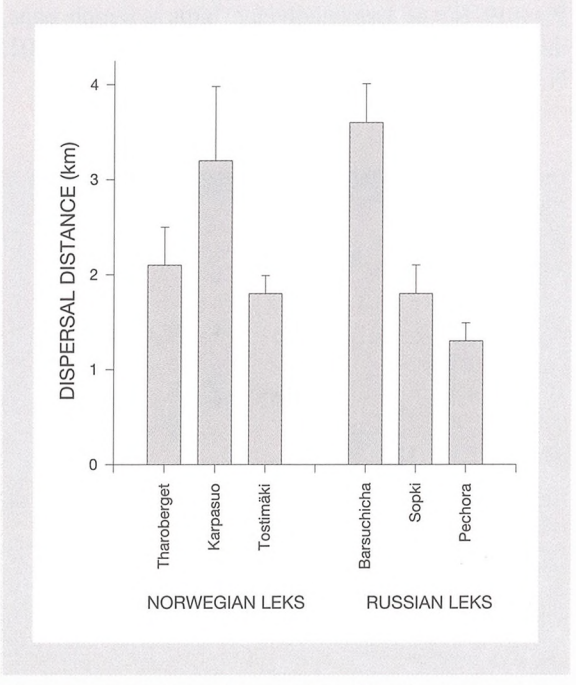

Figure 1. Average dispersal distance (km + SE) of males from leks to summer range for three Norwegian leks (Tharoberget, N = 11; Karpasuo, N = 6; and Torstimäki, N = 13) all from the Varaldskogen study area, and for three Russian leks, two from the Central Russian Forest Reserve (Barsuchicha, N = 6; Sopki, N = 6) and one from the Pechora-Illych Nature Reserve (Pechora, N = 16).

Results

The average dispersal distance of males to summer range for all six leks was 2.3 km (SE = 0.37) (in Russia 2.2 km (SE = 0.70); in Norway 2.4 km (SE = 0.43); Fig. 1). Distances varied within 1.3-3.6 km among the three Russian leks, and within 1.8-3.2 km among the three Norwegian leks. The distance was shorter among males at the Pechora than among males at the Barsuchicha lek (3.6 km) and the Karpasuo lek (3.2 km) (Student-Newman-Keuls test: $P < 0.05$), but due to rather large variation at each lek (Fig. 2), no other differences were statistically significant. One male at the Sopki and two at the Barsuchicha lek disappeared during summer and were not detected within 6-7 km from their display sites. However, the males reappeared at their respective leks with functioning transmitters the following spring. Inclusion of these birds would increase the average dispersal distance on the respective leks and make the difference to Pechora even larger.

For the Norwegian leks, percent coverage of summer spruce habitat increased from the 1-km zone nearest the leks through the two zones further away, as did the relative numbers of males settling in these zones (Fig. 3). Also two of the Russian leks, Pechora and Barsuchicha, had their centres in pine-dominated forest where spruce covered only 7.7 and 3.0% of the inner 1-km zone, respectively, compared to 16.4-23.2% in the outer two zones. The third Russian lek, Sopki, was located in spruce-dominated forest interspersed with scattered

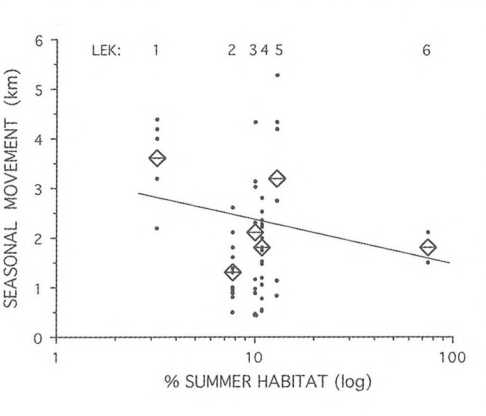

Figure 2. Dispersal distance of individual males at three leks in Norway (3: Tharoberget; 4: Torstimäki; 5: Karpasuo), and three leks in Russia (1: Barsuchicha; 2: Pechora; 6: Sopki) in relation to the proportion of summer habitat (i.e. spruce forest > 50 years) within a1-km radius of lek centres (r = -0.44, P = 0.39, N = 6).

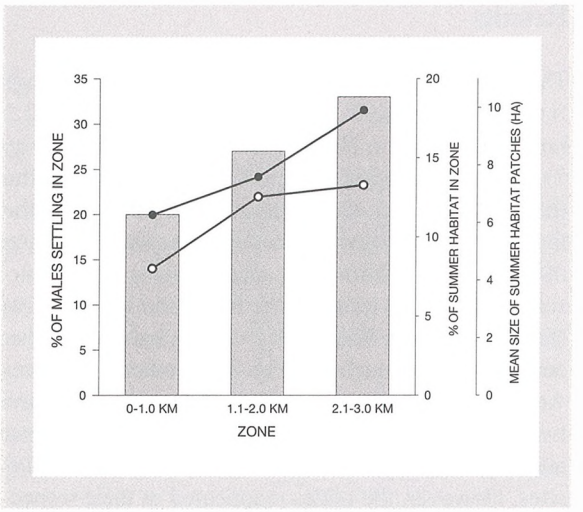

Figure 3. Relationship between the percentage of spruce summer habitats (●) and sizes of spruce summer habitat patches (○) within three zones around three leks at Varaldskogen, Norway, and the proportion of males (N = 30) settling in these zones (columns).

pine trees. Around this lek there was no significant difference in the proportion of old spruce forest between the three successive 1-km zones around the lek (75, 68 and 85%, respectively). The two males that were monitored at this lek moved an average of 1.8 km to their summer ranges.

Except for the Sopki lek, pine dominated at lek sites and significantly less old spruce forest occurred within 1 km of lek centres (8.0-12.9%) than within 1.1-2.0 km and 2.1-3.0 km from centres (9.3-23.2% and 16.5-20.6%, respectively; Student-Newman-Keuls test: $P < 0.01$; Fig. 4). However, when pooling the data from all six leks, there was no correlation between dispersal distance and the proportion of mature spruce forest within the 1-km zone from the lek centre ($r = -0.44$, $P = 0.39$, $N = 6$; see Fig. 2).

As a result of forest cutting and general variation in topography and soil quality, the Norwegian leks were situated in a more fragmented landscape than were the three Russian leks. Graininess of habitat, as expressed both in terms of the average size of spruce patches and by the number of edge crossings/unit linear distance was fine-grained in Norway and coarse-grained in Russia. However, dispersal distance did not correlate with grain size when the data for all six leks were pooled ($r = 0.37$, $P = 0.42$). Only among the three Norwegian leks was there a tendency for males to disperse further with increasing size of preferred spruce summer habitat patches (see Fig. 3). When fitting the data to a curvilinear (second polynomial) regression function, birds on leks in moderately-grained landscape mosaics appeared to move farther than birds on leks in both fine- and coarse-grained landscapes, although this relationship was not significant ($r = 0.82$, $P = 0.19$, $N = 6$). Using individual birds as sample units, this pattern was highly significant ($r = 0.49$, $P = 0.002$, $N = 47$; Fig. 5).

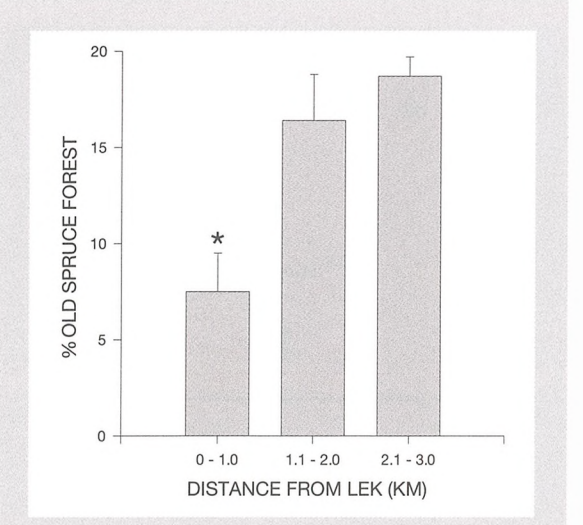

Figure 4. Distribution of spruce forest (% + SE) within three zones around the two leks in Russia and the three leks in Norway. The asterisk (*) indicates that the percentage of old spruce forest is statistically smaller in the inner zone than in the two outer zones ($P < 0.01$).

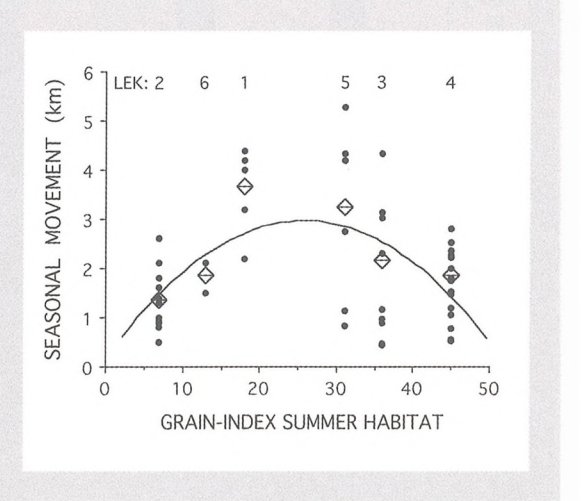

Figure 5. Relationship between dispersal distance from the lek to the summer range and habitat grain size within a 3-km radius of lek centres at the three leks in Russia (1: Barsuchicha; 2: Pechora; 6: Sopki) and the three leks in Norway (3: Tharoberget; 4: Torstimäki; 5: Karpasuo). Second polynomial regression functions for leks: $r = 0.82$, $P = 0.19$, $N = 6$; and for all birds: $r = 0.49$, $P = 0.002$, $N = 47$.

Discussion

The data from the Russian leks confirmed that capercaillie males undertake distinct seasonal movements from pine-dominated winter/spring ranges to rich spruce-dominated summer ranges. Pine needles are a staple food of most capercaillie populations during winter, and their winter habitat contains a preponderance of pine whereas continuous, homogenous spruce forests are avoided (Seiskari 1962, Gjerde & Wegge 1989). Low occurrence of spruce in the zone adjacent to lek centres, therefore, seems logical, assuming that display sites originated from the winter habitat (Gjerde, Wegge & Rolstad 2000). Where pine-dominated forest is scarce, as on Sopki, capercaillie leks may be found in spruce-dominated forest. However, the Sopki lek area contains scattered pine trees which are utilised during winter by capercaillie (O. Hjeljord, unpubl. data).

Despite quite contrasting landscapes and habitat mosaics, the dispersal distances were surprisingly similar among the three geographical regions. With leks being spaced ca 2 km apart (Wegge & Rolstad 1986, Beshkarev et al. 1995, Storch 1997), the average dispersal distance of 2.3 km means that the males from one lek settle on summer ranges closer to neighbouring leks. Earlier studies (Rolstad, Wegge & Larsen 1988, Ims, Rolstad & Wegge 1993) have shown that in Norway males are non-territorial and tend to have a clumped distribution during summer. Also, males from adjacent leks may share the same summer range. Assuming this is a general phenomenon, males at adjacent leks seem to mix during summer in richer, spruce-dominated forest in the interlek zones, more often closer to other leks than to their own.

The relationship between graininess of preferred summer habitat (i.e. patch size of spruce forest) and dispersal distance was ambiguous: in the highly fragmented and fine-grained Norwegian landscape there was a tendency for males to track the preferred patch size, but in the total material the relationship was curvilinear with the shortest dispersal distances in both the most coarse-grained and the most fine-grained landscape. The Pechora lek in Russia differed markedly from all the other leks. At this lek, the landscape consists of large, contiguous patches of pine and spruce forest. The sample lek was located relatively close to large blocks of riparian spruce forest along nearby rivers, which appeared to form a 'fence' which stopped further dispersal. Beyond this corridor there are several kilometres of pine forest with little occurrence of the preferred summer range of spruce on rich soils. Apparently, the short dispersal distance (1.3 km) recorded at Pechora is caused by a combination of high quality summer range close to the lek and a large stretch of unattractive range beyond this zone.

There was no relationship between lek size and dispersal distance. For instance, at the large Pechora lek with >30 males regularly attending each spring, the males only moved an average of 1.3 km, the shortest distance among all six leks studied.

The average dispersal distance of 2.3 km from leks to the summer range in this study compares well with a similar distance of 2.2 km reported from Finland (Helle et al. 1990). However, some birds both in Norway (Rolstad et al. 1988) and Russia (radio-collared birds re-appearing at the lek but not found within ca 5 km of the lek during the preceding summer) apparently undertake much longer dispersal distances, passing potential patches of suitable summer habitat during their early June migration. They may retrace their natal dispersal routes, as suggested by Ellison (1973), Herzog & Keppie (1980), Schroeder (1986; spruce grouse) and Rolstad (1989) and P. Wegge & J. Rolstad, unpubl. data (capercaillie).

In an earlier study, Rolstad & Wegge (1989) showed an inverse relationship between male dispersal distance and the proportion of old spruce forest within 1.5 km of the leks. They hypothesised that a coarse-grained habitat structure and scarcity of one of the seasonal habitat types would promote long distance seasonal movements. Our comparison of fine-grained (Norway) and coarse-grained (Russia) habitat mosaics shows that this relationship may be more complex. It appears that local configuration of preferred habitat patches at the landscape scale (e.g. meandering river-bank habitat in Pechora) may affect movement direction and distance to a larger extent than predicted from the general 'landscape mosaic model' based on graininess and extent of spatial habitat interspersion. Thus, special habitat configurations, in addition to graininess as such, probably play a role in shaping the seasonal movement from leks to summer range in male capercaillie.

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