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GPS satellite telemetry provides new insight into capercaillie *Tetrao urogallus* brood movements

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High mortality among chicks, due to fragmentation and changes in habitat caused by commercial forestry, is considered one of the main reasons for the general decline in capercaillie *Tetrao urogallus* in boreal forests. Using GPS satellite telemetry, we studied the movement patterns of young capercaillie broods: 1) to test if this new technology could be applied to gain more detailed insight into behaviour and habitat selection at a small spatial scale, and if so, 2) to compare the broods' relative use of planted and older, naturally regenerated forests. Hens of four broods with chicks 2-7 days old were captured and fitted with 90-g backpacks containing GPS units and VHF transmitters. The GPS units were programmed to record positions every 15 minutes, the shortest interval possible. With a storage capacity of 450 positions, movements could be monitored for ca 4.5 days. In our study area (Varaldskogen) with moderate topography, the GPS technology performed quite well. A total of 1,277 positions were obtained (84% of potential maximum), of which 77% were within 20 m of the true position of the brood. The movement patterns of the four broods were quite similar, with a mean speed of $83.2 \text{ m} \pm 9.9 \text{ (SE)}$ per hour during the 4.5-day tracking period. Broods moved almost continuously during the 24-hour cycle, presumably foraging, although their speed was slower at night. The two oldest broods whose initial age was seven days moved faster than the two younger broods whose initial age was two and three days, respectively. Strong autocorrelation among successive positions made us examine habitat selection using a binominal choice method for each brood separately. When broods were inside old 'natural' forest, they remained there instead of moving into plantations. When inside plantations, they did not discriminate between remaining there and moving into nearby old forest, but they tended to move faster in plantations than in old forest. Clearly, the new, cost-effective GPS telemetry offers new and better opportunities for studying small-scale brood movement. Very frequent and accurate positions can be obtained without either disturbing the birds or leaving scent marks that may attract predators.

Key words: boreal forest, brood habitat, capercaillie, GPS, habitat selection, tetraonids

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The capercaillie *Tetrao urogallus* is declining throughout most of its geographical range, mainly because of loss and fragmentation of habitat (Storch 2001). The proximate causes are poorly known, but are believed to be associated with low recruitment resulting from increased losses of eggs and chicks (Kurki et al. 2000) rather than to higher mortality of adults.

High losses of eggs and chicks may be related to a higher abundance of predators, particularly mammalian, in man-modified landscapes (Storaas & Wegge 1987, Henttonen 1989, Wegge et al. 1990, 1992, Kurki et al. 1998, 2000, Kauhala & Helle 2002, Storch et al. 2005). Storaas et al. (1999) predicted that an increased density of mammalian predators hunting by scent would increase chick loss more than egg loss. In boreal forests, young broods preferentially use moist old forests rich in ericaceous shrubs (Wegge et al. 1982), presumably because such habitats are rich in high-quality insect food, particularly Lepidoptera larvae (Kastdalen & Wegge 1985, Stuenkel & Spidssø 1988, Picozzi et al. 1999, Wegge et al. 2005).

Fragmentation by commercial forestry disrupts continuous brood habitats, creating a patchy distribution separated by less suitable habitat. Young broods of grouse, including capercaillie, move extensively during their first weeks of life, presumably in search of high-quality insect food (Godfrey 1975, Wegge et al. 1982). Break-up of the forested landscape that results in 'barriers' between optimum brood habitats may contribute to high chick losses, caused either by starvation or exposure to predators. Capercaillie hens are quite traditional in their use of seasonal habitats (Wegge 1985, Wegge & Rolstad 1986, Storch 2001), and hens with broods appear to take their chicks along the same route in successive years (Wegge et al. 1990). Thus, a clearcut will create a new obstacle because the hen may then have to take the brood around the new opening, thereby increasing the energetic cost, or, if she crosses it, the brood will be more vulnerable to avian predation.

To understand how broods move and select habitat on a small spatial scale, we equipped four broods with GPS satellite backpacks. Because such GPS telemetry has not been used on capercaillie before, we were particularly interested in testing if this methodology was suitable for addressing the type of ecological questions outlined above.

Methods

Study area

Our study was conducted at Varaldskogen and Fjella in southeastern Norway. Both areas are typical of boreal forest landscapes modified by commercial forestry. Main predators are goshawk *Accipiter gentilis*, red fox *Vulpes vulpes* and pine marten *Martes martes*. For further description of the forest and fauna in the study area, see Wegge & Rolstad (1986).

Fieldwork

Using pointing dogs and nets, we captured four hens with newly hatched broods in 2004 and 2005; three at Varaldskogen and one at Fjella. We estimated the age of the broods from chick size and presence/absence of the egg tooth. Age ranged within 2-7 days. We weighed the hens and determined their age (i.e. yearling or older) on the basis of pigmentation of the outer primaries (Helminen 1963). The GPS units were attached as backpacks (Brander 1968), with silicon rubber harness to minimise skin abrasion. The weather was warm and sunny, and instrumentation and handling lasted < 30 minutes. To verify that the hens returned to their broods, we tracked them from the ground later the same day using a VHF receiver from distances of > 200 m. Thereafter they were only occasionally located by VHF telemetry, e.g. to confirm that the chicks were still alive at the end of the GPS session and to record subsequent hen and chick survival. We needed to retrieve the collars to download the positions. Because drop-off attachment was not an option (the harness was considered unsuitable) and recapture during the moult might have caused the hen to abandon her brood, the hens were shot in early autumn with the authorisation of the Norwegian Directorate of Nature Management. The positions stored in the collars were downloaded by TVP Positioning (Sweden) and then forwarded to us. We then transferred the positions to digitised habitat maps prepared in ArcView 3.2 GIS. Because the habitat classification in Fjella was not comparable with that in Varaldskogen, inference on habitat use was only made on the basis of the three broods at Varaldskogen.

Technical data of equipment

We used GPS PosRec70 backpack 'collars', weighing 90 grams and produced by TVP Positioning AB, Sweden. Further to the GPS unit, the collars

Table 1. Number and accuracy of GPS positions recorded from four young capercaillie broods at Fjella (F) and Varaldskogen (V) during four consecutive days in June 2004 and 2005. Average age (in days) of the broods during the GPS session is given.

Precision Number of positions	Age	> 20 m (2D)		< 20 m (3D/3D+)		Total	
		N	%	N	%	N	% ¹
Brood 102 (F/2004)	5	81	25	240	75	321	85
Brood 121 (V/2004)	9	96	23	331	77	427	96
Brood 141 (V/2005)	9	48	34	93	66	141	63
Brood 161 (V/2005)	4	65	17	323	83	388	92
All		290	23	987	77	1277	84

¹ Percent of potential maximum number of positions, which varied among units due to pre-testing.

also contained a VHF transmitter in the 142 MHz frequency range, thus enabling tracking from the ground with a portable antenna. By extending the pulse intervals to 40/minute, we obtained a battery capacity for ground tracking of ca three months. The GPS unit could record a maximum of 450 positions. Because our objective was to study the movements of broods at a very small spatial scale, we programmed the units to take positions every 15 minutes, the shortest time interval possible. With such intensive positioning, GPS data could only be obtained for a period of 4-5 days. The accuracy of each GPS position varied with time-specific satellite coverage and location of the bird in relation to the surrounding topography and forest cover. Thus, downloaded positions were classified by the supplier of the GPS units into three different categories: 2D (least accurate) = > 25 m from the true location, 3D = within 15-25 m of the true location, and 3D+ = < 15 m from the true position (TVP Positioning AB, pers. comm.).

Data analyses

Because this was a pilot study with small sample size, we decided to categorise the habitat into only three main types: old forest > 70 years old (OF), plantations < 20 years old (PF1) and plantations 21-70 years old (PF2). Chicks < 10 days old cannot yet fly, hence, they can only select among the habitats that are available in their immediate surroundings. If another different habitat type was available nearby, we tested habitat selection of each brood by a binominal choice method. We defined a nearby habitat as one that was within a distance that the brood could reach within the 15-minute interval. We set this distance equal to a distance of 25 m, slightly longer than the calculated mean movement distance of 21 m per 15 minutes. Thus, the other habitat had to be within 25 m in order to represent an alternative, and the brood had the choice of staying in the same habitat or moving to the alternative habitat. For simplicity,

we assumed a 50:50 chance of staying or leaving and tested this using a binomial test. We assessed habitat use, diel differences in activity, and possible differences due to brood age by comparing their speed of movement using the 15-minute pre-programmed sampling intervals as a basis. We only used successive 3D and 3D+ locations and report the results as mean (\pm SE) distance (m) travelled per hour in the different categories for each brood separately. In the statistical comparisons (t-tests) we used brood means as observation units.

Results

General

All four hens were alive and with their chicks when checked from the ground 5-8 days after they were equipped with the transmitters. They produced 1,277 brood positions over ca four days (Table 1), corresponding to a mean of 84% of the potential number that the units could record, with individual units varying from 63 to 96% among the different broods. Most GPS locations (77%) were category 3D or better, i.e. within ca 20 m of the supposedly true location of the brood. There were no differences in either distribution of accuracy categories or proportion of recorded positions among the four broods (χ^2 -tests: $P > 0.05$ for both tests).

Three hens were adults and one was a yearling. In late August, two of the adult hens had ≥ 3 chicks each, the yearling hen (brood 161) was alone (she lost her brood in July); the fourth hen was killed by a fox in July.

Pattern

Movement was mainly continuous, interrupted by occasional 'stops' for intensive foraging (hotspots) or brooding (Figs. 1 and 2). The yearling hen with a 2-day-old brood (see Fig. 1) moved 1.2 km away from the place of capture during the next three days.

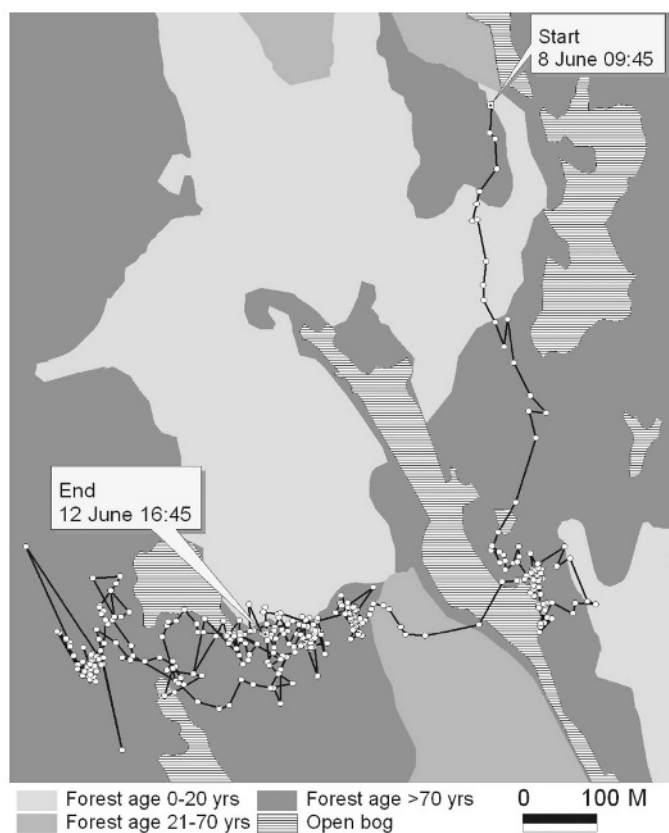


Figure 1. Movement pattern of a 2-day-old brood (yearling #161) during four successive days in June 2005. White dots indicate positions at 15-minute intervals. We omitted two excursions, i.e. positions when the hen had temporarily moved > 150 m away from the brood, probably due to disturbance.

Although the broods tended to move along the edges of bogs (see Fig. 2), this was not a consistent pattern, as they also frequently moved inside plantations and old, natural forest. During brooding, when the hen is stationary, GPS positions will be distributed in random directions around her, at varying distances depending on the accuracy of the recorded positions. Thus, clusters of locations do not necessarily indicate brooding stops, as these cannot be distinguished from foraging activities in preferred 'hotspots'.

Speed and distance

Including brooding stops, the mean speed of movement was 83.2 ± 9.9 m per hour, which corresponds to 2 km per 24 hours. The two oldest broods (initial ages estimated at seven days) moved faster than the two younger broods, and all four moved somewhat slower during the night (i.e. during 18:00-06:00) than during daytime (paired $t = 8.354$, $P = 0.004$, $df = 3$; Fig. 3).

Habitat use

All broods used mainly old, natural forest, particularly the ecotone next to open peat bogs (see Fig. 2). In Table 2, we show how they selected among old, natural forest and two age classes of plantations. A total of 119 occasions were recorded when the broods could choose between staying within their current habitat or moving into an adjacent one. When they were inside old forest ($N = 73$ occasions), the broods chose to remain there 58 times (79%). Conversely, when inside young planted forests ($N = 46$), they moved into old forest 21 times (46%). For two broods (#121 and #161), we obtained enough locations to test for selection (see Table 2). Both selected to remain in old forest. When in plantations, the broods did not seem to make any selection between the habitat they were in and nearby old forest (see Table 2).

We also compared the broods' use of habitats by measuring their speed of movement in the three habitat types. All three broods tended to move fast-

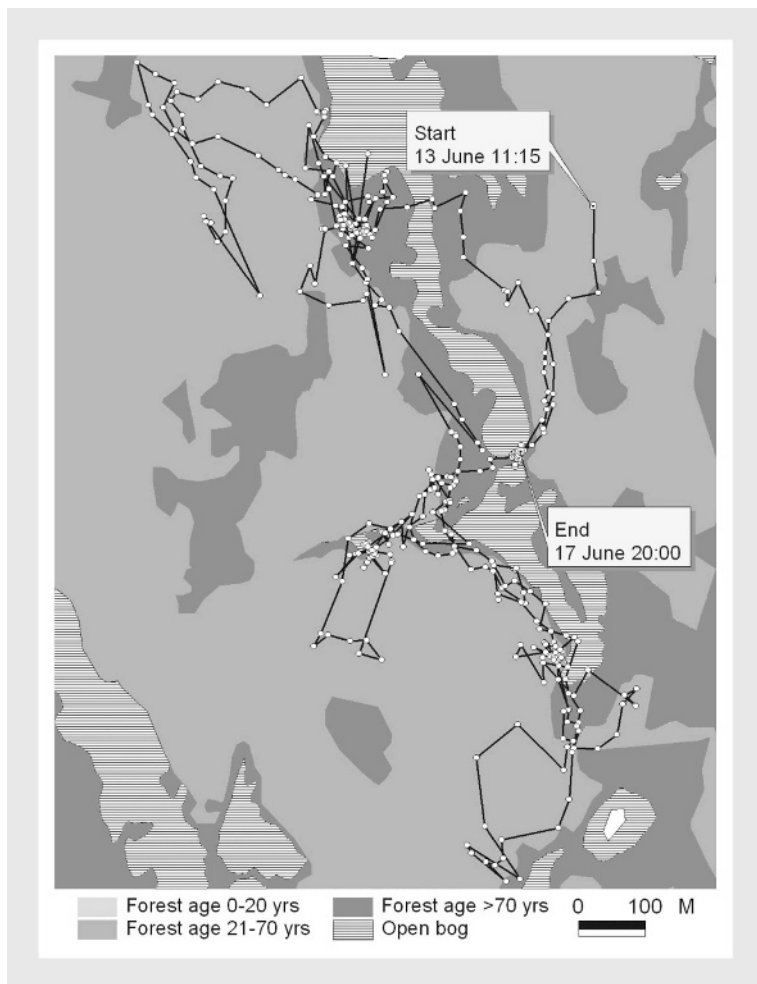


Figure 2. Movement pattern of a 7-day-old brood (adult #121) during four successive days in June 2004. White dots indicate positions at 15-minute intervals. One excursion was omitted.

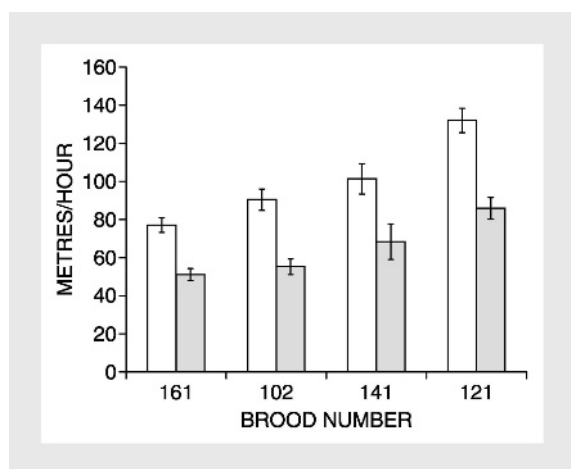


Figure 3. Distance (in m) moved per hour (mean \pm SE) during day (\square) and night (\blacksquare) by four young broods of different ages during four successive days in June 2004 and 2005. Average age of each brood is given in Table 1.

er when in plantations than in old, natural forest (paired $t = 2.824$, $P = 0.053$, $df = 2$, one-tailed; Fig. 4).

Discussion

Equipment performance

GPS satellite telemetry used on hens with young broods worked well. We were surprised that the units recorded as many as 84% of the potential number of positions, considering that brood hens move on the ground in rather dense vegetation and under a canopy of trees. The heavy backpack, 5-6% of the bird's weight, did not seem to affect them negatively. When shot in early autumn, the hens were in 'normal' physical condition, with minimal feather and skin abrasion from the harness, and they flew well. The loss of two broods could not

Table 2. Habitat selection by three young capercaillie broods when in old forest (OF), in plantations 1-20 years old (PF1), and in plantations 21-70 years old (PF2) in Varaldskogen in 2004 and 2005. Numbers in OF-PF1, OF-PF2, PF1-OF, PF1-PF2, PF2-OF and PF2-PF1 refer to the number of times a particular habitat was chosen when opportunity to choose between forest types existed. Numbers in italics indicate significant difference between pairs at $P < 0.01$ and n/a indicates that no data were available.

Brood	Old forest		Plantation 1-20 years old		Plantation 21-70 years old	
	OF-PF1	OF-PF2	PF1-OF	PF1-PF2	PF2-OF	PF2-PF1
121	n/a	<i>20-6</i>	n/a	n/a	12-9	n/a
141	9-3	n/a	6-3	0-1	n/a	n/a
161	<i>29-5</i>	0-1	6-8	n/a	0-1	n/a
All	38-8	<i>20-7</i>	12-11	0-1	12-10	n/a

be attributed to the backpacks, because this rate of chick mortality was no higher than what had been reported in previous studies at Varaldskogen (Wegge et al. 1992, Wegge & Kastdalen in press).

We found that 77% of positions were in either category 3D or 3D+, thereby providing locations accurate enough for studying habitat use on a small spatial scale. However, owing to random GPS error, the positions of a hen that remains stationary for > 15 minutes will be recorded in random directions and at varying distances around her, depending on the accuracy category. Thus, it is almost impossible to distinguish between concentrated foraging and brooding stops with GPS telemetry. Other limitations of the equipment were storage capacity (450 positions) and fixed, pre-programmed recording intervals. A new, lighter model with a capacity of >1,000 positions and an activity sensor will soon be available, which will facilitate separating brooding stops from short-distance movements. An improved harness with a drop-off function will also make it easier to retrieve the collar.

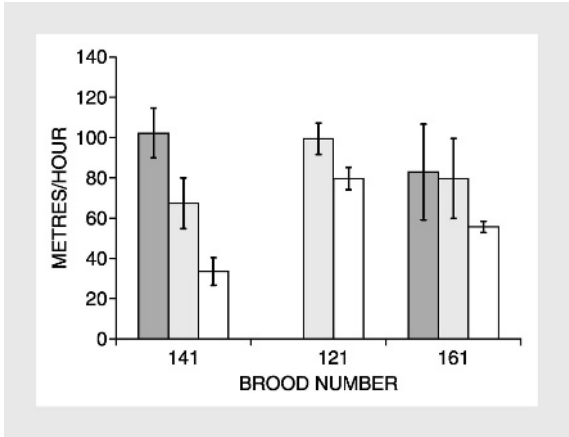


Figure 4. Distance (in m) moved per hour (mean \pm SE) by three young broods (#121, #141 and #161) in forest habitats of different ages (■: 0-20 years old; ▒: 21-70 years old; □: > 70 years old) at Varaldskogen in June 2004 and 2005.

Aside from these drawbacks, the GPS technology provides data on the movements of young broods that are difficult to obtain by other means. To get accurate positions by conventional VHF ground tracking, trackers need to approach within ca 30 m and move around the brood, which may cause disturbance and affect their behaviour. Such bias is eliminated by using satellite telemetry. For the same reason, possible attraction of predators to the brood from scent marks and tracks left by the ground trackers is eliminated. However, the most important advantage of the GPS telemetry is undoubtedly that the movements of broods can be monitored at very short time intervals with a high level of accuracy, thus enabling researchers to study habitat selection at a small spatial scale. Presumably, fragmentation of habitat by clearcutting or other human activities creates barriers to movements, thus putting energetic strain on the small chicks and increasing their risk of mortality. Moreover, human disturbance, for instance hiking and cross-country running events, is another factor that is believed to affect broods negatively (Menoni & Magnani 1998). Combining VHF and GPS telemetry makes it possible, by simulation experiments or by examining the broods' movements in relation to monitored temporal disturbance, to measure critical threshold levels of various sources of disturbance.

Movements and habitat use

Our broods showed more or less directional movements, interrupted by more concentrated 'back-and-forth' movements. Such a pattern was not unexpected and probably reflected 'hotspots' rich in food, as suggested by Barikmo et al. (1985), or longer brooding stops as indicated by the random pattern of GPS positions around a fixed point. Brooding stops are likely to occur more often and to last longer during cold and rainy weather. During the 24-hour cycle, the coldest temperatures occur late at

night, and all four broods showed clustered positions during that time. However, clusters also occurred during other times, and then they probably reflected concentrated foraging rather than brooding.

The directional routes may have reflected movement through poor habitats, as inferred from a study of willow grouse *Lagopus lagopus* brood behaviour (Erikstad 1985), or innate behaviour evolved to minimise predation by raptors (Sonerud 1985, Wegge et al. 2005). Or such movements may have been canalised by the spatial distribution of optimum habitat in our study area, where the highly preferred moist ecotone rich in bilberry *Vaccinium myrtillus* occurs in narrow, elongated belts situated between treeless bogs and drier, upland forests. Movement within such narrow passages would necessarily be directional.

The broods appeared to move faster in plantations than in natural, old forest. Also, when they could choose between habitats, the broods more frequently opted to remain within the old forest rather than to move into plantations. We interpret this as further evidence that conifer plantations are less preferred habitats than old, natural forest, as has been reported from earlier studies in our study area (Wegge et al. 1982, Rodem et al. 1984, Bodal 2001), in Germany (Storch 1994) and in Scotland (Jones 1982). When the broods were inside plantations and could choose to enter old forest, they did not make any significant habitat selection. Also, one of the broods spent a large part of its time in plantations, although old, natural forest was within reach. This somewhat ambiguous result was probably due to the heterogeneous structure of the plantations. Owing to variation in topography and soils, many plantations contained patches rich in bilberry and associated insect larvae, thus providing both food and cover for broods (Kolstad et al. 1985). Furthermore, early thinning stimulates growth of bilberry and other ground plants, which improves the habitat quality for young chicks (Lehn 2002). Field inspection of the route of this particular brood confirmed that it had selected such bilberry-rich patches inside recently thinned plantations.

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