Disturbance effects of hunting activity in a willow ptarmigan *Lagopus lagopus* population

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Hunting disturbance may affect individuals in a population by modifying their behaviour and spatial movements, which can lead to changes in home-range size and habitat use or displacement, for example into refuge areas. To evaluate effects of disturbance by recreational hunting activity, we conducted a study with 87 individually radio-marked willow ptarmigan *Lagopus lagopus*, in experimentally hunted and non-hunted units in central Norway during a four-year period. Contrary to a common belief among many hunters, i.e. that willow ptarmigan abandon a hunting unit in response to hunting activity, none of the birds left hunted units during the first two weeks of the hunting season in our study. Neither, did hunting affect the size of areas used by the ptarmigan or the distance between locations on consecutive days. In fact, day-to-day movements tended to be longer in non-hunted units than in hunted units. Willow ptarmigan responded to the risk of being shot by increasing their use of habitat with dense forest/scrub cover, which provided secure escape sites where birds were more difficult to locate and to shoot by hunters using pointing dogs. The increased use of cover with secure escape sites found for willow ptarmigan indicates that the catch per unit effort of hunters will vary not only with population density, but also with the amount and distribution of dense forest/shrub habitat in hunted units. Where the site-specific catch per unit effort of hunters is difficult to predict, we recommend a management scheme of harvests based on allowing a predefined number of hunters to hunt for the whole season and a seasonal bag limit per hunter.

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Human hunting activities affect game populations directly through the removal of individuals and indirectly through disturbance effects. The literature on the theoretical and empirical effects of hunting is dominated by studies of the direct impact of harvesting on populations (e.g. Czetwertynski et al. 2007, Norman et al. 2004, Pedersen et al. 2004, Solberg et al. 1999). However, indirect effects of hunting disturbance might also be important for management and conservation of harvested populations, as it can lead to temporary or permanent displacement of individuals (Fox & Madsen 1997). Animal movements between accessible hunting areas and surrounding areas (for example non-hunted refuges), are important in the evaluation of

the impact of hunting and the sustainability of harvesting (Novaro et al. 2000). The majority of studies on the effects of hunting disturbance have focused on ungulates and waterfowl (Bender et al. 1999, Fox & Madsen 1997, Kilgo et al. 1998, Madsen & Fox 1995, Vercauteren & Hygnstrom 1998), with little attention being given to upland game birds.

In Asia, Europe and North America, most of the 19 species of grouse and ptarmigan are subject to hunting (Johnsgard 1983, Storch 2007). In Scandinavia (Norway and Sweden), the willow ptarmigan *Lagopus lagopus* is one of the most popular game bird species which each year attracts many recreational small-game hunters into the mountains

(Kaltenborn & Andersen 2009). In Norway alone, it is estimated that about 60,000 persons hunt for ptarmigan each year, and the annual national bag of willow ptarmigan and rock ptarmigan *L. muta* is between 300,000 and 750,000 birds (Statistics Norway; available at: www.ssb.no/jakt).

Hunting, like any other kind of predation, may influence prey behaviour on both an evolutionary time scale and during an animal's lifetime (Lima & Dill 1990). Predation risk may be influenced by predator distribution and habitat features (Hebblewhite et al. 2005, Kauffman et al. 2007), and prey may alter their choice of habitats to decrease predation risk (Gilliam & Fraser 1987). Such a habitat choice might occur in willow ptarmigan when exposed to hunting (Olsson et al. 1996).

Among ptarmigan hunters and landowners in Scandinavia, it is a common belief that hunting disturbance leads to temporary displacement of willow ptarmigan out of hunted areas, which makes them inaccessible for hunters. Such a displacement could create a management situation in which one would not be able to reach the prescribed harvest levels, and the hunting rights in the management units might become difficult to hire out. To assess effects of hunting disturbance in willow ptarmigan, we conducted a study with individually radio-marked birds in experimentally hunted and non-hunted units in central Norway. Our objectives were to determine if recreational hunting activity leads to increased movements, changes in size of their home ranges or selection of different habitats. We explore the hypothesis advanced in an earlier study from Sweden by Olsson et al. (1996), who suggested that willow ptarmigan habitually reduce the risk of being shot by retreating to a familiar area with cover that provides known escape sites.

Material and methods

Study area
Our study was conducted in a 130-km^2 area in the municipalities of Meråker and Selbu in central Norway (63°10'-63°20'N, 11°30'-11°45'E) during 1996-1999. Most of the area is situated below the alpine tree line, which occurs at 600-700 m a.s.l. The subalpine habitat of our study area is dominated by scattered mountain birch *Betula pubescens* and Norway spruce *Picea abies* forest interspersed with some drier areas and bogs. The shrub layer is dominated by dwarf birch *B. nana*, juniper *Junipe-*

rus communis and some species of *Salix*, whereas in the field layer, heather species such as *Vaccinium myrtillus*, *V. uliginosum* and *Arctostaphylos alpinus*, black crowberry *Empetrum nigrum*, sedges *Carex* spp. and grasses are most common. At higher altitudes, the vegetation in the low-alpine habitat mainly consists of dwarf birch, heath and moraine ridges with lichens and sedges. Generally, snow covers the ground from late October to May.

Our study area was divided into five administrative hunting units of 20-30 km^2 each. Harvest regimes with no harvest or a prescribed harvest level were applied randomly to the hunting units each year (Pedersen et al. 2004). All hunting units were subjected to both non-harvest and harvest treatment during our four-year study period (1996-1999). As an example hunting unit 1 was hunted in 1996, 1998 and 1999 but not in 1997, whereas hunting unit 2 was hunted in 1997, 1998 and 1999 but not in 1996, and so on. The group of recreational hunters with access to a hunting unit was given a quota (seasonal bag limit) specific for the unit and based on autumn population estimates and the prescribed harvest regime. The total harvest pressure in hunted units was between 6.9 and 10.4 hunter hours/km^2 during the initial two weeks of the hunting season, and each day, there were typically 4-6 hunters with pointing dogs within a hunted unit. In harvested units, the average bag was 26% (range: 11-48%) of the autumn population (Pedersen et al. 2004). The average autumn density of non-hunted units was 22.0 birds/km^2 (range: 18.9-25.1 birds/km^2), while the average density on hunted units after harvesting was 16.4 birds/km^2 (range: 11.4-27.5 birds/km^2). The habitat in the surrounding area was the same as in the study area and was subject to unregulated recreational hunting (Brøseth & Pedersen 2000, Pedersen et al.1999, 2004). Disturbance by humans other than the hunters was negligible to non-existent in the study area. During the four-year period, we observed backpackers walking through the area only a couple of times, but we never saw them flush any willow ptarmigan.

Data collection
We captured adult willow ptarmigan during March and April from snowmobiles using a spotlight and a net. Juvenile birds from broods (being 1-2 months of age), and a few adults, were captured in August using pointing dogs and hand-held nets (Skinner et al. 1998). Birds were classified as adults or juveniles according to the amount of pigmentation on the

three outermost primaries relative to the rest of the wing (Bergerud et al. 1963). During our study, we captured 248 birds which we fitted with a necklace radio-transmitter and a uniquely numbered ring. We located radio-tagged birds daily by triangulation at distances of 50-100 m, and recorded positions with hand-held, non-differentially corrected 12-channel GPS receivers (Brøseth & Pedersen 2000, Brøseth et al. 2005, Pedersen et al. 1999). Our study was conducted from the start of the hunting season on 10 September and lasted for two weeks each year during 1996-1999. The two weeks were based on the fact that the annual quota was usually reached by the end of this period in the hunting units. Furthermore, some juvenile birds start their autumn dispersal in late September, which could have interfered with our study of the effects of disturbance on movements.

Data analysis

We calculated an index to daily movements by measuring the straight-line distance between consecutive day-to-day telemetry locations during the first two weeks of the hunting season. We applied a square root transformation to the distances to normalise the data (Kolmogorov-Smirnov: $z = 0.04$, $P = 0.05$). Then, we analysed the contributions of different explanatory variables to variation in these distances by applying linear mixed effect models (Pinheiro & Bates 2000). Bird identity was included as a random factor to account for the interdependence of data due to repeated measures of birds during the hunting season. We tested whether the day-to-day movement distance was affected by hunting treatment (hunting vs non-hunting), age (adult vs juvenile) and day of season (10-24 September). In the analysis, hunting and age were entered as fixed factors whereas day of season was treated as a covariate. We also included all possible interactions between hunting, age and day of season. We used Akaike Information Criterion (AIC) corrected for small sample size (AIC_c) to find the most parsimonious model (the 'best' model) applied to the data (Burnham & Anderson 2002). In the mixed effect models, parameters for fixed effects were estimated using restricted maximum likelihood (REML), but because we compared models with different fixed effects, we used maximum-likelihood (ML) for model selection.

We used data from birds with ≥ 10 telemetry locations during the two weeks of the hunting season to evaluate differences in home-range size between birds in hunted and non-hunted units. We used both minimum convex polygon methods (MCP) and adaptive kernel density estimation methods to calculate five different home-range estimates (100% MCP, 90% MCP, 95% kernel, 75% kernel and 50% kernel; Harris et al. 1990, White & Garrott 1990). The 100% MCP estimator and the 95% kernel represent different measures of 'total' area used, whereas the reduced probability distributions of 90% MCP, 75% kernel and the 50% kernel delineate different measures of the 'core' area used. We tested for differences in home-range size between birds in hunted and non-hunted units using a non-parametric Mann-Whitney U-test. Insufficient telemetry data on radio-tagged birds prior to the hunting season prevented us from testing for home-range shifts in hunted and non-hunted units.

We quantified habitat use on the basis of a vegetation raster map with 15×15 m cell resolution created from a Landsat 7 satellite image from August 1999. Originally, the vegetation had been divided into 26 classes based on different vegetation types in Norway (Moen 1999). We reclassified the vegetation map into two main habitat categories ('cover' and 'non-cover'). The cover habitat provides escape sites for the birds where they can hide and are more difficult to shoot. Ptarmigan hunters prefer to hunt in the transition zone between the subalpine birch forest and the open alpine habitat (Kaltenborn & Andersen 2009). Areas classified as cover included vegetation types of forest (birch and spruce) and tall shrub (*Salix* spp. and juniper), whereas non-cover habitat included clear-cuts, bogs, heather moors, alpine pastures, snow fields, exposed soil and bedrock. To test if the birds increased their use of cover when exposed to hunting, two different measures of habitat use were calculated. First, we calculated the percentage of locations recorded in cover habitat of birds in hunted vs non-hunted units. Secondly, we compared the use of cover given by the telemetry locations relative to available cover within the home ranges used by the birds ('third-order' selection *sensu* Johnson 1980). We calculated relative use as the difference in log-ratios ($\ln(p/q)$) between use and availability of cover (Aebischer et al. 1993), where p is the proportion of cover and $q = 1-p$, i.e. the proportion of other habitats. Relative use of zero indicates that cover is used as available, while positive and negative values indicate that cover is used more or less, respectively, than available within the areas used by the birds. To compare differences in relative use of cover, we used

Table 1. Mixed effect models explaining the effects of hunting (hunting or non-hunting), age (adult or juvenile) and day of season (10-24 September) on the day-to-day movement distances in willow ptarmigan. Hunting treatment and age were entered as fixed factors whereas day of season was treated as a covariate. Bird identity was included in all models as a random factor to account for the interdependence due to repeated measures of birds during the hunting season. K is the number of parameters in the model (intercept, effects, random factor and residuals) and w_i is AIC_c weights for the different models.

Model	K	AIC_c	ΔAIC_c	w_i
Intercept	3	1718.66	0.00	0.239
Intercept + Age	4	1719.04	0.38	0.197
Intercept + Hunting	4	1719.71	1.05	0.141
Intercept + Day	4	1720.45	1.79	0.098
Intercept + Hunting + Age	5	1720.47	1.81	0.097
Intercept + Age + Day	5	1720.82	2.16	0.081
Intercept + Hunting + Day	5	1721.56	2.90	0.056
Intercept + Hunting + Age + Day	6	1722.32	3.66	0.038
Intercept + Hunting + Age + Day + Hunting*Age	7	1723.61	4.95	0.020
Intercept + Hunting + Age + Day + Hunting*Day	7	1723.85	5.19	0.018
Intercept + Hunting + Age + Day + Age*Day	7	1724.32	5.66	0.014
Intercept + Hunting + Age + Day + Hunting*Age + Hunting*Day + Age*Day + Hunting*Age*Day	10	1729.30	10.64	0.001

the kernel density estimators of home ranges as they include the outer boundaries from 'total area' to 'core area' used by the birds during the two weeks of the hunting season. We then tested using a parametric t-test whether birds in hunted vs non-hunted units had a higher preference for cover habitat (Aebischer & Robertson 1992).

All estimates of day-to-day movements, habitat- and home-range size were calculated using Animal Movement 2.0 extension (Hooge et al. 1999) for ArcView® GIS 3.3 (ESRI, Redlands, California, USA). Statistical tests were done in SPSS® for Windows 15.0.1 (SPSS Inc., Chicago, USA).

Results

At the start of the hunting season 10 September, 87 willow ptarmigan were alive with functional radio-transmitters, of which 60 birds were in hunted units (33 adults and 27 juveniles) and 27 in non-hunted units (10 adults and 17 juveniles). The mixed effects model analysis showed that the best model included no effect of hunting treatment, age, day of season or interactions between the effects on day-to-day movement distances in willow ptarmigan during the two weeks of the hunting season (Table 1). The baseline model including only the fixed intercept (t = 69.4, P < 0.001) and the random factor of bird identity had the lowest AIC_c value among the alternative models. However, the alternative models with ΔAIC_c < 2 included hunting treatment, age and day of season. When examining the parameter estimates for these effects (Table 2), we see that the effect of hunting treatment tends to be in the opposite direction of what we predicted, with shorter day-to-day distances in hunted units. From the same model, we also see that juvenile birds tend to have longer day-to-day distances than adult birds, which is further supported in the model selection, where the model with an age effect is the second highest ranked (see Table 1). Bird identity accounted for 17% of the observed variation in day-to-day distances (z = 3.39, P = 0.001). Willow ptarmigan moved on average 458 m (95% CI = 397-519 m) from one day to the next in our study (median = 313 m, 95% percentile = 1,274 m; Fig. 1).

High mortality in marked birds during the two weeks of the hunting season, both by natural causes and hunting, resulted in 33 willow ptarmigan with sufficient telemetry locations to evaluate the effect of hunting on size of home ranges and habitat use (13 birds in non-hunted and 20 birds in hunted units). We found no significant effects of hunting on any of our five home-range estimators (100% MCP, 90% MCP, 95% kernel, 75% kernel and 50% kernel; Table 3). Birds in non-hunted units used on average

Table 2. Parameter estimates and test statistics for the model with all three fixed effects (Intercept + Hunting + Age + Day; see Table 1).

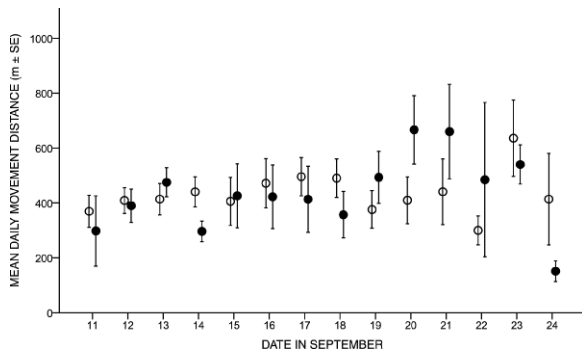| Variables	β	± SE	P
Intercept	4.233	0.198	< 0.001
Hunting treatment: non-hunted	0.090	0.126	0.478
Age: adult	-0.142	0.126	0.264
Day	0.005	0.011	0.665

Figure 1. Day-to-day movement distances (in m ± SE) for willow ptarmigan in hunted (•) and non-hunted (○) units during the first two weeks of the hunting season in Meråker, central Norway.

areas as large as those in hunted units. However, there was large individual variation in size of area used by birds in both groups (see Table 3).

Willow ptarmigan in hunted units were located more often in cover habitat than were birds in non-hunted units (t = 2.17, df = 31, P < 0.05). In hunted units, birds were found in cover habitat on average 50.4% (SE = 4.6) of the time, whereas in non-hunted units the cover habitat use was reduced to 38.6% (SE = 3.0). Comparison of the use of cover habitat relative to the amount available in the home range used by each bird also showed the same tendency of increased use of cover when exposed to hunting (95% kernel: t = 1.89, df = 31, P = 0.07; 75% kernel: t = 2.17, df = 31, P = 0.04; 50% kernel: t = 2.30, df = 31, P = 0.03; Fig. 2). There were no significant differences in use of cover habitat between surviving and shot birds in hunted units (all Ps > 0.4).

Discussion

Willow ptarmigan respond to the risk of being shot by recreational hunters with pointing dogs by in-

Table 3. Comparison of home-range size (in ha ± SE) in willow ptarmigan in hunted (N = 20) and non-hunted units (N = 13) during the first two weeks of the hunting season in the municipalities of Meråker and Selbu, central Norway. Home-range size is calculated with five different estimators (100% MCP, 90% MCP, 95% kernel, 75% kernel and 50% kernel), illustrating a range in area use from 'total area' to 'core area'.

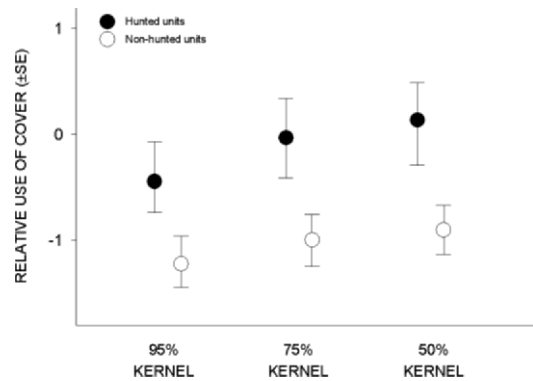|	Hunted units	Non-hunted units	P-value
100% MCP	65.5 ± 20.1	53.7 ± 12.3	0.971
90% MCP	40.3 ± 10.5	31.7 ± 7.6	0.531
95% kernel	101.7 ± 14.8	87.9 ± 16.8	0.439
75% kernel	40.6 ± 6.1	32.9 ± 5.2	0.531
50% kernel	16.5 ± 2.6	13.3 ± 2.7	0.338

Figure 2. Differences in relative use of cover habitat in willow ptarmigan in hunted and non-hunted units during the first two weeks of the hunting season in the municipalities of Meråker and Selbu, central Norway. Relative use of cover is based on the difference in log-ratio between use of cover habitat (telemetry locations) and available cover within the home ranges of individual birds (95% kernel, 75% kernel and 50% kernel).

creased use of cover habitat, which provides more secure escape sites where birds are difficult to locate and to shoot. A similar response to hunting disturbance has been found in ungulates, which increase their use of cover habitats to reduce vulnerability to hunting (Kilgo et al. 1998, Kufeld et al. 1988, Naugle et al. 1997, Swenson 1982). Willow ptarmigan respond to potential threats by crouching, which makes them a popular small game for recreational hunters, both with and without pointing dogs (Pedersen & Karlsen 2007). The birds do not flush until the dog or hunter is quite close, and if this occurs in open habitat, the risk of being shot is higher than if they flush in dense forest/shrub habitat where the success rate of hunters is lower (Foster et al. 1997, Harden et al. 2005). By spending more time in dense forest/shrub habitats, birds will increase their probability of surviving the hunting season. However, there may be costs associated with this strategy. Increased use of dense forest/shrub cover may reduce foraging opportunities and the availability of foods such as bilberry and crowberry, which may compromise body condition. Also, increased use of cover could augment the risk of mammalian predation, for example by red fox *Vulpes vulpes* (Wiebe & Martin 1998).

How birds perceive the threats from hunters will most likely depend on the total hunting effort in the area. In our study, the hunted units were exposed to moderate to high levels of hunting pressure (Pedersen et al. 1999). The hunting pressure within the area used by individual birds predicts their probability of surviving the hunting season (Brøseth & Pedersen

2000). In a detailed study of willow ptarmigan hunters, Brøseth & Pedersen (2000) showed by use of GPS tracking that hunting pressure within a hunting unit can be quite heterogeneous. Even if the hunting pressure was relatively high during the first two weeks of the hunting season (9.8 hunter hours/km^2) and the hunters claimed to have hunted 'everywhere', still about 30% of the area was unaffected by hunting activity. Therefore, within a hunted unit one might expect to see individual variation in the response of birds to hunting disturbance.

Willow ptarmigan can live in open habitats, i.e. without forest or scrub cover (Johnsgard 1983). Whether individuals in such places respond to hunting disturbance by staying or moving out of the area is uncertain. We suspect that the response will depend on the hunting pressure and whether the birds have access to topographical features or vegetation types that are perceived to be secure escape sites.

Displacement as a response to hunting disturbance has been shown in many species in the form of increased use of designated refuges or range shifts (Casas et al. 2009, Kilpatrick & Lima 1999, Laursen & Frikke 2008, Madsen 1998, Madsen & Fox 1995, Vercauteren & Hygnstrom 1998). However, we found no indication of such effects in the hunted populations of willow ptarmigan. Contrary to the common opinion of many hunters, i.e. that the birds leave a hunted area, none of the birds in our hunted units left during the first two weeks of the hunting season. Neither did we see any differences in day-to-day movements or size of home ranges between birds in hunted and non-hunted units (see also Olsson et al. 1996). Our results are in accordance with those for other hunted species which are reluctant to leave familiar areas with known escape coverts, e.g. mule deer *Odocoileus hemionus* (Kufeld et al. 1988), white-tailed deer *O. virginianus* (Vercauteren & Hygnstrom 1998, but see Naugle et al. 1997), moose *Alces alces* (Neumann et al. 2009), raccoon *Procyon lotor* (Hodges et al. 2000) and mountain hare *Lepus timidus* (Dahl 2005).

From the analysis of day-to-day movement distances, we found that a few juvenile birds made long movements at the end of the two weeks of the hunting period. We suspect that these juveniles were showing signs of autumn dispersal from their natal area (Brøseth et al. 2005). Hunting disturbance might hasten the onset of dispersal for juveniles, with unknown population consequences. Future studies of hunting disturbance should explore its effects on recruitment and colonisation of new habitats. The increased use of cover habitat by birds in hunted areas has consequences for harvest management of willow ptarmigan populations. Today, many willow ptarmigan populations as well as many other game species are managed under the assumption that the catch per unit effort for hunters depends only on population density. The increased use of cover with secure escape sites for birds in hunted units found in our study suggests that the catch per unit effort will also depend on the habitat of the hunted unit. Areas with few or no secure escape sites with cover will then have a higher catch per unit effort, and therefore a higher proportion of the population will be harvested given a fixed number of hunter days compared to areas with more cover escape sites. In Norway, this effort regulated system, even in combination with daily bag limits, has resulted in overharvesting in some management units with poor cover habitat. We argue that if the site-specific catch per unit effort for hunters is unknown in an area, a management system based on allowing a predefined number of hunters to hunt for the whole season, and a seasonal (annual) bag limit for each hunter, will allow managers to more accurately predict the number of birds shot.

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