

5. February 2010

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2 Title:

3 **Disturbance effects of hunting activity in a willow ptarmigan population**

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16 Word count: 4889

17

18 Key words: willow ptarmigan, disturbance, hunting, habitat use, movements, Norway

1 **Abstract**

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

20

21 **Introduction**

22 Human hunting activities affect game populations directly through the removal of individuals
23 and indirectly through disturbance effects. The literature on the theoretical and empirical
24 effects of hunting is dominated by studies of the direct impact of harvesting on populations
25 (e.g. Czetwertynski et al. 2007, Norman et al. 2004, Pedersen et al. 2004, Solberg et al. 1999).

1 However, indirect effects of hunting disturbance might be as important for management and
2 conservation of harvested populations, as it can lead to temporary or permanent displacement
3 of individuals (Fox & Madsen 1997). Movements of animals between accessible hunting areas
4 and surrounding areas (for example non-hunted refuges), is important for evaluating the
5 impact of hunting and the sustainability of harvesting (Novaro et al. 2000). The majority of
6 studies on the effects of hunting disturbance have focused on ungulates and waterfowl
7 (Bender et al. 1999, Fox & Madsen 1997, Kilgo et al. 1998, Madsen & Fox 1995, Vercauteren
8 & Hygnstrom 1998), with little attention being given to upland game birds.

9 In Asia, Europe and North America, most of the nineteen species of grouse and
10 ptarmigan are subject to hunting (Johnsgard 1983, Storch 2007). In Scandinavia (Norway and
11 Sweden), the willow ptarmigan *Lagopus lagopus* is one of the most popular game birds that
12 each year attracts many recreational small game hunters into the mountains (Kaltenborn &
13 Andersen 2009). In Norway alone it is estimated that about 60,000 persons hunt for ptarmigan
14 each year, and the annual national bag of willow ptarmigan and rock ptarmigan *L. muta* is
15 between 300,000 and 750, 000 birds (Statistics Norway; www.ssb.no/jakt).

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

22 Among ptarmigan hunters and landowners in Scandinavia it is a common belief that
23 hunting disturbance leads to temporary displacement of willow ptarmigan out of hunted areas,
24 making them inaccessible for hunters. Such displacement could create management situations
25 where one is not able to reach the prescribed harvest levels and the hunting rights on

1 management units become difficult to hire out. To assess effects of hunting disturbance in
2 willow ptarmigan, we conducted a study with individually radio-marked birds on
3 experimentally hunted and non-hunted units in central Norway. Our objectives were to
4 determine if recreational hunting activity leads to increased movements, changes in size of
5 home ranges or selection of different habitats. We explore the hypothesis advanced in an
6 earlier study from Sweden by Olsson et al. (1996) who suggested that willow ptarmigan
7 habitually reduce the risk of being shot by retreating to a familiar area with cover that provides
8 known escape sites.

9

10 **Materials and methods**

11 **STUDY AREA**

12 The study was conducted in a 130-km² area in the municipalities of Meråker and Selbu in
13 central Norway (63°10'-63°20' N, 11°30'-11°45' E) from 1996 to 1999. Most of the area is
14 below the alpine tree line, which occurs at 600-700 m a.s.l. The subalpine habitat of the study
15 area is dominated by scattered mountain birch *Betula pubescens* and spruce *Picea abies* forest
16 interspersed with some drier areas and bogs. The shrub layer is dominated by dwarf birch *B.*
17 *nana*, juniper *Juniperus communis* and some *Salix* spp., whereas in the field layer heather
18 species (*Vaccinium myrtillus*, *V. uliginosum* and *Arctostaphylos alpinus*), black crowberry
19 (*Empetrum nigrum*), sedges (*Carex* spp.) and grasses are most common. At higher altitudes
20 the vegetation in the low-alpine habitat mainly consists of dwarf birch, heath and moraine
21 ridges with lichens and sedges. Generally snow covers the ground from late October to May.

22 The study area was divided into five administrative hunting units of 20-30 km² each.
23 Harvest regimes with no harvest or a prescribed harvest level were applied randomly to the
24 hunting units each year (Pedersen et al. 2004). All hunting units were subjected to both non-
25 harvest and harvest treatment during the four-year study period (1996-1999). As an example

1 hunting unit 1 was hunted in 1996, 1998 and 1999 but not in 1997, while hunting unit 2 was
2 hunted in 1997, 1998 and 1999 but not in 1996, and so on. The group of recreational hunters
3 with access to a hunting unit was given a quota (seasonal bag limit) specific for the unit and
4 based on autumn population estimates and the prescribed harvest regime. The total harvest
5 pressure in hunted units was between 6.9 and 10.4 hunter hours/km² during the two-week
6 hunting season, and each day there were typically 4-6 hunters with pointing dogs within a
7 hunted unit. In harvested units, the average bag was 26% (range: 11-48%) of the autumn
8 population (Pedersen et al. 2004). The average autumn density of non-hunted units was 22.0
9 birds/km² (range: 18.9-25.1 birds/km²), while the average density on hunted units after
10 harvesting was 16.4 birds/km² (range: 11.4-27.5 birds/km²). Habitat in the surrounding area
11 was the same as that found in the study area and was subject to unregulated recreational
12 hunting (Brøseth & Pedersen 2000, Pedersen et al. 2004, 1999). Disturbance by humans other
13 than the hunters was negligible to non-existent in the study area. During the four-year period
14 we observed backpackers walking through the area only a couple of times, but we never saw
15 them flush any willow ptarmigan.

16

17 DATA COLLECTION

18 We captured adult willow ptarmigan during March and April from snowmobiles by using a
19 spotlight and a net. Juvenile birds from broods (1-2 months old), and a few adults, were
20 captured in August using pointing dogs and hand-held nets (Skinner et al. 1998). Birds were
21 classified as adults or juveniles according to the amount of pigmentation on the three
22 outermost primaries relative to the rest of the wing (Bergerud et al. 1963). During the study,
23 248 birds were captured and fitted with a necklace radio transmitter and a unique numbered
24 ring. We located radio-tagged birds daily by triangulation at distances of 50-100 m, and
25 recorded positions with hand-held, non-differentially corrected 12-channel GPS receivers

1 (Brøseth & Pedersen 2000, Brøseth et al. 2005, Pedersen et al. 1999). The study was
2 conducted from the start of the hunting season on 10 September for a two-week period each
3 year from 1996-1999. The two weeks were based on the fact that the annual quota was usually
4 reached by the end of this period on the hunting units. In addition some juvenile birds start
5 their autumn dispersal in late September, which could have interfered with our study of the
6 effects of disturbance on movements.

7

8 DATA ANALYSIS

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

1 Data from birds with ten or more telemetry locations during the two-week hunting
2 season were used to evaluate differences in home range size between birds on hunted and non-
3 hunted units. We used both minimum convex polygon methods (MCP) and adaptive kernel
4 density estimation methods to calculate five different home range estimates (100% MCP, 90%
5 MCP, 95% kernel, 75% kernel and 50% kernel [Harris et al. 1990, White & Garrott 1990]).
6 The 100% minimum convex polygon estimator and the 95% kernel represent different
7 measures of 'total' area used, while the reduced probability distributions of 90% MCP, 75%
8 kernel and 50% kernel delineate different measures of 'core' area used. Differences in home
9 range size between birds on hunted and non-hunted units were tested with a non-parametric
10 Mann-Whitney U-test. Insufficient telemetry data on radio-tagged birds prior to the hunting
11 season prevented us from testing for home range shifts in hunted and non-hunted units.

12 Habitat use was quantified on the basis of a vegetation raster map with 15×15 m cell
13 resolution created from a Landsat 7 satellite image from August 1999. Originally the
14 vegetation had been divided into 26 classes based on different vegetation types in Norway
15 (Moen 1999). We reclassified the vegetation map into two main habitat categories ('cover'
16 and 'non-cover'). The cover habitat provides escape sites for the birds where they can hide
17 and are more difficult to shoot. Ptarmigan hunters prefer to hunt in the transition zone
18 between the sub-alpine birch forest and open alpine habitat (Kaltenborn & Andersen 2009).
19 Areas classified as cover included vegetation types of forest (birch and spruce) and tall shrub
20 (*Salix* spp. and juniper), while non-cover habitat included clear-cuts, bogs, heather moors,
21 alpine pastures, snow fields, exposed soil and bedrock. To test if birds increased their use of
22 cover when exposed to hunting, two different measures of habitat use were calculated. First,
23 we calculated the percentage of locations recorded in cover habitat of birds on hunted vs non-
24 hunted units. Secondly, we compared the use of cover given by the telemetry locations relative
25 to available cover within the home ranges used by the birds ('third-order' selection *sensu*

1 Johnson 1980). We calculated relative use as the difference in log-ratios ($\ln(p/q)$) between use
2 and availability of cover (Aebischer et al. 1993), where p is the proportion of cover and $q = 1 -$
3 p , i.e. proportion of other habitats. Relative use of zero indicates that cover was used as
4 available, while positive and negative values indicate that cover was used more or less than
5 available within the areas used by the birds. To compare differences in relative use of cover,
6 we used the kernel density estimators of home ranges as they include the outer boundaries
7 from ‘total area’ to ‘core area’ used by the birds during the two-week hunting season. We then
8 tested with a parametric t -test whether birds on hunted vs non-hunted units had a higher
9 preference for cover habitat (Aebischer & Robertson 1992).

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

14

15 **Results**

16 At the start of the hunting season on September 10, 87 willow ptarmigan were alive with
17 functional radio-transmitters, 60 birds on hunted units (33 adults and 27 juveniles) and 27
18 birds on non-hunted units (10 adults and 17 juveniles). The mixed effects model analysis
19 showed that the best model included no effect of hunting treatment, age, day of season or
20 interactions between the effects on day-to-day movement distances in willow ptarmigan
21 during the two weeks of the hunting season (Table 1). The baseline model including only the
22 fixed intercept ($t = 69.4$, $P < 0.001$) and the random factor of bird identity had the lowest AICc
23 value among the alternative models. However, the alternative models with \bullet AICc < 2
24 included hunting treatment, age and day of season. When examining the parameter estimates
25 for these effects (Table 2), we see that the effect of hunting treatment tends to be in the

1 opposite direction of what we predicted, with shorter day-to-day distances on hunted units.
2 From the same model we also see that juvenile birds tend to have longer day-to-day distances
3 than adult birds, which is further supported in the model selection, where the model with an
4 age effect is the second highest ranked (Table 1). Bird identity accounted for 17% of the
5 observed variation in day-to-day distances ($z = 3.39$, $P = 0.001$). Willow ptarmigan moved on
6 average 458 m (95% CI = 397-519) from one day to the next in this study (median = 313 m,
7 95% percentile = 1,274 m, Fig. 1).

8 High mortality in marked birds during the two weeks of the hunting season, both by
9 natural causes and hunting, resulted in 33 willow ptarmigan with sufficient telemetry locations
10 to evaluate the effect of hunting on size of home ranges and habitat use (13 birds on non-
11 hunted and 20 birds on hunted units). We found no significant effects of hunting on any of our
12 five home range estimators (100% MCP, 90% MCP, 95% kernel, 75% kernel and 50% kernel,
13 Table 3). Birds on non-hunted units used on average areas as large as those on hunted units.
14 However, there was large individual variation in size of area used by birds in both groups
15 (Table 3).

16 Willow ptarmigan on hunted units were located more often in cover habitat than were
17 birds on non-hunted units ($t = 2.17$, $df = 31$, $P < 0.05$). On hunted units, birds were found in
18 cover habitat on average 50.4% (SE = 4.6) of the time, while on non-hunted units this was
19 reduced to 38.6% (SE = 3.0). Comparison of the use of cover habitat relative to the amount
20 available in the home range used by each bird also showed the same tendency for increased
21 use of cover when exposed to hunting (95% kernel: $t = 1.89$, $df = 31$, $P = 0.07$; 75% kernel: t
22 = 2.17, $df = 31$, $P = 0.04$; 50% kernel: $t = 2.30$, $df = 31$, $P = 0.03$, Fig. 2). There were no
23 significant differences in use of cover habitat between surviving and shot birds on hunted
24 units (all $P > 0.4$).

25

1 **Discussion**

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

17 How birds perceive the threats from hunters will most likely depend on the total
18 hunting effort in the area. In our study, the hunted units were exposed to moderate to high
19 levels of hunting pressure (Pedersen et al. 1999). Hunting pressure within the area used by
20 individual birds predicts their probability of surviving the hunting season (Brøseth & Pedersen
21 2000). In a detailed study of willow ptarmigan hunters, Brøseth and Pedersen (2000) showed
22 by GPS tracking that hunting pressure within a hunting unit can be quite heterogeneous. Even
23 if the hunting pressure was relatively high during the first two weeks of the hunting season
24 (9.8 hunter hours/km²) and the hunters claimed to have hunted 'everywhere', there still was

1 about 30% of the area unaffected by hunting activity. Therefore, within a hunted unit one
2 might expect to see individual variation in the response of birds to hunting disturbance.

3 Willow ptarmigan can live in open habitats, without forest or scrub cover (Johnsgard
4 1983). Whether individuals in such places respond to hunting disturbance by staying or
5 moving out of the area is uncertain. We suspect that the response will depend on the hunting
6 pressure and whether the birds have access to topographical features or vegetation types that
7 are perceived to be secure escape sites.

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

21 We found from the analysis of day-to-day movement distances that a few juvenile
22 birds made long movements at the end of the two-week hunting period. We suspect that these
23 juveniles were showing signs of autumn dispersal from their natal area (Brøseth et al. 2005).
24 Hunting disturbance might hasten the onset of dispersal for juveniles, with unknown
25 population consequences. Future studies of hunting disturbance should explore its effects on

1 recruitment and colonization of new habitats. The increased use of cover habitat by birds on
2 hunted areas has consequences for harvest management of willow ptarmigan populations.
3 Today, many willow ptarmigan populations as well as many other game species are managed
4 under the assumption that the catch per unit effort for hunters depends only on population
5 density. The increased use of cover with secure escape sites for birds on hunted units found in
6 this study suggests that the catch per unit effort will also depend on the habitat of the hunted
7 unit. Areas with few or no secure escape sites with cover will then have a higher catch per unit
8 effort, and therefore a higher proportion of the population will be harvested given a fixed
9 number of hunter-days compared to areas with more cover escape sites. In Norway, this effort
10 regulated system, even in combination with daily bag limits, has resulted in overharvesting in
11 some management units with poor cover. We argue that if the site-specific catch per unit
12 effort for hunters is unknown in an area, a management system based on allowing a
13 predefined number of hunters to hunt for the whole season, and a seasonal (annual) bag limit
14 for each hunter, will allow managers to more accurately predict number of birds shot.

15

16 *Acknowledgements* - We would like to thank S.Å. Domås, O.A. Hestmo, K.O Johnsen, T.
17 Melhus, I. Rimul, O. Rimul, S.S. Skjæveland, S. Stølan, S.L. Svartås, A. Sjøreng, G. Østerås
18 and E. Aavik for assistance during various parts of this study. B. Sandercock, E. Solberg and
19 two anonymous referees provided helpful comments on the manuscript. This study was
20 financed by contributions from the Norwegian Directorate for Nature Management, the
21 Norwegian Research Council's programme "Use and management of outlying fields" and the
22 Norwegian Institute for Nature Research.

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1 Table 1. Mixed effect models explaining the effects of hunting (hunting or non-hunting), age (adult or juvenile) and day of season (10–24
2 September) on the day-to-day movement distances in willow ptarmigan. Hunting treatment and age were entered as fixed factors while day
3 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
4 repeated measures of birds during the hunting season. K is the number of parameters in the model (intercept, effects, random factor and
5 residuals) and w_i is AICc weights for different models.

Model	K	AICc	• AICc	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

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

Variables	•	±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

3

4

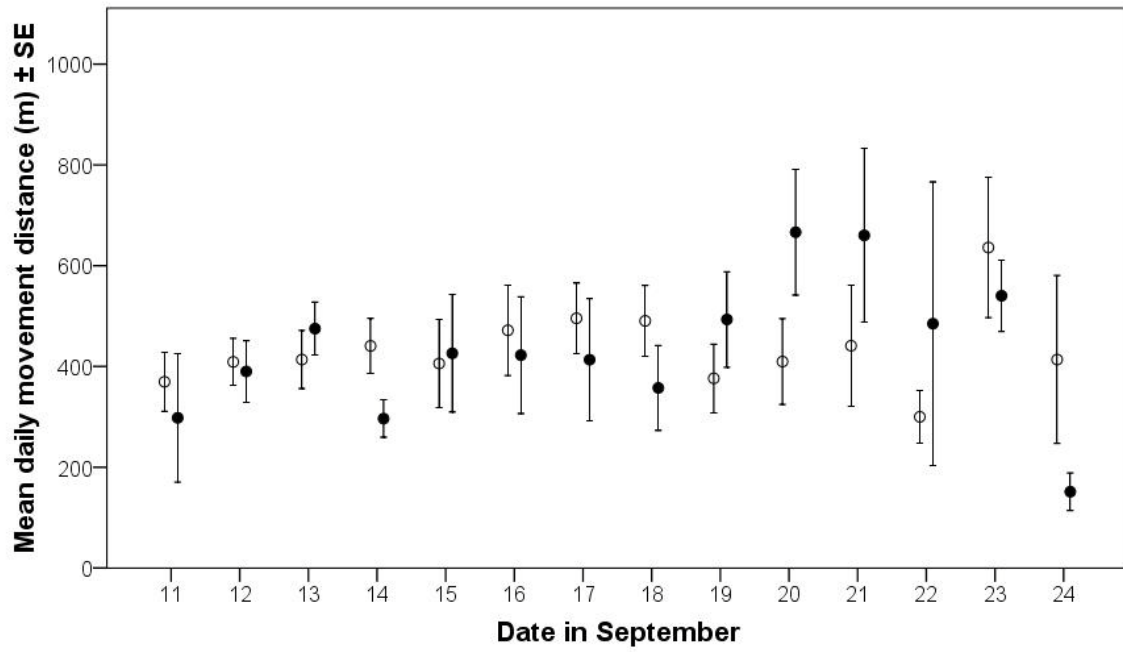
1 Table 3. Comparison of home range size in willow ptarmigan on hunted (N = 20) and non-
 2 hunted units (N = 13) during the first two weeks of the hunting season in Meråker, central
 3 Norway. Home range size is calculated with five different estimators (100% MCP, 90% MCP,
 4 95% kernel, 75% kernel and 50% kernel), illustrating a range in area use from ‘total area’ to
 5 ‘core area’.

	Hunted	Non-hunted	P-value
	(ha ± SE)	(ha ± SE)	
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

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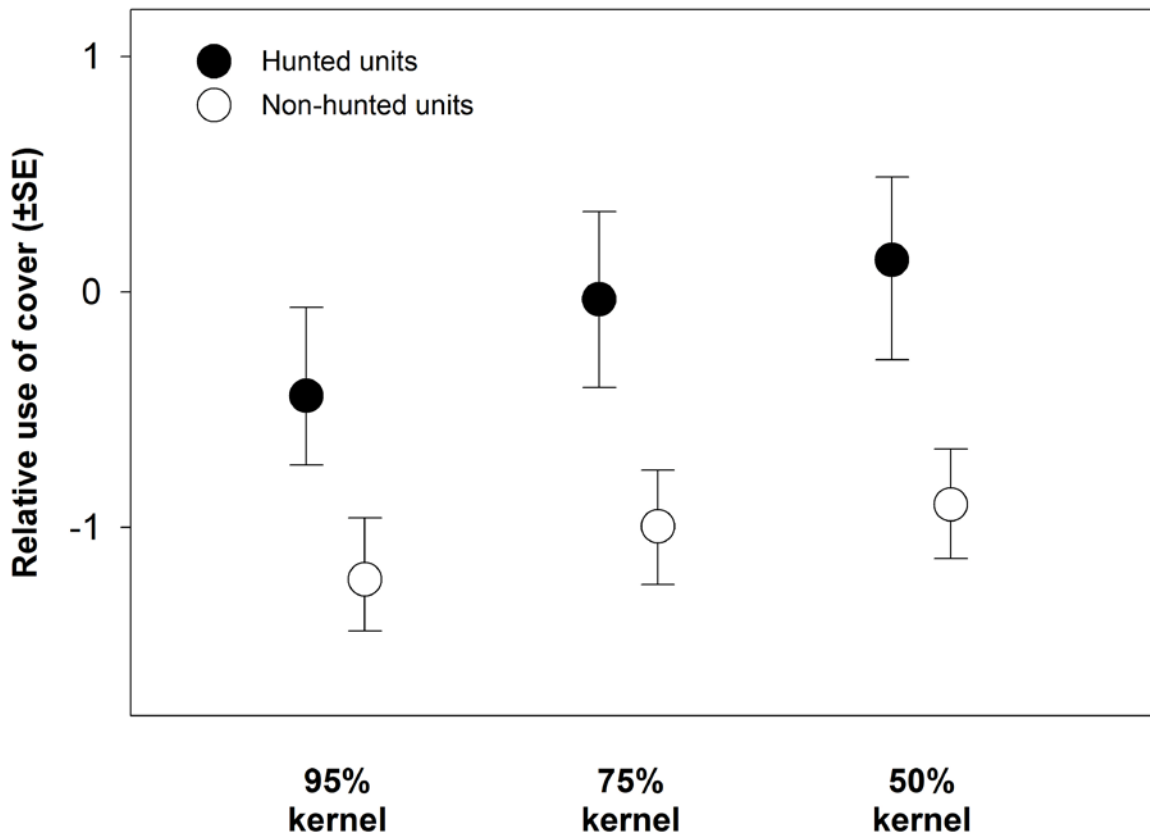
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3 Figure 1. Day-to-day movement distances for willow ptarmigans on hunted (filled symbols)
4 and non-hunted (open symbols) units during the first two weeks of the hunting season in
5 Meråker, central Norway.

1



2

3 Figure 2. Differences in relative use of cover habitat in willow ptarmigan on hunted and non-
4 hunted units during the first two weeks of the hunting season in Meråker, central Norway.

5 Relative use of cover is based on the difference in log-ratio between use of cover habitat
6 (telemetry locations) and available cover within the home ranges of individual birds (95%
7 kernel, 75% kernel and 50% kernel).

8