



Harvesting a red-listed species: determinant factors for willow ptarmigan harvest rates, bag sizes, and hunting efforts in Norway

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Abstract

A main objective of game management on public lands in Norway is to ensure that harvest levels are sustainable while securing hunting access to the public. The willow ptarmigan is a popular but red-listed small game species, and it is challenging for managers to optimize harvest levels based on uncertain population estimates and limited knowledge of the factors influencing hunting impact. We studied how willow ptarmigan hunting effort, catch per unit effort, and harvest rates were influenced by ptarmigan density, topography, vegetation, and infrastructure. Data were collected during 2013–2016 from 162 hunting blocks covering 26,828 km² state-owned land in the counties Nordland and Troms, northern Norway. Hunting effort averaged 1.27 days/km² (SD = 2.08), and it was the highest in areas close to roads and cabins. We found an opposite effect on the catch per unit effort (CPUE, mean = 0.77 ptarmigan/day, SD = 0.48), which was lower close to roads. There was a marked positive effect of density on CPUE, whereas terrain steepness (slope) had a negative effect. On average, harvest removed < 10% of the autumn population in the hunting areas during the study period. This indicates a relatively low and partially compensatory hunting mortality in most years and areas. Although this study shows a low harvest rate, we recommend managers to survey ptarmigan populations, hunting effort, and harvest, especially in easily accessible areas close to infrastructure and in periods of low population density.

Keywords Small game · *Lagopus lagopus* · CPUE · Hunting effort · Overharvest · Sustainability

Introduction

For a harvest regime to be sustainable, annual harvest rates should not exceed net population growth rates over a long time span (Boyce et al. 1999; Getz and Haight 1989; Hilborn et al. 1995; Lande et al. 1995). Although conceptually simple, a range of factors complicate the application of this principle. Firstly, estimates of population sizes and demographic rates are challenging to obtain in the field and are therefore ridden with large uncertainties (Aanes et al. 2002;

Boyce 1992; Eriksen et al. 2017; Saccheri and Hanski 2006). In addition, environmental and/or demographic stochasticity may lead to rapid population fluctuations that further complicate the adoption of a sound level of harvest (Engen et al. 1997). Moreover, there is often not a clear and simple link between harvest regulations and harvest off-take in these game management systems (Johnson and Williams 1999). An example of this is the willow ptarmigan (*Lagopus lagopus*), hereafter ptarmigan, whose high intrinsic rate of increase and highly variable breeding success produce marked annual variation in abundance (Henden et al. 2011; Hörnell-Willebrand 2005; Kvasnes et al. 2010; Moss and Watson 2001; Myrberget 1988).

Historically, hunting of small game has been considered as compensatory mortality and thus having little effect on the populations (Pedersen et al. 2004a, and references therein). However, these assumptions were often based on weak quantitative studies assuming density dependent growth (Ellison 1991). In Norway, small game hunting is a privilege of the landowner, who has the right to hunt and trap without restrictions in numbers of harvested individuals within a wide hunting season. The largest landowner in Norway, the Norwegian State-Owned Land and Forest Enterprise (hereafter Statskog),

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aims to secure wide public access to hunting (Statskog 2017). In recent years, there has been a rising concern among hunters, managers, ornithologists, and the general public related to decreasing ptarmigan populations (Kaltenborn et al. 2012; Pedersen and Storaas 2013). In Norway, willow ptarmigan was classified as near threatened (NT) in 2015 (Henriksen and Hilmo 2015), following a country-wide population decline during the last decades. For example, in the northern counties of Nordland and Troms, the number of bagged ptarmigan declined from 107,300 during the hunting season of 2000/2001 to 37,750 during 2015/2016 (Statistics Norway 2017a). This has invigorated a debate on the role of sport hunting and the need for improved management strategies. As a consequence, intensive monitoring and hunting restrictions have been applied in many areas (Pedersen and Storaas 2013). However, there is still limited information on the actual impact of hunting and the efficiency of regulations (Hörnell-Willebrand 2005; Sandercock et al. 2011; Willebrand and Hörnell-Willebrand 2001; Willebrand et al. 2011). Several papers have shown a strong relationship between hunting effort and harvest rates, indicating that bag size is determined more by effort than by density of birds (Hörnell-Willebrand 2005; Tomeček et al. 2015; Willebrand et al. 2011). Factors influencing the harvest effort are thus important and may include topography, vegetation, and infrastructure (Brøseth and Pedersen 2000; Lyon and Burcham 1998; Tanner et al. 2016).

Whether harvest is mainly additive or compensatory is influenced by the species' life-history strategy, i.e., compensatory mortality is expected predominantly in small-bodied, short-lived species with high fecundity (Sandercock et al. 2011 and references therein). Sandercock et al. (2011) demonstrated partial compensatory hunting mortality in willow ptarmigan below a harvest rate of 15%, while hunting mortality was additive at 30% harvest. Smith and Willebrand (1999) showed that hunting mortality was additive at a harvest rate of 24%, while Braun and Rogers (1971) suggested that harvesting 30% of the autumn population of White-tailed ptarmigan (*Lagopus leucurus*) had no effect on the breeding density the following spring.

Different harvest strategies have been theoretically evaluated and recommended for willow ptarmigan: constant harvest (a fixed number of individuals are removed annually), threshold harvest (harvesting all individuals above a given threshold), and proportional harvest (harvesting a fixed proportion of individuals) (Aanes et al. 2002; Andersen and Kvasnes 2013; Engen et al. 1997; Fryxell et al. 2005; Lande et al. 1997). However, actual thresholds are commonly unknown due to uncertainty in population estimates and fluctuating population sizes. Few studies have investigated this issue (but see Engen et al. 1997 and Aanes et al. 2002).

In Norway, common restrictions in ptarmigan hunting include daily or seasonal bag limits, prohibiting the use of dogs, geographic zoning, and shortening or delaying hunting

seasons (Aanes et al. 2002; Andersen et al. 2014; Willebrand and Hörnell-Willebrand 2001). Access to hunting, rather than bagging many birds, seems to be most important for hunters, and management that aims to reduce access tends to be very unpopular (Breisjøberget et al. 2017; Wam et al. 2013). Daily bag limits are widely used, but in many cases, harvest is only affected during periods of high population densities, i.e., when restrictions are less important, (Breisjøberget et al. 2017; Guthery et al. 2004; Peterson 2001). Willebrand et al. (2011) found that hunters are more efficient at low population densities, probably because they spent longer days in the field to compensate for few bird encounters. The largest potential effect of harvest will thus occur at low densities, making small game management at low population density difficult.

Harvest rate is the ratio of the number of harvested birds and population abundance. The numbers harvested, in turn, is determined by hunting effort (the cumulative number of hunters per unit area) and their catch-per unit effort, i.e., birds shot per hunting day. These components may be influenced by several interacting factors. For instance, variation in hunting effort may be influenced by factors related to the accessibility of the hunting areas, e.g., infrastructure, topography, and distances to cabins (Gratson and Whitman 2000; Thomas et al. 1976). Catch per unit effort may be influenced by both bird density, vegetation, and topography (Brøseth and Pedersen 2010; Willebrand et al. 2011). Hence, in order to disentangle the relative importance of different factors affecting ptarmigan harvest, we focused on three aspects: (1) hunting effort; (2) hunter efficiency, i.e., catch per unit effort; and (3) ptarmigan harvest rate. We expected hunting effort to be mainly determined by factors associated with the accessibility to the hunting areas, i.e., infrastructure, and that catch per unit effort was determined by population abundance, topography, and vegetation structure. We expected harvest rates to vary spatially and annually according to ptarmigan density, i.e., that harvest rates are highest in areas of low ptarmigan density.

Study area

This study was carried out during 2013–2016 on Statskog's land in the eastern parts of Nordland and Troms counties in northern Norway, covering 26,828 km² (Fig. 1). Per 1 January 2017, the two counties had a human population density of 6.3 inhabitants per square kilometer, mainly residing in small towns and villages (Statistics Norway 2017b). Below the tree line, the vegetation is dominated by mountain birch (*Betula pubescens*) with some coniferous forests consisting of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Above the tree line, alpine heath, shrubs, and patches of dwarf birch (*B. nana*) dominate. The climate is continental with low annual precipitation, cold winters (− 5 to − 10 °C in January) and moderately

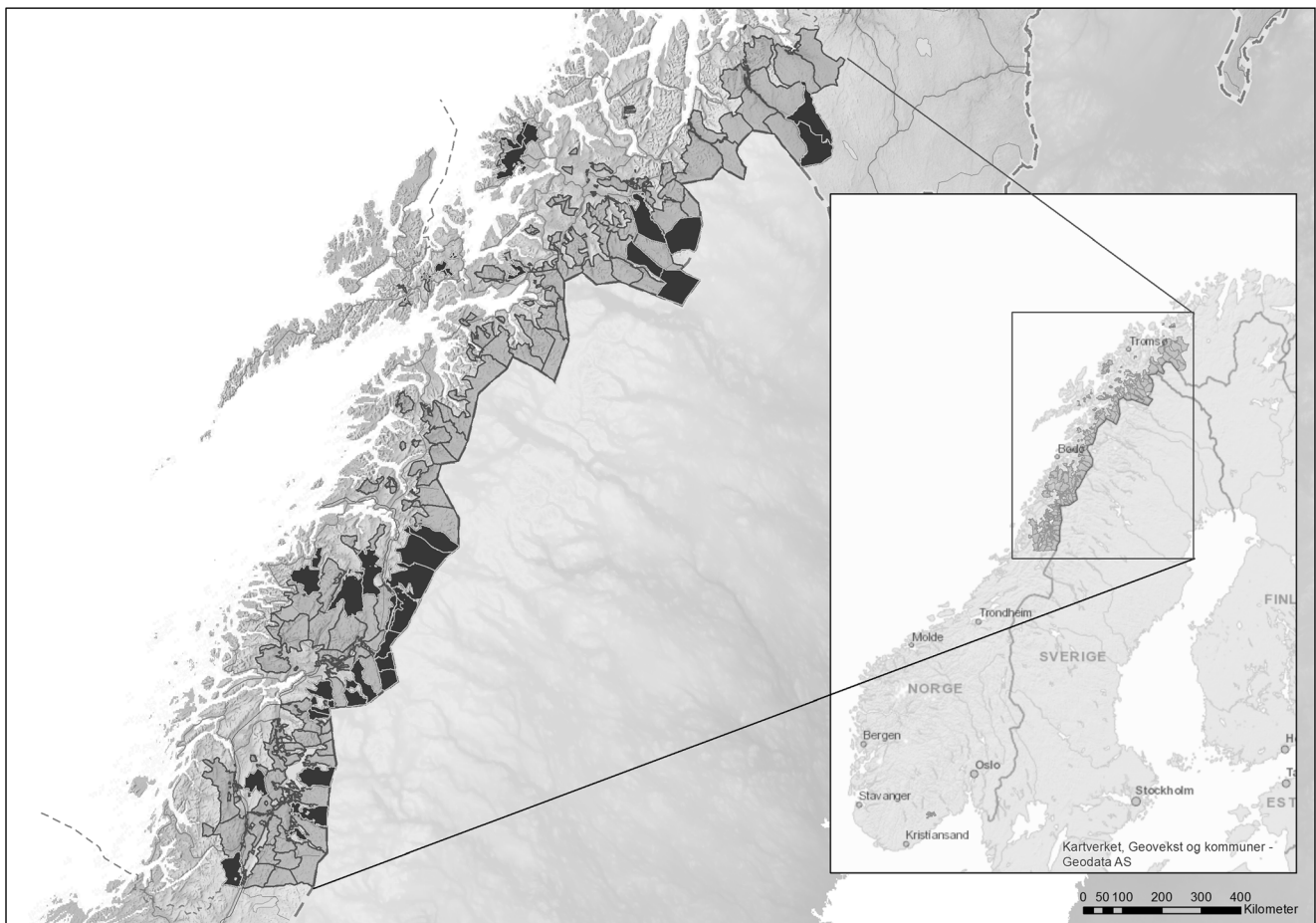


Fig. 1 Map of the study area showing 162 hunting blocks for small game on state-owned land in Nordland and Troms Counties, Norway. We have willow ptarmigan density estimates from the 36 areas marked in black

warm summers (14–15 °C in July), (Norwegian Meteorological Institute 2017). The mountainous landscape is naturally fragmented with valleys surrounded by mountain tops up to 1900 m asl in Nordland. Main predators on ptarmigan are large raptors (golden eagle *Aquila chrysaetos* and gyrfalcon *Falco rusticolus*) in addition to red fox (*Vulpes vulpes*) and stoat (*Mustela erminea*). Hunting is performed by hunters on foot with shotguns, with or without a pointing dog for locating and flushing the birds. Accessibility to the areas varies mainly by the distribution of forest roads or cabins.

We collected annual harvest statistics from 162 hunting blocks ranging in size from 8 to 667 km² (mean = 167 km², SD = 139). In addition, we obtained estimates of ptarmigan population density from 36 of these blocks. We limited the period of this study from the opening of the hunting season 10 September until 30 September, before brood-break up and natal dispersal (Brøseth et al. 2005; Smith 1997). This is the most intensive hunting period as studies have shown that 2/3 of all harvest takes place during the first 10 days in both Sweden and Norway (Kastdalen 1992; Willebrand 1996). Daily bag limits varied between 1 and 6 birds among years.

Methods

Willow ptarmigan population surveys

We surveyed ptarmigan populations in 36 hunting blocks each year in early August 2013–2016. We followed a distance sampling line transect protocol with parallel transect lines placed 500 m apart (Buckland et al. 2001; Pedersen et al. 1999; Pedersen et al. 2004b; Solvang et al. 2007). The counts were performed by volunteers from the Nordland and Troms Chapters of the Norwegian Association of Hunters and Anglers using dogs searching both sides of the transect lines. The dog handlers recorded the observed birds at each encounter (chicks, adult females/males, and birds of unknown age/sex) and measured the perpendicular distance in meters from the birds to the transect line. Pedersen et al. (1999) tested this procedure with radio-collared willow ptarmigan and found the technique suitable and in accordance with the assumptions of the distance sampling method. The total transect length in each survey area varied between 17 and 167 km (median = 53.5, mean = 58.0, SD = 34.2), with estimated

densities (sum of young and adult birds) between 2.1 and 132.5 birds/km² (median = 12.4, mean = 19.7, SD = 25.2).

Bag records and hunting effort

We used Statskog's web-based bag record system where the hunters had to submit a mandatory and detailed bag report every 14 days of hunting in order to continue hunting. Bag records with the number of ptarmigan killed ($n_{\text{total}} = 29,749$) and days hunted ($n_{\text{total}} = 44,875$) were received from 91 to 97% of small game hunters in all areas (Table 1), thus providing detailed information about hunters harvest and effort. We did not extrapolate the missing data, due to the small proportion that had not reported their bag, and the assumption that this group had bagged few birds (Asferg 1996). We calculated the abundance of ptarmigan in each hunting block by multiplying autumn density (young and adult birds/km²) with the total area of suitable ptarmigan habitat (see description of habitat suitability below). We defined hunting effort as the total number of hunting days/km². Catch per unit effort (henceforth CPUE) was defined as ptarmigan harvested divided by the cumulative number of hunting days. Harvest rate was defined as the proportion harvested in each hunting block where ptarmigan population densities had been estimated, i.e., the number of birds shot divided by the estimated abundance.

Environmental variables

As proxies for hunter accessibility to ptarmigan hunting areas, we calculated the mean distance to roads and cabins within each hunting block. We included all passable (for vehicles) roads > 50-m length extracted from the dataset Transport Networks and cabins from the Cadaster (The Norwegian Mapping Authority 2017b, c). There are many building types in the Cadaster, but we included only those we consider as potential starting points for ptarmigan hunting trips, i.e., recreational homes, tourist cabins, rental cabins, and forest huts. Slope and vector ruggedness measures were estimated from a digital elevation model (DEM) with a resolution of 30 × 30 m (The Norwegian

Table 1 Summary showing total number of hunters, effort (total hunting days), bag (total harvested willow ptarmigan), density (mean population of ptarmigan/km² in 36 hunting blocks with density estimates) and CPUE (mean ptarmigan shot per hunter/day in every hunting block), the two latter with median values in parentheses, from 162 hunting blocks on state-owned land in North-Norway during September 10–30, 2013–2016

Year	Hunters	Effort	Bag	Density	CPUE
2013	2548	9485	4012	17.60 (12.60)	0.35 (0.26)
2014	4426	15,271	11,647	16.58 (16.90)	0.59 (0.44)
2015	4058	12,878	8355	27.59 (14.40)	0.47 (0.31)
2016	2761	7241	5735	15.97 (9.35)	0.65 (0.67)

Mapping Authority 2017a). Slope describes the average steepness of the hunting block in degrees (0–90). The vector ruggedness measure (VRM) (Sappington et al. 2007) is a combination of slope and aspect from the DEM and was calculated among nine neighboring pixels in the DEM. The VRM ranges from 0 to 1 where 1 is a complex landscape with high topographic variation commonly termed as rugged (Sappington et al. 2007). We calculated the proportion of forest cover in each block based on a digital vegetation map, NORUT (Johansen 2009) with a resolution of 30 × 30 m. Lastly, we used a resource selection map developed for willow ptarmigan to calculate the aerial coverage of suitable habitat (Kvasnes and Nilsen 2017). Predictions from the resource selection function (RSF) developed by Kvasnes and Nilsen (2017) were quantile binned into five categories from low to high relative selection. The lowest ranked bin was then separated in two new bins where the 25% lowest predictions were placed in a new bin 1 and the remaining 75% predictions placed in new bin 2. This resulted in six categories of relative probability of willow ptarmigan selection. We considered map predictions in the lowest ranked bin (new bin 1) as unsuitable habitat for willow ptarmigan and the remaining categories (2–6) as suitable habitat.

Statistical analysis

Willow ptarmigan density from the line transects was estimated using the add-on library Distance (Miller 2017) in the statistical program R version 3.3.3 (R Core Team 2017). All other data handling and analyses were also conducted using program R. We estimated mixed effects logistic regression models to model effort and CPUE using the *glmer* command in the *lme4* package (Bates et al. 2015). Each of the two global models were estimated with a negative binomial family distribution (due to overdispersion), and with the same explanatory variables: density, mean distance to roads, mean distance to cabins, ruggedness (VRM), mean slope in degrees, and proportion of forest, with year and hunting block as a random effects (Tables 2 and 5). We used the accumulated number of hunting days, with the area of suitable willow ptarmigan habitat as offset, when modeling hunting effort. We removed one outlier from the dataset because this hunting block ("Leina") had high hunting activity due to easy access by boat despite a long distance to roads (> 5.5 km). For modeling CPUE, we used the total number of harvested birds as a response variable with the accumulated days of ptarmigan hunting as an offset. When modeling harvest rate, the response variable was the total number of ptarmigan harvested, and the total estimated ptarmigan population size was the offset variable. We performed an automated model selection with subsets of the supplied global model using the *dredge* function with a limit of five terms in a single model. To incorporate model selection uncertainty, we used the function *model.avg* in the MuMin package for the top models returning a conditional and a full model (Burnham and Anderson 2002). We followed Nakagawa and

Table 2 Results from the model selection based on Akaike information criterion (AIC) within $\Delta AIC \leq 6$, comparing models of how hunting effort on willow ptarmigan is affected by forest cover, mean distance to cabins,

terrain slope, terrain ruggedness, and mean distance to roads within 162 hunting blocks on state-owned land in North-Norway during September 10–30, 2013–2016

Model	Forest cover	Distance to cabins	Terrain slope	Terrain ruggedness	Distance to roads	df	AIC	ΔAIC	w_i
52	x	x			x	7	5469.9	0.00	0.34
56	x	x	x		x	8	5470.3	0.49	0.27
60	x	x		x	x	8	5471.7	1.86	0.13
51		x			x	6	5472.9	3.06	0.07
50	x				x	6	5473.7	3.83	0.05
54	x		x		x	7	5474.4	4.54	0.04
55			x		x	7	5474.5	4.60	0.03
59		x		x	x	7	5474.8	4.95	0.03
49		x			x	5	5475.6	5.76	0.02
58	x			x	x	7	5475.7	5.87	0.02

Freckleton (2011) and used the full model since our aim was to determine which factors have the strongest effect on the response variable. We used a 95% confidence level as a cut-off criterion to delineate the top model set (summed weight) according to Burnham and Anderson (2002). The performance of the models were assessed based on their AIC values (Burnham and Anderson 2002).

Results

Hunting effort

The average hunting effort in all the 162 hunting blocks during the study period was 1.27 (median = 0.86, SD = 2.08) days/km² (Appendix Table 8 in ESM). The total hunting effort in all hunting blocks varied markedly among years (see Table 1). The most parsimonious model explaining how hunting effort varied between the hunting blocks included the

proportion of forest cover and the distance to cabins and forest roads, (Tables 2, 3, and 4). The model averaged parameter estimates showed that efforts decreased with increasing distances to roads and cabins, and decreased with increasing forest cover (Tables 3 and 4).

Catch per unit effort

The average number of ptarmigan shot per hunting day (CPUE) in the 162 hunting blocks was 0.77 (median = 0.71, SD = 0.48, see Appendix Table 8 in ESM). The most parsimonious model explaining how CPUE varied between hunting blocks included terrain slope, ruggedness, and distance to forest roads (see Tables 5, 6, and 7). The effect of terrain slope on CPUE was negative (M61, AIC; 4393.8), whereas the distance to roads had a positive effect, i.e., CPUE was higher in areas with longer distances to roads (Tables 6 and 7). For the subset of the data with access to ptarmigan density estimates, we found a marked positive effect of density on CPUE (Fig. 2).

Table 3 Parameter estimates for the three best models (i.e., lowest AIC values) in the global set of models presented in Table 2, within 162 hunting blocks on state-owned land in North-Norway during September 10–30, 2013–2016. Parameters are estimated based on maximum likelihood

Model/term	Parameter	Parameter value (SE)
52	Forest cover	-0.16 (0.07)
	Distance to cabins	-0.18 (0.08)
	Distance to roads	-0.31 (0.09)
56	Forest cover	-0.19 (0.07)
	Distance to cabins	-0.19 (0.08)
	Terrain slope	-0.09 (0.02)
60	Forest cover	-0.17 (0.07)
	Distance to cabins	-0.19 (0.08)
	Terrain ruggedness	-0.03 (0.07)

Table 4 The relative importance of parameters presented in Tables 2 and 3 based on the sum of Akaike weights across all models where the parameter is present (Burnham and Anderson 2002), and model averaged parameter estimates, within 162 hunting blocks on state-owned land in North-Norway during September 10–30, 2013–2016

Parameter	Relative importance	Model averaged parameter (SE)
Distance to roads	1.00	-0.32 (0.10)
Distance to cabins	0.88	-0.16 (0.09)
Forest cover	0.84	-0.14 (0.09)
Terrain slope	0.34	-0.03 (0.06)
Terrain ruggedness	0.18	0.00 (0.03)

Table 5 Results from the model selection based on Akaike information criterion (AIC) within $\Delta AIC \leq 6$, comparing models of how CPUE on willow ptarmigan is affected by forest cover, mean distance to cabins,

terrain steepness, terrain ruggedness, and mean distance to roads within 162 hunting blocks on state-owned land in North-Norway during September 10–30, 2013–2016

Model	Forest cover	Distance to cabins	Terrain slope	Terrain ruggedness	Distance to roads	df	AIC	ΔAIC	w_i
61			x	x	x	7	4393.8	0.00	0.27
62	x		x	x	x	8	4394.4	0.64	0.19
63		x	x	x	x	8	4394.9	1.16	0.15
53			x		x	6	4395.3	1.54	0.12
55		x	x		x	7	4395.8	2.03	0.10
54	x		x		x	7	4396.5	2.75	0.07
56	x	x	x		x	8	4396.9	3.18	0.05
47		x	x	x		7	4397.7	3.97	0.04
39		x	x			6	4399.3	5.57	0.02

Harvest rate

During 2013–2016, the average harvest rate was 0.076 (median = 0.055, min = 0.001, max = 0.245) in the 36 hunting blocks where estimates of ptarmigan density were available (Appendix Table 8 in ESM). In only two hunting blocks, the average harvest rate exceeded 15%. Based on CPUE predicted from the models described above, we predicted ptarmigan removal within a range of densities from 0 to 30. As illustrated in Fig. 3, removal increased markedly below ptarmigan densities of ca 10 birds/km². Hence, hunters bagged a larger proportion of the population in areas of relatively low density.

Discussion

In accordance with our prediction, hunting effort decreased with distance to roads and cabins, and similar results were reported in studies of hunting impact on ruffed grouse (Fischer and Keith 1974; Small et al. 1991), willow ptarmigan

(Brøseth and Pedersen 2000), and elk (*Cervus elaphus nelson*) (Lyon and Burcham 1998). Brøseth and Pedersen (2000) found that the area around the starting point of the hunting trip had the highest hunting activity. The wide distribution of construction and forest roads in our study area provide easy access for hunters and may result in a more homogenous and high hunting pressure in large parts of the hunting blocks. Before this infrastructure was established, much of the hunting pressure may have been concentrated close to human settlements, whereas the remote areas were probably left relatively undisturbed. With a heterogeneous distribution of hunting activity, source-sink dynamics may arise (Novaro et al. 2005). In a source-sink system, the persistence of populations in habitat sinks will depend on dispersal from high-quality habitat sources (Novaro et al. 2005). Kastdalen (1992) and Willebrand and Hörnell-Willebrand (2001) found a close relationship between hunting effort and harvest rates on forest grouse. Thus, reducing the number of hunters in hunting blocks with many roads and cabins may therefore be an appropriate intervention to reduce harvest. Alternatively, allowing hunting, but restricting access to roads, may concentrate hunting efforts in smaller parts of the blocks (i.e., sinks) while remote areas are left undisturbed (i.e., sources).

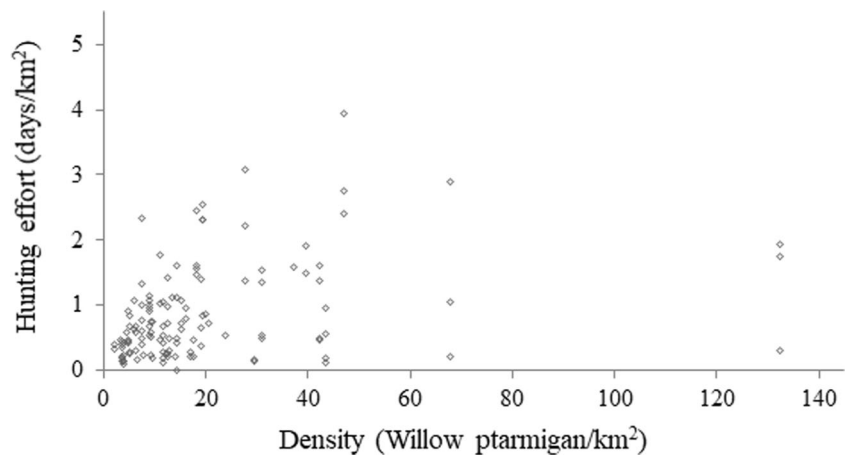
Table 6 Parameter estimates for the three best models (i.e., lowest AIC) values in the global set of models presented in Table 5, within 162 hunting blocks on state-owned land in North-Norway during September 10–30, 2013–2016. Parameters are estimated based on maximum likelihood

Model/term	Parameter	Parameter value (SE)
61	Terrain slope	−0.22 (0.08)
	Terrain ruggedness	−0.11 (0.07)
	Distance to roads	0.22 (0.10)
62	Forest cover	0.07 (0.08)
	Terrain slope	−0.20 (0.03)
	Terrain ruggedness	−0.12 (0.07)
63	Distance to roads	0.26 (0.11)
	Distance to cabins	0.06 (0.08)
	Terrain slope	−0.19 (0.03)
	Terrain ruggedness	−0.03 (0.07)

Table 7 The relative importance of parameters presented in Tables 5 and 6 based on the sum of Akaike weights across all models where the parameter is present, and model averaged parameter estimates, within 162 hunting blocks on state-owned land in North-Norway during September 10–30, 2013–2016.

Parameter	Relative importance	Model averaged parameter (SE)
Terrain slope	1.00	−0.23 (0.07)
Distance to roads	1.00	−0.21 (0.05)
Terrain ruggedness	0.69	−0.08 (0.07)
Distance to cabins	0.36	0.02 (0.05)
Forest cover	0.26	0.02 (0.03)

Fig. 2 The relationship between hunting effort and density in the 36 hunting blocks with density estimates on state-owned land in North-Norway, 2013–2016

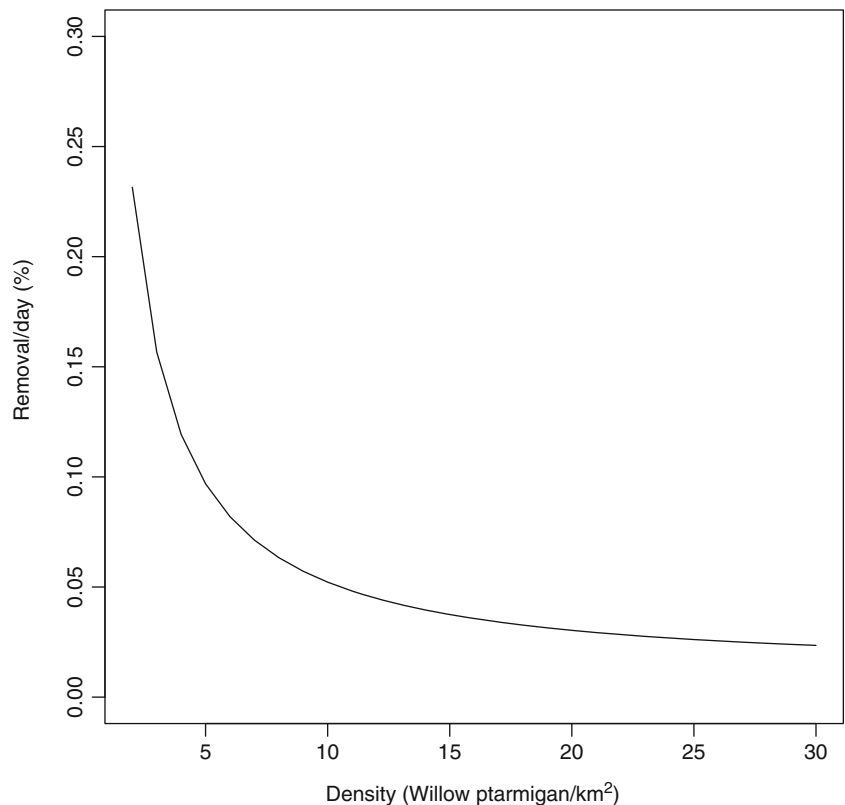


Contrary to our predictions, CPUE increased with distance to roads. An explanation may be that more dedicated hunters seek areas with few other hunters, more birds and less previous disturbance. Wam et al. (2013) showed that the most eager hunters were crowd-avoiding, and Brøseth and Pedersen (2000) found that ptarmigan hunters on average walked long distances and hunted long days. Furthermore, Brøseth and Pedersen (2010) showed that willow ptarmigan selected dense habitat with fewer disturbances during the hunting season. Moreover, a study on grouse displacement behavior and survival revealed overall negative effects of anthropogenic structures, i.e., roads and oil installations (Hovick et al. 2014). We propose that

the hunters that moved further from roads may have benefitted from higher bird densities and few encounters with other hunters.

Overall, the harvest of ptarmigan on public land in Nordland and Troms counties the during first 3 weeks of the season was found to remove < 10% of the autumn population in the hunting areas where we could estimate ptarmigan abundance. This is the same level as estimated by Hagen (1952) more than 60 years ago, but he added that an additional 10% was snared during winter. Snaring is still legal but numbers harvested by this method are insignificant today. A harvest mortality of 10% in small bodied grouse such as ptarmigan is probably compensated to a large extent, as complete additive mortality has not

Fig. 3 Predicted proportions of the ptarmigan population shot per day on 36 hunting blocks in North-Norway, 2013–2016. Based on the models of CPUE, daily removal rates of ptarmigan are estimated by dividing predicted CPUE values with estimated densities within a range of 0–30 birds/km². All the variables included in the model but not presented here, were standardized at their mean



been observed at harvest rates below 20% (Braun and Rogers 1971; Sandercock et al. 2011; Smith and Willebrand 1999). In other small game birds, the extent of compensation from harvesting has been less clear (Ellison 1991; Williams et al. 2004; Small et al. 1991). In larger species with slower population turn-over rates, harvest mortality has been inferred to be more additive; in greater sage-grouse *Centrocercus urophasianus* Sedinger et al. (2010), showed that hunting mortality was additive above 10–15% harvest.

Harvest rates varied greatly between hunting blocks. However, the blocks with the highest harvest rates had relatively low ptarmigan densities. Based on our models, the predicted daily removal of ptarmigan increased markedly when densities became lower than ca 10/km². A similar pattern, i.e., inversely density-dependent harvest rates, was previously reported by Willebrand et al. (2011) and Eriksen et al. (2017). These patterns of density dependence have also been observed in natural predator-prey systems. For instance, a recent experimental study compared different modes of wolf *Canis lupus* predation impact on moose *Alces alces* (Serrouya et al. 2015). The authors found that the best model of moose population dynamics included depensatory predation mortality, i.e., mortality increased when densities declined. This, in turn, was caused by type II functional and numerical responses of the predators, which entails that both kill rates and predator abundances remain relatively stable over a wide range of prey densities (see also Nilsen et al. 2009). At high prey densities, predator functional responses become satiated by handling time, whereas numerical responses may stabilize due to social interactions (Cubaynes et al. 2014). The two main aspects of our study, hunting effort and CPUE, resemble numerical and functional responses, respectively, and the numbers of ptarmigan harvested are equivalent to the total response. As in the wolf-moose system (Serrouya et al. 2015), hunting mortality may be higher at low ptarmigan densities due to non-linear relationships between ptarmigan density and both CPUE and hunting effort. When a red-listed species is being hunted, the general public and conservation organizations tend to explain the declining population trend on overharvest. With the current management system, the annual harvest rates of willow ptarmigan in Nordland and Troms was relatively low in the years studied here and probably partially compensatory (Sandercock et al. 2011). However, in order to reduce the risk of overharvest, ptarmigan populations need to be carefully monitored and hunting restrictions should be considered at low densities.

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Compliance with ethical standards

This article does not contain any studies with human participants or animals performed by any of the authors. The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Conflict of interest The authors declare that they have no conflict of interest.

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