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Using empirical data to quantify
implementation uncertainty in
small game harvest management

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Abstract

Sustainable resource management requires that managers are able to control the harvest offtake. This is challenging in systems with multiple objectives and great uncertainties, which is often the case in small game harvest management. The difference between the strategies implemented by management and the actual harvest bag size (i.e. implementation uncertainty) may be substantial, but few studies have so far explored this. In this study I investigated how different management strategies and system parameters affected actual offtake in willow ptarmigan (*Lagopus lagopus* L.) harvest, using empirical data and simulating performance of strategies and risk of harvest above selected harvest rate thresholds under varying population states. I used data from nine independently managed state owned hunting areas in Central and South Norway. Two paths were explored; analysing harvest directly (as bagged birds per km²) and indirectly by combining models for hunting pressure (hunting days per km²) and hunter efficiency (bagged birds per hunting day). My results show that the best model explaining bagged birds per km² included total allowable catch per km² (TAC) set by managers and willow ptarmigan density, where number of bagged birds at high TAC and low density was comparable to the number at lower TAC and higher density. Hunting pressure was best explained by number of sold permits per km² and type of quota, while the best hunter efficiency model only included density. The results strongly suggested that hunters were relatively more effective at low densities and removed a higher proportion of birds from the area when densities were low. The simulations with alternative harvest management scenarios revealed that this effect was present for all strategies, whether managers used a constant harvest strategy (TAC or effort) or had adapted their strategy to the density estimates. High risks at lower densities of harvest rates above the levels associated with sustainability, indicate the need for knowledge of population state before hunting permits are sold, and urges the use of threshold strategies to balance the competing objectives of hunting opportunities and sustainability. Quantified risks of harvest rates over a range of densities enable informed manager decisions of trade-offs between competing objectives. This study is one of the first approaches to quantifying implementation uncertainty in small game harvest, and shows how estimates from empirical analyses may be used as elements of a full management strategy evaluation (MSE) framework.

Keywords: hunter efficiency, MSE, simulation, suitable habitat, sustainable exploitation, willow ptarmigan

Introduction

Small game harvest for recreational purposes is a popular activity in many countries, and has ecological, sociocultural and economic implications (Storch 2007; Newey, Dahl & Kurki 2010). Management strategies are differing between regions and species (Willebrand & Hörnell 2001; Marboutin *et al.* 2003; Nichols *et al.* 2007), and ownership structures have impact on the management objectives. In many countries the majority of hunting areas are privately owned (e.g. in the UK), while in other areas (e.g. North America and partially Fennoscandia) hunting areas or hunting rights are state owned (Mustin *et al.* 2011). The latter often implies that hunting rights is perceived as a common good, although often with some restrictions to anticipate “the tragedy of the commons” (sensu Hardin 1968). Many of these state controlled areas share similar management features, with common practice of selling hunting permits accompanied by individual day or period quotas (Leal & Grewell 1999; Andersen *et al.* 2014). In Norway, managers of state owned land are required by laws and regulations to provide hunting opportunities to the public (<https://lovdata.no/lov/1975-06-06-31>), while also ensuring sustainability for the hunted population (<https://lovdata.no/lov/2009-06-19-100>). In addition, considering that small game hunting in Norway is a recreational activity, the traditional harvest models optimising the yield (e.g. Lande, Sæther & Engen 1997) are not necessarily the most suited. An approach including social aspects in addition to the ecological and economic, may be more appropriate for these kinds of systems (Wam, Pedersen & Hjeljord 2012).

Small game harvest managers set restrictions to improve sustainability of hunting, but they often lack methods that give them direct control of the actual harvest offtake (unless quotas are set very low or hunting is banned). This is apparent from a number of studies involving harvest bag size or population responses to harvest (e.g. Connelly *et al.* 2003; Patton *et al.* 2010). Such partial controllability seems evident also in recreational fresh water fishing (Allen, Miranda & Brock 1998), and is likely to be a common feature of systems where detailed management of both resource and resource users is difficult. Unlike big game hunting where the number, sex and age of individuals to be harvested can be decided more accurately (Nilsen & Solberg 2006), most small game harvest systems are often associated with substantially more uncertainty when it comes to detailed control of harvest. Until now, management systems have often incorporated population dynamic uncertainties to a much larger extent than other sources of uncertainty (Milner-Gulland, Bunnefeld & Proaktor 2009). An important part of harvest management is understanding what drives the actual harvest, but

uncertainties on the path between population estimates, management actions and harvest yields also should be focused on (Milner-Gulland *et al.* 2010). Research on the difference between management strategies and actual harvest, commonly termed ‘implementation uncertainty’ (Christensen 1997), is generally rare (Milner-Gulland *et al.* 2010). Studies of implementation uncertainty has often focused on to which extent resource users comply with control rules (Bunnefeld, Hoshino & Milner-Gulland 2011). While this is important in many systems, other forms of implementation uncertainty may be of greater concern in other situations. In management of large carnivores an important aspect of implementation uncertainty is when hunters fail to obtain the set quota, hence management targets of removal are not met (Bischof *et al.* 2012). In recreational small game harvest the objective is the opposite, i.e. avoiding overexploitation while still providing hunting opportunities to the public. To date, most studies on the link between management decisions and actual harvest rate do not address the issue of implementation uncertainty, despite being of great importance (Deroba & Bence 2008).

A framework that specifically includes uncertainties is Management Strategy Evaluation (MSE), which enables managers to explore outcomes compared to their objectives (Smith, Sainsbury & Stevens 1999; Bunnefeld, Hoshino & Milner-Gulland 2011). MSE investigates effectiveness for alternative management strategies through simulations, while incorporating lack of accurate knowledge (Milner-Gulland *et al.* 2010). This framework has so far not had many applications in terrestrial systems so far, but has proven to be a useful tool in situations with lack of precise information of a system (Edwards *et al.* 2014). Small game harvest is also believed to be appropriate for this framework, given the uncertainties in monitoring, management, implementation and population dynamics. This may yield a more holistic view of the effect of harvest, and will be a valuable tool for exploring different management scenarios. An important step in this process is to explore management strategies and implementation uncertainty for exploited populations.

Long term sustainability of the harvested population is a main objective for any harvest management strategy. Exploring all parts of an MSE framework, including levels of sustainable harvest, is beyond the scope of this study. Here I investigate the path between management decisions and harvest, and explore how the implementation uncertainty affects the ability to control offtake. I am using willow ptarmigan (*Lagopus lagopus* L.) as a model species for exploring the drivers of small game harvest, seeking to find functions that predict the number of bagged birds. Willow ptarmigan is a medium sized tetraonid (Pedersen &

Karlsen 2007), and harvest of the species is a highly relevant topic at a Fennoscandian scale. It was recently listed as near threatened (NT) in the Norwegian Red List of Endangered Species (Henriksen & Hilmo 2015) as a result of a long-term decrease in abundance (Kålås *et al.* 2014; Lehikoinen *et al.* 2014). Ptarmigan hunting pressure has seen an increase over time (Storch 2007), and in some cases harvest rates on willow ptarmigan as high as 50 % have been reported (Kastdalen 1992; Smith & Willebrand 1999). As harvest mortality to a large extent is additive to natural mortality (Pedersen *et al.* 2004; Sandercock *et al.* 2011), sustainable harvest management is imperative.

The data utilised in this study is from state owned hunting areas with a clear ‘common good’ strategy. Their harvest regulations are evaluated by exploring the link between management decisions and their implementation, and management decisions are assumed to be linked to the current population state (primarily willow ptarmigan density). Parameters included for analyses are all expected to have a potential impact on harvest, and include population estimates (widely assumed to be correlated with harvest, e.g. Cattadori *et al.* (2003)), different harvest limitations and hunting pressure (implicitly assumed to affect harvest), habitat structure (as indicated by Pedersen *et al.* (1999)) and weather (may affect performance or effort). The target here is not to identify all possible predictors that might be related to harvest bags, but to discover the best model among the selected parameters. Best functions for predicting number of bagged birds are further incorporated with their uncertainties into simulations, revealing how several common management strategies lead to a varying level of harvest at different population estimates.

A prerequisite for sustainable harvest management is to understand how the management strategies affect the actual harvest offtake. The objectives of this study are to explore this by

- 1) empirical evaluation of several common harvest regulations and strategies for willow ptarmigan in Norway, focusing on i) what was the role of management strategies and system parameters in the observed harvest (i.e. number of birds shot per km²), and ii) how did managers adapt their strategy in relation to population changes,
- 2) modeling implementation uncertainty under different harvest decision scenarios and population states, as part of an MSE framework with estimates from the empirical data, by quantifying risk of exploitation above specific harvesting thresholds.

Materials and methods

Study area and period

I approached all of the 23 management units (MUs) currently registering population estimates in a nationwide database (Hønsefuglportalen, <http://honsefugl.nina.no>; Nilsen, Pedersen and Vang (2013)). These 23 MUs together represent a high proportion of the areas offering willow ptarmigan hunting of some magnitude. An additional eight MUs involved in a previous study (Pedersen & Storaas 2013) were also contacted, but this group were all either non-respondents or lacked the required data. 16 MUs provided data for this study, but as the data was initially collected for management purposes, not all managers had gathered all types of data. Data was collected as anonymised raw data or as partial or complete variable values. For each MU there were several points of contact after the first reception of data, to validate data quality and collection method and to ensure comparability between data from different areas. National regulations limit hunting season from September 10th to February 28th (<https://lovdata.no/forskrift/2012-03-01-190>), but MUs usually implement stronger restrictions and collect data more extensively in the first month of the season. Also considering that most of the birds are bagged in this period (Kastdalen (1992); supported by raw data in this study) and the added population estimate uncertainty arising from movements of birds between areas later in the season (Brøseth *et al.* 2005), I analysed data only from the early hunting period. Using data from 2008-2015, a total of 42 observations within nine MUs were included in the analyses (Appendix Fig. S1), not including two observations removed due to outliers (described later). In all areas willow ptarmigan hunting was performed as walked-up hunting with shotguns, with or without use of pointing dogs, and none of the areas have had extensive predator control or habitat management. Generally it is easier to obtain access to hunting opportunities for locals in an area, but the dominant feature in all areas is that most hunters are visitors from other municipalities (Wam, Andersen & Pedersen 2013), making it likely that hunters are undistinguishable between areas.

The study areas are of different sizes and parameter values needed to be scaled for this. All MUs are located mainly in the northern boreal and alpine bioclimatic zones (Moen 1999). As willow ptarmigan only utilise parts of this habitat (Pedersen & Karlsen 2007), suitable areas sizes were obtained to reduce an otherwise large bias. All habitat and area size estimations were performed in ArcGIS 10.3 (Esri Inc., www.esri.com). Shapefiles for MU borders publicly available from The Norwegian Mapping Authorities (<http://kartverket.no/Kart/>) were

altered correspondingly to hunting refuges and other area reductions or expansions. Based on satellite vegetation maps (Johansen, Aarrestad & Øien 2009), I used a map of bioclimatic zones (Blumentrath & Hanssen 2010 after Moen 1999) to remove high and middle alpine zones, since willow ptarmigan generally prefer the lower zone (Pedersen & Karlsen 2007). The method is an adaption from Gjershaug *et al.* (2010), who considered willow ptarmigan habitat as all lower alpine areas plus forests dominated by birch (*Betula pubescens* Ehrh.). While this definition seems reasonable in a large scale study over a variety of landscapes, even more precise estimates could be calculated as the study areas were exclusively in or near mountains. By including suitable bogs and other open areas below the lower alpine zone, and excluding all lakes and rivers, I obtained an approximation of area sizes reflecting suitable habitat for willow ptarmigan (for a complete description of vegetation types in my analysis, see Appendix Tab. S1).

Harvest and management strategy data

Data from MUs was collected primarily by e-mail, with supporting phone calls. I included only year by MU combinations that contained all the necessary information (Table 1). Number of bagged birds and active hunting days were scaled by the proportion of responding hunters (range 0.37-1.00, mean 0.71). The number of sold hunting permits would be expected to be important for both harvest offtake and effort. Permits were valid for five or seven days, with the exception of a small number of permits sold for ten or fifteen days in two of the MUs. Initial data exploration did not indicate differences between these groups large enough to raise concerns, and they were not separated for the analyses. In three MUs the number of local permits had not been recorded for the early years. In these cases I assumed an equal proportion of locals between years and estimated the number of missing permits from the years with complete records (9-14 % added). The MUs differ in length of the period they distribute hunters during the first month, from 10 to 25 days of ‘early hunting period’. As most birds are probably shot in the beginning (Kastdalen 1992), length of prime season might affect the total harvest offtake. A related parameter that was considered was the start of the hunting season. The MUs either provide hunting opportunities from September 10th, or they postpone the start with five to ten days (categorised in the analyses as ‘early’ or ‘postponed’ start).

Data on the proportion of hunters using pointing dogs is rarely available, but it seems fair to assume that this proportion is equal between areas, thus being of less importance here. In all the study areas willow ptarmigan was by far the most important hunted small game species (based on information from the MUs). Sold permits were generally valid for all small game, where other species were mostly a bycatch. Possible bias caused by variations in amount of this bycatch is not considered. Quotas were of three types; daily quotas (bag-limits), period quotas and two observations with both the previous types simultaneously. I did not include quota sizes directly in the harvest analyses because of relatively few observations within each quota type and limited amount of variation in period quota sizes. Instead I used total allowable catch scaled by area size (TAC) as a function of sold permits and quota sizes. For period quotas $TAC = \text{number of sold permits} \times \text{quota size}$, while for day quotas $TAC = \text{number of hunting days in sold permits} \times \text{quota size}$. For the combination quotas, TAC was calculated similarly to period quotas, as this represented the maximum possible catch in these two cases. Revealing the impact TAC had on harvest is of major importance, as it incorporates the two main strategies managers apply to restrict harvest; restricting effort and restricting bag size.

System data

Estimates of population density for willow ptarmigan were obtained through line transects, following distance sampling methods (Thomas *et al.* 2010). In August each year, volunteer personnel used trained pointing dogs to search both sides of the transect line, and recorded cluster size and perpendicular distances to observed birds. This procedure has been shown to be a suited variation of distance sampling techniques, respecting the assumptions of the method (Pedersen *et al.* 1999). The nationwide database for population estimates (Nilsen, Pedersen & Vang 2013) contained raw data from line transects traversed in many of the years for my study areas. Missing records were obtained from the MUs, either as spreadsheets or the original field forms. Three data entries contained coordinates of observed birds, but without a cluster size. Here the minimum possible cluster size (i.e. 1) was entered, assuming this alteration affected the results less than deleting the observation.

Line transects have been positioned by the respective MUs (often in cooperation with research institutions), and visual inspection of line placement according to the suitable habitat analyses supported an assumption of transects being representative for the terrain. The total data set

(n=2885) was analysed in R version 3.2.3 (R Core Team 2015), using the package ‘Distance’ (Miller 2015). Each year by management unit (n=42) was analysed separately, as the intention here was to provide independent population estimates for each observation. There is notable uncertainty in the data, partially a result of number of bird spottings within each management unit often bordering the recommended minimum value of 40 to 60 observations (Buckland *et al.* 1993). As there is no fixed line width and some dogs might have searched wider than others, I chose to truncate the highest 10 % of observations in each analysis. To avoid overfitting models, I used a half-normal detection function for all (assuming a fixed slope of the detection curve and only estimating the scale), shown in previous studies to be suitable (Pedersen *et al.* 1999). By this I avoid that model selection is affected by small changes in amount of data, which I consider important given the uncertainties. Further, by applying the same function and truncation to all models there is high comparability between years and MUs. Clusters are defined as the object of interest to avoid dependent observations, and I expect no size bias from clusters. The number of chicks per female willow ptarmigan (“production”) was calculated from the assumptions of equal sex ratios and that all broods consist of two adults, where the exceeding number in the clusters is chicks. An overall mean of 8.8 % of suitable terrain was sampled (effective strip width mean = 108 m with coefficient of variation (CV) = 12.8 %). One outlier with high density (33.9) was removed because data inspection revealed low sampling effort (50 % effort compared to other years in the same MU).

To investigate if there had been variation in hunting success related to how open the landscape is, distribution of vegetation features was used as a proxy. The principal idea is that suitable open landscape yields more shooting opportunities than forested areas. Reusing the satellite vegetation maps (Johansen, Aarrestad & Øien 2009), I calculated the amount of birch forest (map categories 6-8, see Tab. S1) within the suitable habitat. As much of these areas are in the low alpine zone, the mean proportion of forest habitat was 10.4 % (range 2.9 – 17.2), and the rest being bogs, heathland or other open areas. I have no small scale information of locations of shot birds, but assume that proportion of forest within suitable habitat gives a realistic image of the average hunting terrain. One observation had a very high proportion of forest (31.5 %) relative to the others. While this value without doubt is representative for the habitat, it has still been removed from the data set because it was the only observation from a tenth MU, and had a clear impact on the statistical analyses.

Climatic conditions is a potential predictor for the number of days a hunter with a permit chose to hunt, and could also have impact on effectiveness because it may affect the performance of hunters or dogs. As I was interested in how different weather conditions acted on a local scale over a short time span, I used weather variables measured locally, as recommended by Frederiksen *et al.* (2014). Based on data from The Norwegian Meteorological Institute (publicly available from <http://eklima.met.no>), I withdrew daily registrations of temperature and precipitation for the time span of the early period length for each MU and year. For all areas I chose the closest weather stations providing the requested data, on average 2.2 stations (min 1 – max 3) for precipitation and 1.2 stations (1 – 2) for temperature (more stations measure precipitation than temperature). Where data from more than one station had been used, I took the arithmetic average of the stations around each MU to include in the analyses. In total, data from 21 stations with a mean distance of 8.2 km (range 3.2 – 21.7) from the MU borders were used (distances analysed with ArcGIS 10.3, ESRI Inc.).

Empirical evaluation

To achieve the study objective of investigating observed harvest related to management strategies and system parameters, I chose two paths for analyses (Fig. 1); one where I analysed harvest directly with number of bagged birds per km² as response (model 1), and another where I analysed harvest as a function of hunting pressure and hunter efficiency (model 2). Defining hunting pressure as ‘hunting days per km²’ (model 2a) and hunter efficiency as ‘bagged birds per hunting day’ (model 2b; commonly known as catch-per-unit-effort, CPUE), I used the relationship $\text{hunting days} / \text{km}^2 \times \text{bagged birds} / \text{hunting days} = \text{bagged birds} / \text{km}^2$ to explore an alternative path to actual harvest. All the following analyses were performed in R version 3.2.3 (R Core Team 2015).

There was a likely spatial and temporal dependency in the data set, as the observations are repeated counts within the same areas. I checked for dependency by fitting a full model and inspecting the residuals versus MUs, then versus years (Zuur *et al.* 2009). As residuals for several MUs and years were completely above or below the zero line, dependency had to be accounted for. No obvious sequence was discovered for the dependency, thus temporal autocorrelation was not considered. As I wanted to model effect of predictors conditional on group characteristics, without wanting to explore the differences between the individual years

or MUs, I chose to use MU and year as random factors with random intercept only in mixed models (package 'lme4', Bates *et al.* (2015)). This procedure takes the dependency into account while maintaining models more parsimonious (Bolker 2007).

As the study areas are very different in size, the number of bagged birds in model 1 needed to be scaled for area size. Instead of analysing bagged birds divided by area as a density with normal distribution, I used area as an offset to get the response per km² as recommended by e.g. Zuur *et al.* (2009). Similar approaches were done for the other models with count data (model 2a with hunting days as response and area size as offset, model 2b with bagged birds as response and hunting days as offset). This allows for heterogeneity, and fits the distribution of my data. By visual inspection, the data appeared to be in a negative binomial distribution. All models were overdispersed if using a Poisson distribution, thus I used negative binomial models (Zuur *et al.* 2009).

For all candidate models I favoured simplicity, and included a maximum of three predictors simultaneously. Only logical candidate models were tested. I modeled number of bagged birds per km² (model 1) as functions of TAC, sold permits, quota type, hunting pressure, start of hunting season and length of hunting season, and the system predictors density, production, temperature, precipitation and habitat structure. TAC and sold permits were scaled by area size in all analyses to be modeled as values per km². One logical two-way interaction was included; start of hunting season with TAC (if starting the season early TAC may have a stronger effect than otherwise). The interaction term was modeled with other predictors one at the time, and no three-way interactions were considered in the analyses. Model 2a with hunting pressure as response instead of predictor, was modeled with the same predictors as model 1, except from habitat structure which is not believed to affect hunting pressure once a permit has been bought in a given area. Hunter efficiency in model 2b was modeled as functions of the management predictors TAC, quota type and start of hunting season (all expected to be relevant for the number of birds bagged per hunter day), and the system predictors of the first two models.

A Pearson correlation of 0.6 between predictors was used as a collinearity threshold. For categorical variables correlated predictors were identified through logic and boxplots. Several predictors were correlated, including density and production, TAC and quota type, starting time with temperature and length of hunting period (later start was often accompanied by shorter hunting period), and sold permits with habitat structure. The last correlation implied

more permits in more forested areas, possibly a result of managers considering denser areas to tolerate higher crowding. In addition, hunting pressure when used as a predictor was correlated with TAC and sold permits, which could be expected, and also with quota types. All removed predictors were tested again in the best models by replacing the variable it was correlated with (Zuur, Ieno & Elphick 2010). Best models were selected using Akaike information criterion corrected for small sample sizes (AICc; package ‘AICcmodavg’, Mazerolle (2016)) where models with $\Delta\text{AICc} < 2$ were considered equal (Akaike 1973; Johnson & Omland 2004).

To explore how different willow ptarmigan densities lead to a response in the TAC set by managers, I first performed a Spearman correlation test on density versus TAC on subsets of all MUs. Positive correlation values above 0.5 was used as a criterion for a more than random positive relation between the parameters. This method implies that MUs that had a low TAC in all years without increasing it at higher densities was not included. One MU was ignored due to too few observations for an effective correlation test. Visual inspection of paired line plots of TAC and density through years confirmed the selection of three MUs in a group that adapted their TAC in relation to density estimates, hereby referred to as an adaptive management strategy (Walters 1986). The remaining six MUs were categorised as having a non-adaptive strategy. These two groups were analysed separately (TAC model, Fig. 1) to reveal strength of the relation with density, using linear models with Gaussian error distribution and with no random effects warranted.

Simulating harvest rates

The results from the empirical evaluations were used as estimates with uncertainties in simulations of harvest levels under different scenarios, by use of the two structurally different pathways between management and implementation models (Fig. 1). As I was not targeting to explore the true feedback from the biological system on different harvest levels, I used a simplified theta-logistic density dependent population model (E.Nilsen, unpubl.) and parametrised it to simulate densities mainly within the range of densities in my study areas. Thus, all simulation runs were fitted with a start population equal to the median value in my data set (11.5 birds per km²), carrying capacity $k = 17$ to limit the upper tail, intrinsic rate of increase $r_m = 0.6$ and theta $\theta = 0.5$ to reflect density dependent growth of a small animal, environmental stochasticity $\sigma^2 = 0.02$ (Aanes et al 2002) and time frame $t = 100$. Uncertainty

in the observation model was set according to the median uncertainty from the distance sampling analyses, $CV = 0.24$. All simulations were replicated 10,000 times.

For the first path, the harvest decision model used the simulated population state from the observation model, yielding values for TAC as output. Here, and in all the following models, the estimates and standard errors from the empirical analyses (Tab. 2) were used to replicate model uncertainty. The relationship between density and TAC for the two groups of management strategies were divided in further analyses. For the non-adaptive group, a model with only intercept was the best model (i.e. a constant TAC), and three levels of TAC are being tested in the simulations. The output from the TAC model was part of the input for the first implementation model (1), which was also directly related to the population density estimate (Fig. 1).

In the second path, the empirical analyses showed that one of the predictors for hunting effort was the 'school' of quota type the management preferred, and there was no clear indication of groups with adaptive versus non-adaptive management within different quota types. Visual plot inspection suggested that the previously categorised adaptive group differed slightly from the non-adaptive group also when looking at sold permits alone, but the intercept-only model was better. Because of this I chose to explore harvest offtake at different constant effort strategies only, although still assuming that there is some connection between population estimates and the management decisions affecting effort (model 2a). Population state was on the other hand input for the hunter efficiency model (model 2b), which together with the hunting effort model was used to build implementation model 2. Strategies explored contained the two main quota types and three representative levels of sold permits per km^2 . For both implementation model paths, estimate uncertainties are included in all steps, as there is not only uncertainty in the implementation; even if managers decide to set a TAC or effort based on a given criteria, this may well be slightly adjusted later as a result of e.g. social pressure from hunters. Final output for each observation from the two implementation models was the expected harvest in number of willow ptarmigan per km^2 .

Sandercock *et al.* (2011) found that harvest of 15 % of the population was at least partially compensated by a decrease in natural mortality, while 30 % harvest lead to super-additive mortality. Another study showed that willow ptarmigan harvest rates of 20-30 % was common in Sweden (Willebrand, Hörnell-Willebrand & Asmyhr 2011). Based on these indications for what might be sustainable, the quantitative output from my simulations were

used to estimate the risk of exploitation above harvest rates of 15 and 30 %, for the management strategies tested. In addition, different values for uncertainties in the observation model and implementation model were applied to investigate robustness to changes in population estimate precision, and vulnerability to underestimation of errors in the implementation models.

Results

The initial habitat analyses revealed that on average 70.3 % (range 28.3 – 92.3 %) of the MU areas are suitable habitat for the species, giving an effective size range of the study areas of 113.7 to 1058.0 km² (mean 473.4 km²). Densities ranged from 4.0 to 24.7 willow ptarmigan per km², with mean density 11.8 (mean CV = 24.8 %). Production estimates were between 2.0 and 6.1 chicks per hen, averaging at 3.5 (mean CV = 14.1 %).

Empirical analyses

The number of bagged birds per km² (model 1) was modeled as a function of management controlled parameters and system variables. Model selection by AICc (Tab. 3) indicated that the best model included total allowable catch per km² (TAC) and willow ptarmigan density (Tab. 2). Both TAC and density was positively related to number of bagged birds, and the combined effects suggest that a low TAC at higher densities gives harvest rates comparable to a high TAC at low densities (Fig. 2). The number of bagged birds increased with density in a non-linear fashion, indicating that a higher proportion of birds are removed from the area at low densities.

The model selection procedure provided strong support (Tab. 3) for number of sold permits per km² and type of quota as predictors of hunting pressure (hunting days per km²; model 2a). The number of sold (purchased) hunting permits explained much of the variation in hunting pressure, but there were also clear differences between quota types (Tab. 2). Daily quotas generally resulted in higher hunting pressure than period quotas, when the number of sold permits was the same (Fig. 3). Quotas that were combinations of these had an effect in between the main types, but no inference should be made from this with only two observations with combination quotas in the data set.

For hunter efficiency (model 2b), two models performed equally well, within $\Delta\text{AICc} = 2$ (Tab. 3). Bagged birds per hunting day could either be modeled as a function of density alone, or as density and habitat structure together. For density as sole predictor, hunters clearly responded with higher efficiency with increasing density (Tab. 2). The slope of the relationship also suggests that hunters were relatively more effective at lower densities, as an increase in density was not met with a proportional increase in catch per hunting day (Fig. 4). The model with density and habitat structure together, suggests (with notable uncertainty in

the estimate) that an increasing proportion of forest in the hunting area reduced the efficiency. I chose the most parsimonious model as the sole best model, but acknowledge the fact that the other model might be important. Considering also that one observation was removed because it was an outlier in the habitat parameter, and that the inclusion of this observation would have lowered the estimate errors substantially, I present the alternative model in Appendix Fig. S2. The residuals versus fitted values for all the above selected models were in accordance with a negative binomial distribution, and the random effects were normally distributed within each level.

The grouping of MUs into categories with either adaptive or non-adaptive management strategy, gave two main scenarios for simulating effects of harvest decisions (TAC model). For both groups, TAC was modeled as a function of density, to reveal the response of managers to different population states. For the adaptive group, the model with density was better than the alternative intercept-only model ($\Delta\text{AICc} = 4.22$, $\text{AICc weight} = 0.89$, slope \pm SE: 0.546 ± 0.197 , $r^2 = 0.33$). For the non-adaptive group it was the other way round, with the intercept-only model being better than the model with density included ($\Delta\text{AICc} = 2.23$, $\text{AICc weight} = 0.75$, intercept \pm SE: 8.545 ± 1.294). This implies that for the non-adaptive group I defined, the model that best describes the management strategy is a constant TAC where density is disregarded.

Simulations

Exploration of implementation uncertainty in the first pathway from population state to harvest (Fig. 1), was performed through simulating harvest rate under four different scenarios; the adaptive strategy, using estimates from the empirical analyses, and three scenarios of constant TAC. The TAC of the non-adaptive group ranged from 1.2 to 21.2, and the chosen scenarios represent the majority within this range with TAC equaling 5, 10 and 15 (SE = 1.5). The adaptive strategy had a fairly constant harvest rate (proportion of population harvested) along medium and high density values, but this increased notably as densities decreased (Fig. 5). At 5 birds per km² there was a 41.5 % risk of harvest above the 15 % level (cf. Tab. 4 for all means and standard errors). This is comparable to a constant TAC of 5, which, being the most conservative of the scenarios, also yielded lower harvest rates at higher densities. A TAC of 10, slightly above average in the data, had a 21.7 % risk of harvest above the 15 % level at 10 birds per km², but this risk increased to 90.5 % when density dropped to 5 birds per

km². For TAC equal 15 harvest rates were generally high, with a 41.8 % risk of harvest above the 30 % level at 5 birds per km² and notable risks of harvesting above 15 % also at medium and high densities.

The second pathway to harvest rates involved two main quota types, with three scenarios of sold permits per km² within each type. The data ranged from 0.27 to 1.86 permits, but with uneven spread, thus most of the data set was represented within scenarios of 0.5, 0.75 and 1.0. Day quotas overall gave higher harvest rates (Fig. 6), and even with a modest 0.5 permits per km² there was a 31.8 % risk of harvest above the 15 % level at 5 birds per km² (Tab. 5). Risk rapidly increased with increasing number of sold day quota permits, and at 1.0 permits harvest rates averaged at 15 % at high density and 30 % at 3.9 birds per km². For period quotas with 1.0 permits sold there was still substantial risk of overshooting the 15 % level at lower densities, but the risk was greatly reduced when going down to 0.75 permits per km².

Comparing the performance of the adaptive TAC model under the low and high 90 % interval of the density estimations' coefficients of variation (CV = 0.15 and 0.38 respectively), demonstrated high robustness to observation uncertainty. Increasing the implementation models' uncertainties however, while still giving small differences in harvest rate means, risk of harvesting above the tested thresholds was increased. This was especially clear for the 30 % threshold, where risk of harvest above the level was unproportionately high compared with the increase in model uncertainty. This implies that the effect of potential bias not taken into account in this study could be severe.

Discussion

Managers use a number of strategies to avoid excessive harvest in small game populations, e.g. to limit the number of sold hunting permits, implement quotas or alter the hunting season (Kurki & Putaala 2010)). However, without knowledge of the effect of such measures, managers have no real control of harvest offtake even if they implement limitations. The results from the analyses of harvest data in this study clearly indicated that both density and management procedures have to be taken into account when predicting actual harvest. When analysing number of bagged birds per km² directly (implementation model 1), the best model included both TAC and willow ptarmigan density. As TAC is a function of sold permits and quota size, managers may use this knowledge to adjust one or both of these parameters to get closer to the desired harvest level. Predicting number of bagged bird per km² under a range of densities within different levels of TAC (Fig. 2) suggests that if TAC is set at a high level (third quartile in this study; TAC = 11.2), harvest at 5 birds per km² is 59 % higher than if TAC was set at a low level (first quartile; TAC = 3.6). However, a great proportion of permits for willow ptarmigan hunting in Norway (including in this study) is sold before density estimates are obtained in August. This practise leaves less flexibility to the management to react to current population states with a change in TAC, and would be assumed to force the use of stricter quota regulations. On the other hand, the managers may also ignore the predicted increase in harvest, and the lack of flexibility in this situation might have contributed to the small number of MUs categorised in this study as managing in an adaptive way.

The modest positive relationship between density and number of bagged birds indicate that harvest offtake is more stable when density decrease, than what would be expected if there was a linear relationship between density and bagged birds per km². This is in line with the findings of Willebrand, Hörnell-Willebrand and Asmyhr (2011), with only slight differences in the model estimates, but not supporting the linear relationship found by Cattadori *et al.* (2003) when log-transforming both response and predictor. Willebrand, Hörnell-Willebrand and Asmyhr (2011) suggested that hunters compensate for few encounters by hunting longer days at low densities, and that there may be a saturation effect at higher densities. An additional explanation may come from density often being correlated with production (Steen & Erikstad 1996), shown as brood sizes in the beginning of the hunting season. A hunter encountering two birds together will have a chance of killing both (using a shotgun with two shells), but if there were e.g. twelve birds together in a brood, two birds would normally still

be the maximum amount of birds killed in a single encounter, but then with a smaller relative effect for the harvest rate.

The second path to exploring implementation uncertainty involved combining the models for hunting pressure and hunter efficiency. Hunting pressure affects total bag size (Caro *et al.* 2015) and extinction risk (Keane, Brooke & McGowan 2005), and needs to be taken into account in harvest management strategies. I found that sold permits together with quota type best explained hunting pressure, where period quotas yielded the lowest effort. Period quotas (interquartile range 5 – 10) in the study areas in most cases provided a lower TAC than day quotas (interquartile range 2 – 3). While the possibility to distribute the period quota over available days occasionally might have increased offtake, it is a likely assumption that the majority of hunters were unable to fulfill their quotas (Bischof *et al.* 2012; Eriksen, Moa & Hagen 2014), regardless of quota type. Still, in cases where the period quotas were fulfilled, the successful hunter had to stop hunting regardless of any days left in the permit, thus hunting pressure would be limited. However, I propose that the lower hunting pressure related with period quotas also had a behavioural basis, where hunters with period quotas might have expected to fulfil their quota within the period, thus holding back on the effort to avoid fulfilling it too early. Another aspect to consider in quota choice is the hunters' general satisfaction (Wam, Andersen & Pedersen 2013), where hunters seem to prefer quotas for longer periods instead of day quotas (Andersen *et al.* 2014).

When modeling hunter efficiency, i.e. bagged birds per hunting day, density was the only predictor in the most parsimonious model. This relationship is not very different from the relationship of density and bagged birds per km², and the effect is comparable here; efficiency is higher with decreasing density, relative to the proportion of the population being harvested. Similar effects have been found previously, both for willow ptarmigan and in other systems (Harley, Myers & Dunn 2001; Post *et al.* 2002; Hörnell-Willebrand 2005). A maximum number of hunting days allowed in an area is a common strategy implemented to limit overexploitation (Hörnell-Willebrand 2010), but as hunters are relatively more effective at lower densities this method should be used with caution. If managers fail to adjust the allowed number of hunting days in accordance with the increased relative efficiency, they face greater uncertainty of the actual harvest and risk high harvest levels at low densities.

The competing model for hunter efficiency indicated that efficiency decreased with an increase of forest. This supports the suggestions by (Pedersen *et al.* 1999), that birds are

bagged at a higher rate in open areas than in more forested habitat. The relationship may reflect habitat use of willow ptarmigan during early hunting season, or it may be a result of better shooting opportunities in open landscape. In my study areas there were generally low proportions of birch forest, but as this may be an important aspect for understanding hunter efficiency in denser areas, further studies should be done to shed more light on this. The weather parameter was expected to be more important than the results show, as poor weather could be assumed to affect both effort and harvest success negatively. Either there were no relations between weather and these responses, or the way weather was analysed did not reveal it. I speculate that by using average values over entire periods, differences that could have affected the responses on a day-to-day basis may have been clouded. Another matter that might have affected the analyses is the possibility of non-response bias in hunting reports. While no such bias is known, the importance for the analyses would be decreased as non-responders in one area are unlikely to differ from those in others. It is also possible that the difference between permits valid for five or seven days may have influenced the results slightly, but I have no indication of this happening. A final aspect to consider is the possibility of non-compliance with harvest rules, which would have increased harvest compared to my findings. Although rule breaking in recreational harvesting has been shown by others (St John *et al.* 2010), the MUs infrequently controlled hunters and information provided for this study indicated that cheating is not a major issue. Also considering that quotas were relatively high, non-compliance with rules was assumed to be minimal and covered by the model estimate errors, thus following the recommendation of Bunnefeld, Hoshino and Milner-Gulland (2011) of keeping a simpler framework. If, however, managers wish to quantitatively explore the uncertainties arising from hunters not abiding by the rules, a management procedure facilitating control measures would be preferred. Period quotas would in this matter require suitable systems, while controlling compliance with day quotas is simply a matter of inspecting the bag in the terrain.

The managers reacted in different ways to low population estimates; either they closed the hunting terrain (not included in the study, but one of the MUs closed their area in 2015), adapted by adjusting sold permits or quota sizes to give a lower harvest, or they did not change their procedures in a manner affecting harvest (non-adaptive). Managers make adjustments between years to achieve sustainability, but there is a general lack of defined goals for sustainable harvest (Andersen 2015), which may explain why many of the MUs ended up in the non-adaptive group. Although not part of my study objectives, the current

data showed a clear trend of decrease in TAC proportional to abundance through the years (see Appendix Fig. S3 for details). The intent here is not to infer on amount of MUs with different procedures, but to show the effect on harvest from strategies adapting to density levels or not. Also, given that the population model was parametrised to yield a range of densities present within the study, the simulations should be seen as predictions of harvest in time t , and not as population development in $t+i$.

Overexploitation of a harvested species may lead to continued low abundance (Courchamp, Clutton-Brock & Grenfell 1999) or in worst case extinctions (Sutherland 2001), and constant management strategies are problematic in this aspect (Fryxell *et al.* 2010). The reasoning behind choosing a constant TAC model is assumed to be that managers either believe that hunting mortality is compensatory, contrary to a number of studies (Small, Holzwardt & Rusch 1991; Smith & Willebrand 1999; Pedersen *et al.* 2004; Gibson *et al.* 2011; Sandercock *et al.* 2011), or that they trust hunters to bag less when densities are low. This study strongly contradicts the latter aspect, as all competing scenarios gave increased harvest levels at lower densities. Harvest rates and risk of harvest above the specified thresholds were always substantially increased at low density, even with TAC as low as 5. A further implication for the non-adaptive strategies is that even if managers set a low constant quota, there is still a need for obtaining population estimates to know when densities are low. The exception would be if TAC is set extremely low, implying that both quotas and number of sold permits are close to zero, which would compromise satisfaction for hunters and objectives for managers (Andersen *et al.* 2008; Andersen *et al.* 2010). In the second implementation model path, where managers control effort to limit harvest offtake, the general image was not very different. Thus, to avoid high harvest rates without knowledge of the population state, managers would have to choose very precautionary strategies (Bunnefeld, Hoshino & Milner-Gulland 2011). Within the quota sizes represented in my data, reducing the number of sold permits will lower the risk of high harvest rates by affecting TAC and effort. Setting period quotas may give higher hunters satisfaction (Andersen *et al.* 2014), and will often enable managers to sell more permits before reaching the TAC decided upon, than they would with day quotas.

For the adaptive group TAC was increased with increasing density estimates, enabling more permits to be sold when there were more birds to hunt. Through the simulations, this strategy was shown to give an offtake at a steady rate and with low risk of harvest levels higher than 15 % from approximately 10 birds per km² and upwards. However, even if the risks of harvesting

above the 15 % threshold might have been acceptable to managers at medium densities and higher, this strategy also gave a substantially increased harvest when there were few birds to hunt. As shown theoretically before (Lande, Sæther & Engen 1997), managers must consider the pit-falls of high harvest rates at low densities. A reasonable option given the results of this study is implementing proportional threshold strategies (Lande, Sæther & Engen 1997; Andersen & Thorstad 2013). This would imply that managers mirror their TAC or effort to changes in density, but also that they close the area for hunting when population estimates are below a certain limit.

The adaptive TAC model was the only management model directly related to density, and simulations indicated that it was very robust to different observation uncertainties in the current data. However, risk of high harvest levels increased notably with increased implementation model uncertainty, suggesting that this should be a matter of continued focus. More research is recommended to uncover other potential sources of bias and measure their effect.

Management implications

The quantified ecological risks of harvest levels above 15 and 30 % is applicable for informed trade-off decisions against economic and social advantages by offering hunting opportunities. Although ecological sustainability will supersede the other two in long terms (if the harvest is not ecologically sustainable the resource will implicitly not last), manager decisions on short terms may be influenced by other factors than population state (McAllister *et al.* 1999). When risk of high harvest rates is substantial, managers defying this risk increase the probability that harvest affect population development negatively (Sandercock *et al.* 2011). This study shows that in a small game harvest system where detailed control of actual offtake is connected with uncertainty, the proportion of the population being harvested typically increase with decreasing density. A consequence of this is that management should not only be based on controlling effort or constant relations between total allowable catch and density, but must include thresholds for taking the increased proportion into account. The result of inadequate management strategies to deal with this is a substantial risk of harvest rates above previous indications of sustainable harvest levels (Sandercock *et al.* 2011; Willebrand, Hörnell-Willebrand & Asmyhr 2011).

I have shown a method for quantifying implementation uncertainty in small game harvest management by using knowledge from empirical evaluations, and suggest this to be evolved to further explore adaptive harvest management options. The next step from here is to incorporate the method into a full MSE framework for this system, including all known sources of uncertainty and investigations of management objectives (Rademeyer, Plagányi & Butterworth 2007), to increase the ability of informed decision-making for managers.

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Tables

Table 1. Parameters used to explore the relationship between harvest, management strategies and system characteristics.

Parameter	Description
Responses	
Bagged birds per km ²	Total number of bagged birds per km ² suitable habitat, scaled by hunter response rate
Hunting pressure (also predictor)	Hunting days per km ² suitable habitat, scaled by hunter response rate
Hunter efficiency	Number of bagged birds per hunting day, scaled by hunter response rate
Management decisions	
Sold permits	Number of sold permits per km ² suitable habitat
Length of prime season	Number of days hunters are distributed on
Season start	Categorical: 1) Season opening September 10th, or 2) postponed (i.e. 5-10 days later)
Quota type	Categorical: 1) Day quota, 2) period quota or 3) a combination of the two
Total allowable catch per km ² (TAC)	Function of 1) number of hunting days in sold permits × daily quota, or 2) number of sold permits × period quota, both per km ² suitable habitat
System characteristics	
Willow ptarmigan density	Estimates from distance sampling line transects
Willow ptarmigan production	Number of chicks per female, assuming equal sex ratio and brood sizes > 2
Habitat structure	Proportion of highland birch forest in suitable terrain
Precipitation	Daily average precipitation (local weather stations) for available hunting days in each area
Temperature	Daily average temperature (local weather stations) for available hunting days in each area

Table 2. Parameter estimates from the best negative binomial models following AICc model selection, with model 1) bagged birds per km², 2a) hunting days per km² (hunting pressure) and 2b) bagged birds per hunting day (hunter efficiency) respectively. For the hunter efficiency model, both models within $\Delta\text{AICc} = 2$ is shown.

Parameter	Estimate (log)	SE (log)
1)		
(Intercept)	-0.725	0.189
Density	0.033	0.008
TAC	0.061	0.007
2a)		
Quota type (Intercept)*	0.009	0.147
Quota type: Combination	-0.152	0.116
Quota type: Period	-0.428	0.085
Sold permits	1.128	0.159
2b)		
(Intercept)	-1.204	0.169
Density	0.058	0.010
(Intercept)	-0.905	0.357
Density	0.057	0.010
Habitat	-2.653	2.830

TAC = total allowable catch per km²

*Quota type (Intercept) represents daily quotas

Table 3. AICc model selection tables of top five models and null models from empirical analyses, where 1) is models bagged birds per km², 2a) hunting days per km² (hunting pressure) and 2b) bagged birds per hunting day (hunter efficiency).

Model	par	AICc	Δ AICc	AICc weight
1)				
Density + TAC	6	528.86	0.00	0.59
Density + TAC + Habitat	7	531.68	2.83	0.14
Density + TAC \times S.start	8	532.53	3.68	0.09
Density + Hunting pressure	6	533.70	4.85	0.05
Prod. + Quota type + Temp.	8	534.12	5.27	0.04
Null	4	577.51	48.66	0.00
2a)				
Sold permits + Quota type	7	540.20	0.00	0.89
Sold permits + TAC	6	545.92	5.72	0.05
Sold permits + TAC + S.start	7	546.51	6.31	0.04
Sold permits + TAC \times S.start	8	548.38	8.18	0.01
Sold permits + Precipitation	6	550.94	10.74	0.00
Null	4	602.11	61.91	0.00
2b)				
Density	5	542.71	0.00	0.36
Density + Habitat	6	544.63	1.91	0.14
Density + TAC	6	544.94	2.22	0.12
Density + Precipitation	6	545.13	2.42	0.11
Density + Temp.	6	545.45	2.73	0.09
Null	4	565.40	22.69	0.00

TAC = total allowable catch per km², S.start = season start, Prod. = production, Temp. = Temperature

Table 4. TAC strategy harvest rates. The table shows harvest rate means, and risks of harvest rates, above two specified levels (15 and 30 %) for simulated scenarios within the TAC strategies (model 1). Means and risks are presented for three levels of willow ptarmigan density, where the values are calculated over the range ± 1 of the density level (e.g. 4-6 for density 5).

TAC strategy	Density 5 \pm 1			Density 10 \pm 1			Density 15 \pm 1		
	HR Mean (SD)	RHR > 0.15	RHR > 0.30	HR Mean (SD)	RHR > 0.15	RHR > 0.30	HR Mean (SD)	RHR > 0.15	RHR > 0.30
Adaptive TAC	0.147 (0.040)	41.5 %	0.3 %	0.109 (0.034)	11.1 %	0.0 %	0.103 (0.039)	10.7 %	0.2 %
Constant, TAC = 5	0.149 (0.036)	43.2 %	0.2 %	0.094 (0.022)	1.6 %	0.0 %	0.075 (0.019)	0.2 %	0.0 %
Constant, TAC = 10	0.211 (0.052)	90.5 %	5.9 %	0.128 (0.031)	21.7 %	0.0 %	0.102 (0.026)	4.7 %	0.0 %
Constant, TAC = 15	0.295 (0.077)	99.5 %	41.8 %	0.175 (0.044)	69.0 %	1.1 %	0.138 (0.036)	32.7 %	0.0 %

HR = Harvest rate, SD = Standard deviation, RHR = simulated risk of harvest rates above specified levels, TAC = total allowable catch per km²

Table 5. Effort strategy harvest rates. The table shows harvest rate means, and risks of harvest rates, above two specified levels (15 and 30 %) for simulated scenarios within the effort strategies (model 2), given the quota sizes in the study. Means and risks are presented for three levels of willow ptarmigan density, where the values are calculated over the range ± 1 of the density level (e.g. 4-6 for density 5).

Effort strategy		Density 5 \pm 1			Density 10 \pm 1			Density 15 \pm 1		
Quota type	Permits per km ²	HR Mean (SD)	RHR > 0.15	RHR > 0.30	HR Mean (SD)	RHR > 0.15	RHR > 0.30	HR Mean (SD)	RHR > 0.15	RHR > 0.30
Day	0.50	0.137 (0.035)	31.8 %	0.1 %	0.098 (0.026)	3.8 %	0.0 %	0.088 (0.025)	2.0 %	0.0 %
	0.75	0.190 (0.052)	77.1 %	3.3 %	0.131 (0.036)	26.5 %	0.1 %	0.118 (0.035)	16.3 %	0.0 %
	1.00	0.260 (0.077)	95.9 %	26.2 %	0.175 (0.052)	65.4 %	2.3 %	0.157 (0.051)	49.7 %	1.4 %
Period	0.50	0.089 (0.025)	1.7 %	0.0 %	0.064 (0.018)	0.1 %	0.0 %	0.058 (0.017)	0.0 %	0.0 %
	0.75	0.118 (0.033)	15.9 %	0.0 %	0.085 (0.025)	1.6 %	0.0 %	0.077 (0.024)	0.9 %	0.0 %
	1.00	0.163 (0.050)	54.6 %	1.4 %	0.114 (0.036)	14.8 %	0.0 %	0.103 (0.034)	8.9 %	0.0 %

HR = Harvest rate, SD = Standard deviation, RHR = simulated risk of harvest rates above specified levels

Figures

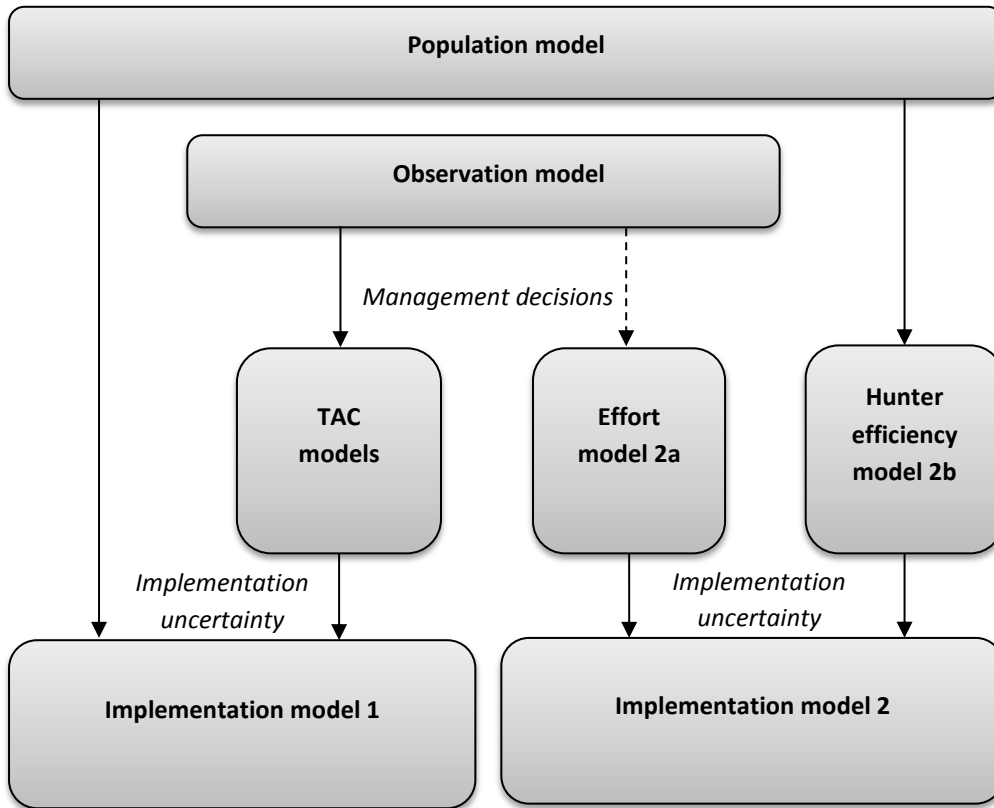


Figure 1. Schematic structure of two paths between population states and the implementation models. Solid lines indicate connections modeled in this study, where implementation model 1 (bagged birds per km²) depended on density and management decisions from the TAC models (TAC = total allowable catch per km²). Implementation model 2 is a function of management decisions of effort from model 2a (hunting pressure, defined as hunting days per km²) and hunter efficiency from model 2b (defined as bagged birds per hunting day), using the relationship $\text{hunting days} / \text{km}^2 \times \text{bagged birds} / \text{hunting days} = \text{bagged birds} / \text{km}^2$. The TAC models include two groups and their relation to the estimated density. The dashed line indicates an assumed connection between estimated density and the management decisions in the effort model.

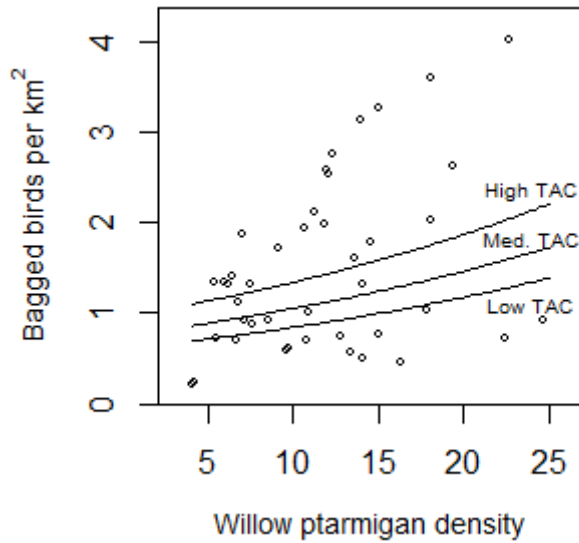


Figure 2. Number of bagged birds per km² in relation to willow ptarmigan density and total allowable catch per km² (TAC). The relationship is plotted with three selected values (representing the first, second and third quartile in the current data set) of TAC as examples, to visualise the number of bagged birds at various densities, conditional on a level of TAC. The individual observations are included as points for additional information, but as the parameters are conditional on the random structure (area and year) in the model, the observations cannot directly be interpreted to belong to the nearest prediction line. For standard errors, cf. Tab. 2.

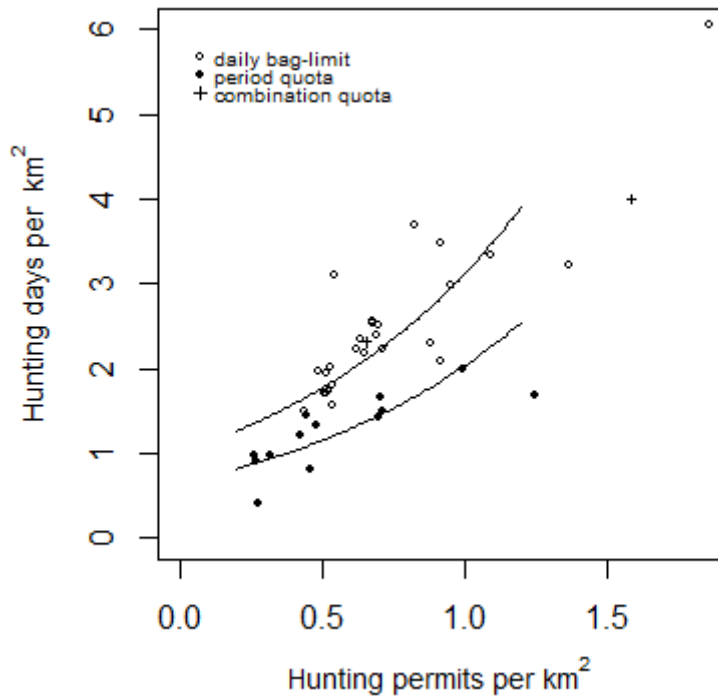


Figure 3. Hunting days per km² (i.e. hunting effort) as a function of sold hunting permits per km² and quota type. The upper line predicts the hunting effort with daily bag-limits, and the lower line vice versa with period quotas. The two observations with quotas that are combinations of the others are not included in the predictions. For standard errors, cf. Tab. 2.

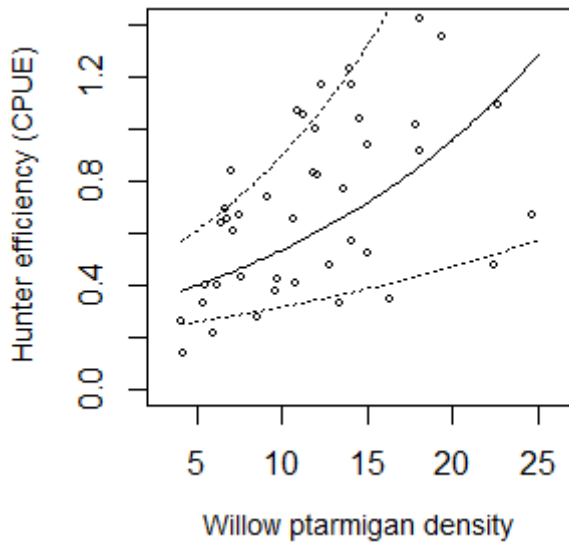


Figure 4. Hunter efficiency, measured as bagged birds per hunting day (commonly referred to as catch-per-unit-effort, CPUE) modeled in relation to willow ptarmigan density. Dashed lines are 95 % CI.

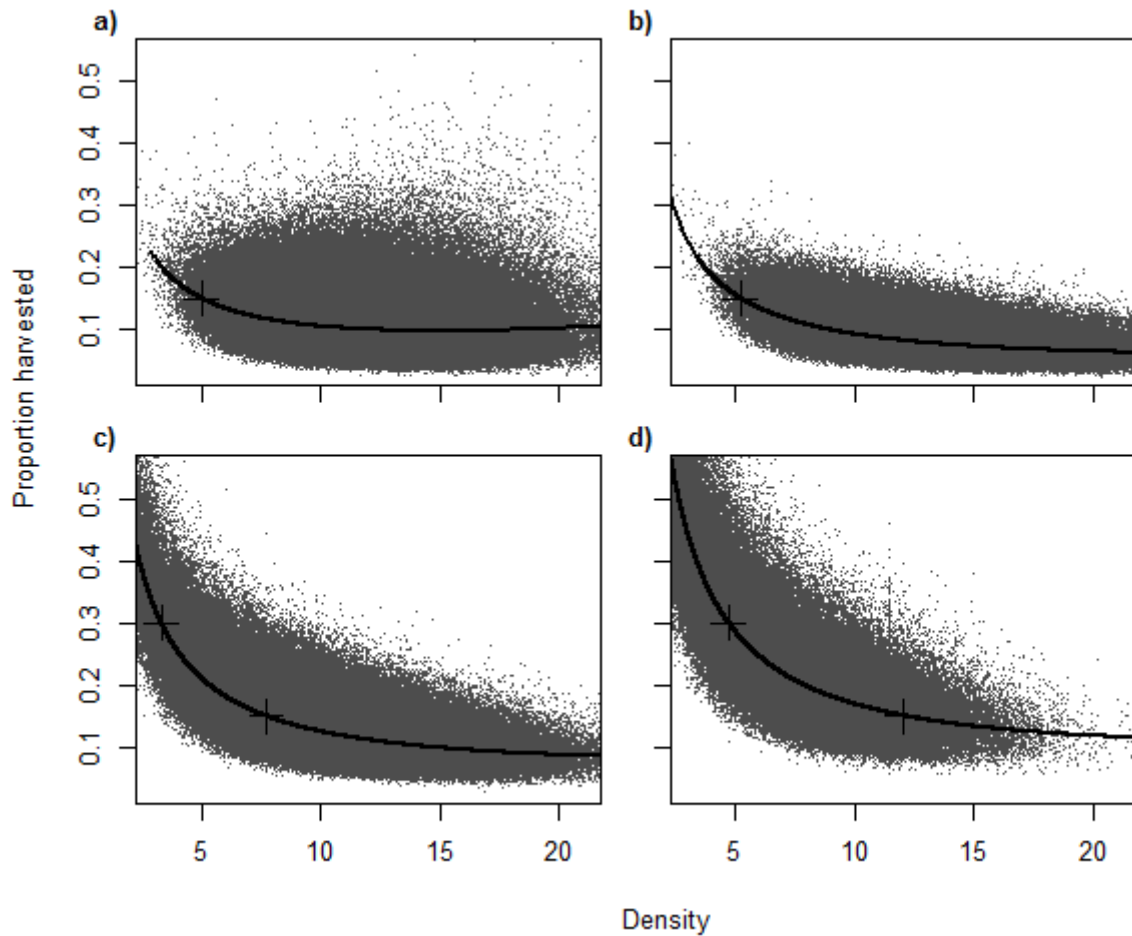


Figure 5. Simulations of four TAC strategy scenarios. The plots show proportion harvested in relation to willow ptarmigan density under a) adaptive TAC strategy, where the management adjusts total allowable catch per km² (TAC) in relation to the observed density, and three constant TAC strategy scenarios; b) constant TAC = 5, c) constant TAC = 10 and d) constant TAC= 15. Simulated values ($t = 100$ with 10,000 replications) are shown in grey. Black line is the line for the same simulation without uncertainty in any parameters, representing average mean values along the x-axis over an infinite number of simulations. Black crosses indicate where the average mean value reaches 15 and 30 % harvest rate levels (where applicable).

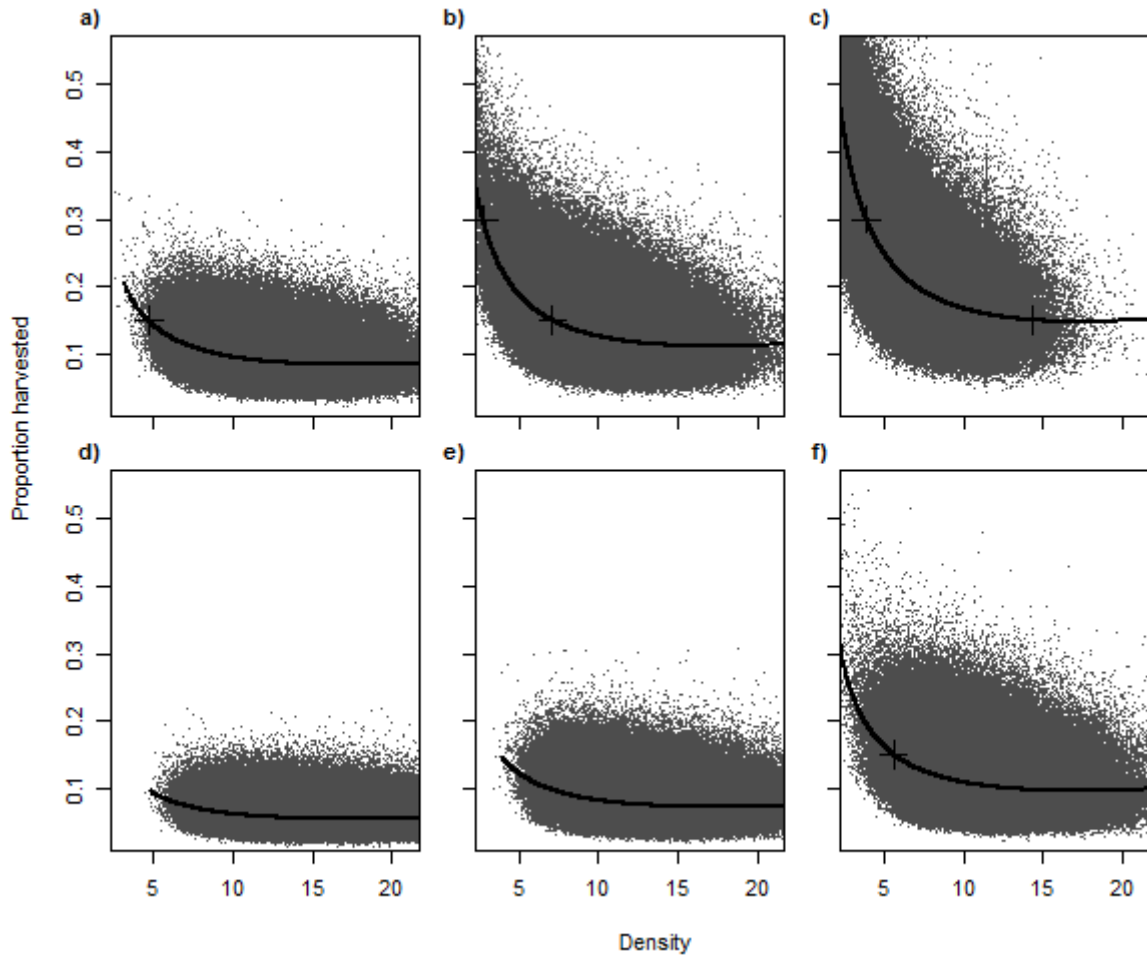


Figure 6. Simulations of six effort strategy scenarios. The plots show proportion harvested in relation to willow ptarmigan density), given the quota sizes in the study, under day quota scenarios with a) 0.5, b) 0.75 and c) 1.0 sold permits per km², and period quota scenarios with d) 0.5, e) 0.75 and f) 1.0 sold permits per km². Simulated values ($t = 100$ with 10,000 replications) are shown in grey. Black line is the line for the same simulation without uncertainty in any parameters, representing average mean values along the x-axis over an infinite number of simulations. Black crosses indicate where the average mean value reaches 15 and 30 % harvest rate levels (where applicable).

Appendix: Supplementary material

Table S1. Vegetation types included and excluded in the calculations to obtain area size of suitable habitat for willow ptarmigan. The table is adapted from Johansen, Aarrestad and Øien (2009) p.34, and the method an adaptation from Gjershaug *et al.* (2010). After removing all areas within high and medium alpine zones with a map of bioclimatic zones (Blumentrath & Hanssen 2010), categories 6-10 and 12-21 (filled circles) were included as suitable terrain. The open circle represents smaller areas (0.0 - 1.7 % of total) in satellite shadow (or otherwise unclassifiable areas). The values within this category were distributed on the other categories, proportionally to the amount of the others in each management unit area. The habitat structure parameter was calculated as proportion of birch forest (cat. 6-8) in relation to other suitable categories. Vegetation types are typically distributed as mosaics in the landscape, and for some types only parts of the areas would be suitable (e.g. in the snow-patch vegetation types), but removing higher alpine zones is assumed to greatly improve precision.

Vegetation type	Included as suitable terrain
Forests	
1 Coniferous forest, dense canopy layer	
2 Coniferous and mixed forest, open canopy layer	
3 Lichen-rich pine forest	
4 Low herb forest and broad leaved deciduous forest	
5 Tall herb - tall fern deciduous forest	
6 Bilberry - low fern birch forest	●
7 Crowberry birch forest	●
8 Lichen-rich birch forest	●
Bogs and swamps	
9 Ombrotrophic bog and low-grown lawn vegetation	●
10 Tall-grown lawn vegetation	●
11 Wet mires, sedge swamps and reed beds	
Open areas in mountains or lowland	
12 Exposed alpine ridges, scree and rock complexes	●
13 Graminoid alpine ridge vegetation	●
14 Heather-rich alpine ridge vegetation	●
15 Lichen-rich heatland	●
16 Heather- and grass-rich early snow patch communities	●
17 Fresh heather and dwarf-shrub communities	●
18 Herb-rich meadows	●
19 Grass and dwarf willow snow-patch vegetation	●
20 Bryophyte late snow patch vegetation	●
21 Glacier, snow and wet snow-patch vegetation	●
Other	
22 Water	
23 Agricultural areas	
24 Cities and built-up areas	
25 Unclassified/shadow areas	○

Table S2. Comparison between simulations of base models (adaptive TAC, constant TAC = 10, day and period quotas with 0.75 sold hunting permits per km²) and models where implementation model errors have been increased by 20, 50 and 100 % respectively. For the adaptive TAC model, comparisons with different levels of uncertainties in the observation model is also included (using the outer 90 % interval values of coefficients of variation (CV) from the data set, base model CV = 0.24). The table shows harvest rate means, and risks of harvest rates, above two specified levels (15 and 30 %) for simulated scenarios, given the quota sizes in the study. Means and risks are presented for three levels of willow ptarmigan density, where the values are calculated over the range ± 1 of the density level (e.g. 4-6 for density 5).

Strategy	Density 5 \pm 1			Density 10 \pm 1			Density 15 \pm 1		
	HR Mean (SD)	RHR > 0.15	RHR > 0.30	HR Mean (SD)	RHR > 0.15	RHR > 0.30	HR Mean (SD)	RHR > 0.15	RHR > 0.30
Adaptive TAC									
Model	0.147 (0.040)	41.5 %	0.3 %	0.109 (0.034)	11.1 %	0.0 %	0.103 (0.039)	10.7 %	0.2 %
Impl.error \times 1.2	0.149 (0.045)	43.2 %	0.6 %	0.110 (0.038)	13.5 %	0.1 %	0.104 (0.043)	12.7 %	0.3 %
Impl.error \times 1.5	0.152 (0.054)	43.9 %	1.7 %	0.112 (0.045)	16.9 %	0.4 %	0.107 (0.051)	15.7 %	0.7 %
Impl.error \times 2.0	0.159 (0.072)	46.6 %	4.7 %	0.117 (0.060)	22.1 %	1.5 %	0.112 (0.068)	20.4 %	2.1 %
Obs.model CV = 0.15	0.146 (0.039)	40.4 %	0.2 %	0.109 (0.032)	10.4 %	0.0 %	0.103 (0.036)	9.9 %	0.1 %
Obs.model CV = 0.38	0.147 (0.041)	41.5 %	0.4 %	0.110 (0.037)	12.4 %	0.1 %	0.105 (0.045)	12.6 %	0.5 %
Constant TAC = 10									
Model	0.211 (0.052)	90.5 %	5.9 %	0.128 (0.031)	21.7 %	0.0 %	0.102 (0.026)	4.7 %	0.0 %
Impl.error \times 1.2	0.213 (0.061)	87.0 %	8.6 %	0.129 (0.037)	25.0 %	0.1 %	0.103 (0.031)	7.8 %	0.0 %
Impl.error \times 1.5	0.218 (0.075)	83.3 %	13.1 %	0.132 (0.046)	29.2 %	0.5 %	0.105 (0.040)	12.3 %	0.1 %
Impl.error \times 2.0	0.228 (0.103)	77.6 %	19.6 %	0.138 (0.064)	33.7 %	2.4 %	0.110 (0.057)	19.1 %	1.0 %
Day quota, 0.75 permits/km²									
Model	0.190 (0.052)	77.1 %	3.3 %	0.131 (0.036)	26.5 %	0.1 %	0.118 (0.035)	16.3 %	0.0 %
Impl.error \times 1.2	0.191 (0.058)	75.2 %	4.7 %	0.132 (0.041)	28.6 %	0.2 %	0.119 (0.040)	19.0 %	0.1 %
Impl.error \times 1.5	0.195 (0.067)	72.7 %	7.3 %	0.134 (0.048)	31.1 %	0.6 %	0.121 (0.048)	22.6 %	0.5 %
Impl.error \times 2.0	0.201 (0.086)	69.8 %	12.0 %	0.139 (0.063)	34.9 %	2.2 %	0.127 (0.065)	27.9 %	2.1 %
Period quota 0.75 permits/km²									
Model	0.118 (0.033)	15.9 %	0.0 %	0.085 (0.025)	1.6 %	0.0 %	0.077 (0.024)	0.9 %	0.0 %
Impl.error \times 1.2	0.121 (0.037)	19.4 %	0.1 %	0.086 (0.028)	2.7 %	0.0 %	0.078 (0.027)	1.7 %	0.0 %
Impl.error \times 1.5	0.123 (0.042)	22.4 %	0.0 %	0.087 (0.032)	4.6 %	0.0 %	0.079 (0.032)	3.4 %	0.0 %
Impl.error \times 2.0	0.126 (0.055)	26.8 %	1.1 %	0.091 (0.042)	8.6 %	0.2 %	0.083 (0.043)	7.3 %	0.2 %

HR = Harvest rate, SD = Standard deviation, RHR = simulated risk of harvest rates above specified levels, TAC = total allowable catch per km²

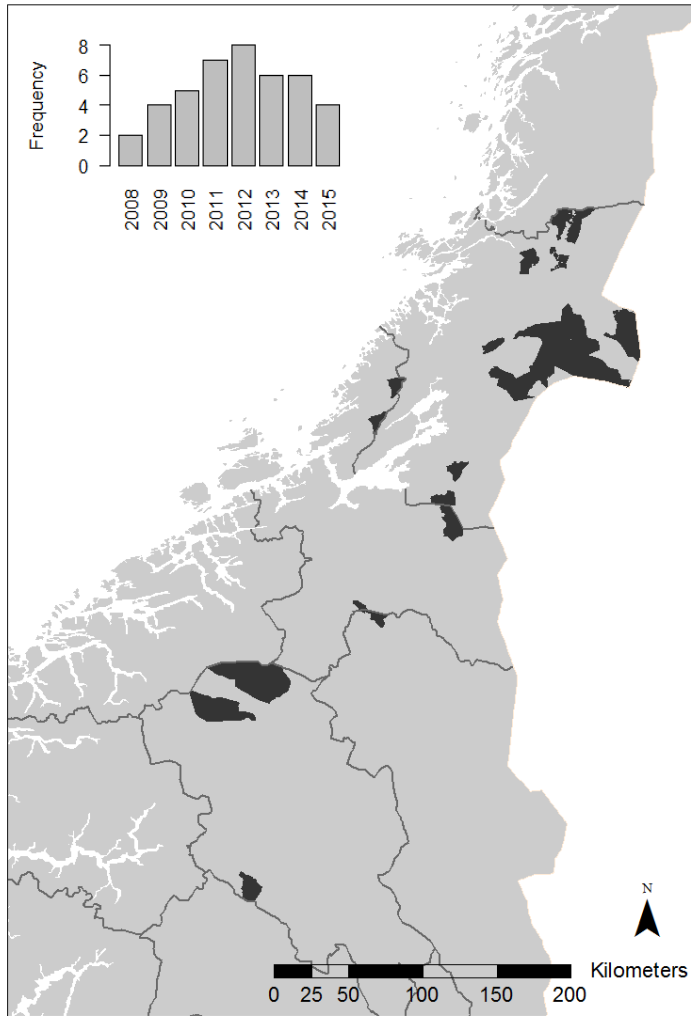


Figure S1. Map showing the spatial distribution of study areas (dark polygons) in Central and South Norway, and the frequency of observations in the different years of the study period ($n = 42$). Generally there has been an increase in the number of management units (MUs) collecting harvest data. The lower number of observations again in 2015 is a result of one MU being closed for hunting and several others not finishing the data collection from hunters in time for this study.

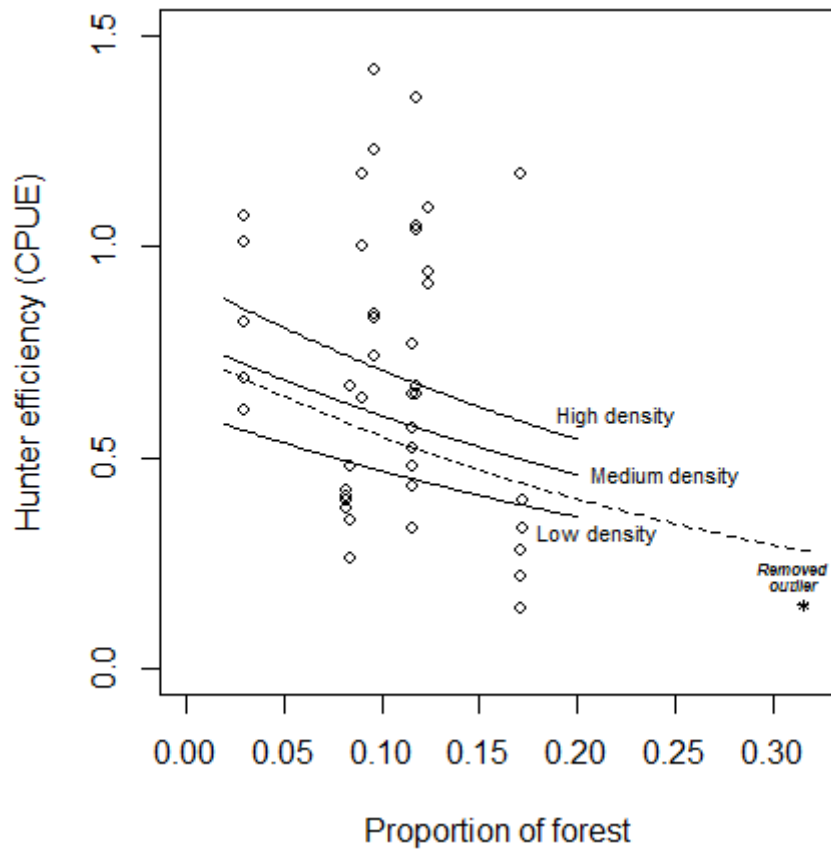


Figure S2. Hunter efficiency, measured as bagged birds per hunting day (commonly known as catch-per-unit-effort, CPUE), modeled as a function of density and proportion of forest in hunting grounds. The solid prediction lines for three fixed example levels of density (first, second and third quartile of the data set), show a decreasing hunter efficiency with increasing proportion of forest. These predictions and the observations (circles) are from the data set used in all other analyses. The asterisk is the previously removed outlier, and the dashed line shows the prediction line for the low density level with the habitat outlier included.

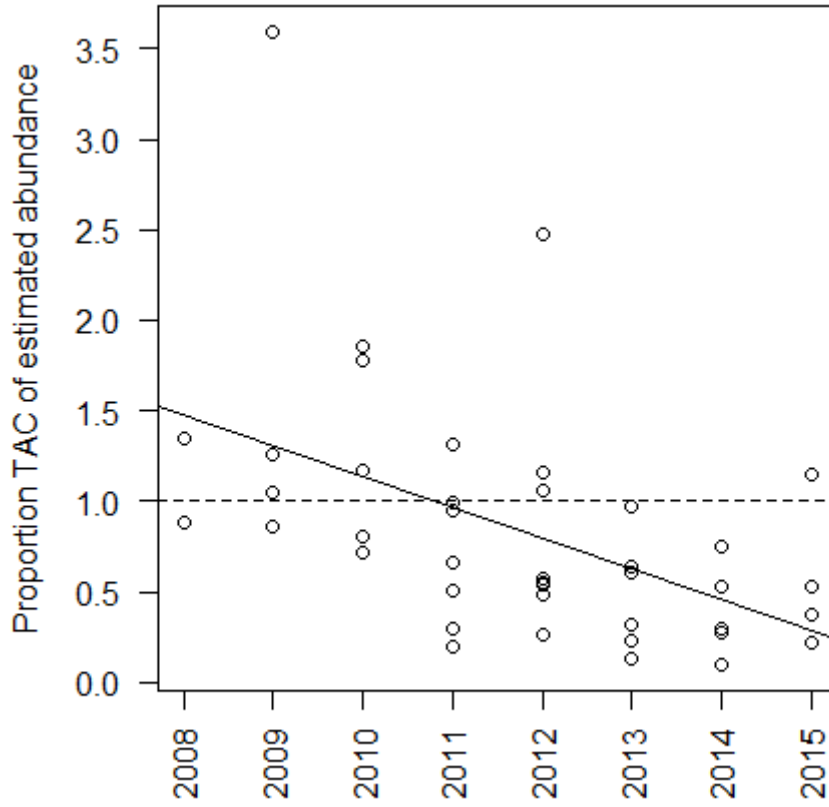


Figure S3. Decrease in TAC proportional to estimated abundance over the study period. Solid line is a regression line through the observation, dashed line indicates the logical limit for what might actually be shot, i.e. 100 % of the population. Average proportional TAC = 82 %.