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Spatial and temporal variation in abundance of willow ptarmigan *Lagopus lagopus* and rock ptarmigan *Lagopus muta* in Finnmark county, Norway:

– evaluation of methods for population monitoring

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NAB-3900 Master's thesis in
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Abstract

Sustainable harvesting requires reliable quantitative estimates of pre-harvesting population size, however, within low management budgets, good quality predictions are often difficult to obtain. For the popular game species willow ptarmigan (*Lagopus lagopus*) estimates of population density or relative indices are often obtained from line transect surveys. Such methods can provide accurate information on pre-harvest populations, however, the quality of estimates could be sensitive to low sampling effort. Additional ptarmigan population data are hunting statistics, but the potential lack of convergence between population density and hunting bag remains a concern. The sympatric rock ptarmigan (*Lagopus muta*) is commonly given much less management attention, and the species is often arbitrarily expected to show synchronised dynamics with willow ptarmigan. In this paper we evaluate different population indices obtained from willow ptarmigan line transects surveys in late summer, and catch reports of subsistence snare trapping in late winter, and specifically assess these indices' ability to predict subsequent ptarmigan hunting bags in eight municipalities in northernmost Norway. We use line transect data from 6–7 years of varying monitoring effort, snare trapping statistics from between 6 and 12 years in different municipalities, and hunting statistics from 7–8 years in all municipalities. By means of statistical modelling we evaluate to what extent these indices are able to predict the subsequent hunting bags of both ptarmigan species in our study area.

Generalised linear mixed-effect models indicated that only crude predictions of the subsequent willow ptarmigan hunting bags could be made from the line transect estimates under the current management regime. The snare trapping index made only a minor improvement of the prediction, and although the potential effects varied between municipalities, its inclusion as a predictor is not generally recommended in future ptarmigan management. The rock ptarmigan hunting bags could not be predicted by any of the available pre-harvesting indices. Variance component analyses revealed pronounced lack of systematic variation in all indices for both ptarmigan species, consequently any prediction of subsequent hunting bag outcome, should be highly conservative. Although we did not find clear tendencies of better predictions in municipalities with higher line transect effort, we suspect that the monitoring effort needed to provide useful pre-harvest indices is highly underestimated in the current management regime. Potentially unknown ptarmigan population processes and an elevated hunting pressure, should encourage management to increase, knowledge-based ptarmigan monitoring in the future.

Key words: willow ptarmigan; rock ptarmigan; sustainable harvesting; population density indices; line transect; snare trapping statistics; hunting statistics; population dynamics; population monitoring; game management; arctic ecosystems; Finnmark; Norway.

Contents

1 Introduction

Ptarmigan (*Lagopus* spp.) species play an important role in Arctic and Alpine ecosystems, both as herbivores on plants (den Herder *et al*. 2008) and as prey for predators (Erikstad *et al*. 1982; Myrberget 1985; Huhtala *et al*. 1996; Nielsen 1999; Munkebye *et al*. 2003). In recent years there has been increasing pressure on ptarmigan populations due to hunting (Storch 2007). Ptarmigan species are hunted for recreation throughout their ranges, and harvest rates up to 50% have been reported (Kastdalen 1992; Smith and Willebrand 1999). Harvesting may in general affect species populations directly through density reductions (Pedersen *et al*. 2004) and altered population dynamics (Baines and Lindén 1991; Solberg *et al*. 1999). Harvest mortality has traditionally been believed to be compensatory through density dependent processes (Allen 1954; Ellison 1991). On the contrary, recent studies show that hunting to some extent is additive to natural mortality (Steen and Erikstad 1996; Smith and Willebrand 1999; Pedersen *et al*. 2004). In general, assuming harvest to be compensative has sometimes led to severe over-harvest and non-reversible density reductions as well as extinction of species (Lande *et al*. 1995).

Ecological sustainable harvest is strongly emphasized in modern game management (Hudson and Rands 1988). However, for species such as willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*Lagopus muta*), both well documented to show large annual fluctuations in numbers (Gardarsson 1988; Myrberget 1988; Lindström 1994; Steen and Erikstad 1996; Aanes *et al*. 2002), the estimation of sustainable harvest levels suffers from considerable unpredictability. In order to harvest sustainably, good quality estimation of population density is highly requested, however, within low management budgets, such estimates are often not realistic on large temporal and spatial scales. Further, technical and logistical difficulties in implementation of surveys may result in large uncertainties in estimates. A variety of different techniques are applied to estimate abundance of ptarmigans, many are expressed as indices (e.g. counting of territorial calls, counts of droppings along transects (Evans *et al*. 2007)) instead of unbiased density estimates (Anderson 2001). Currently most surveys are conducted through line transect sampling with trained pointing dogs, using distance sampling methodology (Buckland *et al.* 2001) (Thomas *et al.* 2006). Despite obtaining true density, estimates of sparsely distributed species may still suffer from inaccuracies due to large spatial heterogeneity and insufficient numbers of line transects. Limitations may also apply due to observers experience and the requirements of trained dogs. Indices of relative population density along with information on population dynamics are often obtained from hunting bag statistics. Here, problems may arise due to arbitrary quantifying of hunter effort and low hunting record return rate. Hence, common concerns are that such data may not reflect actual population abundance (Lambin *et al.* 1999; Cattadori *et al.* 2003).

In Norway, willow ptarmigan and rock ptarmigan are the most important small game species. Annually, approximately 60 000 hunters harvest between 200 000 and 500 000 ptarmigans (Statistics Norway 2010a, b). In Finnmark, the northernmost county of Norway, the number of hunters and the total annual bags increased until the season 2005/06, when 30% (~105 000) of all ptarmigans hunted in Norway were shot in this county. Traditionally, vast un-hunted areas have been seen as a guarantee against overharvesting, hence hunting regulations beyond fixed season length, were not implemented until bag-limits were introduced in 2007/08. Elevated hunting pressure together with major changes in governmental management structure have made it particularly important to implement sustainable harvest management actions. Until recent years ptarmigan managements in Finnmark have based their decisions on two types of relative abundance indices, pre-hunting line transect surveys and hunting bag statistics. The line transect surveys have been conducted locally, but due to logistical challenges and funding resources the number of line transects have been limited. Municipality scale bag statistics and hunting effort information have been collected in Finnmark since 2000. The large size (48 649 km^2) and considerable environmental heterogeneity of Finnmark makes data on small scale useful, however the report return rates are low.

In Scandinavia there are old traditions for ptarmigan snare trapping, especially in the northern parts where indigenous people still harvest ptarmigan for subsistence (Helander 1999). The snare trapping is a late winter catch, carried out after most ptarmigan winter mortality has occurred (Pedersen and Karlsen 2007), further, information on both catch and effort are annually reported. As a potential third index on relative abundance of ptarmigan, a long-term dataset on ptarmigan populations from snare trapping reports, were made available for the current study.

In this study we use statistical modelling to evaluate to what extent the pre-harvest population indices obtained from line transect surveys in late summer and snare trapping in late winter are able to predict the subsequent hunting bags in the fall of both ptarmigan species in Finnmark. Demographic analyses have shown that apparent winter survival and chick production may have equal influence on willow ptarmigan population growth rate (Steen and Erikstad 1996), even so to date there has been no systematic attempts for monitoring of ptarmigan breeding population in Finnmark. We hypothesize that the snare trapping statistics by providing an index for size of the spring breeding population of ptarmigan, can improve on managers ability of predicting the subsequent hunting bags in the fall, in particular, if it is combined with line transect indices from late summer. To derive such reliable predictions on the scale of administrative units (e.g. municipalities) should be valuable to all stakeholders involved in ptarmigan harvest. As the accuracy of the predictions will be affected by the magnitude of sampling variance and other sources of spatial and temporal variation, we also conducted variance component analyses to quantify such sources of variability. Based on these analyse we aim to provide recommendations on how and where such index based predictions can be applied.

2 Methods

2.1 Study area

The study area consisted of eight municipalities in Finnmark (68°–71°N, 21°–31°E), the northernmost county of Norway (Figure 1). The area comprises the northern edge of the continuous Euro-Asian taiga in the south, the central part of Finnmarksvidda mountain tundra plateau, and the mountainous Barents Sea coastline. The North East Atlantic current is causing relatively mild climatic conditions in the coastal habitats of Finnmark. However, moving south and east in the study area the climate gradually changes from coastal to continental with mean July temperature in study area in the range of 10–13°C, while mean January temperature varies between coastal west -8°C, coastal east -12°C and continental south -17°C. Annual precipitation varies between 300 and 500 mm (Norwegian Meteorological Institute 2009 (data from 1961–1990)).

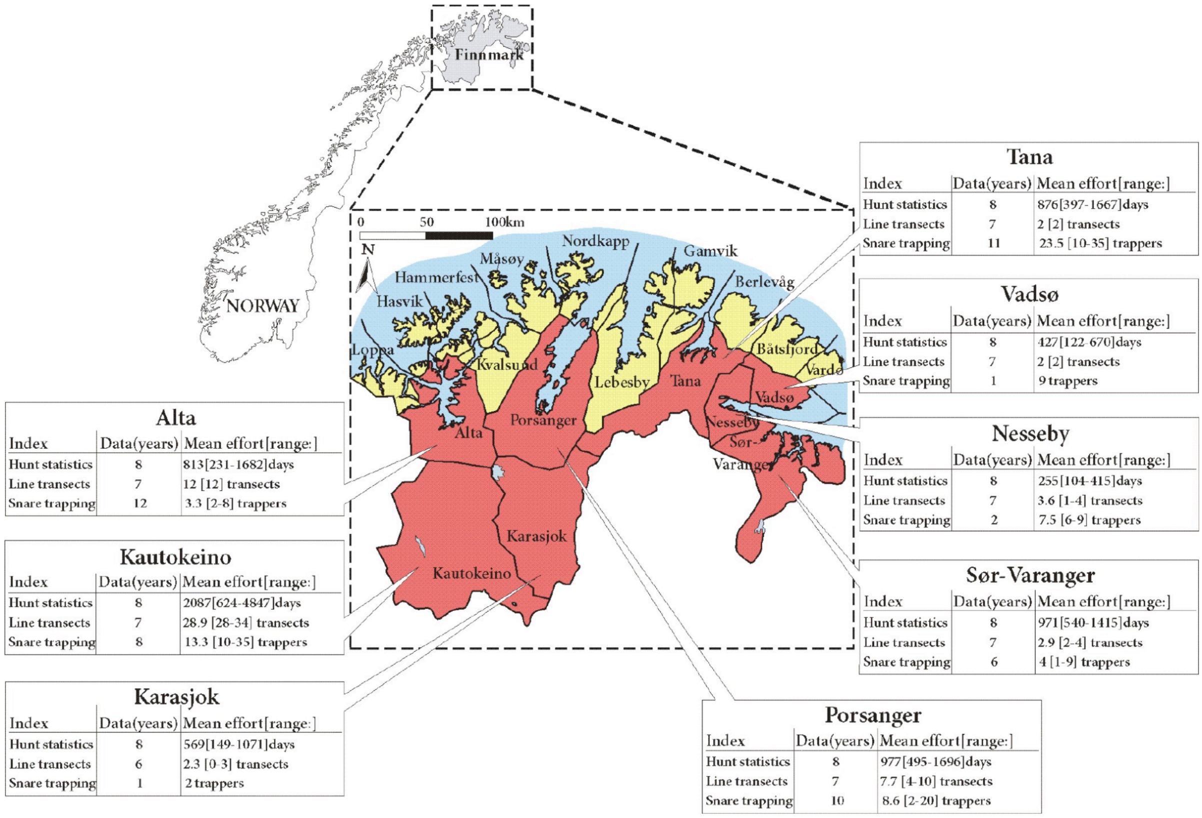


Figure 1. Map of Norway with inset showing Finnmark county and the eight study municipalities. Tables show efforts of different population indices from each municipality (Illustration: T. Midthun).

2.2 Study species

Willow ptarmigan and rock ptarmigan are monogamous, territorial, medium-sized game birds in the Tetraonidae family, with a circumpolar distribution. Populations are characterized by multiannual density variations and Myrberget (1982) showed a correlation between the approximately 4-years cycle of small rodents in the years 1932–1971 and population indices of willow ptarmigan in Finnmark. In Fennoscandia willow ptarmigan and rock ptarmigan are sympatric, although habitats are generally stratified by elevation with willow ptarmigan occupying mainly subalpine habitats, and rock ptarmigan the higher elevated alpine habitats (Andersen 1986; Krempig and Wallerheim 2004; Pedersen and Karlsen 2007). Willow ptarmigan diet in winter is dominated by shoots and seeds of mountain birch (*Betula pubescens*) and willow shrubs (*Salix spp.*). In seasons of accessible field layer, willow ptarmigan also feed on vegetation of dwarf-shrub species (e.g. *Vaccinum myrtilus, Vaccinum uliginosum* and *Arctostaphylos uva-ursi*), sedges and grasses (Myrberget 1979; Pulliainen and Iivanainen 1981; Brittas 1988). The diet of the rock ptarmigan is dominated by a variety of dwarf-shrub species (e.g. *Empetrum nigrum hermaphroditum, Loiseleuria procumbens, Arctostaphylos uva-ursi* and *Andromeda polifolia*) found at exposed snow free areas in the alpine habitats (Hjeljord 1980; Pedersen and Karlsen 2007).

2.3 Vertebrate community

Small rodents have major impact on the dynamics of their foraging resources and predators, hence they play a key functional role in northern boreal forest and arctic tundra ecosystems (Hansson and Henttonen 1988; Ims and Fuglei 2005). In our study area small rodents such as the Norwegian lemming (*Lemmus lemmus*) and the grey sided vole (*Myodes rufocanus*) are particularly abundant (Ims *et al*. 2007). Other herbivores in the study area are mountain hare (*Lepus timidus*), moose (*Alces alces*) and semi-domesticated reindeer (*Rangifer tarandus tarandus*). Common potential ptarmigan predators are red fox (*Vulpes vulpes*), stoat (*Mustela erminea*), weasel (*Mustela nivalis*), common raven (*Corvus corax*) and hooded crow (*Corvus cornix*) (Erikstad *et al*. 1982; Smedshaug *et al*. 1999; Klausen *et al*. in press), and raptors like gyr falcon (*Falco rusticolus*) (Huhtala et al. 1996; Nielsen 1999), golden eagle (*Aquila* *chrysaetos*) (Tjernberg 1981; Systad *et al*. 2007), and northern goshawk (*Accipiter gentilis*) (Tornberg 1997) and rough-legged buzzard *(Buteo lagopus*).

2.4 Databases

The study used data from three different population indices (Appendix 1). The line transect datasets and the hunting statistics were obtained from the Finnmark Estate (FeFo). The snare trapping reports were collected from eight municipalities (Figure 1). The line transect data were exclusively on willow ptarmigan, and snare trapping statistics did not distinguish between willow ptarmigan and rock ptarmigan catches, hence for rock ptarmigan, the only population index available was the hunting statistics.

2.4.1 Line transects

Pre-hunting season line transect surveys were conducted annually in each municipality between 10 and 20 August from 2001 to 2007, by qualified observers with trained pointing dogs from local hunters associations or the Norwegian Nature Inspectorate. Numbers of adults and juveniles (i.e. clutch size) were collected, and the time spent walking the line transects was reported. Hence, number of willow ptarmigan per hour (termed line transect index), number of adults per hour (termed adult index) and juveniles per two adults (termed production index) could be calculated as relative abundance indices.

In the eight municipalities 60 line transects (average 7.6 line transects per municipality [range: 2–28]) were surveyed annually. The effort varied to a great extent between the municipalities (mean 14.2 hours yearly per municipality [range: 4.0–52.3], median 6.6). All municipalities in sum averaged 113.2 hours [range: 99–138.5] of line transect walked each year.

In two of the municipalities, Alta and Kautokeino, there were sufficient data for willow ptarmigan density estimation by use of DISTANCE software (Thomas *et al*. 2006). The line transect index used in the study, and the willow ptarmigan density estimates, were highly correlated (Pearson correlation (r), Alta ($r = 0.97$, $P < 0.0001$); Kautokeino ($r = 0.84$, $P < 0.01$)) (Figure 2), suggesting that the indices mirror the proper estimates of spatial and temporal variation in willow ptarmigan densities.

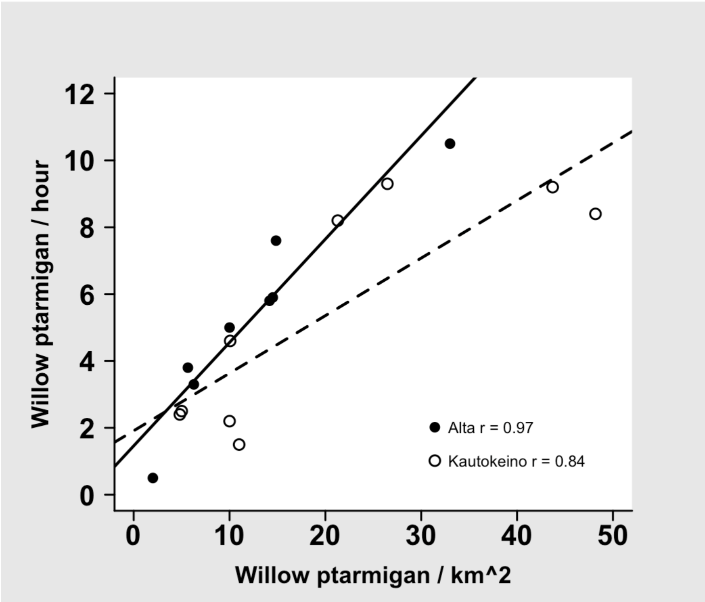


Figure 2. Correlation between willow ptarmigan density estimated by distance sampling and the line transect index (willow ptarmigan observed per hour) from Alta (●) and Kautokeino (○) municipalities. Regression lines for Alta (solid line) and Kautokeino (dashed line) are added.

2.4.2 Hunting statistics

Hunting statistics on municipality scale were collected annually between the seasons 2000/01 and 2007/08. These are retrospective data based on a voluntary bag report system with a return rate at county level averaging 22%. Hunters reported total number of willow ptarmigan and rock ptarmigan bagged, and the total sum of days spent hunting. Hence, willow ptarmigan bag per hunting day and rock ptarmigan bag per hunting day (respectively termed hunting index and rock ptarmigan hunting index) could be calculated. The reported number of days hunted varied among the years and municipality (see Appendix 1). For Kautokeino hunting season 2007/08 was excluded from analysis due to implementation of bag limits.

2.4.3 Snare trapping statistics

The snare trapping statistics were based on annually reported catches from recreational and subsistence snare trapping in eight municipalities between 1996 and 2008, however, due to limited data three municipalities were excluded from analyses. Each snare trapper reports the number of ptarmigan caught, number of snares used and the total amount of days spent trapping. Hence, we were able to calculate the number of ptarmigan caught per snare per day (termed snare trapping index) on municipality scale. The number of snare trappers and the effort per trapper varied between the municipalities (see Appendix 1). Snare trapping is legal during the entire ptarmigan hunting season (10 September–15 March). However, only the period between mid January and the 15 March is offering sufficient snow depth and light conditions for snare trapping. The essence of snare trapping practise is presented in Figure 3.

Figure 3. The snare trap is made of a wire that kills the ptarmigan by strapping around the bird's neck during browsing. Snares are placed in the shrub vegetation, according to the trapper's awareness of preferred ptarmigan habitats and old trapping traditions.

2.5 Statistical analyses

To examine variation in the hunting index for the two ptarmigan species, attributed to variation between year and between municipalities, variance component analyses were conducted using generalised linear random effect models. Models were fitted in R (R Development Core Team 2008) using the lme4 package (Bates and Maechler 2007). Likewise, to examine variation in line transect data and snare trapping data, we conducted separate variance component analyses for the line transect index and the snare trapping index. On county scale all line transects and snare trappers were assigned an identification number, and these were treated as random effects nested within municipality. The year variable was fitted in the model as a random intercept.

We examined the potential of five population indices (Table 1) in explaining the prospective ptarmigan hunting index by conducting model selection based on generalised linear mixed-effects models implemented in the lme4 package in R (Bates and Maechler 2007). The modelling was conducted separately on two data sets: (1) The eight municipalities with line transect data (termed 'line transect based models') and (2) the five municipalities with both line transect and snare trapping data (termed 'snare trapping + line transect based models'). The response variables in both sets of models were the annual hunting index or the annual rock ptarmigan hunting index. The response variables were log transformed. The potential fixed predictor variables examined in the 'line transect based models' were the line transect index, production index, adult index and hunting index (t-1) or the rock ptarmigan hunting index (t-1). For summary of indices and modelling terms see Table 1.

The potential fixed predictor variables examined in the 'snare trapping + line transect based models' were the snare trapping index in addition to the predictor variables used in the 'line transect based models' (see above). In both sets of models municipality was fitted as random intercepts. Random slopes for municipalities were tried, but as the numerical algorithms did not converge such random effects could not be included. All possible model combinations were ranked using the Akaike´s Information Criterion corrected for small sample sizes (AIC_c) and AIC_c weights (Anderson and Burnham 2002; Burnham and Anderson 2004), assuming models with lower AIC_c (and higher weights) to be better. The contribution of each of the fixed terms to the overall predictive powers of the models was assessed by the reduction in the residual variance when including the term compared to a constant model. As it may be of interest to use municipalities as units in future management of ptarmigan populations in Finnmark, we assessed the power of the two mixed models to predict the hunting index for each municipality. We did this by regressing the predicted values from the mixed models against the observed values of the hunting index. Finally we assessed the predictive power of the line transect index (i.e. the observed values) against the observed hunting index for each municipality.

Tabel 1. Explanation of indices- and modelling terms.

	Terms	Explanations
Indices	Hunting index	Willow ptarmigan bag per hunting day
	Rock ptarmigan hunting index	Rock ptarmigan bag per hunting day
	Line transect index	Willow ptarmigan observed per hour
	Production index	Willow ptarmigan juveniles observed per two adults
	Adult index	Willow ptarmigan adults observed per hour
	Snare trapping index	Ptarmigan caught per snare per day
	Hunting index (t-1)	Willow ptarmigan bag per hunting day the previous year
	Rock ptarmigan hunting index (t-1)	Rock ptarmigan bag per hunting day the previous year
Modelling	'Line transect based models'	Models based on dataset from eight municipalities with line transect data
	'Snare trapping + line transect based models'	Models based on dataset from five municipalities with snare trapping data and line transect data

3 Results

3.1 Sources of variation in ptarmigan indices

The variance component analyses showed that variation in the hunting index for both ptarmigan species was mostly attributed to variation between municipalities (Table 2). For willow ptarmigan there was also some of the total variation that could be attributed to a year variance component, which implies a common temporal trend in the hunting index between the municipalities (Figure 4). For rock ptarmigan there were fewer birds bagged per hunting day, and no variation was attributed to between-year variation (Table 2, Figure 4). Moreover, the proportion of rock ptarmigan in the total ptarmigan hunts over eight study years varied from inland Kautokeino (average: 2.1% [range: 1.5%–4.5%]) to coastal Alta (average: 29.0% [range: 18.7%–42.5%]).

Table 2. Variation in hunting index (bag per hunting day) for both ptarmigan species attributed to between municipality variation and between-year variation.

	Willow ptarmigan		**Rock ptarmigan**	
	Std. Dev.	**Variance (%)**	**Std. Dev.**	**Variance (%)**
Between municipalities	0.80	68.1	0.16	68.9
Between years	0.36	13.6	0.00	0.0
Residual	0.42	18.3	0.98	31.1

The variance component analyses of the line transect- and snare trapping datasets revealed large residual variance (i.e. variance within individual line transects and snare trappers) in both the line transect index and the snare trapping index (Table 3). Further, for the line transect index year and municipality contributed about equally to the total variance, whereas variance between line transects within year and municipality contributed substantially less. For the snare trapping index the variance between individual snare trappers within year and municipality was the most important variance component besides the residual variance.

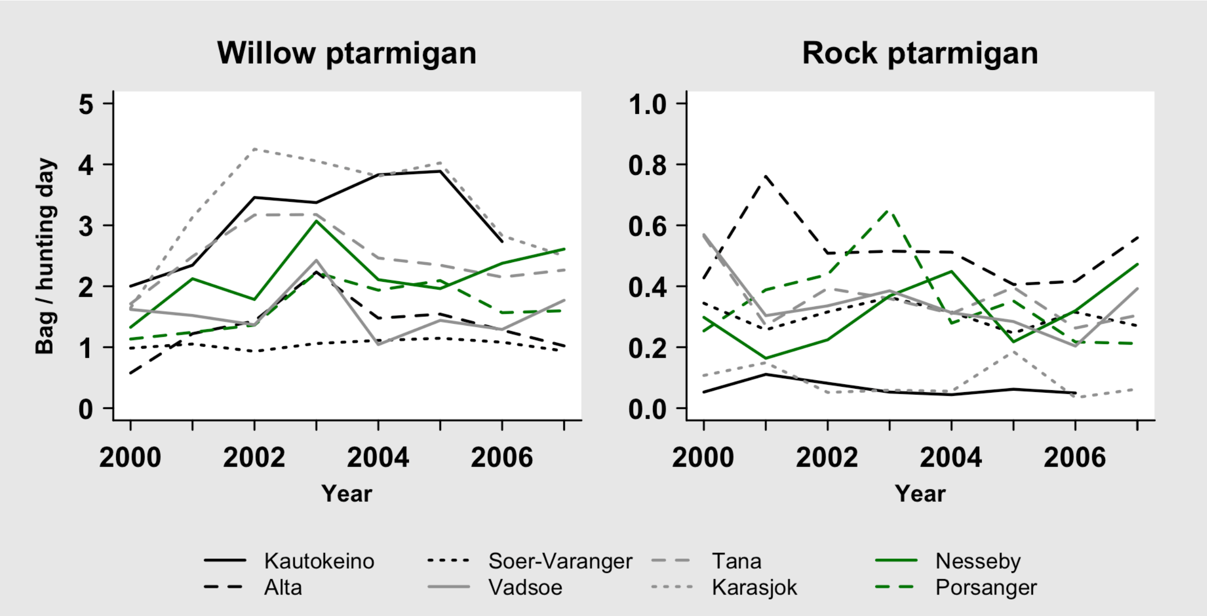


Figure 4. Willow ptarmigan and rock ptarmigan hunting index (bag per hunting day) in the different municipalities over the years 2000–2007.

Table 3. Variation in the two indices line transect (willow ptarmigan observed per hour) and snare trapping (ptarmigan caught per snare per day) attributed to within year and municipality, between municipalities, between years and residual.

	Line transect index		Snare trapping index	
	Std. Dev.	**Variance (%)**	**Std. Dev.**	**Variance (%)**
Within year and municipality	1.15	2.5	1.20	24.6
Between municipalities	2.46	11.6	0.48	3.9
Between years	2.59	12.9	0.36	2.2
Residual	6.16	73.0	2.02	69.3

3.2 Willow ptarmigan hunting statistics predictions

The selection of mixed effect ‘line transect based models’ (i.e. based on eight municipalities) of willow ptarmigan hunting index gave as the best model one that included the two variables, hunting index (t-1) and production index (Table 4) (termed ‘line transect model’). The reduction in residual standard deviation was, however, minor relative to a constant model (Table 4).

Table 4. The three best models and estimated effects (± standard error) describing the variability of hunting index (willow ptarmigan bag per hunting day) from the ‘line transect based models’ (i.e. based on eight municipalities). Hunting index (t-1) = willow ptarmigan bag per hunting day in the previous year. Line transect index = willow ptarmigan observed per hour. Production index = juveniles per two adults. Last column shows the reduction (%) in residual standard deviation (Std. Dev.) in willow ptarmigan hunting index prediction models, relative to a constant model with no fixed predictor variables.

Intercept	Hunting index (t-1)	Line transect index	Production index	ΔAIC_c	AIC_c (w)	Reduction (%) in residual Std. Dev.
0.32 (±0.18)	0.13 (±0.05)	–	0.02 (±0.01)	0.00	0.22	1
0.47 (±0.16)	0.10 (±0.05)	–	–	0.24	0.19	–
0.68 (±0.15)	–	–	–	1.88	0.08	–

For the ‘snare trapping + line transect based models’ (i.e. based on five municipalities), the willow ptarmigan hunting index was best predicted by the model fitted with three variables line transect index, snare trapping index and hunting index (t-1) (termed ‘snare trapping + line transect model’) (Table 5). This demonstrates that in the study municipalities with available snare trapping data, the snare trapping index could, to some extent, improve the prediction of the hunting index for willow ptarmigan. The best model gave a 28% reduction in the residual standard deviation, relative to a constant model (Table 5). Line transect index and snare trapping index alone gave residual standard deviation reductions of 12% and 1% respectively. The model including both the hunting index (t-1) and the snare trapping index provided the best early (i.e. prediction obtained > four months ahead of hunting start) hunting index prediction, reducing the residual standard deviation with 10% relative to the constant model. The negative effect on the hunting index from the snare trapping index, when fitted additively to the other variables, is partly a consequence of positive correlation between snare trapping index and line transect index (mean correlation coefficient: 0.46 [range: 0.19–0.72], directing negative correlation between model coefficients. The model solely including the snare trapping index variable gave a positive coefficient (Table 5). Predictions from the model including hunting index (t-1) and production index, and the model including hunting index (t-1) and line transect index provided the second and third best models respectively.

Table 5. 'Snare trapping + line transect based models' selection (i.e. based on five municipalities). Above dashed line: The three bests models predicting the variability of hunting index (willow ptarmigan bag per hunting day). Below dashed line: Two models with early (i.e. prediction obtained > four months ahead of hunting start) indices including hunting index (t-1) and snare trapping index, further two models including solely the line transect index and the snare trapping index respectively. Estimates (± standard error) are shown. Hunting index (t-1) = willow ptarmigan bag per hunting day in the previous year. Line transect index = willow ptarmigan observed per hour. Production index = juveniles per two adults. Snare trapping index = ptarmigan caught per snare per day. Last column shows the reduction (%) in residual standard deviation (Std. Dev.) in willow ptarmigan hunting index prediction models relative to a constant model with no fixed predictor variables.

Intercept	Hunting index (t-1)	Line transect index	Production index	Snare trapping index	ΔAIC_c	AIC_c (w)	Reduction (%) in residual Std. Dev.
0.21 (±0.19)	0.16 (±0.05)	0.03 (±0.01)	–	-9.26 (±4.62)	0.00	0.19	28
-0.05 (±0.19)	0.23 (±0.05)	–	0.04 (±0.01)	–	0.13	0.18	21
0.09 (±0.18)	0.16 (±0.05)	0.03 (±0.01)	–	–	0.61	0.13	22
0.35 (±0.20)	0.18 (±0.06)	–	–	-7.32 (±5.64)	6.52	0.01	10
0.41 (±0.21)	–	0.03 (±0.01)	–	–	6.88	0.01	12
0.69 (±0.23)	–	–	–	0.69 (±0.23)	12.42	0.00	1

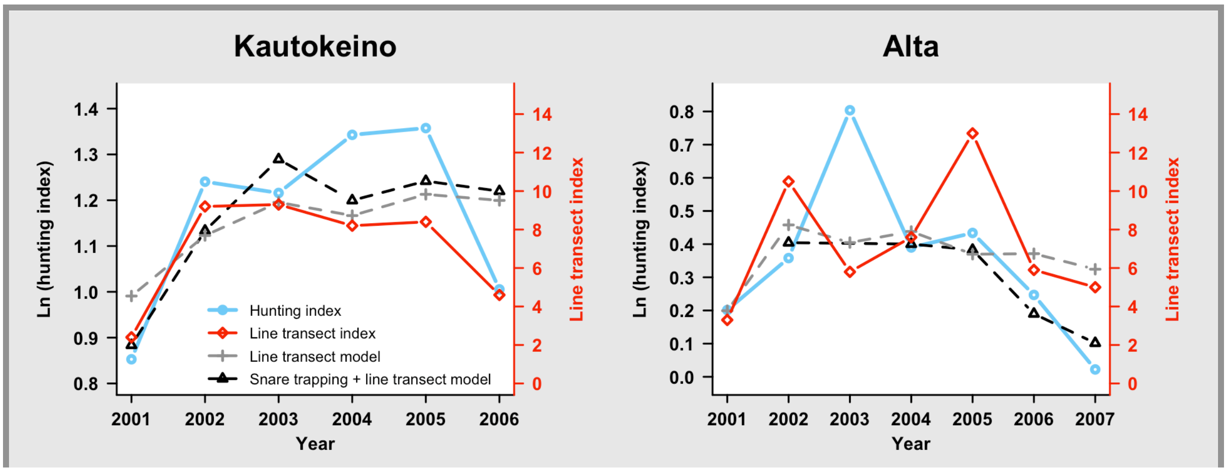
3.3 Validation of municipality level predictions

For the 'line transect model' the predictions of hunting index had generally low predictive power in all municipalities (Table 6). The model could for some municipalities (for example Kautokeino and Tana) predict the general direction of the hunting index trajectory in the subsequent hunting season (Figure 5). However, there was no general tendency for the predictive power of the model to be better for municipalities with high line transect effort (Table 6). There were tendencies of overestimating in years of low hunting index, and of underestimating in years of larger hunting index (Figure 5).

The 'snare trapping + line transect model' made a slightly better overall prediction than the 'line transect model' (Figure 5). There was still some tendency of overestimating in low years, however this tendency appeared to be less severe than with the 'line transect model'. Except for one municipality (i.e. Kautokeino) the best mixed model (i.e. 'snare trapping + line transect model'), gave better predictions than the simple linear regression for each municipality based on only line transect observations (Table 6).

Table 6. Validation of predictions of hunting index (willow ptarmigan bag per hunting day) from the two best mixed models (i.e. 'line transect model' and 'snare trapping + line transect model') against observed hunting index for the individual municipalities by means coefficient of determination (R^2) and p-values from linear regression. For comparison equivalent statistics are given for the regression between line transect index (willow ptarmigan observed per hour) and hunting index (termed line transect observation). Significant coefficients are in bold. In two last columns line transect- and snare 0trapping effort parameters (annual mean line transect numbers and annual mean snare trapper numbers) are shown.

Models / Municipality	Line transect model		Snare trapping + line transect model		Line transect observation		Mean line transect numbers	Mean snare trapper numbers
	R^2	p	R^2	p	R^2	p		
Kautokeino	0.47	0.13	0.51	0.11	**0.83**	**0.01**	28.9	13.1
Alta	0.22	0.29	**0.88**	**0.02**	0.07	0.56	12	3.3
Tana	0.27	0.23	0.56	0.05	0.19	0.32	2	24.7
Porsanger	0.05	0.63	0.37	0.40	0.04	0.67	7.7	8.6
Sør-Varanger	0.11	0.46	0.08	0.72	0.06	0.58	2.9	4
Nesseby	0.07	0.56	–	–	0.25	0.25	3.6	–
Vadsø	0.27	0.24	–	–	0.02	0.76	2	–
Karasjok	0.27	0.30	–	–	**0.74**	**0.03**	2.3	–



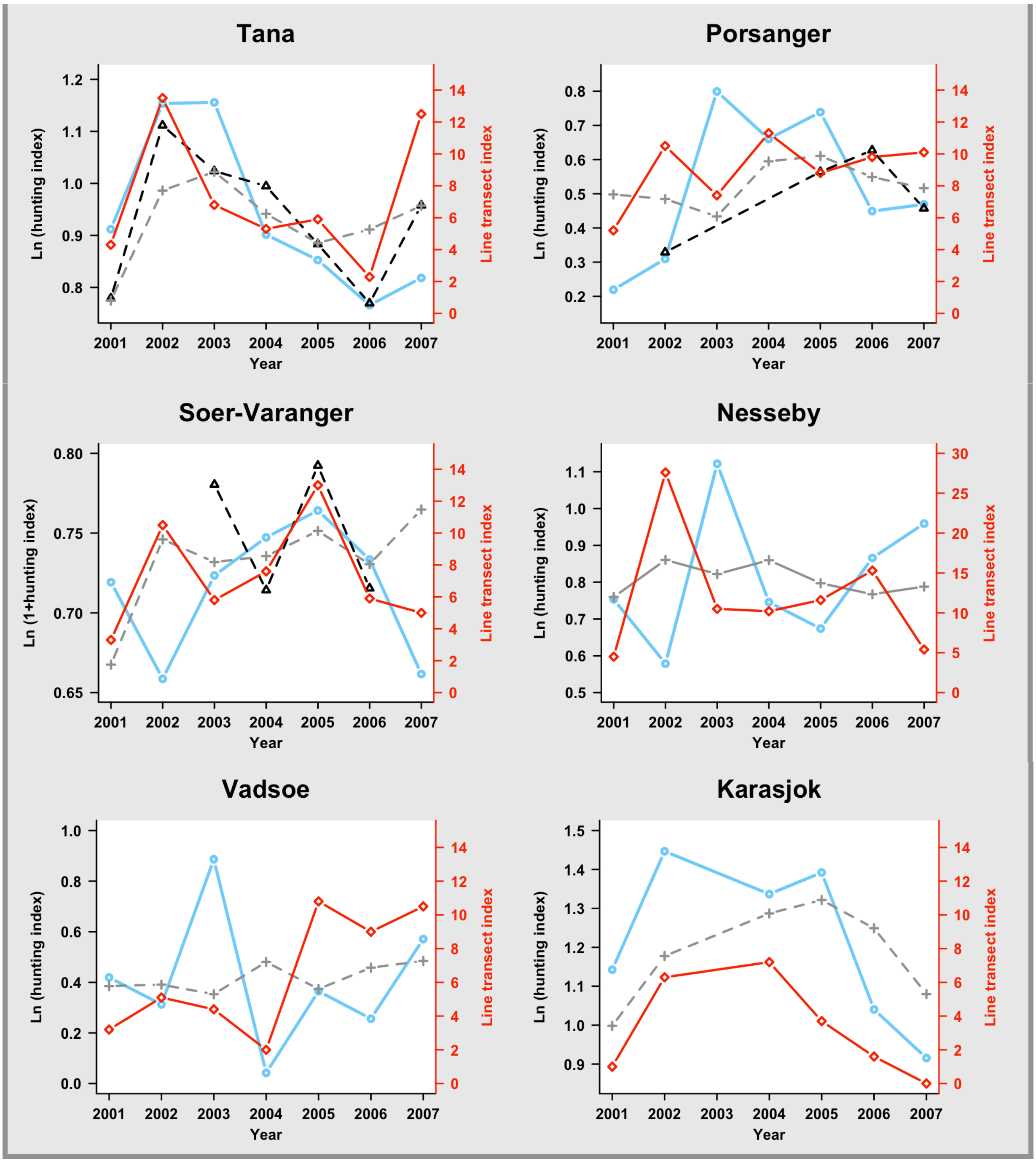


Figure 5 (page 18 and 19). Observed and predicted hunting index (willow ptarmigan bag per hunting day) in eight municipalities. Observed hunting index (○, blue line), predictions from 'snare trapping + line transect model' (△, broken black line), and predictions from 'line transect model' (+, broken grey line). Observed line transect index (willow ptarmigan observed per hour) are plotted on right axis (○, red line). Hunting index is log transformed (note that a constant of 1 is added to Sør-Varanger).

3.4 Rock ptarmigan hunting statistics predictions

The rock ptarmigan hunting index was best predicted by a constant model from the 'line transect based models' (i.e. eight municipalities) indicating that none of the study indices could predict the rock ptarmigan hunting index (Table 7). Second best model included a negative effect from the adult index (willow ptarmigan). All other models had very low predictive powers. Best model from the 'snare trapping + line transect based models' selection (i.e. five municipalities), remained the constant model, and the model including the snare trapping index variable was the fifth best model with accordingly very low predictive power (Table 8). However, in this model the snare trapping index influenced the rock ptarmigan hunting index positively, suggesting a weak positive relationship between the spring ptarmigan population and the rock ptarmigan hunting index in fall.

Table 7. The three best models and estimated effects (± standard error) describing the variation in rock ptarmigan hunting index (rock ptarmigan bag per hunting day) in eight municipalities. Line transect index = willow ptarmigan observed per hour. Adult index = adult willow ptarmigan observed per hour. Last column shows the reduction (%) in residual standard deviation (Std. Dev.) in rock ptarmigan hunting index prediction models, relative to a constant model with no fixed predictor variables. Note that all predictor variable indices are based on willow ptarmigan line transect data.

Intercept	Line transect index	Adult index	ΔAIC_c	AIC_c (w)	Reduction (%) in residual Std.Dev.
-1.48 (±0.27)	–	–	0.00	0.261	–
-1.38 (±0.29)	–	-0.05 (±0.05)	1.309	0.135	0
-1.39 (±0.29)	-0.01 (±0.01)	–	1.362	0.132	0

Table 8. The three best models describing the variation in rock ptarmigan hunting index (rock ptarmigan bag per hunting day). Below dashed line: Two models including snare trapping index and line transect index respectively. Estimates (± standard error) are shown. Line transect index = willow ptarmigan observed per hour. Production index = willow ptarmigan juveniles per two adults. Adult index = adult willow ptarmigan observed per hour. Snare trapping index = ptarmigan caught per snare per day. Last column shows the reduction (%) in residual standard deviation (Std. Dev.) in rock ptarmigan hunting index prediction models relative to a constant model with no fixed predictor variables. Note that all predictor variable indices, except snare trapping index (no species information), are based on willow ptarmigan line transect data.

Intercept	Line transect index	Adult index	Production index	Snare trapping index	ΔAIC_c	AIC_c (w)	Reduction (%) in residual Std. Dev.
-1.41 (±0.35)	–	–	–	–	0.00	0.22	–
-1.23 (±0.38)	–	-0.08 (±0.07)	–	–	1.25	0.12	2
-1.56 (±0.37)	–	–	0.03 (±0.03)	–	1.40	0.11	1
-1.47 (±0.38)	–	–	–	4.21 (±9.96)	2.61	0.06	0
-1.39 (±0.37)	-0.00 (±0.02)	–	–	–	2.79	0.05	0

4 Discussion

4.1 The validity of population indices as predictive tools

The objective of this study was to evaluate the applicability of conventional and new population indices in sustainable hunting management regimes for two ptarmigan species in northern Norway. We did this by evaluating the ability of line transect indices to predict subsequent ptarmigan hunting bags, and to evaluate the possible improvement of predictions by including a new index constructed from subsistence snare trapping statistics. Any improved prediction by using snare trapping statistics, would provide a cost effective means for more accurate management on local administrative scale (e.g. municipalities).

For willow ptarmigan the best mixed model based on only line transect indices and previous year hunting index (i.e. 'line transect model'), gave in most cases only crude predictions of the current year hunting index when all municipalities were included in the model. Simple regression using the line transect index as a predictor per municipality did in most cases not predict the willow ptarmigan hunting index. The mixed line transect model gave a slightly better prediction when based on the five municipalities, for which snare trapping statistics were available. Moreover, for these five municipalities the prediction was vaguely improved my adding the snare trapping index to the model. Except for one municipality (i.e. Kautokeino) where a disproportional large annual line transect effort took place, the mixed model gave a better prediction than the simple linear regression based on line transect observations per municipality. This suggests that the mixed modelling approach, including the snare trapping predictor worked best for some of the municipalities with scanty line transect data. In such cases the model could "borrow strength" from the information available from the other municipalities. However, all approaches gave generally uncertain predictions, thus a conservative use is recommended in the future management. Rock ptarmigan hunting index could not at all be predicted from any ptarmigan population index in the study, thus at present there seem to be no information available to perform an evidence based management of the rock ptarmigan.

4.2 Sources of variance in population indices

As revealed by the variance component analyses, there were large residual variances in all predictors and hence only marginal variance was attributed to year and municipality, which may have been some of the reasons for their low capabilities of predicting the hunting index. With a pronounced lack of systematic variation attributed to municipalities and year, the failure to perform powerful model predictions at these levels are to some extent inevitable.

4.2.1 Line transects

The potential of making predictions from line transects depend on a minimum of line transect effort, and reasonable precision of density estimation by DISTANCE methodology, has been achieved at > 40 observations (Buckland *et al.* 1993; Pedersen *et al.* 1999; Buckland *et al.* 2001, 2004). We were not able to calculate absolute density estimates since the line transect efforts were too low in most municipalities. We did not find any obvious tendency for improved predictions in municipalities with high line transect effort. Anyhow, for the municipality where sufficient data were available (Kautokeino) the simple line transect indices were strongly correlated with the proper density estimates. Nevertheless, it seems reasonable to suggest that prediction in most study municipalities would benefit from increased line transect effort and proper analysis accounting for imperfect detection (Buckland *et al.* 2001). As numbers of observations per effort would vary with changing ptarmigan density, the required effort of line transects in Finnmark may differ spatially and temporally. For example, the good fit between the line transect index and hunting index in the two southernmost study municipalities (Kautokeino and Karasjok) with relatively high ptarmigan density, could suggest that in areas with high population density better estimates are obtained. Perhaps, even the hunting index was more related to the true population density in these municipalities.

4.2.2 Snare trapping statistics

There were huge variations between individual snare trappers, and together with the high residual variance this impede the utility of the snare trapping index as a powerful predictor.

Further, different limitations and biases in the use of snare trapping index are evident, including both individual snare trappers qualities and other sources of variation associated with the snare's ability to catch the ptarmigan (e.g. snow depth, shifting daylight). Seeking to minimize the variation between snare trappers, truncation of trappers with low effort (< 5000 snare days) was tried, but the variation between snare trappers did not decrease. Based on the highly variable snare trapping reports available in most municipalities, we also suspect the report return rate to be generally low, and thus be a source of unexplained variability.

4.2.3 Hunting statistics

Hunting statistics have been used as a population index in several studies (Holmstad *et al.* 2005; Kvasnes *et al.* 2010). Cattadori *et al.* (2003) showed that hunting statistics were a good proxy for population abundance of red grouse (*Lagopus lagopus scoticus*) in Great Britain, however, the authors emphasised the need of comparative studies to reveal the potential of hunting statistics in different species and applied to different harvesting strategies. In northern Finland, bordering Finnmark in the south, contrasting results were found in hunting statistics from three grouse species (Ranta *et al.* 2008), hence concerns questioning the quality of hunting statistics in neighbouring grouse species , such as willow- and rock ptarmigan in Finnmark, seems relevant. Ranta *et al.* (2008) further suggested potential factors that could result in variable reliability of hunting indices, such as management policy changes and regional differences in management recommendations and hunting traditions. A further sign of divergences between hunting statistics and census data are the bias in the age and sex structure observed in the bag data (Hudson 1986). A higher juvenile to adult ratio in the line transect estimates, compared to the hunting statistics is reported in several ptarmigan studies (Pedersen *et al.* 1999; Taylor 2000; Hörnell-Willebrand *et al.* 2006). In our study the negative effects of the snare trapping index on the hunting index may suggest a similar pattern in Finnmark willow ptarmigan populations.

4.3 Uncertainty in underlying ptarmigan population processes

In this study we use hunting bag statistics both as response (i.e. hunting index) and predictor (i.e. hunting index (t-1)), hence potential bias and sources of variation in hunting statistics may have influenced the results. Some of the bias and variance is likely to result from to the low report return rates in Finnmark. However, when included as a predictor hunting index (t-1) had a positive effect on current year hunting index. This is in contrast to the expectation of direct negative density-dependence in ptarmigan populations (e.g. Pedersen *et al*. 2004). This may suggest lack of agreement between hunting statistics and actual population processes. Alternatively, ptarmigan populations in Finnmark may currently display dynamics less prone to direct density-dependence. Conventional ptarmigan dynamics in Finnmark show population synchrony with small rodent cycles (Myrberget 1982), however during the study period small rodents peaked in the years 2002 and 2007 (Ims *et al*. 2010, manuscript). The hunting index showed no apparent population peak associated with these small rodent years, hence present ptarmigan populations in Finnmark may experience hitherto unexplained dynamic patterns. A similar recent change in the temporal dynamics of ptarmigan is also known from the neighbouring county of Troms where 3–4 years cyclicity has been replaced by more long term fluctuations (Holmstad *et al*. 2005). The recent changes in the cyclic amplitude of small rodents in northern Fennoscandia have implications on ptarmigan population (Strann *et al*. 2002; Hörnfeldt *et al*. 2005; Ims *et al*. 2008), both through changed trophic interactions (e.g. the effect of shared predators) and through shared susceptibility to the same climatic changes (Kausrud *et al*. 2008). Other interactions affecting ptarmigan populations are increased resource competition from large herbivore overabundance (Ims *et al*. 2007). With the recent doubling of ptarmigan hunter numbers and a threefold increase in willow ptarmigan hunting bags in Finnmark during the study period, one might also speculate that such elevated harvest levels could affect the general population dynamics. The combined effects of increased harvest pressure and new kinds of natural population regulation represent an immense challenge making ptarmigan population predictions.

4.4 Management implications

This study shows that large sampling variability and potential biases in ptarmigan population indices together with potentially unknown processes underlying population dynamics, lead to considerable difficulties in making reasonably good prediction under current management regime in Finnmark. Potential spatial differences in natural ptarmigan population carrying capacity as well as hunting pressure, may call for differentiated recommendations in the individual municipalities. However, generally increased line transect effort would potentially improve overall predictions. Given low management budgets and incapacity of increased monitoring effort, we recommend that a higher number of line transects are placed in fewer and larger management regions representative for ptarmigan populations across municipality borders. Furthermore, that appropriate methods accounting for imperfect detection are applied. This could potentially improve estimates and further provide a basis for direct density estimations of ptarmigan populations (Rosenstock *et al*. 2002). The potential loss of prediction on the local (i.e. municipality) scale is justified to the benefit of higher total predictive power for the county as a whole. To improve precision from the hunting statistics we also recommend that hunting report return rates must be increased. The recent implementation of municipality scale reporting in the national hunting statistics is promising. Estimates from snare trapping could potentially be applied in selected municipalities (e.g. Alta and Tana). However, on a larger scale the utility of snare trapping predictions likely depends on an improved report return system. No prediction of rock ptarmigan hunting statistics could be made from any of the study indices. Rock ptarmigan is the second most harvested game species in Finnmark and Norway, hence, developing population monitoring programmes for rock ptarmigan should be a prioritized issue for future research. In anticipation of improved population prediction for both ptarmigan species in Finnmark, cautiousness in harvesting practise is recommended.

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7 Appendix 1

Summary of the datasets by municipality.

	Parameter	Alta	Porsanger	Tana	Kautokeino	Sør-Varanger	Nesseby	Vadsø	Karasjok
	Area (km^2)	3845	4873	4055	9704	3967	1442	1259	5464
Hunting statistics (2000–2007)	Years with data	8	8	8	7	8	8	8	8
	Mean hunting days reported	813 [231–1682]	977 [495–1696]	876 [397–1667]	2087 [624–4847]	971 [540–1415]	255 [104–415]	427 [122–670]	569 [149–1071]
	Mean hunting days stipulated from report return rate [range]	3499 [1283–5607]	4360 [2494–6222]	3758 [2205–5209]	9458 [3467–16157]	4360 [3000–7861]	1138 [578–1646]	1986 [678–3722]	2464 [828–3570]
Line transects data (2001–2007)	Years with data	7	7	7	7	7	7	7	6
	Mean line transect numbers [range]	12 [12]	7.7 [4–10]	2	28.9 [28–34]	2.9 [2–4]	3.6 [1–4]	2	2.3 [0–3]
	Mean line transect time in hours [range]	24 [22–28]	10 [6–12]	4 [4–5]	52 [38–71]	8 [3–22]	6 [2–7]	4 [3–5]	6 [5–8]
Snare trapping statistics (1996–2008)	Years with data	12	10	11	8	6	2	1	1
	Mean snare trappers per year [range]	3.33 [2–8]	8.6 [2–20]	23.5 [10–35]	13.13 [7–20]	4 [1–9]	7.5 [6–9]	9	2
	Mean snare days per year [range]	3034 [165–8913]	9126 [172–23659]	111441 [54447–150234]	50795 [6228–108221]	3812 [216–5998]	25857 [25830–25884]	7997	312