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THE ARCTIC  
UNIVERSITY  
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Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

## An assessment of survey methods to estimate spring density of two ptarmigan species in arctic Norway

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**Aurélie Delaye and Marita Anti Strømeng**

*BIO-3950 Master thesis in Biology, Northern populations and Ecosystems*

*May 2016*





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Cover photos by

Left: Aurélie Delaye; Rock ptarmigan (*Lagopus muta*) in Varanger, spring 2015

Right: Marita Anti Strømeng; Willow ptarmigan (*Lagopus lagopus*) in Varanger, spring 2015

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Aurélie Delaye  
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## Abstract

Both Willow ptarmigan (*Lagopus lagopus*) and Rock ptarmigan (*Lagopus muta*) are important game species in mainland Norway, but were recently added to the Norwegian Red List due to long-term population declines. Yet the knowledge about the population dynamics and the underlying drivers of both species is limited, especially for *L. muta*. Developing robust methods for long-term monitoring of population densities is required to increase ecological insight. The partially overlapping distribution of *L. lagopus* and *L. muta* in our study area in northeastern Norway provided a rare opportunity for inter-specific comparison of methods of population surveys and analyses to estimate spring density of breeding pairs. We used identical survey designs conducted simultaneously during 3 weeks in April-May within the same geographical area for both species. Despite having similar survey efforts we obtained considerably more data for *L. lagopus* than for *L. muta*, mainly due to differences in their densities, but also because their different behaviours and spatial distributions influenced their detectability. While distance sampling appeared to accurately estimate the density of *L. lagopus*, the same method was not possible to apply to *L. muta*, as the number of observations was too low. When using point count methods, the density for both species seemed to be overestimated. This appeared to be mainly due to the violation of the assumption of closed population. This violation was due to a proportion of birds still being aggregated in mobile flocks and because unusually warm weather and loss of snow cover for transportation of observers caused the survey period to be terminated before the birds were stably established on their breeding territories. The density as well as species-specific phenological and behavioural traits should decide the choice of monitoring methods, herein timing, survey design and effort. The initiation of territorial behaviour in ptarmigan is mainly induced by change in day length, but can also be affected by weather conditions. In light of increasingly earlier onset of spring in alpine and arctic tundra under climate change, the temporal mismatch between the peak of territorial activities and sufficient snow cover for transportation of field personnel for the survey may increase. Thus, it may become even more challenging to perform manual spring surveys on ptarmigan in the Norwegian terrestrial arctic by conventional methods. The use of new automated survey technology, such as acoustic sensors, may help to overcome such challenges.

Keywords: *Lagopus lagopus*, *Lagopus muta*, inter-specific comparison, density estimation, distance, detection probability, survey design, spring survey, point count





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## Introduction

Willow ptarmigan (*Lagopus lagopus*) and Rock ptarmigan (*Lagopus muta*) are two genetically closely related tetranoid bird species (Dimcheff et al. 2002). They have a circumpolar distribution and overlap in some regions, including mainland Norway. The core of the distribution range of *L. lagopus* is within the low-arctic tundra, but also extends into forest tundra and open sub-arctic forest (Potapov and Sale 2013). In northern alpine ecosystems (e.g. in Fennoscandia), it is found in the low-alpine vegetation zone. Erect shrubs of *Salix* spp. or *Betula* spp. characterize the breeding habitat of *L. lagopus*. *L. muta* is present further north (i.e. in high Arctic) and at higher altitudes than *L. lagopus*, e.g. in high-alpine ecosystems in Svalbard, Greenland, Fennoscandia and the Alps. Its breeding habitat is typically rock-dominated and interspersed with dry heath vegetation (Pedersen et al. 2014). If the two species are found within the same region they will tend to segregate into separate habitats according to their preference in breeding sites and diet, which is mainly vegetarian for both species but more restricted for *L. muta* (Sale and Michelsen 2006, Wilson and Martin 2008).

As the most abundant year-round resident birds in arctic-alpine ecosystems, the two ptarmigan species are considered to have high societal and ecological importance (Ims et al. 2013, Tape et al. 2010). *L. lagopus* and *L. muta* are important game species that have been hunted for a very long time and are still the two most popular game species in northern Fennoscandia (Ims et al. 2013, SSB 2015). Several studies have attempted to estimate the impact of hunting on the species' population dynamics in order to improve the regulation of the harvest (Aanes et al. 2002, Bergerud and Huxter 1969, Pedersen et al. 2004, Sandercock et al. 2011). Their ecological functioning is much due to their importance as significant prey species for numerous predators, in particular for ptarmigan specialists such as the Gyrfalcon (*Falco rusticolus*) (Nielsen 1999) and the Golden Eagle (*Aquila chrysaetos*) (Nystrom et al. 2006), but also for generalists such as corvids, mustelids and foxes (Erikstad et al. 1982, Ims et al. 2013). Trophic interactions are thought to be the main drivers of cyclic changes in abundance (Henden et al. 2016, Ims et al. 2013, Isaev 2011, Myrberget 1982).

Similar to many other tetranoid bird species (Storch 2007), population declines in both ptarmigan species have been witnessed in several regions, including Fennoscandia (Henden et al. 2011, Kausrud et al. 2008, Lehtikoinen et al. 2014), and as a result both species were recently added to the Norwegian Red List as “near threatened” (Kålås et al. 2015). Changes in

species' abundance as a result of direct or indirect human activities (e.g. climate change, pollution, overhunting, livestock overgrazing) need to be fully understood in order to take appropriate management decisions. Scientifically robust monitoring of both the species of concern as well as potential drivers of changes is necessary for this purpose. The Climate-ecological Observatory for Arctic Tundra (COAT) launched by the Fram Center has the purpose to accumulate knowledge for long-term adaptive monitoring of arctic species of high ecological and societal importance. COAT is composed of several modules and one of them focuses on *Lagopus* spp. in the Norwegian sector of the terrestrial arctic; i.e. Varanger peninsula and Svalbard (Ims et al. 2013). Essential to COAT's ptarmigan module are unbiased estimates of breeding birds' densities. For the Svalbard rock ptarmigan (*L. muta hyperborea*) monitoring of spring densities has been properly developed (Pedersen et al. 2012) and presently run over a period of sixteen years. However, for both ptarmigan species on the Varanger peninsula and the rest of mainland Norway similar monitoring of the breeding populations' densities has not been established.

Several survey methods have been used to estimate density or abundance of each of the two ptarmigan species and these vary among the areas. For instance, distance sampling and site occupancy are presently used in Svalbard for *L. muta hyperborea* (Pedersen et al. 2012), total counts has been used in Newfoundland (Canada) for *L. lagopus* (Bergerud 1970), aerial surveys of both species in Yukon (Canada) (Pelletier and Krebs 1998) and point counts in the Pyrenean for *L. muta* (Marty and Mossoll-Torres 2012). There is a great lack of information about the population dynamics of *L. lagopus* from its vast circumpolar distribution. Likewise, *L. muta* is mainly surveyed at local scales and, in vast parts of its range of distribution, the monitoring is poor or entirely absent and thus population trends are unknown (Storch 2007). However, in general, there are more surveys and more knowledge about *L. lagopus* than about *L. muta*. In mainland Norway, *L. lagopus* is surveyed annually, using permanent line transects and distance sampling in late summer/early autumn, thus not targeting densities of territorial pairs in the spring. These line transect surveys are conducted using teams of trained observers with pointing dogs. By assessing the demography and brood sizes, the summer production of chicks can be estimated. Similar line transect surveys are not applied on *L. muta* as this species does not sit properly for pointing dogs. Hence, systematic monitoring of *L. muta* in Norway is lacking, except for Svalbard. The abundance dynamics and distribution of *L. muta* in Norway is thus mainly inferred from hunting bags as an index of abundance (Nilsen et al. 2012).

Surveying of bird species is a big enterprise worldwide and the need to estimate populations' abundances has led to the development of a wide range of methods for both obtaining data from the field and analyzing them (Borchers et al. 2010, MacKenzie et al. 2002, Thomas et al. 2010). The different methods greatly differ in the time and effort required to be spent in the field, but also in terms of the quality of the estimates they yield (Rosenstock et al. 2002, Schwarz & Seber 1999). Data obtained can broadly be divided into index- and survey-based information. Long-term monitoring of wildlife by means of proper surveys are scarce and, for harvested species, hunting bags have been used as an index for assessing populations' densities and their dynamics in space and time. However, studies that have assessed the validity of using hunting bag data as population indices have given contrasting results, i.e. with sometimes poor correlation between hunting statistics and direct survey-based estimates (Cattadori et al. 2003, Kvasnes et al. 2010, Soininen et al. 2016, Willebrand et al. 2011). This cautions against the use of such indices. High-quality surveys, such as mark-recapture and total-counts, are expensive as well as time and effort consuming. The methods used to survey birds must account for the particularities of the species studied, like abundance (rare species are more difficult to monitor and often need special adjustments), conspicuousness or habitat.

The most commonly used techniques for bird surveys are line transects and point counts. These can be conducted in a variety of ways, among others repeated visits within seasons, i.e. temporal replicates, using multiple observers, using exact counts and distance to individuals observed, or presence and absence counts can be used. With each method follows a suite of assumptions that should be met, although some assumptions may be relaxed (Borchers et al. 2010). Imperfect detection may arise when individuals are present but not detected. The animal's camouflage, behaviour, distance from observer, weather and habitat characteristics can influence its detection probability, and imperfect detection can lead to measurement errors if not accounted for (Freckleton et al. 2006, Link and Nichols 1994, Santin-Janin et al. 2014, Yoccoz and Ims 2004). Some of the methods that incorporate imperfect detection in wildlife surveys are distance sampling, repeated counts, occurrence sampling and double observer sampling (Fiske and Chandler 2011). Many statistical methods also include covariates to assess causes of variability in detection probability and animal presence, attempting to increase precision and decrease bias. These covariates are mainly recorded at site (e.g. elevation, habitat type and/or quality) and observation level (e.g. weather parameters, time of day, date, observers) (Fiske and Chandler 2011, Marques et al. 2007, Pedersen et al. 2012). Acquiring accurate density estimates should be of great concern when choosing census and

analysis methods, but species' behaviour, type and accessibility of terrains and habitats as well as allocation of effort, available time and personnel should be taken into consideration (Joseph et al. 2006, MacKenzie and Royle 2005, Marty and Mossoll-Torres 2012).

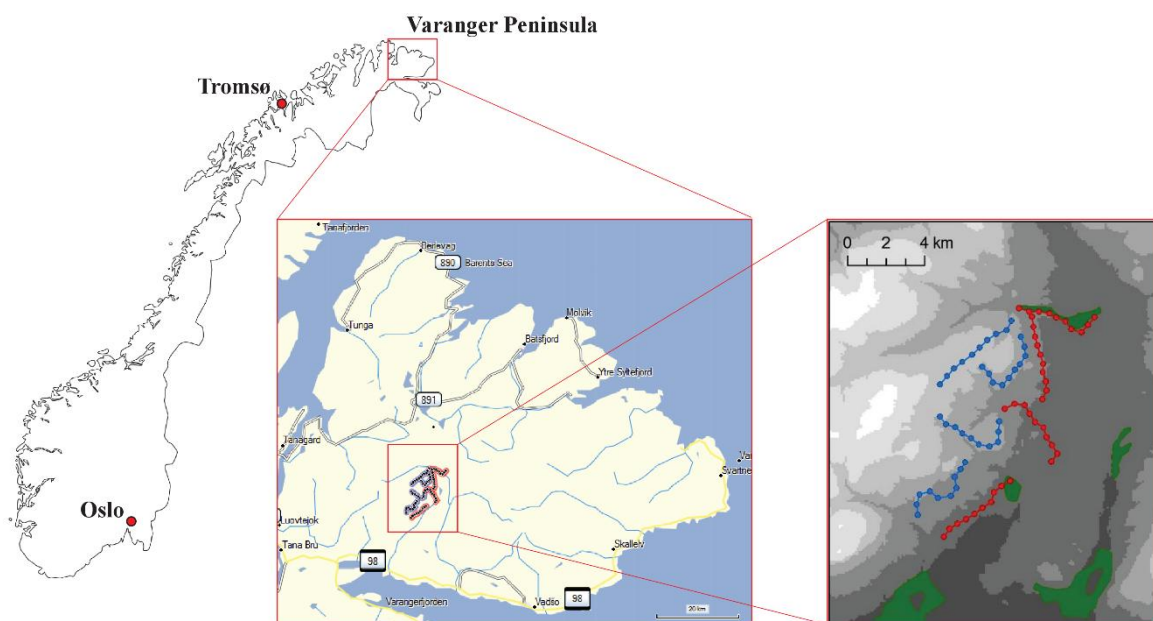
The aim of the present study was to assess the feasibility of conducting survey-based estimates of spring densities of both ptarmigan species in the Varanger peninsula. At the outset we used the extensive experience gained from spring surveys by means of the point-transect methods applied to *L. muta hyperborea* in Svalbard (Pedersen et al. 2012) to guide the design of the survey. However, important unknowns were due to the timing of the survey in spring in order to encompass the time when pairs are firmly settled on their territories.

There could potentially be differences between subspecies (i.e. *L. muta* vs. *L. muta hyperborea*) and species (*L. muta* vs. *L. lagopus*) both with respect to phenological aspects as well as general behavioural differences of birds relative to the observers. Moreover, spring surveys are susceptible to weather conditions and in particular whether the snow conditions are suitable for transport of observers on skis or snow mobiles. Thus, another aim of the study was to fill such knowledge gaps. It was also our purpose to compare point transects with line transects both in respect to performance of the two methods in the field and in statistical estimation of population densities of the two species. Finally, simulations would aid in assessing the needed survey effort in order to obtain precise estimates of the populations.

## Methods

### Study area

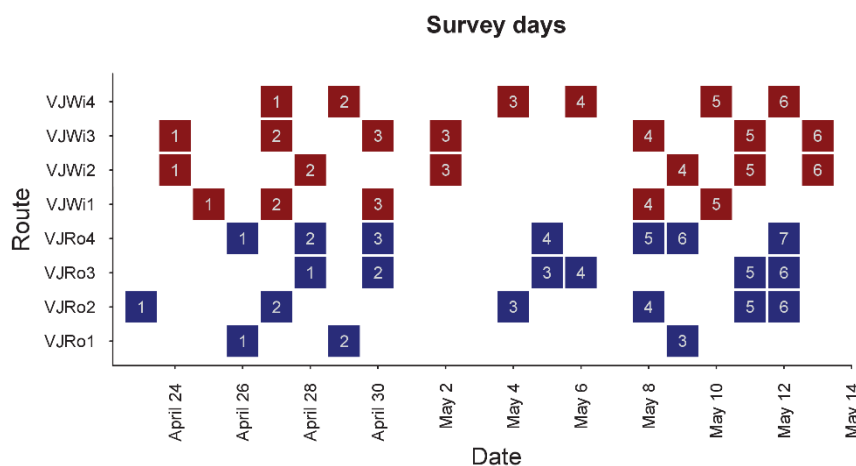
The survey was conducted in 2015 in the Varanger peninsula in northeastern Norway, where the Varanger peninsula national park encompasses most of the peninsula and extends over 2000 km<sup>2</sup>. It is located just above the 10°C July isotherm and its northern part is considered as erect low-shrub tundra of the low-Arctic subzone E (Walker et al. 2005). The southern part of the peninsula extends into sub-arctic mountain tundra and sub-arctic forest tundra (Ims et al. 2013). Originally, the study intended to include the two regions of Komag (KO) and Vestre Jakobselv (VJ) (70-71°N, 29-31°E) with equal field effort in both regions. However, KO had to be discarded from the study due to the early onset of spring in the end of April, because of open rivers and only patchy snow cover that did not allow transport of personnel with skis and snow mobiles between the designated surveys routes in this region. Thus, all efforts were focused in VJ (Figure 1). The VJ study region is composed of low arctic and sub-arctic shrub tundra with erect dwarf-shrub heaths, willow thickets and with patches of forest in the southern and low-lying parts.



**Figure 1: Study area.** Placement of the line and point transects for *Lagopus lagopus* (red) and *Lagopus muta* (blue) in the area of Vestre Jakobselv. The shadings of grey in the inset to the right denote altitude (white > 450m; equidistance = 50 m), while green denotes patches of tall willow and birch shrubs.

## Study design – data collection

The field protocol was partly adapted from the study of Pedersen et al. (2012) on *L. muta hyperborea* in Svalbard. The study period was initiated on April 23<sup>rd</sup> (Figure 2) at a time we expected that both species were at the onset of their spring courting season when male ptarmigan start to defend territories and acquire females for reproduction. At this time of the year, the birds are particularly conspicuous as they vocalize and perform physical displays (Potapov and Sale 2013). Originally, the study period was planned to extend until the latter half of May to ensure that it included the peak of the courting season when pairs are spaced out on stable territories. However, due to above-normal temperatures, rapidly diminishing snow cover and flooded tundra, efficient transport of observers was prohibited and the study period had to be terminated on May 13<sup>th</sup>. During the survey period, the snow cover decreased and unveiled patches of bare ground and small shrubs that could be occupied by both species of ptarmigan. This development was noted during the surveys. Moreover, during the survey period we noted the behaviour of the ptarmigan, i.e. whether they appeared in flocks (i.e. clusters) or displayed territorial behaviour.



**Figure 2: Survey dates among the different routes. The numbers indicate the temporal replicates. For VJWi3, the third temporal replicate was done over two days. VJWi corresponds to Willow Ptarmigan Routes and VJRo to Rock Ptarmigan Routes, and “VJ” in the name denotes the study region Vestre Jakobselv.**

*A priori* routes were created in MapSource (version 6.16.3); 3 in KO and 4 in VJ for *L. lagopus*, and 3 in both KO and VJ for *L. muta*. As *L. lagopus* and *L. muta* differ in habitat use, the routes for each of the species were placed in areas that were expected to represent a strata of their respective preferred habitat, although both species could appear on the routes of the opposite species. For *L. lagopus*, we chose “Willow Ptarmigan Routes” in low-lying riparian areas with presence of shrubs of willow or birch that protruded the snow cover already at the onset of the study period. For *L. muta*, “Rock Ptarmigan Routes” were placed in elevated and



rugged terrain along slopes and ridges without presence of shrubs. Some small changes were made to the *L. muta* routes and one *L. lagopus* route in order to avoid hazardous terrain. Because we were not able to go through with survey in KO, one additional route for *L. muta* was created *ad hoc* in VJ.

Each route consisted of 10 points linked together by 9 line transects and all together, we had 4 routes with a total of 40 points and 36 line transects for each species (Figure 1, Table 1). The routes for *L. lagopus* were surveyed 6 times (i.e. temporal replicates), except one that was surveyed 5 times. Two of the routes for *L. muta* were surveyed 6 times, one route 7 times and one route 3 times only (Figure 2), because the deep snow cover made it very unlikely that rocks and bare ground would be available early enough in the season for *L. muta* to breed there. The study period encompassed the calving season of semi-domestic reindeer and, to avoid disturbance, surveys were not conducted on line transects and points with presence of reindeer.

**Table 1: Sampling effort per survey type and species.**

Survey type	Parameter	<i>L. lagopus</i>	<i>L. muta</i>
<b>Line transects</b>	No. of surveys	207	198
	Cumulative distance covered	104 km	103 km
	Transect lengths (range)	426 – 562 m	401 – 650 m
<b>Point transects</b>	No. of surveys	230	217
	Cumulative survey time	57 h	54 h
	Altitude (range)	210-265 m. a. s. l.	275 – 380 m. a. s. l.

The routes were done by skiing, starting from either ends or at a mid-point of the route and with alternating both direction and observers as well as varying the time of day for the survey. Each point was surveyed for 15 minutes, where we started by registering start time of survey and site level parameters such as temperature (°C), wind speed (m/sec), cloud cover and bare ground (intervals of 25%) and whether erect shrubs were present within the 250 m radius from the point (Table 2). The range of wind speeds was determined by a hand held anemometer and the mean was taken afterward for the analysis. The altitude of each point was also noted. We listened for ptarmigan and scanned the surroundings with and without binoculars. Because it was important to be able to both hear and see the ptarmigan, the surveys were limited to days with wind speeds at 6 m/sec or below, and without fog or

precipitation. We registered ptarmigan within a 250 meters radius from the point and within 250 meters perpendicular distance on each side of the line. The points were spaced by approximately 500 meters, and the 250 meters truncation was set in order to avoid overlap of observations between the points, as well as to have a similar truncation distance for both the line- and point-transects.

When ptarmigan were observed, we registered the number of birds and if they were airborne (i.e. flying by) or seen on the ground. When ptarmigan were on ground, we registered degrees to the north of their position, our coordinates (UTM WSG 84), and distance in meters to the individual using binoculars with laser-rangefinder (Victory RF by Zeiss). The magnetic declination is about 11 degrees to the west of the true north in Finnmark. This was corrected for by subtracting 11 degrees from the recorded sighting angles. For the line transects, the distances recorded were sighting distances. In order to calculate the perpendicular distances between the line and the ptarmigan, we first used the coordinates of the observer with the distance and the corrected angle to the bird to get its coordinates. Basic trigonometry was used as the Earth's surface can be assimilated to a plane surface on relatively short distances. Knowing the coordinates of the object and the endpoints of the line, the perpendicular distance could be calculated.

For each observation we identified the species to *L. lagopus*, *L. muta* or unknown, the sex of each individual (or unknown), whether there was a displaying or vocalizing male present (i.e. territorial behaviour), and whether the ptarmigan was associated with bare ground or shrubs (Table 2). The frequencies of observations of the “wrong species” in the species-specific survey routes were relatively small; i.e. *L. muta* accounted for only 6% of the total number of individuals in the Willow Ptarmigan Routes (23 *L. muta* and 349 *L. lagopus*), while *L. lagopus* accounted for 24% of the observations done on Rock Ptarmigan Routes (36 *L. lagopus* and 168 *L. muta*). However, 34 of these *L. lagopus* individuals were observed on the 11<sup>th</sup> and 12<sup>th</sup> of May during 20 observations and all were on the southernmost Rock Ptarmigan Route, which was in the vicinity of shrubs and a nearby forest patch. This incident may have coincided with the spring breakup of rivers and flooding of the plains in the lowland, leading to relocation of *L. lagopus*. These observations were discarded in the statistical analyses.

**Table 2: Summary of recorded environmental variables.**

<b>Variable</b>	<b>Description</b>	<b>Survey type</b>	<b>Level covariate</b>
<b>Altitude</b>	Altitude from sea level, with map information	Point only	Site level
<b>Temperature</b>	Ambient temperature on each sites, recorded in Celsius degrees with a small portable digital thermometer	Point and line	Observation level
<b>Wind speed</b>	Mean wind speed on each sites, recorded in meters per second with a small portable digital anemometer	Point and line	Observation level
<b>Overcast</b>	Estimation of the cloud cover, recorded by categories of percentage covered: 0, 25, 50, 75 or 100, to the closest number.	Point and line	Observation level
<b>Willow</b>	Recorded as 0 or 1 depending on the absence or presence of willow thickets around the points	Point only	Observation level
<b>Bare ground</b>	Estimations of the bare ground visible, in percentage	Point only	Observation level
<b>Associated with willow</b>	If a bird (or cluster) was seen, then it was recorded if it was associated with willow (0 or 1), i.e. if it was in the close vicinity of a willow thicket	Point and line	Observation level
<b>Associated with bare ground</b>	If a bird (or cluster) was seen, then it was recorded if it was associated with bare ground, i.e. if it was on it or very close to it.	Point and line	Observation level

## Statistical analysis

The data sets for each species were first subjected to exploratory analyses (correlation analyses and plotting) focusing on the temporal and spatial variations in the ptarmigan encounter rates and recorded distances and their relations to the environmental factors listed in Table 2.

We were interested in analyzing the data for both species in a similar manner in order to facilitate between-species inference and comparisons of survey methods, abundance- and detection-processes. Distance sampling with covariates (Thomas et al. 2010) was attempted for both *L. lagopus* and *L. muta*, however, only the line transect data for *L. lagopus* had sufficient sample size and quality to fit the detection function. As the sample size from line transects for *L. muta* was very low, they were omitted from further analysis. Moreover, since the data for *L. muta* were too scarce, we decided to add point count analysis for both species in our study.

The point counts of both species were first analyzed using the function *pcount* in the package *unmarked* (Fiske and Chandler 2011) in R (R Core Team 2014), which is a N-mixture model with a Poisson state process and a Binomial observation model (Fiske and Chandler 2011). This method assumes that the population within the survey area is closed during the survey period. As our experience in the field and the exploratory analyses indicated that this assumption did not strictly hold, we continued the analyses using the function *gpcount* in *unmarked*, which explicitly takes temporal emigration into account (Chandler et al. 2011); i.e. assuming that individuals can move in and out of the survey area independently of each other. However, neither of the two methods for analyzing point counts seemed to result in plausible estimates for abundance and detection processes. This was most likely because ptarmigans were moving in groups, violating the closure assumption in *pcount* as well as violating the assumption of independency of movement in *gpcount*.

As a final step we did a simulation study where we modeled populations with varying densities and known parameters for detection and availability (availability is defined as the probability that an individual is present within a temporal replicate of a point, thus allowing for temporal emigration). These simulations were conducted to assess the impacts of these parameters as well as sampling effort (i.e. number of spatial and temporal replicates) on the precision of the estimates. The simulated populations were then sampled and analyzed by *gpcount* and *pcount* to assess bias in abundance models where temporal emigration is not accounted for when present. By varying the number of spatial and temporal replicates in the simulation, we explored the effect of survey effort on the parameter estimates, in an attempted to find a survey design that gave reasonably precise estimates.

#### DISTANCE SAMPLING ANALYSIS

Distance sampling analysis was conducted to obtain density estimates according to Buckland et al. (2001) using the package *Distance* (Miller 2015) in the R software (R Core Team 2014).

There are three key assumptions in distance sampling, and the method allows for one or more of these to be relaxed. Firstly, it is assumed that all animals on the line or on the point (i.e. distance = 0) are detected with certainty, while the detection probability may decrease with increasing distance to the observer. Secondly, it is assumed that the animals are detected at their initial location and do not move in response to the observer, and lastly that the measured distances to the animals are exact.

Distance sampling was used on the data obtained both from the line-transect and point-transect surveys for *L. lagopus*. The exact distances  $x$  to the birds were recorded within the truncation distance  $w$ , 250 m. Total length of line-transects  $L$  could then be used to give the surveyed area,  $a = 2wL$ . If each individual  $n$  within the surveyed area had  $P_a$  probability of being detected, the estimated probability  $\hat{P}_a$  of detecting an individual at distance  $x$  from the line could be given by a detection function  $g(x)$ .  $P_a$  is expected to decrease with distance from the line, and animals on the line are assumed to be detected with certainty  $g(0) = 1$ . The effective strip half-width  $\mu$  is the distance from the line where the number of detections within  $\mu$  is equal to number of detections beyond  $\mu$ , and this parameter is given by integration of  $g(x)$ . The probability density function (pdf) is given as  $f(x) = g(x)/\mu$ , and the distance function then fits a detection function by choosing a key function and adding series expansions if needed. The density  $\hat{D}$  is estimated by

$$\hat{D} = \frac{n}{2\hat{\mu}L} = \frac{n\hat{f}(0)}{2L} \quad (\text{eq. 1})$$

There were more covariates recorded in the field (Table 2) than could be fit in the same model. So, in order to find the best model, we attempted to fit the model with one covariate at a time. Next, the covariate that seemed to be the more significant according to the AIC (Akaike's Information Criterion) (Buckland et. al 2001) of the model was kept and each of the other covariates was then added to the model, one at a time. The best combination of two covariates was kept in the model and a third one was added. This process was repeated until the AIC did not decrease anymore when adding covariates. *A priori* candidate models (i.e. combination of covariates) were also tried to see if they would yield a better AIC. The goodness of fit was used to determine the best model for both line and point transects. Goodness of fit was good for the line-transect data but significantly poorer for the model using the point-transect data, probably because no *L. lagopus* were observed within the nearest 54 m from the point, challenging the assumption about certain detection at distance = 0 and also that the distances were independent of the presence of observers. The number of observations for *L. muta* in both line- and point-transects was too few to successfully fit a detection function in *Distance*. Thus, density estimates using distance sampling were only obtained using the line transects data for *L. lagopus*.

#### POINT COUNT ANALYSIS

We used the functions *pcount* and *gpcount* in the R package *unmarked* (Fiske and Chandler 2011) to assess abundance for repeated counts of  $i = 1, 2, \dots, R$  sites in  $t = 1, 2, \dots, T$

occasions (i.e. spatial and temporal replicates respectively). While *pcount* assumes that the surveyed population is closed, *gpcount* allows for partial emigration, i.e. that not all individuals are always available for detection.  $N_i$  is the population available for detection at sites  $i$ , and  $p$  is the probability of detecting an individual given that it is present. Both *pcount* and *gpcount* support exact numbers of individuals, thus  $Y_{it}$  are the counts of animals that are recorded in plot  $i$  at occasion  $t$ . This implies that the number of observations for *pcount*, and to some extent also for *gpcount* (see “secondary periods” below), is reduced compared to number of observations in the raw data because the individuals of multiple observations within one temporal replicate  $t$  at site  $i$  are summed into a single value  $Y_{it}$ .

The *pcount* function assumes that the local population is closed between repeat survey occasions within a season, meaning that there is no mortality, recruitment or movement during the sampling period. This assumption can be considered as fulfilled when the birds have established their territories. It is also assumed that counts at a site are independent (Royle 2004). Here,  $\lambda_i$  is the expected abundance at site  $i$ , and  $f$  can be a Poisson or Negative Binomial discrete distribution when  $N_i$  is  $\geq 0$ . Additional parameters are denoted by  $\theta$ , i.e. a dispersion parameter if  $f$  is Negative Binomial, while under the Poisson the dispersion parameter equals zero:

$$N_i \sim f(\lambda, \theta) \text{ for } i = 1, 2, \dots, R$$

$$Y_{ij} | N_i \sim \text{Binomial}(N_i, p) \text{ for } j = 1, 2, \dots, J_i$$

Numerical covariates were scaled (Fiske and Chandler 2011) to ease convergence of the models, and covariates for both state and detection processes can be included. The covariates are modeled through log (abundance) and logit (detection) links to coerce positive values:

$$\log(\lambda_i) = x_i \beta$$

where the vector of site level covariates are denoted  $x_i$  and their effect parameters is the vector  $\beta$ . The vector of observation level covariates  $v_{ij}$  and the vector of their corresponding effect parameters  $\alpha$  are used to model the detection probability:

$$\text{logit}(p_{ij}) = v_{ij} \alpha$$

The *pcount* model then gives the log-scale mean of  $\lambda_i$  across sites, which can be expanded over the area of plots ( $\pi r^2 i$ ) to estimate the density of birds in the surveyed area:

$$\hat{D} = \frac{e^{\bar{\lambda}_i}}{\text{plot area} \times i} = \text{individuals per km}^2 \quad (\text{eq. 2})$$

The *gpcount* (Chandler et al. 2011) is a three-level hierarchical model that in addition allows for estimating abundance of animals with temporal emigration by estimation of the superpopulation size  $M$  at site  $i$ . In our case, the sampling was strictly contained within the three weeks, so we decided to segregate the observations at each point into two distances classes, from 0 to 177 m and from 177 to 250 m. These two “discs” with equal area sizes were considered as our “secondary periods” of sampling, as opposed to “primary periods” which correspond to each temporal replicate, i.e visit. At the first hierarchical level,  $M_i$  is the superpopulation size, i.e. the total number of individuals that could be detected at site  $i$  during a survey season. At the next level,  $N_{it}$  is the proportion of  $M_i$  that is available for detection within the plot area at a given occasion, with the availability  $\varphi$  denoting the probability that a member of  $M_i$  is present. Lastly, the counts of individuals  $Y_{it}$  depends on the detection probability  $p$  of detecting a member of  $N_{it}$ . The three levels of the hierarchical model are thus:

$$M_i = \text{Poisson}(\lambda) \quad (\text{superpopulation})$$

$$N_{it} = \text{Binomial}(M_i, \varphi) \quad (\text{subset of } M_i \text{ present})$$

$$Y_{it} = \text{Multinomial}(N_{it}, \pi_{it}) \quad (\text{subset of } N_{it} \text{ detected})$$

Here, the function of the detection probability  $p$  yields a vector of multinomial cell probabilities,  $\pi_{it}$ . Because of the temporary emigration in the superpopulation, some individuals will have their ranges outside of the plot area ( $A$ ), and the effective plot area ( $A_e$ ) is unknown and larger. The density  $D$  can still be estimated by:

$$\hat{D} = \frac{\hat{\lambda}\hat{\varphi}}{\pi(0.25\text{km})^2 \times i} \quad (\text{eq. 3})$$

Model selection was done step-wise, first by finding the best model according to AIC of the detection process. Second, by keeping the detection model constant we assessed the best covariate combination for the abundance (Hamel et al. 2013). Lastly, for *gpcount* we did not have suitable information to model the availability process, and could therefore not use covariates for it. The best model was selected based on AIC, and we then used the *predict* function in *unmarked* to estimate density. For *pcount*, the predictions are per site, thus density is estimated by

$$\hat{D} = \frac{\text{sum}(\lambda_i)}{A \times i} \quad (\text{eq. 4})$$

For *gpcount*, the prediction gives one value per visit across sites, and we obtain density with

$$\hat{D} = \frac{\hat{\lambda}\hat{\phi}}{A \times i \times t} \quad (\text{eq. 5})$$

#### DATA SIMULATION

The analysis results from *pcount* and *gpcount*, for both *L. lagopus* and *L. muta*, yielded highly unlikely results with a considerable underestimation of the detection function and overestimation of abundance compared to what seemed reasonable based on literature (Marty and Mossoll-Torres 2012, Pedersen et al. 2012). This indicated violation of the assumption of closed populations within the survey period. We thus wanted to model populations with known parameters, and simulate varying survey efforts by changing number of temporal and spatial replicates. Moreover, we wanted to compare the performance of *pcount* and *gpcount* when we knew both the latent population density and availability in the modeled population. Finally, we wanted to assess the survey effort needed in order to yield reasonably precise estimate of the density of the two species.

In order to simulate data for *L. lagopus*, we used the estimated lambda including covariates and availability produced by the model selected with the *gpcount* function. The intercept of the detection probability was set at 0.65 (i.e. from the distance sampling results) as the detection probability estimated from *gpcount* seemed to be too low.

For *L. muta* we decided to use detection probabilities (0.2 and 0.5) and abundance (2 and 5 individuals/km<sup>2</sup>), which are within the known ranges of 0.2 - 0.5 detection probability and 2 - 10 individuals/km<sup>2</sup> of territorial males (Marty and Mossoll-Torres 2012, Pedersen et al. 2012). The dispersion parameter was set at 0.5 (Chandler et al. 2011). For simplicity, the numbers of covariates were reduced to include only a slight negative and a slight positive effect, as well as the effect of the two distance categories.

We first created populations with known parameters, and then sampled from these populations with different survey designs, i.e. varied the number of sites and temporal replicates. Each simulation was then fitted with both *gpcount* and *pcount*, and we could compare the estimated parameters for abundance ( $\lambda$ ), detection ( $p$ ) and for *gpcount* also the availability ( $\phi$ ) with the true parameters of the simulated population. The results were plotted for visual comparison.



## Results

### Observations, encounter rates and environmental covariates

Despite the fact that the survey effort was similar for the two species (Table 1), the total number of observations and individuals observed were more than three times as many for *L. lagopus* compared to *L. muta* (Table 3). The distribution of the observations along the 8 survey routes (Figure 3) showed that the relatively few observations of *L. muta* also tended to be very unevenly distributed within and among the survey routes. Airbornes and individuals observed on the “wrong” route (e.g. *L. lagopus* observed on the Rock Ptarmigan Route) were discarded from the analysis.

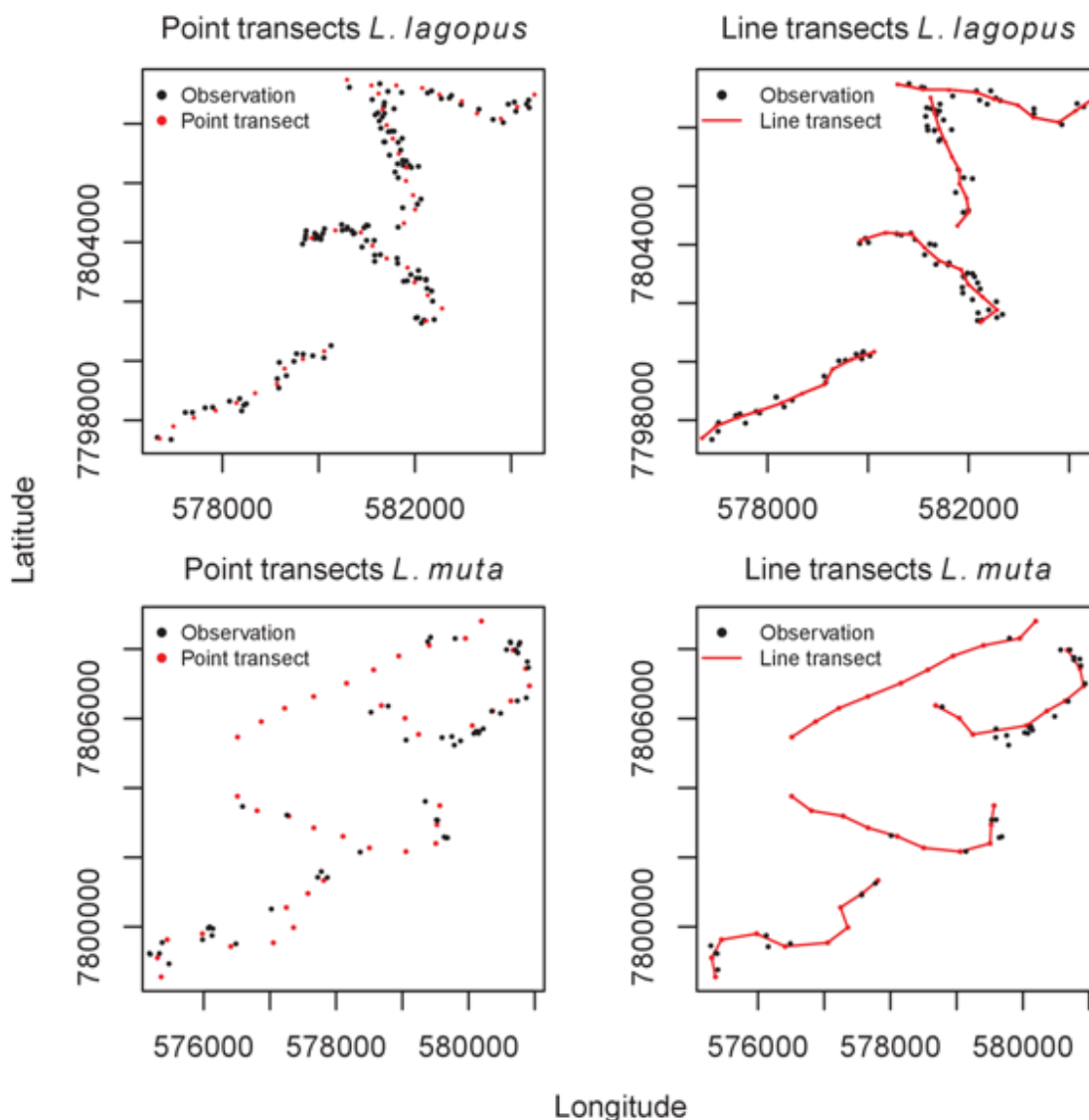
**Table 3: Total number of observations, individuals, group size and distance to observations per survey type and species. Observations of airborne individuals and observations with unknown distances (*L. muta*: 2 observations of 2 territorial males) were omitted from analyses.**

Survey type	Parameter	<i>L. lagopus</i>	<i>L. muta</i>
<b>Line transects</b>	No. of observations	136	36
	Observations with territorial male	45	5
	No. of individuals	323	70
	No. of airborne individuals	45	3
	Encounter rate (mean [range])	1.3 [0-17.2]	0.19 [0.5-3.8]
	Group size (mean [range])	2.5[1-120]	1.94 [1-5]
	Distance (mean [range])	101.4 [1-252]	78.11[3-248]
<b>Point transects</b>	No. of observations	159	55
	Observations with territorial male	66	13
	No. of individuals	301	107
	No. of airborne individuals	38	5
	Encounter rate (mean [range])	0.72 [0-9]	0.48 [0-7]
	Group size (mean [range])	1.92 [1-40]	1.98 [1-7]
	Distance (mean [range])	198.5 [54-298]	167.28 [13–258]

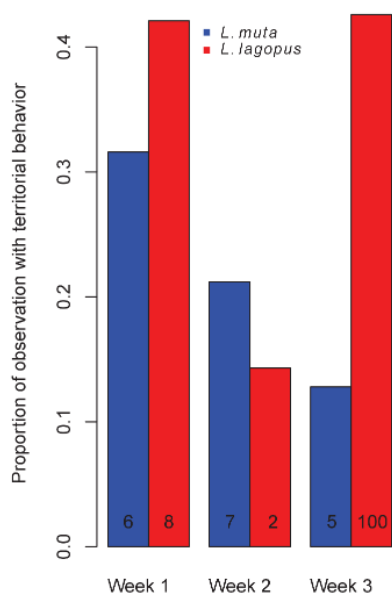
The encounter rates of *L. lagopus*, both on lines and points, increased with temperature and was different among different periods of the day and the three weeks of survey, with a significantly higher encounter rate at dawn and during the third week of survey (correlation coefficients between the encounter rates and environmental variable are provided in Appendix A). For the point transects the encounter rate also increased with amount of bare ground. The encounter rates for *L. muta*, which were lower than for *L. lagopus*, were generally little

influenced by the environmental covariates. There was, however, a tendency for the encounter rates to be negatively correlated with wind speed. For both species, the recorded distances were not correlated with any of the variables measured during the survey (see Appendix A).

The number of male *L. lagopus* displaying territorial activities increased drastically during the survey period as only 8 and 2 territorial males were observed during the first two weeks compared to 100 during the last week (Figure 4). The proportion of territorial males of *L. muta* was most often lower than for *L. lagopus* and showed a tendency to decrease over the survey period (Figure 4).



**Figure 3: Spatial distribution of the observations recorded for both species on the point and line transects. Each black dot represents an observation, i.e. it can be a single individual or a cluster of individuals.**



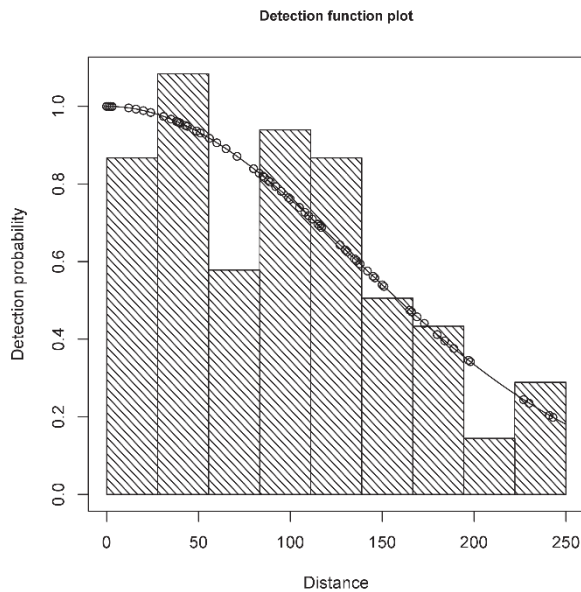
**Figure 4: Proportion of observations recorded where males were displaying territorial behaviour. The numbers at the bottom of the bars indicate the number of observations which included territorial behaviour.**

## Population density estimates

### DISTANCE SAMPLING ANALYSIS

For *L. lagopus*, according to both the Akaike's Information Criterion (AIC) (i.e. lowest AIC value) (Buckland et al. 2001) and the goodness of fit, the half-normal key function was used to fit the data from the line transects. The best model was the null model (i.e. with no covariates) (Figure 5) and included only the observations made during the third, and last, week of survey. Indeed, when the detection function was fitted with all the three weeks of survey, the goodness of fit was poorer. The clusters observed during the survey could range from a pair of birds to an actual flock of several dozen individuals (Table 3). The estimated density of flocks within the survey area was 15.1 flocks/km<sup>2</sup> (+/- 2.1 flocks/km<sup>2</sup>) with an expected cluster size of 1.44 (+/- 0.06). For the individuals, the estimated density was 21.8 individuals/km<sup>2</sup> (+/- 3.3 ind/km<sup>2</sup>). For both these estimates of densities, the coefficients of variation were about 0.15. The estimated number of birds in the covered area (9.03 km<sup>2</sup>) was 95 (+/- 14 ind). The model output can be found in Appendix B.

Distance analysis was also tried on the point transect data for *L. lagopus*, however none of the models had an appropriate goodness of fit. For *L. muta*, the low number of observations did not warrant fitting the detection function on either the point or line transects data as the scarcity of observations led to poor goodness of fit of the detection function.



**Figure 5: The fitted half-normal detection probability function (line and dots) for the null model of distance sampling for *L. lagopus*. The histogram shows the empirical distribution of the distance data.**

#### POINT COUNT ANALYSIS

The point count approach was used to counteract the fact that the number of observations was scarce. As some covariates were highly correlated within both species (e.g. date/week and temperature, Appendix A), we avoided fitting models with correlated covariates. Data from the whole survey period (weeks 1 to 3) was used both for the *pcount* and *gpcount* estimations and details of the models outputs and models selections is provided in Appendices B, C and D. All density population estimates are given in Table 4.

All the following estimates are given on the normal scale except if specified otherwise. For *L. lagopus*, the best *pcount* model based on the AIC included *week* (categorical), *overcast* (cat.), *presence of shrub* (cat.) and *observer* (cat.) as covariates for the detection process of the model and *altitude* for the abundance process. Using eq. 4, the estimated density was 45.66 ind/km<sup>2</sup> within the area covered. The mean detection probability was 0.07.

For *L. muta* the best *pcount* model included *wind*, *observer* (cat.) and *altitude*. With this model, we obtained a mean detection probability of 0.061 and a density of 35.56 ind/km<sup>2</sup>. Characteristic of the data for *L. muta* was that for many of the points where observations occurred, the detection history consisted of many zeroes and actual observations were mostly of clusters with 2-7 individuals.

When *gpcount* was fitted to the data for *L. lagopus*, the best model included *presence of shrub* (cat.) and *altitude* as covariates for abundance and *day*, *hour*, *distance classes* (cat.) and *wind*

*speed* for detection probability. We then obtained an availability ( $\varphi$ ) of 0.72 and the estimated mean detection probability on all the points was only of 0.04. Using *eq. 5*, the estimated density is 86.9 ind/km<sup>2</sup>.

For *L. muta*, the best *gpcount* model based on AIC included *wind*, *observer* and *altitude*. This model yielded mean estimates of 0.03 for detection probability, 0.997 for availability and a density of 35.97 ind/km<sup>2</sup>.

**Table 4: Density estimate for both species depending on the model used. Lambda is the intercept of the abundance (on the log-scale) given by the model. For distance sampling, the estimated density is given directly as ind/km<sup>2</sup> on the normal scale.**

Model	<i>L. lagopus</i>		<i>L. muta</i>	
	Density estimate	Lambda (+/- se)	Density estimate	Lambda (+/- se)
<b>Distance sampling (line)</b>	21.8 ( $\pm$ 3.3) ind/km <sup>2</sup>	∅	Unable to fit	Unable to fit
<b>Distance sampling (point)</b>	Unable to fit	Unable to fit	Unable to fit	Unable to fit
<b>Pcount</b>	45.66 ind/km <sup>2</sup>	2.18 ( $\pm$ 0.59)	35.9 ind/km <sup>2</sup>	1.91 ( $\pm$ 0.42)
<b>Gpcount</b>	86.9 ind/km <sup>2</sup>	1.97 ( $\pm$ 0.64)	35.6 ind/km <sup>2</sup>	1.92 ( $\pm$ 0.44)

## Simulation study

Overall, when *pcount* was used on the simulated data based on parameters for *L. lagopus*, abundance was systematically overestimated and detection underestimated. When *gpcount* was used, lambda ( $\lambda$ ) was close to the parameters entered for every combination of sites and temporal replicates. However, availability ( $\varphi$ ) was consistently underestimated and detection probability *p* overestimated for almost all combinations. (Appendix E).

With *pcount* used for *L. lagopus*, lambda ranged from 1.52 to 2.94 (mean of 2.48, log-scale). The mean of lambda increased with the number of temporal replicates (2.13 for 2 replicates, 2.64 with 12). The mean detection probability obtained was 0.34 (normal-scale), varying from 0.23 to 0.56. The mean detection probability was 0.48 with 2 temporal replicates and 0.31 for the combinations with more replicates.

When *gpcount* was used for the *L. lagopus* simulations, the mean detection probability was 0.72 (ranging from 0.63 to 0.82) and did not vary much depending on the number of temporal replicates. Lambda ranged from 0.9 to 1.99 with a mean of 1.63 (log-scale) for all combinations and it slightly increased with the number of temporal replicates: 1.42 with two replicates and 1.69 with 12. For availability the mean of all the combinations was 0.24,

ranging from -0.15 to 1.22 (logit-scale). Availability was close to the input parameters when there were only 2 temporal replicates (mean of 0.74) but was underestimated with more replicates (mean of 0.13 for all the combination with more than 2 replicates).

We used plausible parameter values for abundance and detection from literature to simulate data for *L. muta*. The analyses with *pcount* underestimated detection probability and overestimated abundance in a similar manner as it did for *L. lagopus*. Analyses with *gpcount* on the other hand resulted in estimates that were close to the parameters in the simulated data (Appendix F). Since the covariates were random samples, a re-run of the simulation and model selection could result in different preferred models with very small  $\Delta$ AICs.

The parameter estimates obtained by *pcount* were highly skewed. Having  $p = 0.2$  in the simulated data resulted in an estimate that mainly ranged from 0.056 to 0.208 (with one estimate of 0.434) and a mean of 0.131. For  $p = 0.5$  in the simulated data, the mean estimate was 0.218 and ranged between 0.167 and 0.309. These low estimates of detection probability in turn led to overestimation of the density and in the case of simulating 2 ind/km<sup>2</sup> in the simulated population the mean estimated density was 6.62 and ranged from 2.51 to 10.86 ind/km<sup>2</sup>. When the density was 5 individuals/km<sup>2</sup> in the simulation, the mean density estimate across models in *pcount* was 19.5, ranging from 10.79 to 34.85 ind/km<sup>2</sup> (Appendix F)

When we used  $p = 0.2$  in the simulated data, the mean estimated detection probability in *gpcount* was 0.175, and the mean precision increased slightly with temporal replicates (mean  $p = 0.162$  with 5 temporal replicates and mean  $p = 0.183$  with 20). With  $p = 0.5$  in the simulated data, the mean was 0.437 (0.417 with 5 temporal replicates and 0.469 with 15). Availability  $\varphi$  was set as 0.5 for all simulations, and the mean for all simulated data was 0.499. However,  $\varphi$  ranged between 0.216 and 1, with the most extreme values obtained with low number of spatial replicates combined with low bird density (2 ind/km<sup>2</sup>). The mean density estimate across models when the density in the simulated data was set to 2 ind/km<sup>2</sup> was 2.09 and ranged between 0.82 and 3.34. When the density was set to 5 ind/km<sup>2</sup>, the mean across models was 5.23 mainly ranging from 2.79 to 7.43, but with one extreme value at 11.62 (40 sites with 5 replicated visits) (Appendix F).

## Discussion

With this study we aimed to assess the feasibility of conducting spring survey to estimate the breeding population densities of the two ptarmigan species on the Varanger Peninsula, by focusing on the performance of different survey methods, their timing in the season and estimation methods. Simultaneously with learning the strengths and suitability of the different methods, it is equally important to know their limits. There were differences in density, timing of territoriality and behaviour of the species that may motivate using disparate methods for surveying *L. lagopus* and *L. muta* populations. We found that reliable density estimates could only be achieved with the line transects distance sampling method for *L. lagopus*. The number of observations for *L. muta* was too low to use the same method. Furthermore, the mismatched timing of the survey relative to the peak of territorial display, at least for *L. lagopus*, lead to a high number of observations of flocks and non-territorial birds. Thus, the primordial assumption of closed populations for *pcount* and the assumption of independent movement in *gpcount* were violated, and consequently densities were overestimated. For *L. muta* we had too few observations in order to determine if a peak in territorial behaviour was occurring. Importantly, rapidly deteriorating snow condition caused termination of the survey before the peak of courting season.

### Density estimations

The principal method that was to be used in this study was distance sampling. Distance sampling analysis can give relatively precise abundance estimates as it uses the information from recorded distances to fit a detection function. This, however, may require a larger sample size than for point counts. Distance sampling performs a stepwise estimation of parameters, where it first determines the detection function, and then based on that it estimates the density. With small sample sizes, as was the case in our study for *L. muta*, it is important that the data are “well-behaved”, meaning that it produces a detection function with a wide shoulder and an even falloff with increasing distance. This means that the estimates are very sensitive to spikes in the observed distances, especially with scarce data (Buckland et al. 2001). In this study, it was impossible to estimate density of *L. muta* using distance analysis because of the scarcity of the data.

For the *L. lagopus* data, the null model appeared to be the best distance-based model according to AIC and goodness of fit. The model gave an estimate of the density (21.8 ind/km<sup>2</sup>) that seems reasonable according to known densities of other *L. lagopus* populations

(usually around 5 to 10 pairs/ km<sup>2</sup> in Scandinavia, exceptionally up to more than 100 pairs/km<sup>2</sup>) (Storch 2007). It was however impossible to fit a good model to the data obtained from the point transects. That could be due to the fact that no observations were made within the nearest 54 meters from the point. This suggests that there was some response movement of *L. lagopus* to the observer, but it is also likely that the predetermined truncation distance at 250 m was inadequate. Indeed, no limits should be taken while recording information to let more space for data manipulation during the analysis, where right truncations can then be used to exclude eventual “tails” (Ekblom 2010). For instance, in point transects where the observer can be standing still while using binoculars, it has been shown by Pedersen et al. (2012) that precision of estimating detection probability and occupancy rate for *L. muta hyperborea* did not change much between the different spatial scales 250 m and 450 m, showing that predetermined distance truncations should be avoided. It is primordial to have ample space between survey points in order to avoid truncating data at a relatively short distance, at the same time fulfilling the assumption of independently placed points.

With regard to *L. muta*, the situation in Varanger resembles the one in Svalbard for *L. muta hyperborea* (Pedersen et al. 2012) in the sense that it was not possible to estimate year-specific density functions due to too few observations, even though the Svalbard surveys had considerably more points and a larger survey effort than we had in Varanger. Pedersen et al. (2012) resolved this by using multiple covariates distance sampling (MCDS) and including year as a covariate, which did not change the shape of the detection function through the 10 years of study, but affected it through a scale parameter. Increasing the survey effort on Varanger combined with multi-annual surveys could solve some of the issues concerning the limited amount of observations encountered in our study. This shows that *L. muta* can be a challenging species to survey as it occurs at very low density in the area.

Distance sampling is a good method of survey when the species occur at a rather high density. It is recommended to have at least 60-80 observations for line transects, and even more for point transects, to be able to fit such models (Buckland et al. 2001). Here we have illustrated that given the same survey design and effort; distance sampling could work well on one species (*L. lagopus*) but not the other (*L. muta*), and this is mainly due to difference in population densities reflected in the sample sizes. However, as the species have been shown to decline in Norway (Henden et al. 2011) this method might become inefficient, even for *L. lagopus*, especially in the light of climate change. Indeed, if the density of the species declines



too much then surveys using distance sampling would become very challenging, as survey effort would need to be increased in order to ensure a sufficient number of observations.

Point-count and presence/absence studies could be of some use as they need fewer observations to be usable. However, when this method was used on our data, the density seemed to be overestimated for both species, both with *pcount* and *gpcount*, and they also both underestimated detection probability for *L. lagopus* compared to distance sampling. The *gpcount* model underestimates detection probability compared to distance analysis and hence overestimates the density of *L. lagopus* to more than three times the density estimated by distance sampling. This observation could lend some support to the idea that the density estimation of *L. muta* by *gpcount* is also overestimated. The overestimation by *pcount* and *gpcount* compared to distance sampling is due to the fact that the latter, contrary to the point counts, does not assume that the population is closed. Moreover, the observations of *L. muta* in our study were relatively few, and they were very unevenly distributed among the spatial replicates. In addition, they also showed high variability within temporal replicates. This variability within the detection history of spatial and temporal replicates resulted in both *pcount* and *gpcount* estimating very low detection probabilities. Segregating the observations into two distance classes for *gpcount*, to take into account temporal emigration, did not improve the estimates, as only a few of the observations within sites became separated into the two distinct classes. Furthermore, since *gpcount* allows for partial emigration (Chandler et al. 2011), it should yield a better estimation of the density than the less complex *pcount* which assumes closed populations. The ability to account for temporary emigration comes at the expense of estimating an additional availability parameter  $\phi$ . Optimally, survey and plot specific covariates, e.g. habitat suitability, could be used to model  $\phi$  to better account for variations in size and center of home range, but we did not have applicable information in our study. Lacking such information may create biased estimators, and it is likely that the estimate of  $\phi$  as well as  $\lambda$  are sensitive (thus yielding overestimations) to underestimation of  $p$ .

From what we observed during the fieldwork, it seems that individual movements within the population of *L. lagopus* in Varanger were not independent but rather shifted between territorial behaviour and movement in flocks, depending on the weather and presence of predators. As long as males have not permanently established their territories, any survey can be challenging because of such movements within the population. This was the reason for employing the *gpcount* modeling that allows for temporary migration within the study period. In addition, many males appeared to be non-territorial, and since we recorded and analyzed

data on all individuals observed, we have probably also included an unknown proportion of “free-floaters” that roam in the area. Studies could be restricted to only include observations of males that clearly display territorial behavior since the assumption of closed population is then more likely to be fulfilled. However, the estimate then changes from population density to density of territorial males (Marty and Mossoll-Torres 2012, Pedersen et al. 2012). In our study, we had to use all the data recorded, i.e. including females and non-territorial males, otherwise the amount of data would have been too scarce to fit models and obtain reasonable estimates. Also, the estimations from the point count included all three weeks of survey. However, during the two first weeks, *L. lagopus* had not established definite territories, hence violating the assumption of closed population. Thus the density estimates were higher with point count methods than with distance sampling which does not assume that the population is closed. Disregarding the data obtained during the first weeks could have improved the closure assumption and thus the density estimates. This again shows the importance of timing for this type of study.

We also simulated data that used predefined parameters for the respective species. From this we aimed to estimate the minimum survey effort in order to improve surveys as well as assess the consequences of violating the closure assumptions. For *L. lagopus* we used estimated parameters, while for *L. muta* we had to resort to parameters estimated in other studies. For the simulations on *L. lagopus* data, the densities estimated by *gpcount* were close to the density estimation on our actual data made by distance analysis while *gpcount* on our real data overestimated the density. This supports the idea that the population of *L. lagopus* in the area display dependent (i.e. flock movements) rather than independent movement. Indeed, *gpcount* takes temporal emigrations into consideration, given that they are independent. No simulations will perfectly reflect a natural population, but it can give an idea of the needed survey effort to be able to efficiently estimate the density of ptarmigan in the region. Our simulations are indicative that two temporal replicates (i.e. primary periods) for each site could give fairly good estimates, and then three or four should be preferred in order to improve their precision. More than four temporal replicates did not further improve the estimates. The increase of the spatial replicates does not greatly improve the estimates either, but it may reduce variance around the estimates. Nevertheless, it would require deeper simulation analyses by running large number of resamples in order to corroborate these conclusions. However, in order to accurately estimate the density in the area, it would be optimal to have a

large area included in the survey, with a representation of a wider range of ptarmigan habitats of different quality.

Detection probability of surveyed animals is known to decrease with increased distance to the observer, which is the fundamental idea behind distance sampling design (Buckland et al. 2001). Detection probability is also influenced by animals' behaviour and conspicuousness and this might vary according to several parameters, for example the season (e.g. rut and mating season, with production of mating calls and/or more conspicuous colours), the time of the day (foraging may occur at particular moment of the day like sunrise or sunset and thus animals might be more visible, as they are active), or also weather conditions. Therefore, the sighting distances of ptarmigan could be influenced by those parameters, making the birds easier or harder to detect. Yet none of the recorded environmental variables seemed to have an impact on the sighting distance for *L. lagopus*.

### Timing of the survey

The encounter rates (defined as the number of individual recorded per kilometer or per point) of *L. muta* did not have significant correlations with any of the variables recorded in either of the survey designs. This may have been due to small sample size, or because surveys for both species were restricted to clear days and days of calm weather. However, some variables had an impact on the encounter rate for *L. lagopus*. There was an increase in *L. lagopus* activity during calm and warm days, in line with the observation made by Pedersen et al. (1983). As the season progressed, more and more *L. lagopus* males were displaying territorial behaviours and the number of birds recorded during the last week (from May the 7<sup>th</sup> to the 13<sup>th</sup>) was substantially higher than in the two preceding weeks. Indeed, during the first two weeks of survey *L. lagopus* were still occurring in big flocks up to more than a hundred individuals. *L. lagopus* is a resident bird in Norway and occurs in flocks in winter (Hornell-Willebrand et al. 2014). Before the breeding season, birds are less approachable and tend to flee at greater distances from the observer, while when males start to acquire territories for breeding they tend to flee at shorter distances. Moreover, calling males are more conspicuous, not only because of auditory detection, but also because they are often displaying on flat ground or in high positions, e.g. on rocks or branches of shrubs. The increase in the encounter rate with the amount of bare ground is partially because birds maintained their white plumage, making them easily detectable against the brown background. Moreover, territorial and breeding activities have been shown to be related to weather conditions and the start of snowmelt (Hannon et al. 1988), thereby increasing the birds' conspicuousness. It has also been shown

that *L. muta* males can be more inactive during and shortly after snowy days and stormy events (Marty and Mossoll-Torres 2012), and this could apply to *L. lagopus* as well. Within our survey period, we observed variations in the proportion of *L. lagopus* observations that included territorial males. This could be related to two weather events with heavy snow and strong winds during the second week, when we recorded lower proportion of territorial males compared to the first and third week. In the third week the number of observations of territorial *L. lagopus* increased by ten-fold, and this can be related to both good weather and increased territoriality through the courting season. During the survey period, the proportion of *L. muta* observations with territorial activity was less than the proportion of territorial activities of *L. lagopus*, and their behaviour was less pronounced. The timing of territorial behaviour of *L. muta* varies with latitude. For instance at high latitude in Svalbard, the territorial behaviour of *L. muta hyperborea* is from late march to mid-July, and territories are established in April (Pedersen 2007). In the Pyrenees however, the peak of territorial activity is in mid-May (Marty and Mossoll-Torres 2010). However, we did not obtain sufficient data on *L. muta* in our study area to reach a conclusion about changes in the proportion of territorial behaviour throughout the survey period.

The timing of a survey, both regarding the choice of season and time of the day for surveying, is primordial to get an accurate estimate of the population. In order to get the correct timing, it is important to know the species' ecology and in particular the phenology of the breeding. It has been shown that breeding, and thus territorial activities, is related to day length, although some phenotypic plasticity is present (Stokkan et al. 1988). For those species that time the breeding season in relation to the photo-period, choosing the starting date of the survey to match the territoriality period of the species should be a relatively easy task. However, ptarmigan spring surveys rely heavily on sufficient snow cover for travel and sampling (i.e. surveys done by ski). With the ongoing climate change, snowmelt tends to occur at irregular dates between years and with a trend towards taking place earlier in the season than before (Ims et al. 2013), thus making spring surveys less feasible. As we were forced to depart from the study region VJ as a consequence of snowmelt, it is very likely that the survey was stopped before the peak of the territorial display season.

## Recommendations

Lots of sampling designs are available to ecologists to estimate density of species. Optimally, the choice for the design should be well matured before going in the field to avoid failure of the study. The design should depend on the estimated, or expected, density of the species (rare

vs. common species). However, in some cases little information may be available beforehand and pilot-type feasibility studies are needed as a first step towards the development of robust survey designs. Our study represents a good example of such a situation. There was no prior information about population densities of the two species nor of the general feasibility of conducting population surveys targeting the density of breeding pairs in the spring. With limitations in mind, the present feasibility study set out with the aim to conduct the same survey design for both species in what was likely to be their preferred habitats. For the same number of survey points and similar survey effort, one species, *L. lagopus*, could be estimated relatively well compared to the other one, *L. muta*, whose lower density caused trouble for the abundance estimation. The choice of survey design should also take the kind of terrain or the funding and people available in consideration (Joseph et al. 2006). Rough terrain can be encountered, especially for *L. muta*, in which case performing line transects can prove to be challenging, and in these conditions point counts should be preferred. Moreover, it is not necessary to do both point and line survey simultaneously in the same study as they cannot be used together for the analysis. Then having the two designs would only increase the field effort without improving the quality of either the data or the estimates.

When planning the study design, several parameters need to be considered. In general, population surveys based on randomized designs are more reliable for estimating the entire population (MacKenzie and Royle 2005). However, if the aim of the study is to perform monitoring to identify mechanisms of change, regarding for example climate change as is the target of COAT, then it is relevant to place transects where the species is known to occur. Then changes in between years can be spotted with limited efforts and resources (i.e. financing, people and time available to do the survey). In our study, the transects were placed in areas that we believed to be a strata of suitable habitats for the respective species. Therefore, the results must be regarded as density in the surveyed area, and in similar habitats, as the estimates may have an upward bias. Nonetheless, this could be used to monitor annual variations of the density in the targeted area, as it has been shown by Pedersen et al. (2012). Depending on the size and nature of the area sampled, it might be better to increase the number of either spatial or temporal replicates (Ralph et al. 1995). MacKenzie and Royle (2005) recommended that given the detection probabilities are similar, the number of temporal replicates should increase with increasing population density, while for rare species the number of sites (i.e. spatial replicates) should be increased instead, i.e. for *L. muta* in our study. If plausible estimates of detection probability and density are assumed, it is possible to

determine the number of sites and temporal replicates needed for the desired precision of the density estimate.

Other methods are presently available in order to overcome some of the difficulties encountered during this study. One of them includes the use of sound recording (Blumstein et al. 2011). Sound recording methods, or bioacoustics surveys, need fewer people and can cover a larger area. Then one would be able to more precisely identify the period when birds stop occurring in flocks and start to be territorial. Moreover, sound recording allows recording the vocal part of the fauna within the area for a long time, without the need of having observers in the field for an extended period of time (Zwart et al 2014). Indeed, one of the greater concerns to survey ptarmigan in the area is the timing according to the spring phenology of the birds. Starting the survey too early in the season would lead to a need of increasing the survey effort by staying in the field for a longer period to obtain suitable data. On the other hand, starting too late could lead to missing the territorial period of the species. All in all, the survey should be made when the population is at the most stable, i.e. when males are well established in their territories. By focusing the survey on territorial males it would have been possible to extrapolate the density estimate to the number of breeding pairs. However, as shown by this study it can be quite challenging to do the survey at the right time and bioacoustics survey could help to pin-point the peak of territorial activities.

## Conclusion

For species with changing behaviour through the seasons, finding the right timing for the population surveys is primordial. The main issues when performing spring surveys of ptarmigan populations is to time the survey period so it coincides with the territorial display seasons for the species concerned as well as with snow conditions that permits transport of the observers. As spring and snow melt in the tundra occurs increasingly earlier in the age of climate change, this becomes more challenging; in some years it could even not be feasible to survey these species whose territorial behaviour is mainly induced by changes in day length. In our study area, there were fewer problematic issues with *L. lagopus* than with *L. muta*. As *L. lagopus* is generally present at higher densities than its more alpine congener, conventional study designs could be used with some improvement from how it was conducted in the present study. Distance sampling seems to offer accurate density estimates for *L. lagopus* and could be improved by avoiding truncating the sighting distances on the field. Point count is another option, at the condition that the methods take into account the kind of movements that were observed. However, it might be hard to assess if and when the populations of *Lagopus* spp. are closed during this period in the area, and therefore point count surveys should be used with caution. For *L. muta*, different methods should be considered and methods adapted from designs used on rare species could be a start. For instance, increasing the survey effort by adding more survey points could be one solution. Other designs could also be explored, like the use of bioacoustics surveys, alone or in combination with other methods.

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## Appendix

### Appendix A

Correlation tables diagrams of observations and variables.

**Table A. 1: Overview of correlations between: Observation distances and variables, E.R. (encounter rate) on lines and E.R. on points. The test statistics used were:  $r$  = Pearsons correlation-test,  $H$  = non-parametric Kruskal-Wallis test and  $W$  = Wilcoxon test. Significant correlations are indicated in bold.**

		<i>L. lagopus</i>		<i>L. muta</i>	
Correlation variables		<i>test statistic</i>	<i>p-value</i>	<i>test statistic</i>	<i>p-value</i>
<b>Observation distances</b>	temperature	$r(206) = -0.09$	$> 0.2$	$r(87) = -0.12$	$> 0.05$
	wind speed	$r(213) = 0.02$	$> 0.7$	$r(87) = 0.01$	$> 0.05$
	overcast	$H(4) = 7.235$	$> 0.1$	$r(87) = 0.10$	$> 0.05$
	% bare ground	$W = 1108$	$> 0.1$	$W = 107.5$	$> 0.65$
<b>Lines: E.R.</b>	temperature	<b><math>r(189) = 0.22</math></b>	<b>0.002</b>	$r(192) = 0.05$	$> 0.05$
	wind speed	$r(201) = -0.20$	0.004	$r(192) = -0.19$	0.007
	overcast	$H(4) = 4.2199$	0.4	$r(192) = -0.149$	0.038
	time of day	<b><math>H(2) = 27.9149</math></b>	<b>8.70E-07</b>	$H(2) = 0.383$	$> 0.8$
	period, weeks	<b><math>H(2) = 53.2666</math></b>	<b>2.71E-12</b>	$H(2) = 4.74$	0.09
<b>Points: E.R.</b>	temperature	<b><math>r(210) = 0.23</math></b>	<b>0.00061</b>	$r(215) = -0.013$	0.848
	wind speed	$r(225) = -0.14$	0.03	$r(215) = -0.124$	0.068
	overcast	$H(4) = 8.8782$	0.6	$r(215) = -0.078$	0.257
	% bare ground	<b><math>r(227) = 0.25</math></b>	<b>0.0002</b>	$r(215) = -0.0114$	0.868
	presence willows	$H(1) = 0.7158$	0.4	$H(1) = 1.0078$	0.3154
	time of day	<b><math>H(2) = 28.9246</math></b>	<b>5.24E-07</b>	$H(2) = 1.743$	0.418
	period, weeks	<b><math>H(2) = 79.2058</math></b>	<b>2.20E-16</b>	$H(2) = 0.950$	0.622

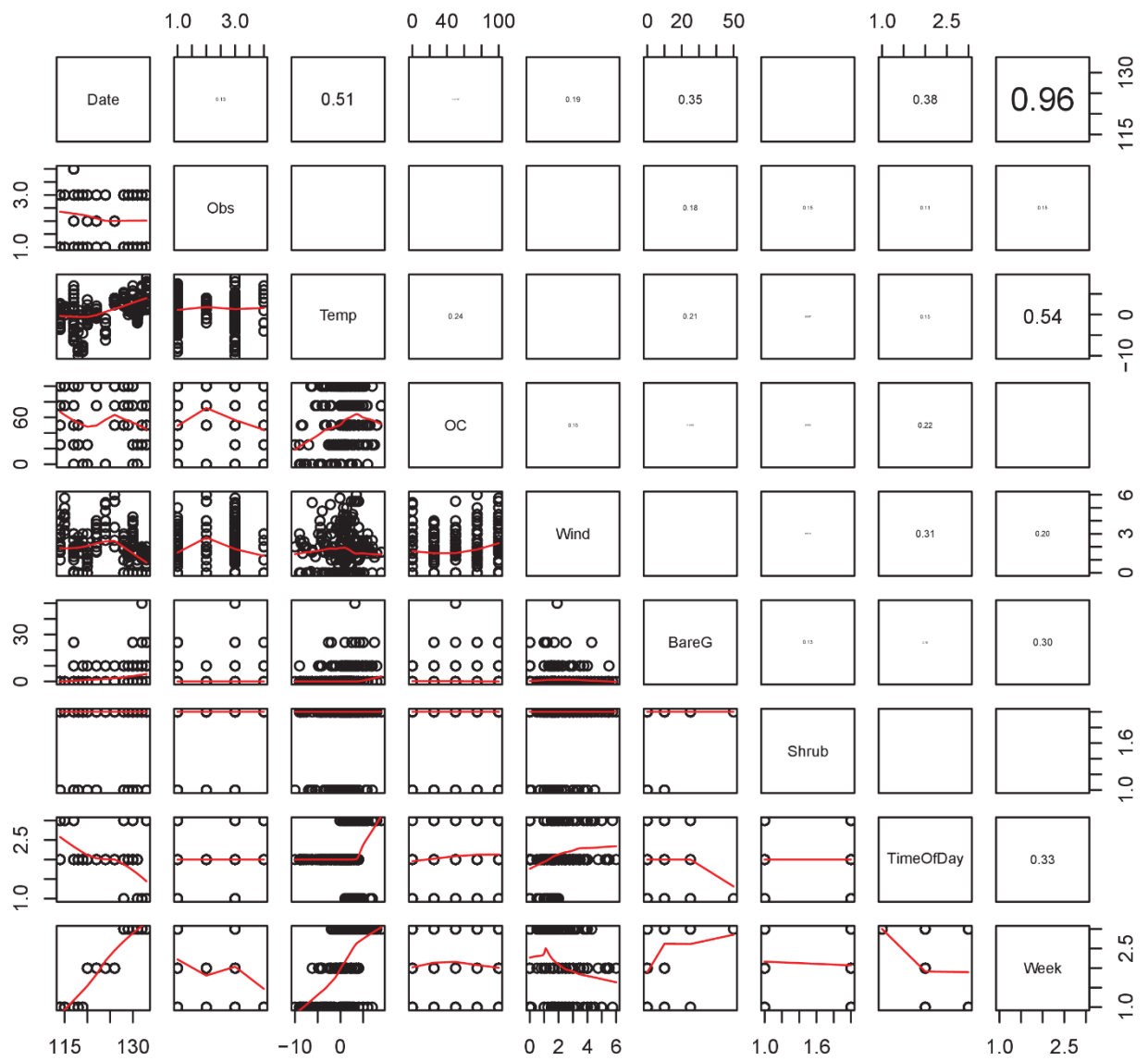


Figure A. 1: Correlation diagram between different variables for the *L. lagopus* routes

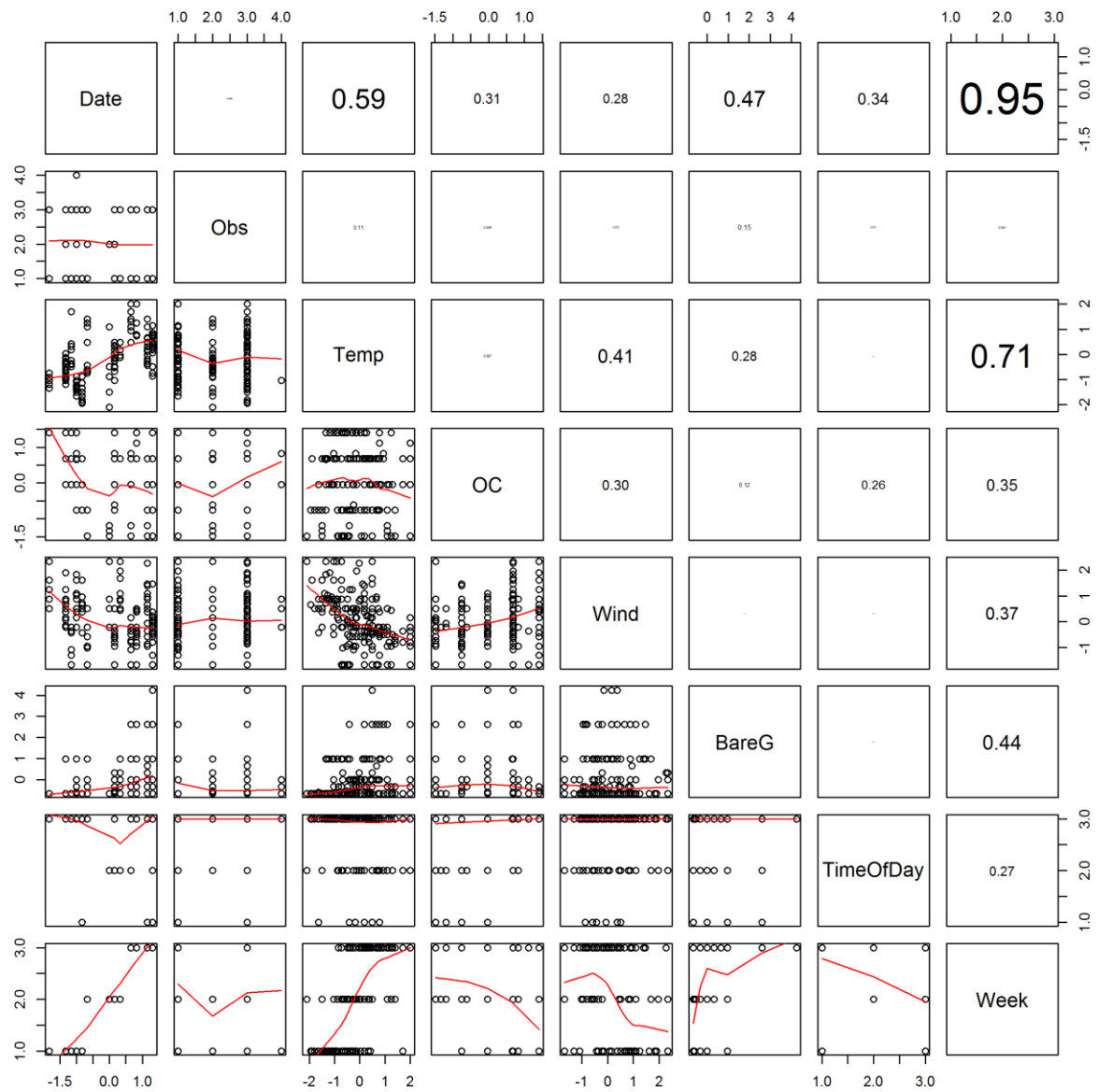


Figure A. 2: Correlation diagram between different variables for the *L. muta* routes

## Appendix B

This appendix contains the summary output from *Distance*

### Output A.1: Summary of the selected distance sampling model – *L. lagopus*:

```
#####
```

```
>summary(vj3_hn)
```

```
Summary for distance analysis
```

```
Number of observations : 79
```

```
Distance range      : 0 - 250
```

```
Model : Half-normal key function
```

```
AIC : 858.8731
```

Detection function parameters

Scale Coefficients:

	estimate	se
(Intercept)	4.906698	0.1429495

	Estimate	SE	CV
Average p	0.6340865	0.06479054	0.1021793
N in covered region	124.5886851	15.29573299	0.1227698

Summary for clusters

Summary statistics:

Region	Area	Covered Area	Effort	n	k	ER	se.ER	cv.ER
VJ	4381203	8246500	16493	79	32	0.004789911	0.0004719964	0.0985397

Abundance:

Label	Estimate	se	cv	lcl	ucl	df
Total	66.19151	9.396092	0.1419531	49.99908	87.62794	91.47363

Density:

Label	Estimate	se	cv	lcl	ucl	df
Total	1.510807e-05	2.144638e-06	0.1419531	1.141218e-05	2.000089e-05	91.47363

Summary for individuals

Summary statistics:

Region	Area	Covered Area	Effort	n	ER	se.ER	cv.ER
VJ	4381203	8246500	16493	114	0.006912023	0.0007924255	0.1146445
mean.size	se.mean						
1.443038	0.06174682						

Abundance:

Label	Estimate	se	cv	lcl	ucl	df
Total	95.51686	14.6686	0.1535708	70.48887	129.4314	79.79933

Density:

Label	Estimate	se	cv	lcl	ucl	df
Total	2.180152e-05	3.348076e-06	0.1535708	1.608893e-05	2.954243e-05	79.79933

Expected cluster size

Region	Expected.S	se.Expected.S	cv.Expected.S
Total	1.443038	0.06394658	0.04431386

#####

Appendix C

This appendix contains the summary outputs from *pcount* and *gpcount*.

**Output A.2: Summary of the the *pcount* model – *L. lagopus***

#####

Call: *pcount*(formula = ~Shrub + Overcast + Observer + Week ~ Altitude,  
data = *pcounts*)



## Abundance:

	Estimate	SE	z	P(> z )
(Intercept)	2.177	0.5879	3.70	0.000213
Altitude	0.182	0.0942	1.93	0.053679

## Detection:

	Estimate	SE	z	P(> z )
(Intercept)	-4.2254	0.793	-5.3264	1.00e-07
Shrub1	0.5300	0.289	1.8347	6.66e-02
Overcast100	-1.2814	0.402	-3.1863	1.44e-03
Overcast25	-0.7982	0.352	-2.2656	2.35e-02
Overcast50	-0.1561	0.321	-0.4861	6.27e-01
Overcast75	-0.5268	0.309	-1.7050	8.82e-02
ObserverGIV	1.0223	0.794	1.2870	1.98e-01
ObserverMAS	0.0999	0.194	0.5152	6.06e-01
ObserverRAI	-13.9533	756.375	-0.0184	9.85e-01
WeekWeek 2	-1.2414	0.786	-1.5800	1.14e-01
WeekWeek 3	2.6443	0.388	6.8089	9.84e-12

AIC: 415.3684

#####

**Output A.3: Output of the best *gpcount* model – *L. lagopus***

#####

Call: `gpcount(lambdaformula = ~Shrubfinal + Altitude, phiformula = ~1, pformula = ~Day + Hour + Dist + Wind, data = pcountgd, mixture = "P", K = 50, method = "BFGS", control = list(trace = TRUE, REPORT = 1))`

## Abundance:

	Estimate	SE	z	P(> z )
(Intercept)	1.969	0.641	3.07	0.00212
Shrubfinal1	0.563	0.302	1.86	0.06221
Altitude	0.143	0.106	1.35	0.17834

## Availability:

	Estimate	SE	z	P(> z )
	0.988	4.2	0.236	0.814

## Detection:

	Estimate	SE	z	P(> z )
(Intercept)	-4.156	0.963	-4.32	1.59e-05
Day	1.357	0.182	7.46	8.58e-14
Hour	0.259	0.100	2.59	9.57e-03
Dist1	0.328	0.179	1.84	6.64e-02
Wind	-0.331	0.132	-2.51	1.21e-02

AIC: 593.7479

#####

**Output A.4: Output of the best *pcount* based on AIC for the *L. muta***

Call: `pcount(formula = ~Wind + Obs ~ Altitude, data = umf_pcount, K = 50)`

Abundance (log-scale):

	Estimate	SE	z	P(> z )
(Intercept)	1.907	0.422	4.52	6.07e-06
Altitude	-0.279	0.139	-2.01	4.44e-02

Detection (logit-scale):

	Estimate	SE	z	P(> z )
(Intercept)	-3.0723	0.468	-6.5604	5.37e-11
Wind	-0.3561	0.115	-3.0987	1.94e-03
ObsGIV	-0.0199	0.332	-0.0598	9.52e-01
ObsMAS	0.5052	0.246	2.0575	3.96e-02
ObsRAI	1.8624	0.475	3.9242	8.70e-05

AIC: 443.6055

Number of sites: 40

optim convergence code: 0

optim iterations: 35

Bootstrap iterations: 0

#####

**Output A.5: Output of the best model in *gpcount* based on AIC for the *L. muta***

#####

Call: `gpcount(lambdaformula = ~Altitude, phiformula = ~1, pformula = ~Wind + Obs, data = GUMF, K = 50)`

Abundance (log-scale):

	Estimate	SE	z	P(> z )
(Intercept)	1.921	0.442	4.35	1.35e-05
Altitude	-0.278	0.140	-1.99	4.70e-02

Availability (logit-scale):

	Estimate	SE	z	P(> z )
	5.9	25.7	0.23	0.818

Detection (logit-scale):

	Estimate	SE	z	P(> z )
(Intercept)	-3.7997	0.481	-7.8969	2.86e-15
Wind	-0.3448	0.112	-3.0672	2.16e-03
ObsGIV	-0.0217	0.327	-0.0662	9.47e-01
ObsMAS	0.4880	0.241	2.0258	4.28e-02
ObsRAI	1.7586	0.450	3.9072	9.34e-05

AIC: 570.9543

Number of sites: 40

optim convergence code: 0

optim iterations: 78

Bootstrap iterations: 0

**Appendix D**

Model selection tables for *Distance*, *pcount* and *gpcount*

Table A. 2: Comparison of different models of distance sampling evaluated for estimating *L. lagopus* abundance in Varanger

Covariates (new distances)	AIC	$\Delta$ AIC
No covariates	858.87	0
Wind speed	859.09	0.22
Ambient temperature	859.67	0.80
Observer	859.96	1.09
Observed on bare ground	860.45	1.58
Observed associated with willows	860.71	1.84
Male territorial	860.74	1.87
Time of the day	862.13	3.26

Table A. 3: Comparison of different *pcount* models for *L. lagopus*

Covariates	AIC	$\Delta$ AIC
Shrub + Overcast + Week + Observer + Altitude	415.37	0.0
Shrub + Overcast + Week + Altitude	422.60	7.23
Overcast + Week	425.22	9.85
Overcast + Week + Wind	426.48	11.11
[...]	[...]	[...]
No Covariates	603.67	188.3

Table A. 4: AIC comparison of *pcount* models for *L. muta*

	nPars	AIC	$\Delta$ AIC
Wind + Observer + Altitude	7	443.61	0
Wind + Observer + Time of day + Overcast + Altitude	10	444.08	0.47
Wind + Observer + Time of day + Altitude	9	444.16	0.56
Wind + Observer + Overcast + Altitude	8	444.17	0.57

Table A. 5: AIC comparison of different *gpcount* models with stepwise model selection for *L. lagopus*.

Covariates	AIC	$\Delta$ AIC
Shrub final* + Altitude* + Day + Hour + Distance + Wind	593.7	0.0
Day + Hour + Distance + Wind	595.2	1.5
Day + Observer + Hour + Distance + Wind	595.5	1.8
Shrub final* + Altitude* + Day + Hour + Distance + Wind	595.53	1.83
Day + Observer + Hour + Distance + Wind + Ground	595.7	2
Altitude* + Day + Hour + Distance + Wind	595.75	2.05
Shrub final* + Ground final* + Altitude* + Day + Hour + Distance + Wind	595.8	2.1
Day + Hour + Distance + Wind + Ground	596.1	2.4
Day + Observer + Time + Distance + Wind	596.3	2.6
Day + Observer + Time + Distance + Wind + Ground	596.5	2.8
Day + Time + Distance + Wind + Ground	596.6	2.9
Ground final* + Day + Hour + Distance + Wind	597.17	3.47
Day + Observer + Hour + Distance + Wind + Overcast	597.3	3.6
Day + Time + Distance + Wind + Ground	597.4	3.7
Day + Observer + Time + Wind	597.9	4.2
Day + Observer + Time + Wind + Ground	598.1	4.4
[...]	[...]	[...]
No covariates	726.4	132.7

**Table A. 6: AIC comparison of *gpcount* models with stepwise model selection for *L. muta*.**

<b>Covariates</b>	<b>nPars</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
<b>Wind + observer + alt</b>	8	570.95	0
<b>Wind + Observer + Time of day + Altitude</b>	10	571.52	0.57
<b>Wind + Observer + Time of day + Overcast + Altitude</b>	11	571.55	0.59
<b>Wind + Observer + Overcast + Altitude</b>	9	571.62	0.66
<b>Wind + Observer</b>	7	573.08	2.12
<b>Wind + Observer + Time of day + Overcast</b>	10	573.33	2.38
<b>Wind + Observer + Time of day</b>	9	573.62	2.67
<b>Wind + Observer + Overcast</b>	8	573.64	2.69

## Appendix E

This appendix contains summary of the simulation results as visual representations and tables.

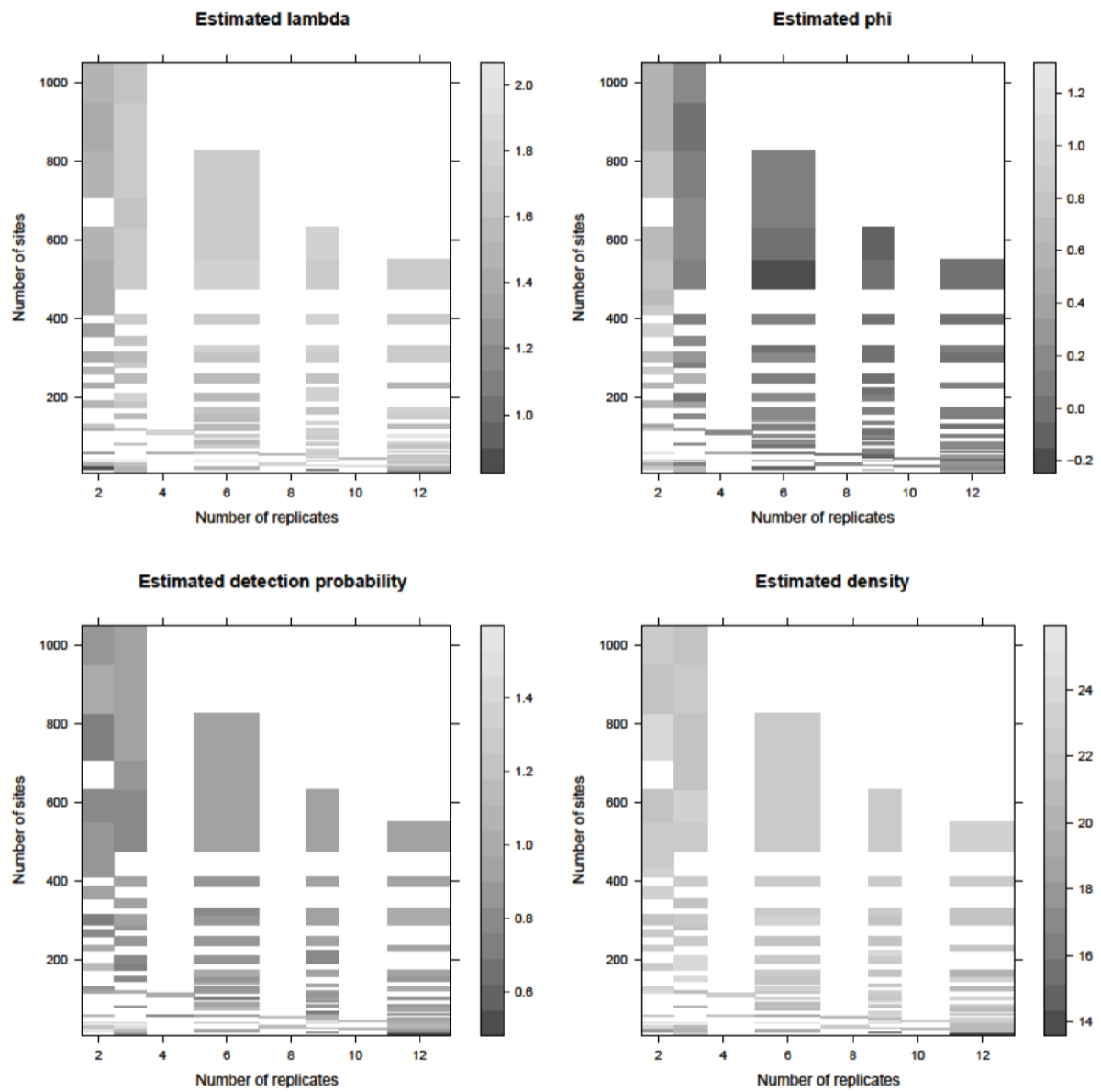


Figure A. 3: Estimated parameters (intercepts) obtained with gpcount on the simulated data, depending on the number of sites and replicates for *L. lagopus*

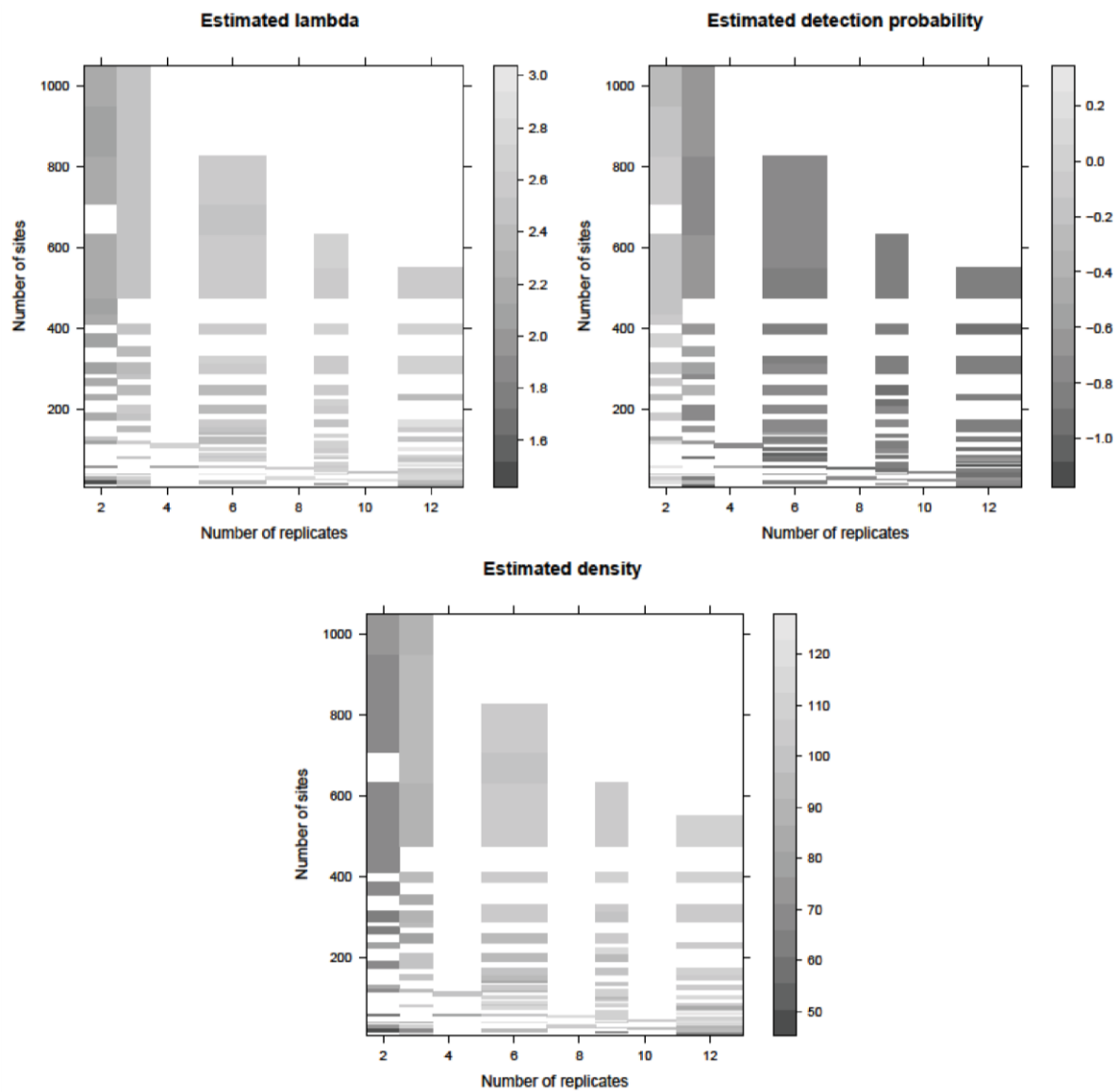
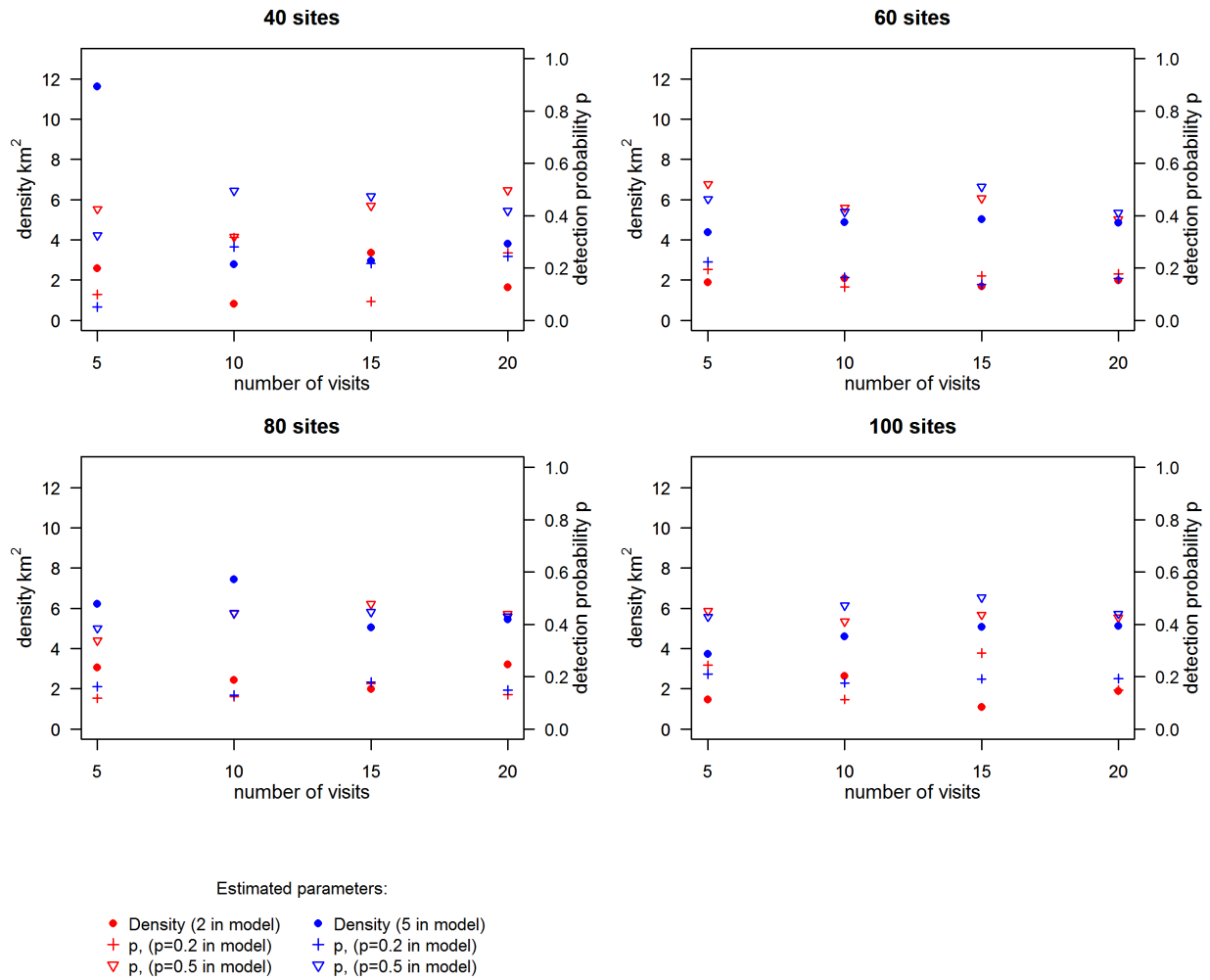
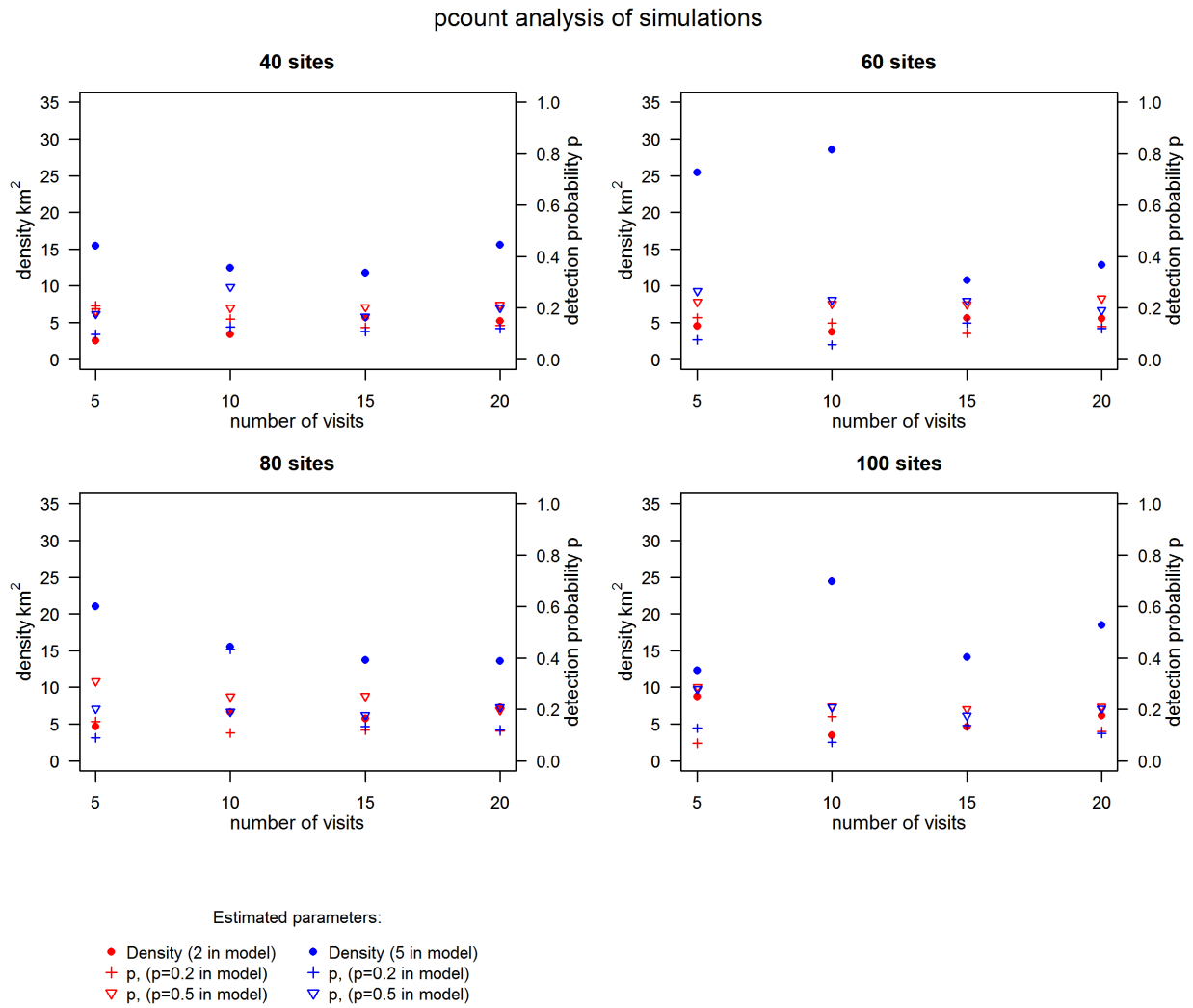


Figure A. 4: Estimated parameters (intercepts) obtained with pcount on the simulated data, depending on the number of sites and replicates for *L. lagopus*

## gpcount analysis of simulations



**Figure A. 5: Simulations analyzed with *gpcount*: Overview of density and detection probability estimates of the simulation study using known parameters for *L. muta*. Red and blue symbols indicate models based on simulating population densities with 2 and 5 ind/km<sup>2</sup>, respectively. Note the scales on the y-axes.**



**Figure A. 6: Simulations analyzed with *pcount*: Overview of density and detection probability estimates of simulation study using known parameters for *L. muta*. Red and blue symbols indicate models based on simulating population densities with 2 and 5 individuals/km<sup>2</sup>, respectively. Note the scales on the y-axes.**



Table A. 7: Simulation results with parameter estimates from *pcount* and *gpcount* for *L. lagopus*

Survey effort			Input parameters				Result gpcount					Result pcount		
SurveyEffort	nVisits	nSites	$\lambda$ intercept	$\phi$	p intercept	sum(M)	logscale est. $\lambda$	logitscale est. $m$	logitscale est. $n$	ind/km <sup>2</sup> Density funct	sum(bup(re))	logscale est. $\lambda$	logitscale est. p	D funct. ind/km <sup>2</sup>
40	2	20	1.5	0.7	0.65	120	0.9	0.92	1.53	18.2	104.8	1.52	0.17	50.41
60	2	30	1.5	0.7	0.65	224	1.49	0.52	1.18	24.39	239.4	2.19	-0.05	75.44
80	2	40	1.5	0.7	0.65	275	1.86	0.35	1.07	21.36	296	2.62	-0.4	75.96
120	2	60	1.5	0.7	0.65	404	1.23	1.22	1.07	22.63	358.7	1.94	0.25	59.09
240	2	120	1.5	0.7	0.65	843	1.4	0.89	0.95	24.24	844.8	2.08	0.11	66.35
250	2	125	1.5	0.7	0.65	877	1.66	0.43	0.87	23.56	999.5	2.44	-0.43	84.66
360	2	180	1.5	0.7	0.65	1260	1.48	0.6	1.14	22.34	1282.9	2.2	-0.1	71.12
450	2	225	1.5	0.7	0.65	1525	1.42	0.56	1.01	22.57	1643.3	2.18	-0.29	77.2
540	2	270	1.5	0.7	0.65	1779	1.48	0.84	0.8	22.58	1805.2	2.16	-0.05	64.28
600	2	300	1.5	0.7	0.65	1939	1.43	0.71	0.75	21.87	2032	2.12	-0.19	64.51
750	2	375	1.5	0.7	0.65	2487	1.34	1.01	0.92	23.44	2463.1	2.11	-0.01	67.04
840	2	420	1.5	0.7	0.65	2853	1.44	0.83	0.85	23.44	2914.5	2.14	-0.06	67.87
900	2	450	1.5	0.7	0.65	3025	1.39	0.69	0.88	22.37	3141.9	2.1	-0.14	68.26
1000	2	500	1.5	0.7	0.65	3352	1.44	0.75	0.87	22.48	3422.1	2.16	-0.14	67.38
1200	2	600	1.5	0.7	0.65	4033	1.46	0.68	0.79	22.07	4154.2	2.19	-0.19	67.53
1500	2	750	1.5	0.7	0.65	5229	1.48	0.82	0.76	23.88	5345.4	2.14	-0.08	67.63
1800	2	900	1.5	0.7	0.65	6101	1.43	0.6	0.98	21.91	6329.3	2.12	-0.16	68.17
2000	2	1000	1.5	0.7	0.65	6885	1.52	0.58	0.9	22.66	7334.4	2.22	-0.23	71.55
30	3	10	1.5	0.7	0.65	59	1.59	0.64	0.9	22.88	69.6	2.76	-1.05	116.49
60	3	20	1.5	0.7	0.65	135	1.49	0.66	1.17	20.32	125.1	2.3	-0.25	67.26
90	3	30	1.5	0.7	0.65	210	1.62	0.1	1.48	20.62	236.3	2.64	-0.87	111.92
120	3	40	1.5	0.7	0.65	286	1.97	0.17	1.06	22.91	243.9	2.07	-0.23	64.01
240	3	80	1.5	0.7	0.65	519	1.54	0.12	0.86	20.44	621.9	2.47	-0.96	102.68
360	3	120	1.5	0.7	0.65	822	1.64	0.28	0.98	21.24	907.9	2.56	-0.68	92.94
450	3	150	1.5	0.7	0.65	1072	1.57	0.23	0.77	24.35	1331.9	2.4	-0.68	99.51
540	3	180	1.5	0.7	0.65	1225	1.63	0.35	0.72	24.1	1496.4	2.49	-0.7	97.31
600	3	200	1.5	0.7	0.65	1356	1.77	0.04	0.83	23.72	1891.9	2.56	-0.74	101.09
750	3	250	1.5	0.7	0.65	1684	1.56	0.6	0.84	22.73	1799.1	2.37	-0.4	79.38
840	3	280	1.5	0.7	0.65	1849	1.72	0.06	0.89	21.85	2431.6	2.51	-0.73	95.7
900	3	300	1.5	0.7	0.65	1999	1.6	0.3	0.95	22.43	2387	2.41	-0.56	88.1
1005	3	335	1.5	0.7	0.65	2220	1.62	0.24	0.93	21.53	2647.7	2.37	-0.51	82.32
1200	3	400	1.5	0.7	0.65	2751	1.69	0.09	0.92	22.39	3484.8	2.49	-0.69	95.3
1500	3	500	1.5	0.7	0.65	3462	1.72	0.13	0.81	22.77	4361.6	2.45	-0.61	89.26
1800	3	600	1.5	0.7	0.65	4098	1.71	0.15	0.79	22.87	5229.9	2.46	-0.63	89.81
1995	3	665	1.5	0.7	0.65	4440	1.65	0.17	0.84	21.92	5471.6	2.51	-0.75	95.16
2250	3	750	1.5	0.7	0.65	5078	1.69	0.08	0.91	21.71	6362.4	2.51	-0.72	94.29
2700	3	900	1.5	0.7	0.65	6240	1.73	0.02	0.94	22.2	8084.1	2.5	-0.65	93.83
3000	3	1000	1.5	0.7	0.65	6846	1.65	0.19	0.95	21.99	8218.2	2.45	-0.61	89.86

## Appendix

120	6	20	1.5	0.7	0.65	124	1.49	-0.13	0.91	19.03	162.3	2.36	-0.85	92.16
240	6	40	1.5	0.7	0.65	279	1.98	0.07	0.86	22.8	353.1	2.9	-0.9	110.67
360	6	60	1.5	0.7	0.65	369	1.6	0.02	0.94	19.63	467.1	2.55	-0.94	100.63
450	6	75	1.5	0.7	0.65	508	1.68	-0.02	1.15	20.96	631.9	2.69	-0.98	115.78
480	6	80	1.5	0.7	0.65	533	1.46	0.3	0.97	21.68	603.4	2.45	-0.81	101.8
540	6	90	1.5	0.7	0.65	574	1.57	0.24	0.92	21.19	678.1	2.65	-1.02	113.49
600	6	100	1.5	0.7	0.65	663	1.75	0.18	0.7	23.42	859.8	2.67	-0.89	107.73
720	6	120	1.5	0.7	0.65	780	1.58	0.21	0.87	21.89	951.1	2.43	-0.7	93.71
750	6	125	1.5	0.7	0.65	843	1.54	0.11	0.86	22.99	1086.9	2.4	-0.81	104.52
840	6	140	1.5	0.7	0.65	938	1.53	0.26	1.04	21.57	1068.8	2.36	-0.51	85.08
900	6	150	1.5	0.7	0.65	986	1.59	0.22	0.9	21.93	1187.8	2.45	-0.7	94.61
990	6	165	1.5	0.7	0.65	1096	1.62	0.19	0.98	22.36	1346.3	2.54	-0.76	101.35
1200	6	200	1.5	0.7	0.65	1313	1.54	0.24	0.9	22.29	1589.8	2.41	-0.72	95.92
1500	6	250	1.5	0.7	0.65	1631	1.53	0.09	0.9	21.5	2067.9	2.37	-0.75	95.36
1800	6	300	1.5	0.7	0.65	2085	1.64	0.2	0.87	23.09	2518.3	2.54	-0.77	102.83
1980	6	330	1.5	0.7	0.65	2202	1.8	0.03	0.82	22.46	2925.8	2.65	-0.84	103.26
2400	6	400	1.5	0.7	0.65	2729	1.71	0.06	0.87	22.12	3441.4	2.58	-0.82	102.20
3000	6	500	1.5	0.7	0.65	3500	1.77	-0.15	0.95	22.66	4955.0	2.55	-0.82	105.87
3600	6	600	1.5	0.7	0.65	4141	1.71	0.04	0.97	22.60	5342.2	2.54	-0.75	102.24
3990	6	665	1.5	0.7	0.65	4543	1.68	0.12	0.92	22.83	5725.9	2.53	-0.71	99.22
4500	6	750	1.5	0.7	0.65	5171	1.71	0.06	0.95	22.60	6604.9	2.57	-0.77	103.73
126	9	14	1.5	0.7	0.65	66	1.03	0.77	0.89	16.68	67.5	1.98	-0.64	67.04
234	9	26	1.5	0.7	0.65	169	1.83	0.2	1.07	20.82	195.9	2.8	-0.79	98.97
360	9	40	1.5	0.7	0.65	258	1.51	0.25	1.02	20.06	284.7	2.48	-0.75	91.2
450	9	50	1.5	0.7	0.65	336	1.76	-0.07	1.09	21.02	434.4	2.69	-0.94	110.94
540	9	60	1.5	0.7	0.65	436	1.74	0.1	0.98	23.65	533.9	2.63	-0.8	110.44
594	9	66	1.5	0.7	0.65	445	1.81	0.08	0.75	23.4	589.7	2.68	-0.87	107.54
720	9	80	1.5	0.7	0.65	525	1.45	0.14	0.92	21.94	652.9	2.41	-0.86	105.54
756	9	84	1.5	0.7	0.65	547	1.81	0.05	0.89	21.5	699.4	2.77	-0.94	109.55
855	9	95	1.5	0.7	0.65	674	1.77	0.03	0.86	23.95	892.2	2.56	-0.73	103.4
900	9	100	1.5	0.7	0.65	652	1.73	0.18	0.91	21.61	791.8	2.58	-0.71	92.97
990	9	110	1.5	0.7	0.65	738	1.77	-0.03	0.87	22.55	1002.8	2.64	-0.86	107.7
1080	9	120	1.5	0.7	0.65	817	1.74	0.11	0.92	22.93	1038.8	2.66	-0.85	109.17
1215	9	135	1.5	0.7	0.65	875	1.81	0.06	0.94	21.6	1131.4	2.7	-0.83	101.64
1485	9	165	1.5	0.7	0.65	1105	1.64	0.08	0.95	21.48	1360.8	2.53	-0.77	98.54
1800	9	200	1.5	0.7	0.65	1371	1.78	0.12	0.83	22.49	1693.2	2.61	-0.73	96.69
1980	9	220	1.5	0.7	0.65	1581	1.83	0.02	0.83	23.89	2066.8	2.73	-0.91	115.45
2250	9	250	1.5	0.7	0.65	1626	1.65	-0.02	0.91	21.37	2144.7	2.56	-0.93	106.67
2700	9	300	1.5	0.7	0.65	2038	1.72	-0.02	0.97	21.48	2593.9	2.58	-0.81	101.53
2970	9	330	1.5	0.7	0.65	2333	1.76	-0.05	0.93	22.5	3036.5	2.59	-0.81	105.05
3600	9	400	1.5	0.7	0.65	2709	1.79	-0.04	0.92	22.31	3634.7	2.67	-0.87	107.95
4500	9	500	1.5	0.7	0.65	3390	1.68	0.03	0.92	22.27	4365.7	2.57	-0.85	106.30
5400	9	600	1.5	0.7	0.65	4086	1.83	-0.06	0.93	22.32	5509.9	2.68	-0.85	106.69
120	12	10	1.5	0.7	0.65	42	1.18	0.51	0.55	14.35	45.68	2.12	-0.82	62.75
240	12	20	1.5	0.7	0.65	127	1.5	0.18	0.87	20.61	149.6	2.41	-0.79	92.71
360	12	30	1.5	0.7	0.65	199	1.87	0.29	1.1	20.86	217.2	2.78	-0.64	90.59

456	12	38	1.5	0.7	0.65	261	1.6	0.29	1.1	21.29	279.4	2.77	-0.93	113.03
504	12	42	1.5	0.7	0.65	304	1.75	-0.04	1.03	22.72	386.3	2.72	-0.93	119.66
600	12	50	1.5	0.7	0.65	348	1.61	0.28	0.93	23.49	407.4	2.6	-0.82	109.55
744	12	62	1.5	0.7	0.65	406	1.81	0.06	0.85	21.77	518.7	2.89	-1.08	122.92
840	12	70	1.5	0.7	0.65	455	1.85	0.07	0.98	21.14	565.2	2.92	-1.04	117.32
900	12	75	1.5	0.7	0.65	464	1.64	0.22	0.91	20.96	563.6	2.47	-0.64	85.9
1008	12	84	1.5	0.7	0.65	556	1.78	0.21	0.87	22.49	679.26	2.72	-0.81	103.04
1200	12	100	1.5	0.7	0.65	676	1.99	0.05	0.85	23.23	901.7	2.94	-0.95	117.07
1500	12	125	1.5	0.7	0.65	830	1.57	0.01	0.99	21.22	1050.4	2.48	-0.86	103.98
1800	12	150	1.5	0.7	0.65	1054	1.73	0.1	0.87	23.22	1316.8	2.61	-0.81	106.86
1980	12	165	1.5	0.7	0.65	845	1.77	0.1	0.94	20.29	1042.6	2.86	-0.84	108.14
2700	12	225	1.5	0.7	0.65	1521	1.45	0.06	0.91	21.88	1898.6	2.37	-0.86	105.63
3600	12	300	1.5	0.7	0.65	2069	1.74	0.01	1.03	21.81	2582.4	2.65	-0.85	107.04
3960	12	330	1.5	0.7	0.65	2253	1.75	0.05	1.01	21.99	2808.4	2.67	-0.83	105.84
4800	12	400	1.5	0.7	0.65	2705	1.75	-0.02	0.95	22.15	3550.1	2.67	-0.90	111.26
6000	12	500	1.5	0.7	0.65	3513	1.70	-0.04	0.96	23.21	4717.5	2.55	-0.83	110.47

**Table A. 8 Simulation results with parameter estimates from *pcount* and *gpcount* for *L. lagopus*. Also included in the simulation were: The log-scale slope “Altitude” (-0.3) as covariate for superpopulation abundance and the logit-scale slopes “Wind” (-0.3), “Julian date” (0.2) and “Difference in detection between Distance classes” (-0.5) as covariates for the detection process.**

Survey effort			Input parameters			Results gpcount							Results pcount		
SurveyEffort	nVisits	nSites	$\lambda$ intercept	$\phi$ intercept	$pInt$	sumM	logscale est. $\lambda$	logitscale est $\phi$	logitscale est. p ind/km <sup>2</sup>	Density funct	sum(bup(re))	logscale est. $\lambda$	logitscale est. p	D funct. ind/km <sup>2</sup>	
200	5	40	2	0.5	0.2	25	-1.10	7.82	-2.20	2.57	38.54	-1.10	-1.34	2.51	
400	10	40	2	0.5	0.2	22	-0.92	-0.34	-0.77	0.82	22.81	-0.41	-1.68	3.40	
600	15	40	2	0.5	0.2	25	-0.42	5.35	-2.55	3.34	36.14	0.05	-1.96	5.69	
800	20	40	2	0.5	0.2	32	-0.31	-0.26	-1.06	1.63	36.26	0.03	-1.89	5.23	
300	5	60	2	0.5	0.2	52	-0.41	0.22	-1.42	1.87	72.13	-0.20	-1.65	4.55	
600	10	60	2	0.5	0.2	22	-0.51	0.76	-1.93	2.08	54.05	-0.31	-1.80	3.73	
900	15	60	2	0.5	0.2	44	-0.38	-0.29	-1.59	1.69	62.47	-0.06	-2.18	5.63	
1200	20	60	2	0.5	0.2	51	-0.26	0.01	-1.53	1.98	56.22	0.09	-1.93	5.56	
400	5	80	2	0.5	0.2	61	-0.23	1.12	-2.02	3.05	90.49	-0.08	-1.72	4.68	
800	10	80	2	0.5	0.2	63	-0.03	-0.05	-1.96	2.42	114.82	0.26	-2.10	6.60	
1200	15	80	2	0.5	0.2	60	-0.34	-0.03	-1.56	1.97	80.85	0.02	-1.99	5.71	
1600	20	80	2	0.5	0.2	83	0.09	0.30	-1.89	3.21	106.26	0.36	-2.03	7.27	
500	5	100	2	0.5	0.2	90	-0.04	-0.97	-1.13	1.47	239.44	0.44	-2.61	8.78	
1000	10	100	2	0.5	0.2	71	-0.53	1.97	-2.06	2.64	83.63	-0.38	-1.57	3.47	
1500	15	100	2	0.5	0.2	71	-0.58	-0.49	-0.90	1.09	71.31	-0.15	-1.84	4.60	
2000	20	100	2	0.5	0.2	80	-0.22	-0.25	-1.74	1.89	102.98	0.12	-2.04	6.13	
200	5	40	2	0.5	0.5	35	0.14	-0.37	-0.30	2.39	63.18	0.76	-1.47	10.86	
400	10	40	2	0.5	0.5	29	-0.40	0.23	-0.76	2.27	37.84	0.12	-1.39	7.09	
600	15	40	2	0.5	0.5	35	-0.20	-0.10	-0.25	1.97	36.06	0.47	-1.37	8.45	
800	20	40	2	0.5	0.5	25	-0.46	-0.32	-0.01	1.38	28.33	0.20	-1.32	6.33	

## Appendix

<b>300</b>	5	60	2	0.5	0.5	47	-0.17	-0.36	0.08	1.8	69.43	0.49	-1.25	8.32
<b>600</b>	10	60	2	0.5	0.5	52	-0.08	-0.06	-0.28	2.27	63.26	0.57	-1.29	9.03
<b>900</b>	15	60	2	0.5	0.5	59	0.03	-0.22	-0.14	2.36	68.43	0.69	-1.30	10.28
<b>1200</b>	20	60	2	0.5	0.5	51	-0.13	0.16	-0.46	2.44	55.69	0.43	-1.17	7.91
<b>400</b>	5	80	2	0.5	0.5	46	-0.55	0.56	-0.67	1.93	66.08	-0.23	-0.80	4.24
<b>800</b>	10	80	2	0.5	0.5	58	-0.36	0.02	-0.24	1.81	63.19	0.30	-1.10	6.85
<b>1200</b>	15	80	2	0.5	0.5	65	-0.25	-0.05	-0.09	2.03	70.70	0.36	-1.09	7.67
<b>1600</b>	20	80	2	0.5	0.5	68	-0.12	-0.20	-0.24	2.05	76.93	0.58	-1.41	9.13
<b>500</b>	5	100	2	0.5	0.5	92	-0.07	0.00	-0.19	2.37	121.92	0.38	-0.91	7.45
<b>1000</b>	10	100	2	0.5	0.5	86	-0.12	0.00	-0.36	2.25	101.76	0.51	-1.31	8.72
<b>1500</b>	15	100	2	0.5	0.5	80	-0.26	-0.10	-0.26	1.88	86.07	0.46	-1.38	8.18
<b>2000</b>	20	100	2	0.5	0.5	75	-0.24	-0.08	-0.30	1.92	83.76	0.42	-1.32	7.75
<b>200</b>	5	40	5	0.5	0.2	63	1.12	1.29	-2.94	11.62	179.55	1.17	-2.23	15.47
<b>400</b>	10	40	5	0.5	0.2	76	0.63	-0.88	-0.94	2.79	96.83	0.89	-1.94	12.46
<b>600</b>	15	40	5	0.5	0.2	75	0.43	-0.57	-1.28	2.95	77.54	0.79	-2.10	11.74
<b>800</b>	20	40	5	0.5	0.2	83	0.65	-0.52	-1.13	3.8	90.16	1.07	-2.00	15.57
<b>300</b>	5	60	5	0.5	0.2	134	1.27	-1.15	-1.25	4.38	259.05	1.61	-2.49	25.47
<b>600</b>	10	60	5	0.5	0.2	123	1.49	-1.29	-1.63	4.87	342.19	1.72	-2.83	28.51
<b>900</b>	15	60	5	0.5	0.2	108	0.42	0.48	-1.83	5.01	112.50	0.71	-1.81	10.79
<b>1200</b>	20	60	5	0.5	0.2	120	0.71	-0.13	-1.66	4.85	139.92	0.93	-1.99	12.87
<b>400</b>	5	80	5	0.5	0.2	178	1.14	-0.46	-1.64	6.21	313.41	1.41	-2.33	21.00
<b>800</b>	10	80	5	0.5	0.2	183	0.91	0.28	-1.91	7.43	251.36	1.12	-0.27	15.53
<b>1200</b>	15	80	5	0.5	0.2	159	0.71	-0.02	-1.52	5.04	185.53	1.00	-1.88	13.68
<b>1600</b>	20	80	5	0.5	0.2	142	0.70	0.15	-1.74	5.45	180.48	0.99	-1.99	13.56
<b>500</b>	5	100	5	0.5	0.2	177	0.50	-0.27	-1.33	3.73	257.49	0.87	-1.93	12.33
<b>1000</b>	10	100	5	0.5	0.2	214	1.20	-0.99	-1.54	4.59	423.89	1.57	-2.55	24.43
<b>1500</b>	15	100	5	0.5	0.2	206	0.61	0.13	-1.44	5.06	211.87	1.00	-1.84	14.09
<b>2000</b>	20	100	5	0.5	0.2	216	0.87	-0.36	-1.44	5.11	273.77	1.26	-2.13	18.50
<b>200</b>	5	40	5	0.5	0.5	70	0.72	0.17	-0.73	5.82	98.34	1.38	-1.54	20.76
<b>400</b>	10	40	5	0.5	0.5	77	0.64	-0.09	-0.02	4.61	84.11	1.17	-0.94	16.23
<b>600</b>	15	40	5	0.5	0.5	103	-0.34	-0.34	-0.10	6.13	121.98	1.88	-1.61	34.85
<b>800</b>	20	40	5	0.5	0.5	94	0.85	-0.05	-0.33	6.44	108.35	1.57	-1.39	26.92
<b>300</b>	5	60	5	0.5	0.5	127	0.64	0.22	-0.15	5.36	131.85	1.30	-1.02	18.68
<b>600</b>	10	60	5	0.5	0.5	124	0.78	0.06	-0.34	5.73	142.93	1.40	-1.20	20.64
<b>900</b>	15	60	5	0.5	0.5	122	0.67	-0.06	0.04	4.65	120.04	1.44	-1.22	20.76
<b>1200</b>	20	60	5	0.5	0.5	106	0.64	0.04	-0.36	4.95	119.93	1.46	-1.45	21.50
<b>400</b>	5	80	5	0.5	0.5	161	0.88	-0.16	-0.47	5.68	213.89	1.44	-1.37	21.53
<b>800</b>	10	80	5	0.5	0.5	163	0.77	-0.12	-0.23	5.13	187.65	1.54	-1.45	23.84
<b>1200</b>	15	80	5	0.5	0.5	162	0.84	-0.24	-0.21	5.18	195.57	1.63	-1.54	26.07
<b>1600</b>	20	80	5	0.5	0.5	177	0.76	0.07	-0.28	5.92	187.13	1.51	-1.34	24.61
<b>500</b>	5	100	5	0.5	0.5	179	0.51	0.21	-0.29	4.74	198.50	1.02	-0.95	14.46
<b>1000</b>	10	100	5	0.5	0.5	186	0.64	-0.20	-0.11	4.33	207.79	1.34	-1.34	19.69
<b>1500</b>	15	100	5	0.5	0.5	189	0.69	-0.19	0.01	4.62	212.21	1.60	-1.55	25.39
<b>2000</b>	20	100	5	0.5	0.5	196	0.68	0.05	-0.24	5.12	205.05	1.48	-1.37	22.20

