Survival and cause-specific mortality of harvested willow ptarmigan (*Lagopus lagopus*) in central Norway

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Abstract

Survival is a key demographic component that often vary as a result of human activities such as recreational harvest. Detailed understanding of seasonal variation in mortality patterns and the role of various risk factors is thus crucial for understanding evolution of life histories, the link between environmental variation and wildlife population dynamics, and to design sustainable harvest management systems. Here, we report from a detailed seasonal and cause-specific decomposition of mortality risks in willow ptarmigan (*Lagopus lagopus*) in central Norway. The analyses are based on radio collared (n=188) birds that were monitored across all seasons, and we used time-to-event models for competing risks to estimate mortality patterns. Overall, annual survival was estimated at 0.43 (SE: 0.04), with no distinct difference between years or sex. Analysis of mortality risk factors revealed that on the annual basis, the risk of harvest mortality was lower than the risk of dying from natural causes. However, during the autumn harvest season (Sept. – Nov.), survival was low and the dominating cause of mortality was harvest. During winter (Dec. – Mar.) and spring seasons (Apr. - May), survival was in general high and did not vary between males and females. However, during the spring season juveniles (i.e. birds born last year) of both sexes had lower survival than adults, potentially because they are more prone to predation. During the summer season (June – Aug.) females experienced a higher hazard than males, underlining the greater parental investment of females during egg production, incubation and chick rearing compared to males. Our analyses provide unique insight into demographic and seasonal patterns in willow ptarmigan mortality risks in a harvested population, and revealed a complex interplay across seasons, risk factors and demographic classes. Such insight is valuable when designing sustainable management plans in a world undergoing massive environmental perturbations.

Key words: demography, grouse, harvest, cause-specific mortality, survival

Introduction

Population dynamics is driven by temporal and spatial fluctuations in demographic rates, that together determine the population growth rate λ (Sæther *et al.* 1999; Sæther & Bakke 2000). Both survival and reproductive output contribute to the observed variation, and their general contribution varies both in time and space (Sæther & Bakke 2000; Nilsen *et al.* 2009). In addition, research focusing on the evolution of life history strategies have found that species can be classified along a slow-fast continuum (Stearns 1983; Sæther & Bakke 2000; Bielby *et al.* 2007). Generally, fast living species have low survival and high reproductive output, whereas slow living species have high survival rates and lower reproductive output (Sæther *et al.* 2013). Species on opposite ends of the continuum also differ in the way age-specific survival contributes to the population growth rate (Sæther *et al.* 2013). The potential contribution of adult survival is higher in slow living species (Sæther & Bakke 2000), whereas the potential contribution of early life survival is higher in fast living species (Bielby *et al.* 2007). Annual mortality patterns are often very different for species on different ends of the continuum. Therefore, understanding the spatiotemporal variation in survival and cause-specific mortality rates are imperative for understanding the population dynamics of wildlife species (DelGiudice *et al.* 2002; Heisey & Patterson 2006; Murray 2006).

Previous studies have reported that demographic factors such as sex and age can significantly affect the survival probability (Shackell *et al.* 1994; Caizergues & Ellison 1997; Beauplet *et al.* 2006) and mortality causes (Hannon, Gruys & Schieck 2003; Delgiudice *et al.* 2006; Chilvers & MacKenzie 2010; Asmyhr, Willebrand & Hörnell-Willebrand 2012) of a range of species. Moreover, in temporally variable environments mortality risk might vary through time (Gauthier *et al.* 2001; Crespin *et al.* 2002), and the ability to deal with unpredictable environmental conditions may vary between life stages (Delgiudice *et al.* 2006). For instance, adult survival is often reported to be higher and less variable than juvenile survival (Guillemain *et al.* 2013). Finally, in seasonal environments certain seasons within the year may also place more stress on one sex than the other, such as the energy demanding process of egg production (Nilsson & Råberg 2001) and incubation (Haftorn & Reinertsen 1985) for female birds or risky behavior undertaken by males in the mating season (Hannon, Gruys & Schieck 2003).

In wild vertebrate populations, individuals are typically facing competing risks from a range of different sources, and these sources might have different intensities in different times of the year. In exploited populations, previous studies have demonstrated that harvest-related mortality risks may be significantly higher than natural mortality risks in parts of the year (Toïgo *et al.* 2008). Harvest mortality is often assumed to be partially compensated through reduced natural mortality (Pedersen *et al.* 2004). However, this may only be true at low harvest rates, where harvest mortality above certain levels may be increasingly additive or even super-additive (Sandercock *et al.* 2011). Knowledge of such thresholds and any compensatory mechanisms is thus essential information for sustainable harvest management (Brøseth *et al.* 2005). For harvested wildlife populations, understanding the interplay between harvest induced mortality and other natural mortality sources is important in order to establish sustainable harvest strategies (Sandercock *et al.* 2011).

Willow ptarmigan (*Lagopus lagopus* L.) is a valued game species, and is hunted in many parts of its distributional range (Storch 2007), including Scandinavia (Aanes *et al.* 2002; Asmyhr, Willebrand & Hörnell-Willebrand 2012). After a strong decline in population numbers, the willow ptarmigan was in 2015 classified as near threatened (NT) in the Norwegian Red List for Species (Henriksen & Hilmo 2015), fueling a debate of harvest effects on population development (Breisjøberget *et al.* 2018). This makes the Norwegian willow ptarmigan population a highly relevant case study for a detailed examination of variation in mortality patterns for a managed wildlife species. To this end, we used five years of telemetry data from central Norway to characterize annual and seasonal mortality risks for different sex- and age classes. In particular, we first (i) estimated annual survival rates for the different demographic groups in the population. Second, (ii) we decomposed the annual cycle into distinct seasons and assessed sex- and age- effects within seasons. Finally, (iii) we estimated the relative risk of natural and harvest induced risks using a competing risks formulation, and estimated seasonal patterns in hazard rates. In sum, these analyses will provide an important description of how different hazards shape the annual mortality patterns for different demographic groups in a wildlife population.

Materials and methods

Study area

The basis of our field study was two locations, Lifjellet (64°25′ – 64°30′N, 13°11′ – 13°24′E) and Gusvatnet (64°15′ – 64°18′N, 13°25′ – 13°37′E) respectively, in Lierne municipality in Central Norway, where all captures and marking of birds occurred (Figure 1). Because some birds migrated long distances (> 25km), our dataset also include several relocations in neighboring municipalities. Radio tagged willow ptarmigan were triangulated inside the total study area, as the birds dispersed or migrated out of the main areas. The capture sites for willow ptarmigan (see next section) spanned elevations from 459 – 757m, and were located in the subalpine to alpine bioclimatic zone. The subalpine bioclimatic zone was dominated by spruce (*Picea abies* L.) interspersed with birch (*Betula pubescens*). Dwarf birch (*B. nana* L.) and willows (*Salix spp*.) comprise most of the shrubbery scattered amongst forest patches. At lower elevations bogs/marshes are covered by grasses and sedges and the forests by ericaceous plants, while the vegetation at higher altitudes is dominated by dwarf birch heather, sedges and lichens. The ground is typically snow-covered from October until May. Main predators on adult willow ptarmigan observed in the study area include, gyrfalcons (*Falco rusticolus* L.), golden eagles (*Aquila chrysaetos* L.) and red fox (*Vulpes Vulpes* L.). In addition, arctic fox (*Vulpes lagopus* L.) and lynx (*Lynx lynx* L.) are present in the study area, but probably does not represent major mortality risks for ptarmigan in the study area due to low densities.

Field methods

During February and March 2015-2019, we captured a total of 188 willow ptarmigan at night using snowmobiles and large hand nets with prolonged handles, as described in Nilsen *et al.* (2020). To prevent birds from flying off before the field personnel were close enough to capture them, a high-powered head lamp was used to dazzle the birds. After capture, we placed the birds in an opaque bag to reduce stress. We aged the birds based on descriptions in Bergerud, Peters and McGrath (1963) and Myrberget (1975), by examining the pigmentation on the outer primaries and categorized them as either juvenile (< 1 year old) or adult (> 1 year old). We assessed the sex of each bird in the field by visual inspection of morphological characteristics and later confirmed the sex by DNA analyses using a feather sample collected during capture. For 17 birds we did not obtain any biological samples or the DNA analysis was unsuccessful, and could thus not confirm sex using DNA. Based on the birds where both field-based and DNA-based sex determination was obtained, field-based determination was correct in 85% of the cases. We therefore opted to include birds where sex was not verified using DNA analyses, aware of the small potential bias here. Before releasing the birds, they were fitted with a uniquely numbered leg ring (~ 2.4g) and a Holohil RI-2BM or Holohil RI-2DM radio transmitter (~ 14.1g). The radio transmitters had an expected battery lifetime of 24 months (RI-2BM) or 30 months (RI-2DM), and included a mortality circuit that was activated if a bird had been immobile for 12 hours. For all marked birds, the combined weight of the leg ring and radio transmitter were < 3.5% of the body mass. From the total number of birds that we instrumented with VHF radio collars (n = 188), some birds (n = 6) were never relocated after release and were thus excluded from the study. This left us with a total sample of n = 182 individual willow ptarmigan included in the analyses. Of these birds, there were 53% females and 47% males. During the study period, we recorded mortalities for 124 birds (i.e., 68% of all birds marked), whereas 58 birds (32%) were censored either because we lost contact or because they were alive at the end of the study period (Table 1). As previous studies did not find adverse effects of radio tags on survival (Thirgood *et al.* 1995; Hannon, Gruys & Schieck 2003; Terhune *et al.* 2007), we assumed the radio tags would not influence the survival of willow ptarmigan.

Following release of the radio tagged birds, they were triangulated from the ground at least once a month for 10 months of the year (February – November) by qualified field personnel. If a mortality signal was heard from the transmitter, we recovered it as soon as possible to determine cause of death. A number of birds dispersed out of the main study areas and was thus out of signal range for field personnel on the ground. To avoid loss of data, we conducted aerial triangulation using a helicopter or airplane three times a year (May, September and November) in the years 2016-2019. In 2015, we only conducted one triangulation from the air in October.

The data used here is based on an ongoing field project, and the dataset is therefore continuously updated as new data is registered. For analyses reported here we used data collected between 16.02.2015 to 27.11.2019.

Individual capture histories

As a basis for our analysis of annual survival probabilities, we set 1 August to represent the start of the biological year. This choice made it possible to directly compare our results with those from previous studies in Scandinavia (Smith & Willebrand 1999; Sandercock *et al.* 2011). With the redefined year, the first time period of the study started 1 August 2014 and ended on 31 July 2015, while the final time period (6 in total) started 1 August 2019 and ends 31 July 2020. Hereafter, “year” refers to the biological year from 1 August to 31 July.

In addition to the analysis of annual survival probabilities, we also assessed patterns of survival in four distinct seasons. First, we defined the autumn season as 1 September to 30 November. This season is strongly affected by the annual recreational harvest season starting 10 September, and previous studies from Scandinavia have shown that harvest is a dominating mortality factor in autumn (Smith & Willebrand 1999; Sandercock *et al.* 2011). Most of the hunting effort usually takes place during the first weeks after the hunting season has started (Smith & Willebrand 1999; Willebrand, Hörnell-Willebrand & Asmyhr 2011). In our case, there were only two harvest-related mortalities outside the defined autumn season (during the winter harvest season in February). Second, we defined the winter season as 1 December to 31 March. Winter survival of willow ptarmigan in Scandinavia have typically been found to be high (Smith & Willebrand 1999; Sandercock *et al.* 2011). Finally, we defined the mating and pre-brooding period as the spring season (1 April to 31 May), while the incubation and chick rearing period was defined as the summer season (1 June to 31 August). The age of each bird (juvenile vs adult) was estimated at capture in February/March and separated into two age categories (< 1 year old and > 1 year old). In the further analyses, age was only included as a predictor variable for the spring survival analysis.

Based on the time schedules described above, we constructed capture histories for each bird following a time-to-event modelling approach (Pollock *et al.* 1989). Birds that were alive at the end of the year (31 July) or season (see above for definitions) were censored, and re-entered in a new row in the dataset for the next year or season. Thus, each observation in the dataset is one bird in one given year. For all years in total, we had 350 observations or 'bird-years'. Naturally, with only one tagging session in February/March the number of observations available for analyses decreased due to mortalities from winter (n = 251), spring (n = 232), summer (n = 206) to autumn (n = 161). In addition to the capture-related variables (ring identification number, sex and age), five new variables were created: time period, entry day, exit day, event (if the bird was alive = 0 or dead = 1) and cause of death (harvest = 1 or natural = 2). Natural causes were defined as any non-harvest related mortality. All unknown mortality causes were assumed to be natural (since harvested marked ptarmigans were reported), but not identifiable to a single natural cause. We assumed that all harvested birds were reported as harvested. Hunters were frequently reminded to report and return radio tags and/or leg rings and since marked birds were not banned from harvest, this should be a valid assumption.

Because the birds were not monitored in continuous time, the exit date (i.e., date for mortality or censoring) had to be estimated in many cases. For birds that were alive at the end of the study, exit day was set to the day that they were last confirmed to be alive. Birds that died due to natural causes, had their exit day defined as the midpoint between the last day they were heard alive and the first time the mortality signal from the transmitter was heard. For birds that were shot by hunters, exit day was set according to the day the bird was shot, as reported by the hunters. A few birds (n = 4) that were censored due to loss of contact (radio transmitter failure or other), re-entered the study when they were reported as shot and their status was changed to alive until the day they were shot.

Survival analyses

Survival rates were estimated using five years of radio telemetry data, collected between 2015 and 2019 in Lierne, Snåsa, Grong and Røyrvik municipalities. We applied Pollock *et al.* (1989) staggered-entry modification of the Kaplan-Meier procedure (Kaplan & Meier 1958) to estimate annual and seasonal survival rates on a daily basis in the statistical software R, version 3.6.1 (R Core Team 2019), employing functions from the *survival* package (Therneau 2015). Other analyses and data handling were also conducted in R.

To examine variation in mortality risk due to sex, age and year, we used Cox proportional hazards regression models fitted using the function *coxph* (Therneau 2015). To account for non-independence caused by the fact that some individuals were represented by more than one observation, individual ID (ring identification number) was included as a random variable. The proportional hazards assumption of all cox regression models were assessed by running model diagnostics with the *cox.zph* function (Therneau 2015). Annual cause-specific mortality under the competing risks of natural and harvest mortality was estimated by employing a nonparametric cumulative incidence function estimator (NPCIFE) described by Heisey and Patterson (2006), using the code modified by Sandercock *et al.* (2011). The same procedure was also used to estimate the cumulative risk of natural and harvest mortality during autumn only. To test for any dependencies in harvest or natural mortality risk due to sex, we used a stratified Cox proportional hazards analysis. We first stratified the data by mortality cause (natural or harvest) and then ran two separate Cox proportional hazards regressions, one for natural mortality risk and one for harvest mortality risk, testing for an effect of sex in each model. Finally, we estimated separate continuous annual hazard functions for both mortality causes combined, for harvest mortality only and natural mortality only by employing Gu (2014) smoothing spline functions.

All survival analysis figures were created using package *ggplot2* (Wickham 2016), while the map in Figure 1 was created with packages *leaflet* and *mapview* (Cheng, Karambelkar & Xie 2018; Appelhans *et al.* 2019).

Results

Annual survival probabilities

Annual survival probability of willow ptarmigan across all years was estimated to be 0.43 ± 0.04 SE (Figure 2a). For females and males, annual survival was estimated to be 0.40 ± 0.05 SE and 0.45 ± 0.05 SE respectively (Figure 2b). When stratified by sex, the proportional hazards assumption was not met ($\chi^2 = 5.71$, $P = 0.02$), and we therefore did not use Cox proportional regression to assess this difference statistically. We further examined if there was any between-year variation in annual survival (Figure 2c), but no significant between-year variation in annual survival was found (Wald test = 1.67, df = 3, P = 0.60). The assumption about proportional hazards for the global model was met ($\chi^2 = 7.27$, $P = 0.06$). Therefore, annual survival estimates remained relatively stable for all years.

Seasonal survival rates

In the second part of the analysis we created distinct datasets for the various seasons (as defined in the methods), and estimated survival probabilities for each season separately. As expected, autumn survival was low (0.67 ± 0.04 SE), and there were some indications that males had higher mortality risk than females during this season (HR = 1.53, 95% CI = 0.90 – 2.60, z = 1.58, P = 0.11; Figure 3a). The assumption of proportional hazards was met when stratified by sex (χ^2 = < 0.01, P = 0.98). During the winter season, overall survival probability was high (0.90 ± 0.03 SE), with no discernible difference in mortality risk between males and females (HR = 0.65, 95% CI = 0.24 – 1.78, z = -0.84, P = 0.40). The assumption of proportional hazards when stratified by sex was met (χ^2 = 2.28, P = 0.13). Also during spring, survival probabilities were high (0.90 ± 0.02 SE). The proportional hazards assumption was met for sex (χ^2 = 0.07, P = 0.79) and age (χ^2 = 0.08, P = 0.78), for the spring survival data. There were no difference in survival between males and females (HR = 1.10, 95% CI = 0.47 – 2.58, z = 0.23, P = 0.82) in spring, but juveniles (< 1 year old) had a substantially higher risk of mortality than adult birds (HR = 2.35, 95% CI = 1.01 – 5.45, z = 1.98, P = 0.05; Figure 3b). During the three month long summer season, survival probability was lower than both winter and spring survival (0.82 ± 0.03 SE), and males had a substantially lower mortality risk than females (HR = 0.33, 95% CI = 0.16 – 0.69, z = -2.93, P = < 0.01; Figure 3c). The summer survival data for sex met the assumption of proportional hazards (χ^2 = 3.09, P = 0.08). For all seasonal analyses, year did not explain a significant amount of the variation in mortality risk for any season and the proportional hazards assumption was met for all seasonal data (except summer) used to test for effects of year (see Appendix 1).

Temporal variation in cause-specific mortality risk

In the third and final part of the analyses we investigated annual and seasonal cause-specific mortality risk. Annually, there was a higher probability of mortality due to natural causes (CIF = 0.33 ± 0.03 SE, 95% CI = 0.28 – 0.38) than being shot (CIF = 0.25 ± 0.04 SE, 95% CI = 0.19 – 0.31) for willow ptarmigan in this study (Figure 4a). Unsurprisingly, this relationship was reversed when we examined the autumn season only, with harvest mortality being substantially higher (CIF = 0.24 ± 0.04 SE, 95% CI = 0.18 – 0.30) than the probability of dying of natural causes (CIF = 0.09 ± 0.03 SE, 95% CI = 0.04 – 0.14; Figure 4b). We did not find any clear difference in mortality risk between males and females for the risk of being shot (HR = 1.51, 95% CI = 0.81 – 2.81, z = 1.28, P = 0.20) or dying of natural causes (HR = 1.60, 95% CI = 0.53 – 4.82, z = 0.83, P = 0.41).

Finally, we estimated smoothed instantaneous mortality risk for natural and harvest mortalities combined (total), harvest mortalities only and natural mortality only (Figure 4c). In general, the mortality risk was highest in September and October, coinciding with the first few weeks of the hunting season (10 September to 28 February). During winter and early spring mortality risk was very low, but increased slowly and gradually until mid-June, yielding another peak in mortality risk. The risk of harvest mortality is mainly relevant in the autumn, and the spring peak in mortality risk is driven exclusively by natural mortality factors.

Discussion

Survival

In our study area we estimated annual survival to be 0.43 ± 0.04 SE, with no discernible distinction between years. This annual survival probability is comparable to previous studies from other localities in Norway (Figure 5; Sandercock *et al.* 2011) and North America (Martin, Hannon & Rockwell 1989; Sandercock, Martin & Hannon 2005). Annual survival in our study area was lower than the estimates by Sandercock *et al.* (2011) for annual survival in non-harvested areas (0.54, 95% CI = 0.38 – 0.70) and areas with experimental treatments of 15% harvest (0.47, 95% CI = 0.35 – 0.59), as well as the estimate in Smith and Willebrand (1999) for non-harvested areas (0.53, 95% CI = 0.40 – 0.67). However, the survival probability found in our study area was higher than those reported under 30% experimental harvest in central Norway (Sandercock *et al.* 2011; 0.30, 95% CI = 0.20 – 0.40) and under harvest in central Sweden (Smith & Willebrand 1999; 0.28, 95% CI = 0.18 – 0.38, Figure 5). This gives some insight into the importance of harvest intensity on annual survival for willow ptarmigan in Scandinavia. We did not find any clear difference in annual survival between males and females. This might be the result of counteracting seasonal effects, as suggested by (Hannon, Gruys & Schieck 2003); in general we found that males tended towards lower survival (although not statistically significant) than females in autumn, while females had substantially lower survival than males during summer.

In winter and spring, survival was generally high, and there were no clear signs of sex differences in survival. However, juvenile birds had much lower survival in spring than adult birds. Willow ptarmigan vigorously defend their established territories from any intruders, including juveniles (Pedersen, Steen & Andersen 1983; Rørvik, Pedersen & Steen 1998; Eason & Hannon 2003). We expect that inexperienced yearlings trying to acquire a territory may be less alert to predators during this time, and may therefore suffer greater mortality risk than adults. This difference might arise due to differential predation pressure, and Barichello and Mossop (2011) suggested that gyrfalcon exerts higher predation pressure on young ptarmigan compared to adults. Such a preference would indicate that juveniles are easier prey than adult birds and could explain the lower survival of juveniles in spring found in this study. Inexperience may also affect the foraging ability of young birds during winter-spring, resulting in poor spring body condition (Wiebe & Martin 1998).

We also found a distinct difference in survival between males and females during summer, with female willow ptarmigan having markedly lower survival compared to males. Hannon, Gruys and Schieck (2003) suggest that female willow ptarmigan are more prone to predation in the breeding season than males as a result of their great parental investment. This investment includes the process of egg laying and incubation, as well as any clutch defense behavior towards predators (Martin & Horn 1993). Both male and female willow ptarmigan defend the nest from predators, although males for the most part indirectly defend the nest by defending their female partner (Martin 1984; Martin & Horn 1993). The higher survival of males during summer suggest that they do not invest as much in the nest and are therefore in better condition than females during this time, allowing them to more effectively avoid predation.

There was no significant distinction in autumn survival between male and female willow ptarmigan, but our results did provide some indications that females have higher survival during autumn. Because our sample size in autumn is lower than in the other seasons resulting from mortalities between winter tagging and autumn, the power to detect any trend is also lower in autumn compared to the other seasons.

Cause-specific mortality risk

In our study, we found that natural mortality risk varied throughout the year, revealing a minor peak in late September and a major peak in mid-June. Sandercock *et al.* (2011) found a very similar pattern, although they reported an autumn peak that was more distinct and a summer peak that occurred somewhat earlier than mid-May. In our study, the summer peak in natural mortality risk (Figure 4c) coincided with late incubation or hatching stage, a period which has previously been associated with high mortality risk (Winder *et al.* 2014; Winder *et al.* 2016). The reason for this heterogeneity between the studies is of yet unknown. Differences in climate between the two locations could explain the observed distinctions, with the Lierne study area being located both further north and further inland than Meråker-Selbu, which may cause the breeding dates of willow ptarmigan and/or predators to differ between the two areas. The distance and distinct climates between Lierne and Meråker-Selbu means that there could also be spatial differences in the predator communities of the two areas as well, yielding differing mortality risk patterns. Moreover, our data was collected approximately 20 years later than the data analyzed by Sandercock *et al.* (2011), which means that temporal changes to the predator community is also a potential explanation for the observed differences.

As expected, the vast majority of harvest mortalities occurred during the first weeks of the autumn hunting season, and the annual patterns in harvest mortality risk were mostly driven by these weeks. The estimated autumn harvest mortality risk (0.24 ± 0.04 SE) was identical to the estimate of hunting mortality in autumn in central Sweden (Smith & Willebrand 1999). It is important to note that the core areas in our study (Gusvatnet and Lifjellet) are easily accessible, and areas close to infrastructure are often associated with higher hunting effort compared to more remote locations (Brøseth & Pedersen 2000; Breisjøberget *et al.* 2018).

We found no significant autumnal difference between the sexes for either natural mortality risk or harvest mortality risk. Asmyhr, Willebrand and Hörnell-Willebrand (2012) were also unable to find an effect of sex on harvest risk in a harvested area in central Sweden. Interestingly, Sandercock *et al.* (2011) showed that females were more at risk of harvest mortality under experimental harvest. In their experiment hunters mostly used pointing dogs during the hunt (Sandercock *et al.* 2011), while our study area had a mix of hunters with and without dogs (Nils Vidar Bratlandsmo, pers. comm., 08.04.2020). Male and female willow ptarmigan are to different degrees following the brood during the autumn hunting season, and this may affect the susceptibility for being shot (Bunnefeld *et al.* 2009). We speculate whether this grouping behavior may have different effects on harvest with or without dogs. As using a hunting dog usually gives the hunter more time to prepare before firing in each situation, it is likely that hunters may have time to shoot more individuals from large coveys of ptarmigan than if hunting without a dog. Since females are more prone to grouping, this might imply that more females may be shot when hunting with dogs than without, which would give a possible reason for the observed differences between our study and Sandercock *et al.* (2011).

Harvest management

In our study area the willow ptarmigan harvest mortality risk was substantially higher than what is generally considered to be compensatory (Sandercock *et al.* 2011). Moreover, there seem to be a clear connection between harvest rate and willow ptarmigan survival, where willow ptarmigan in non-harvested areas have higher survival (Figure 5). It is therefore important to implement a harvest strategies that can reduce risks of overharvest. Threshold harvest strategies have often been proposed as a way to counterbalance risk of harvest, especially when the exploited population occur at low densities (Eriksen, Moa & Nilsen 2018), as it only permits harvest above a certain population threshold (Lande, Sæther & Engen 1997). Although, it does imply no harvest in the years where the population size is below this threshold (Lande, Sæther & Engen 1997).

Conclusion

The high temporal resolution of this study allowed us to accurately estimate willow ptarmigan annual and seasonal survival, as well as cause-specific mortality risks. Our results provide insights into the relative importance of harvest and natural mortality for overall survival probability. By identifying demographic differences in mortality risk throughout the year, our results are applicable for highlighting areas where conservationists or small game area managers should focus their efforts.

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Conflict of interest

None declared.

Author contributions

M. F. Israelsen conducted the data analysis, supervised by E. B. Nilsen. E.B. Nilsen conveyed the main research question. All authors contributed to the data acquisition, data interpretation and preparation of the manuscript. All authors approved the submitted version of the manuscript.

Data availability statement

Temporary location of raw data used in the analyses: https://github.com/markusfisra/WillowPtarmiganSurvival/blob/master/rawdataAnalysis.csv

Temporary location of scripts developed to conduct analyses and produce figure illustrations: https://github.com/markusfisra/WillowPtarmiganSurvival/blob/master/Willow%20ptarmigan%20survival.Rmd

Upon acceptance, both data and analysis scripts will be archived in a stable repository with a citable DOI.

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Table 1. Number of radio tagged birds and mortalities for each calendar year of the study. Also shown is the total number of birds used in the analysis and the number of these that died or survived until the end of the study.

Year	**2015**	**2016**	**2017**	**2018**	**2019**	**Total**	**Total in analysis**	**Prop. Mort.**	**Prop. Surv.**
Tagged birds	32	38	40	38	40	188	182	(124 / 182)	(58 / 182)
Mortalities	19	21	34	30	20	124	124	0.68	0.32

Figure captions

Figure 1. Study area (outlined box) showing all marking locations (red triangles) and telemetry positions (blue dots) of the marked birds. The northern cluster of red triangles represent the Lifjellet location and the southern cluster Gusvatnet.

Figure 2. (a) Survival of willow ptarmigan 1 August – 31 July (vertical lines represents censoring events). (b) Annual survival for each sex and (c) annual survival for complete willow ptarmigan years.

Figure 3. Seasonal survival in (a) autumn for males and females, (b) spring for juvenile and adults and (c) summer for males and females. Vertical lines represent censoring events. Note that the probabilities on the y-axis ranges from 0.5 to 1.

Figure 4. (a) Annual mortality probability due to natural causes and harvest. (b) Autumn mortality probability due to natural causes and harvest. Note that the range of probabilities on the y-axis goes from 0 to 0.40 for (a) and (b). (c) Smoothed instantaneous hazard function showing daily hazard risk for total, harvest and natural mortality.

Figure 5. Annual survival estimates for this study (Lierne 2015-2019, harvested area, in orange) in comparison to what was found in Sandercock *et al.* (2011; Meråker-Selbu in central Norway, non-harvested area, 15% and 30% harvest rate) and Smith and Willebrand (1999; central Sweden harvested area and central Sweden non-harvested area).

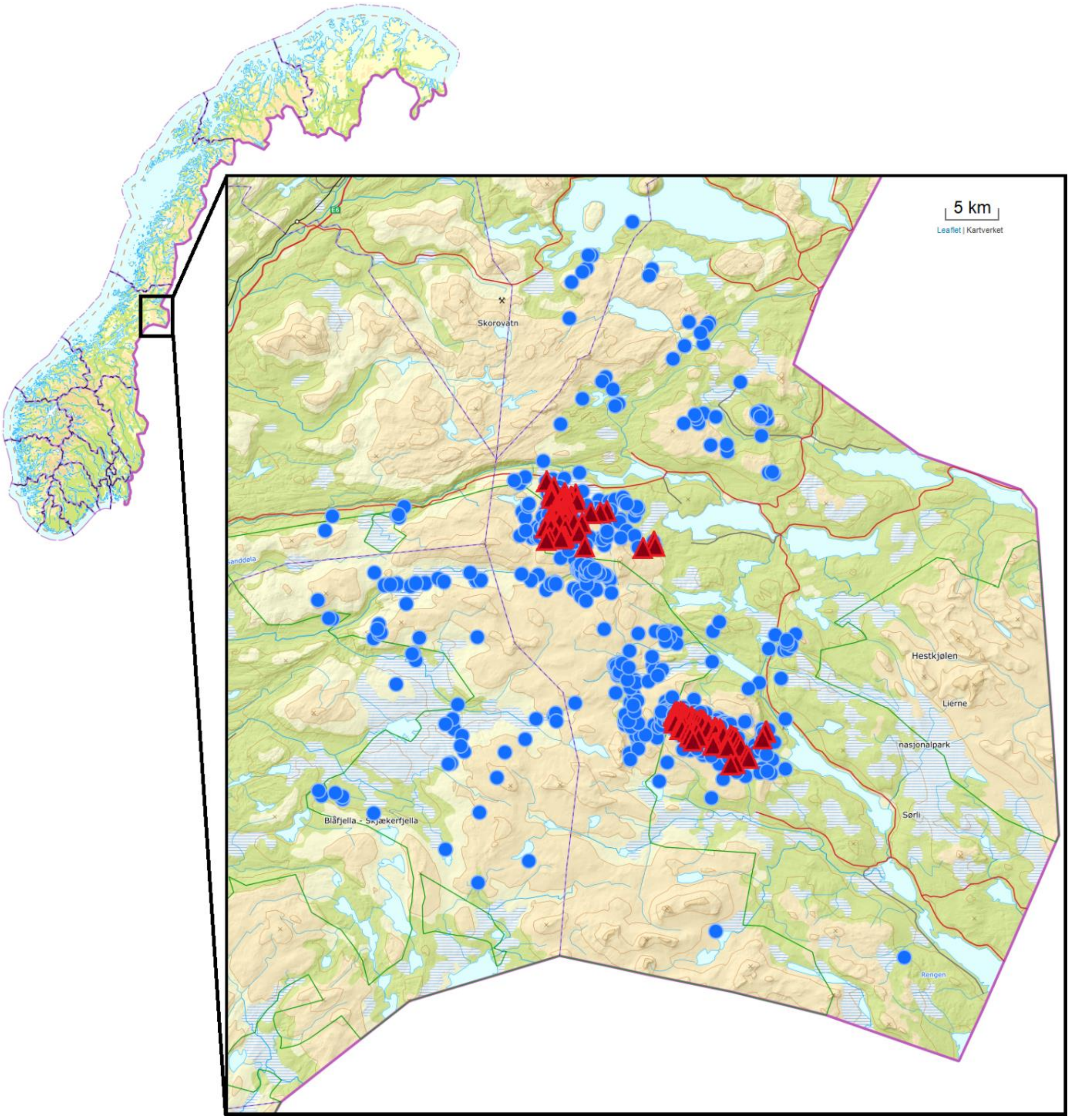

5 km
Leaflet | Kartverket
Skorovatn
Hestkjølen
Lierne
nasjonalpark
Sørli
Blåfjella - Skjækerfjella
Rengen

Figure 1

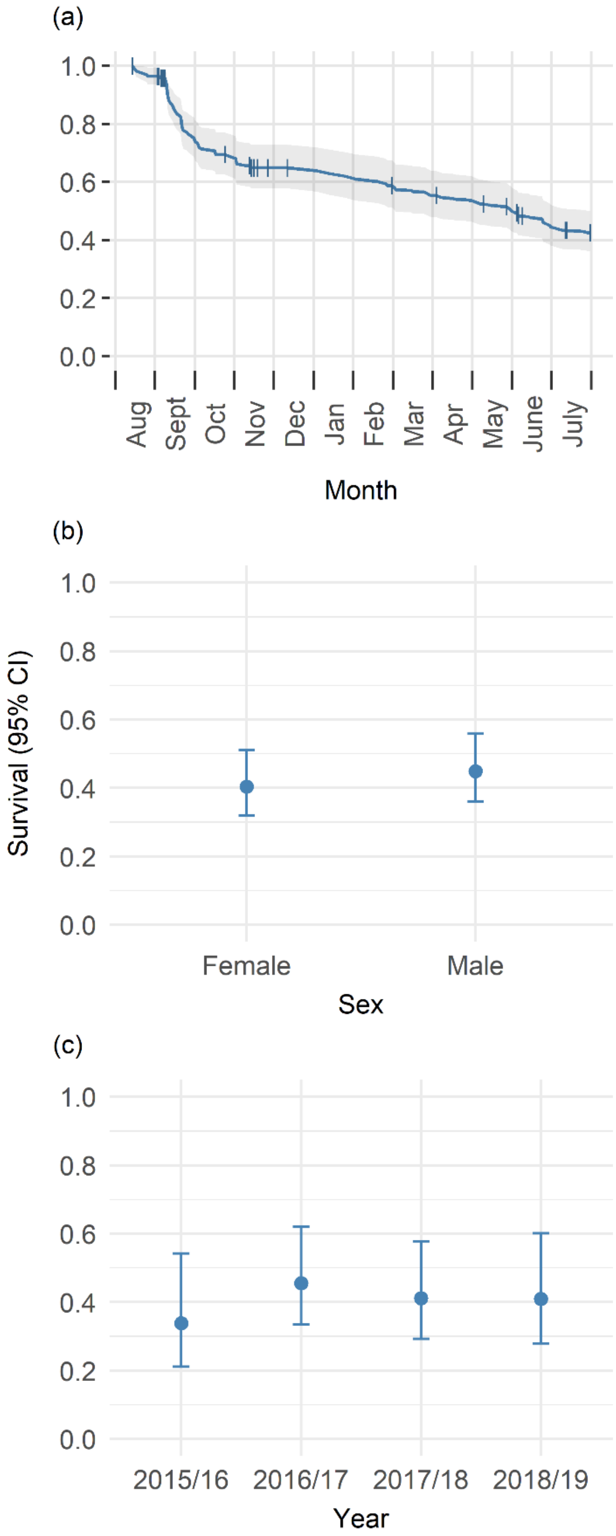
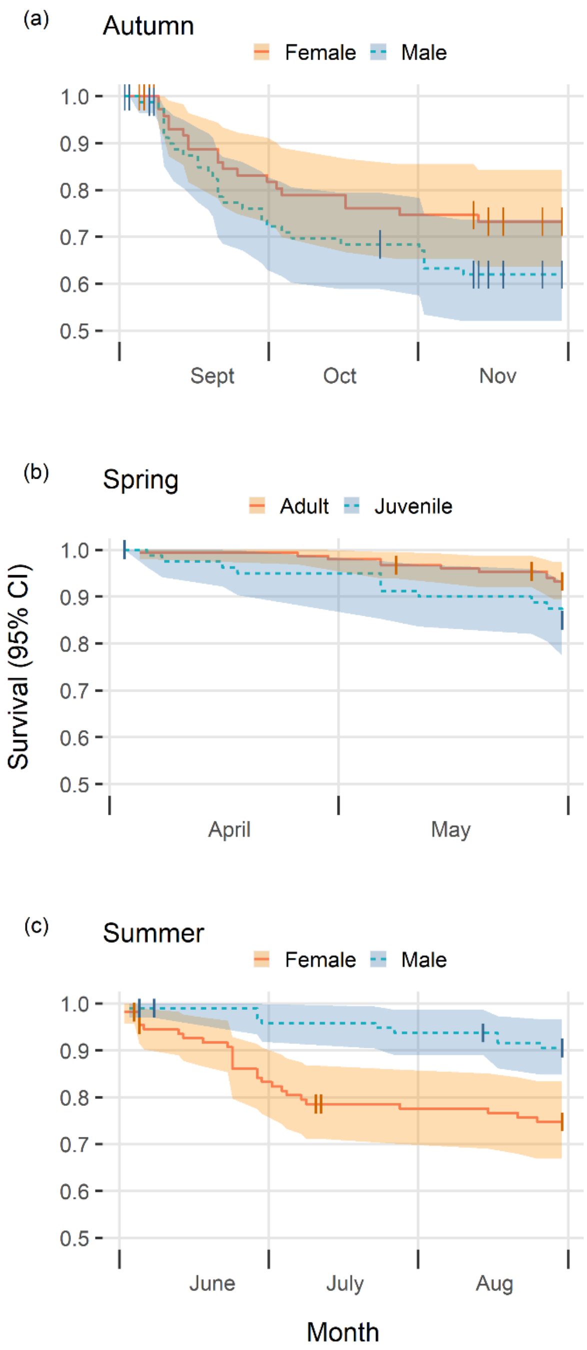

(a)
1.0
0.8
0.6
0.4
0.2
0.0
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
June
July
Month
(b)
Survival (95% CI)
1.0
0.8
0.6
0.4
0.2
0.0
Female
Male
Sex
(c)
1.0
0.8
0.6
0.4
0.2
0.0
2015/16
2016/17
2017/18
2018/19
Year

Figure 2

635



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637

638 **Figure 3**

639

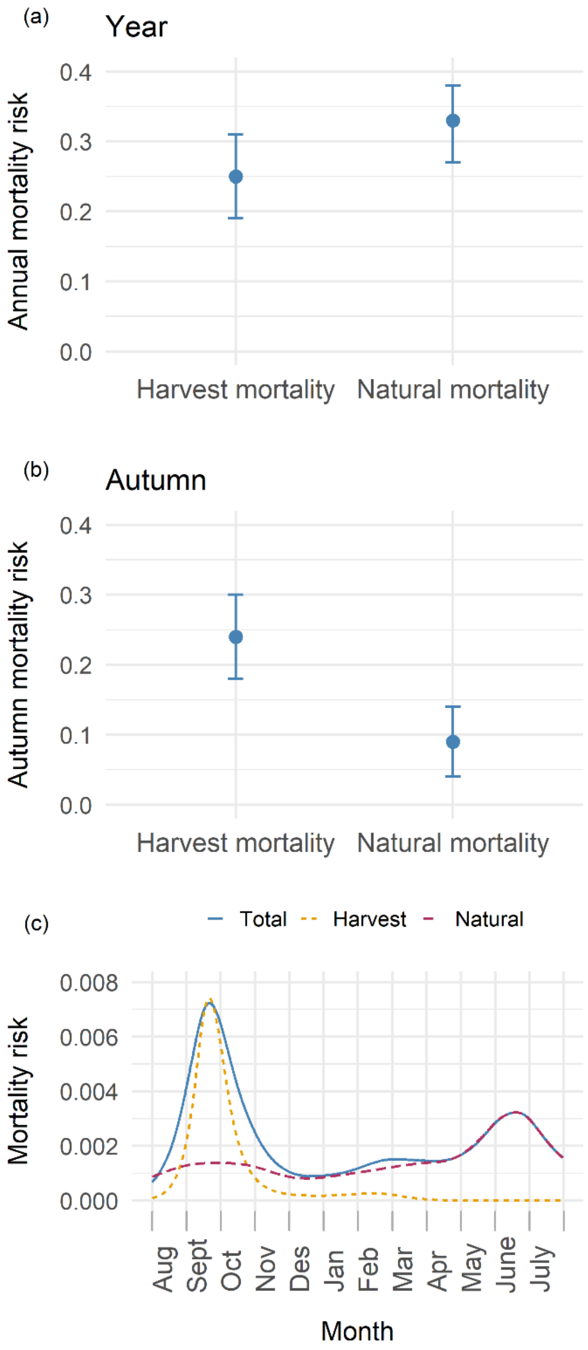
(a)
Year
Annual mortality risk
0.4
0.3
0.2
0.1
0.0
Harvest mortality
Natural mortality
(b)
Autumn
Autumn mortality risk
0.4
0.3
0.2
0.1
0.0
Harvest mortality
Natural mortality
(c)
Total
Harvest
Natural
Mortality risk
0.008
0.006
0.004
0.002
0.000
Aug
Sept
Oct
Nov
Des
Jan
Feb
Mar
Apr
May
June
July
Month

Figure 4

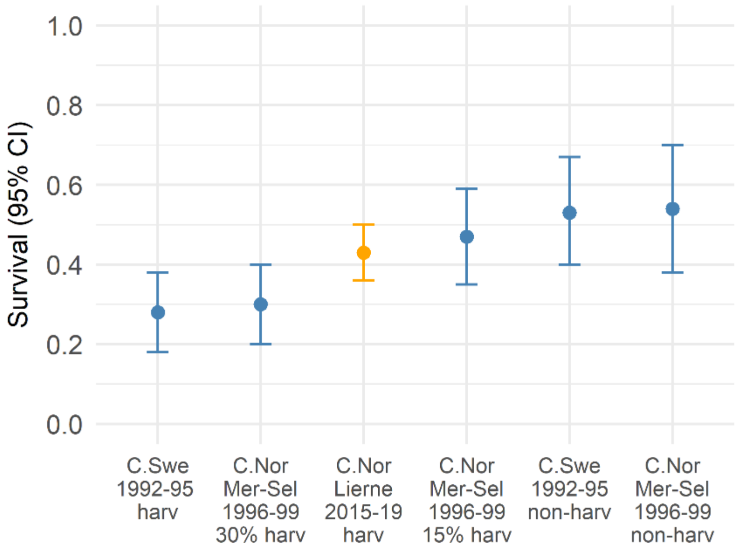
Survival (95% CI)
1.0
0.8
0.6
0.4
0.2
0.0
C.Swe 1992-95 harv
C.Nor Mer-Sel 1996-99 30% harv
C.Nor Lierne 2015-19 harv
C.Nor Mer-Sel 1996-99 15% harv
C.Swe 1992-95 non-harv
C.Nor Mer-Sel 1996-99 non-harv

Figure 5