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Demographic determinants of population growth rate in willow ptarmigan (*Lagopus lagopus*) in Lierne, central Norway

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Abstract

Willow ptarmigan (*Lagopus lagopus*) populations in Norway have declined during the last decade and the species was included in the Norwegian Red list in 2015 as “near threatened”. Accordingly, it is important to identify the drivers of the population decline, which possibly may lead to management mitigations that may increase the viability of the population. This 3-year study presents insight into both recruitment rate and survival rate, and identifies the demographic determinants of the population growth rate (λ) in a willow ptarmigan population in Lierne, central Norway. Radio-telemetry was used to estimate adult survival and cause-specific mortality probabilities, and camera traps on nests were used to estimate breeding success. In addition, line transect surveys was applied to estimate population densities and brood size in autumn. The combined use of these data presents a novel method providing vital estimates on all steps of the life cycle. A stage-structured projection matrix was constructed to calculate sensitivities and elasticities of λ to the demographic parameters. As expected for a fast-living species, the willow ptarmigan population exhibited high reproductive potential and low adult survival. All hatching failures were due to predation. The adult mortality rate was highly influenced by predation and harvest, and the estimated probability of mortality owing to predation and harvest was 0.40 and 0.28, respectively. Juvenile survival during summer and autumn, and hatch probability were identified to have potentially largest impact on λ . Further, the elasticity of λ to recruitment was higher than to adult survival. The observed population growth was positive ($\lambda = 1.20$) and might be explained by immigrating individuals rather than the demography of the population. Based on the elasticity analysis and the estimated harvest rate, this study suggests that management actions including a reduction in the harvest rate would have a substantial positive effect on λ .

Sammendrag

Lirypepopulasjoner i Norge har hatt en nedgang i løpet av det siste tiåret, og arten ble i 2015 oppført i norsk Rødliste under kategorien “nær truet”. Av den grunn er det viktig å identifisere hvilke faktorer som driver populasjonsnedgangen, som kanskje kan føre til forvaltningstiltak som kan øke levedyktigheten til populasjonen. Denne 3-årige studien presenterer innblikk i både rekruttering og overlevelse, og identifiserer de demografiske determinantene til populasjonsvekstraten (λ) i en lirypepopulasjon i Lierne, Midt-Norge. Radiotelemetri ble brukt til å estimere voksenoverlevelse og årsaksbestemte mortalitetssannsynligheter, og viltkamera som ble satt opp på reir ble brukt til å estimere hekkesuksess. I tillegg ble linjetakseringer brukt til å estimere populasjonstettheter og kullstørrelse om høsten. Den kombinerte bruken av disse dataene presenterer en ny metode som gir data på alle steg i livssyklusen. En projeksjonsmatrise, som ble satt sammen basert på aldersklasser, ble konstruert for å kalkulere vekstratens sensitivitet og elastisitet til de demografiske parameterne. Som forventet for en kort-levd art hadde lirypepopulasjonen stort reproduksjonspotensial og lav voksenoverlevelse. Alle egg som ikke klekket skyldtes predasjon. Mortalitetsraten hos voksne individer var svært påvirket av predasjon og jakt, og de estimerte sannsynlighetene for mortalitet forårsaket av predasjon og jakt var henholdsvis 0.40 og 0.28. Juvenil overlevelse gjennom sommer og høst, og klekke-sannsynlighet, ble estimert til å ha størst potensiell innvirkning på λ . Videre hadde λ høyere elastisitet til endringer i rekruttering enn til voksenoverlevelse. Den observerte populasjonsveksten var positiv ($\lambda = 1.20$) og kan mulig forklares av immigrerende individer heller enn demografien i populasjonen. Basert på elastisitetsanalysen og estimatet av høstingsraten, foreslår denne studien at forvaltningstiltak som innebærer en reduksjon i høstingsrate vil kunne ha en vesentlig positiv effekt på λ .

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Introduction

During the last decades, an increasing proportion of populations, across taxa, are have been declining (McRae et al., 2017; WWF, 2016). Among birds, BirdLife International (2018b) reported that 13% of all bird species are currently threatened by extinction. The major causes of decline are related to anthropogenic factors, such as overharvesting, habitat change, negative effects of invasive species and climate change (CBD, 2006; Newton & Brockie, 2003; Owens & Bennett, 2000).

Because fluctuations in the population growth rate (λ) are caused by variation in demographic rates of the population (Fryxell et al., 2014; Sæther et al., 1999), an understanding of demographic mechanisms causing variation in λ might be needed to design robust management strategies. Variation in demographic rates are influenced both by local adaptations in life history traits, partly driven by variation in environmental conditions, density-dependence, and the interaction between these drivers (Fryxell et al., 2014; Gaillard et al., 1998; Sæther et al., 2016a). Understanding the link between current and past environmental conditions and how this influences life history traits is therefore important in order to understand how species population dynamics respond to changing environments (Oksanen et al., 2012).

Empirical studies have documented a strong pattern of covariation between the main life history traits in birds (Gaillard et al., 1989; Sæther et al., 1996; Sæther & Bakke, 2000) and mammals (Gaillard et al., 1989; Oli, 2004), sorting species along a “fast-slow continuum” of life history strategies. The placement is influenced by eco-evolutionary adaptations to varying density-dependence, responses to mortality rates, and adaptations to environmental variability (Benton & Grant, 1999b; Nilsen et al., 2009; Reznick et al., 2002; Ricklefs, 2000; Sæther et al., 2002). Species at the fast end of the continuum typically mature early, have a high reproductive output and a short life span (also called *r*-selected species; Sæther & Bakke, 2000), whereas species at the slow end of the continuum mature late, have a small reproductive output and a long life span (also called *K*-selected species; Oli, 2004). These characteristics result in short and long generation time, respectively (Gaillard et al., 2005; Sæther et al., 2004). Despite a debate of the relevance of the *r*- and *K*-selection categorization (Reznick et al., 2002; Stearns, 1977; Sæther et al., 2016b), it can be a useful concept to consider when evaluating the ability of a population to persist when faced with human-induced perturbations, in particular (Heard et al., 2012). The response of λ to changes in the vital rates depends on the sensitivity and elasticity of λ to the

rates, and a pattern of increasing elasticity of λ to changes in reproductive parameters with decreasing rate of adult survival has been found in both birds (Sæther & Bakke, 2000) and mammals (Gaillard & Yoccoz, 2003; Oli, 2004). Evaluating the magnitude of the sensitivities is important in wildlife management (De Kroon et al., 2000; Manlik et al., 2018). For instance in a population of New Zealand sea lions (*Phocarcetos hookeri*), λ was most sensitive to changes in fecundity, suggesting that management effort should target this rate (Meyer et al., 2015).

The actual contribution from a vital rate on observed variability in λ is determined by the combined effect of the sensitivity and the variability of a rate (Manlik et al., 2018; Sæther & Bakke, 2000), and previous studies have observed a negative correlation between these two traits (Gaillard & Yoccoz, 2003; Sæther & Bakke, 2000). It has been hypothesized that evolution through natural selection has favoured individuals that exhibit less variation in vital rates which λ is most sensitive to (i.e. the "buffering hypothesis"; Pfister, 1998), because large variation in demographic rates generally decreases long-term λ (Lande, 1993; Pimm, 1991), and observed life histories can partially be explained by adaptations to specific environments (Nilsen et al., 2009; Reznick et al., 2001). However, other studies have revealed that when the statistical variance constraints on vital rates were accounted for, the relationship between sensitivity and variance appeared as equivocal in red-tailed tropicbird (*Phaethon rubricauda*; Doherty et al., 2004) and non-existing in Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Bjorkvoll et al., 2016).

Populations of species on the fast end of the fast-slow continuum typically have high mortality rates, and several previous studies have pointed to the important limiting role of top-down factors, such as predation (Ekanayake et al., 2015; Sinclair et al., 2003) and harvest (Rolland et al., 2010). The impact from predation and harvest on populations is additive if the mortality caused by these factors adds to losses due to other natural causes, whereas the impact is compensatory if an enhancement in survival or other vital rates compensate for losses due to predation or harvest (Lebreton, 2005; Mills, 2012). Previous studies have found that compensation is more likely at low harvest rates, for species with high elasticity of λ to adult survival, and at high density due to negative density-dependence (Peron, 2013). Previous meta-analyses have provided evidence for both additive (Salo et al., 2010) and compensatory (Forrester & Wittmer, 2013) effects of predation on natural populations of prey. The strength of the interactions between top-down factors (i.e. predation and harvesting) and density-dependence also varies with the dynamics of alternative prey species (Korpimaki et al., 2005; Kvasnes et al., 2014b). As predicted by the alternative prey hypothesis, the impact from

predation by red fox (*Vulpes vulpes*) on roe deer fawn (*Capreolus capreolus*) was demonstrated to depend on the density of two vole species, as red fox switched its diet from roe deer fawns to vole in years of high vole densities (Kjellander & Nordström, 2003).

Here, I report on the results of a study designed to investigate the complete life cycle of willow ptarmigan (*Lagopus lagopus*), and the impacts of predation and harvest on the demography of this species. Willow ptarmigan is a popular game bird in Norway with ca. 118 000 individuals harvested in 2016-17 (data from www.ssb.no). Willow ptarmigan therefore has both economic and social importance (Brøseth & Pedersen, 2010). In 2015, willow ptarmigan was included in the Norwegian Red list categorized as “near threatened” (NT) due to a 15-30% reduction in the population size during the last 10 years. The negative trend in population size combined with the harvesting regime has raised concern about whether the current management regime is sustainable (Eriksen et al., 2018). Willow ptarmigan is a fast-living species with a high reproductive output (Sandercock et al., 2005b). Empirical knowledge predicts, and previous studies have demonstrated, that λ is most sensitive to changes in the fecundity rate and is thus the main driver of long-term fluctuations in willow ptarmigan populations (Sandercock et al., 2005a; Steen & Erikstad, 1996; Sæther & Bakke, 2000). Further, predation and harvest have been demonstrated as the main sources of mortality in willow ptarmigan population (Sandercock et al., 2011; Smith & Willebrand, 1999), whereas other factors, such as food availability or diseases, appear to be less important (Hannon & Martin, 2006). Thus, it is expected that top-down effects from predation and harvest are the main environmental factors affecting the demographic rates of willow ptarmigan populations. However, the effect of predation and harvest on survival and recruitment of willow ptarmigan, and the sensitivity of λ to changes in these parameters, have to my knowledge never been studied based on direct field observations of the different demographic parameters.

The aim of this study was to quantify the effect of environmental and demographic factors on the dynamics of a willow ptarmigan population in Lierne, central Norway, using stage-structured population matrix models (Caswell, 2001). Three objectives were defined in order to accomplish this: (1) estimate the vital rates of the study population, (2) calculate the sensitivities and elasticities of these vital rates to λ , and (3) quantify the impact of harvest on adult survival rate by estimating cause-specific mortality probabilities. I expected that the population would show vital rates in accordance with a fast life history strategy (i.e. large reproductive output, early maturation and short life span expectancy), and that λ would be most sensitive to changes in the recruitment rate.

Methods

Study species

Willow ptarmigan has a circumpolar distribution in the subalpine zone, from the British Isles, through the northern part of Eurasia, and in North America (BirdLife International, 2018a). In Norway, willow ptarmigans are observed all over the country in the subalpine zone (Kvasnes & Nilsen, 2017). Willow ptarmigan occupy areas associated with mountainous birch (*Betula pubescens ssp. czerepanovii*) forests and willow (*Salix spp.*) species (Pedersen et al., 2013) and prefer habitats that comprises both food availability and cover from predators (Kvasnes et al., 2014a). With the exception of the first few weeks when the chicks feed on insects, willow ptarmigans are herbivorous birds. Buds and shoots of willow, reproductive parts of birch and exposed ericaceous plants (e.g. *Vaccinium sp.*) are the main food source during winter, whereas ericaceous plants and alpine bistort (*Bistorta vivipara*) are preferred during summer and autumn (Steen & Ree, 1989). The natural mammalian predators of willow ptarmigan in the region were red fox, pine marten (*Martes martes*) and stoat (*Mustela erminea*). Further, the main avian predators were hooded crow (*Corvus cornix*) and raptors such as golden eagle (*Aquila chrysaetos*), gyrfalcon (*Falco rusticolus*) and hen harrier (*Circus cyaneus*).

The willow ptarmigan is mainly a sedentary species (Pedersen & Karlsen, 2007), with juveniles staying close to their natal territories until they start natal dispersal movements in early October (Sandercock et al., 2011). Typically, males start to occupy territories for next breeding season right after the juveniles have dispersed, although there is variation between populations in the onset of territoriality (Brøseth et al., 2005). Adults are generally sedentary year-round, and most adult birds disperse less than 1 km from one year to the next (Brøseth et al., 2005; Pedersen et al., 2013). The breeding season begins with a period of territorial activity in mid-March and continues with nesting and brood-rearing from mid-May to mid-August (Sandercock et al., 2011).

Study area

The study was conducted on two localities in Lierne municipality, Trøndelag county, in the borderline of Blåfjella-Skjækerfjella national park (Fig. 1). The study area is categorized as a subalpine zone. The soil conditions in the area are poor (Hofton & Blindheim, 2007), and the vegetation is dominated by birch, ericaceous plants (*Ericaceae spp.*) and pine (*Pinus sylvestris*).

Large areas are also covered by open mires. During the last climatological normal period (1961-1990), the average climatic conditions in the study area comprised an annual temperature of 0 °C, 920 mm precipitation annually, and an average June temperature of 7 °C.

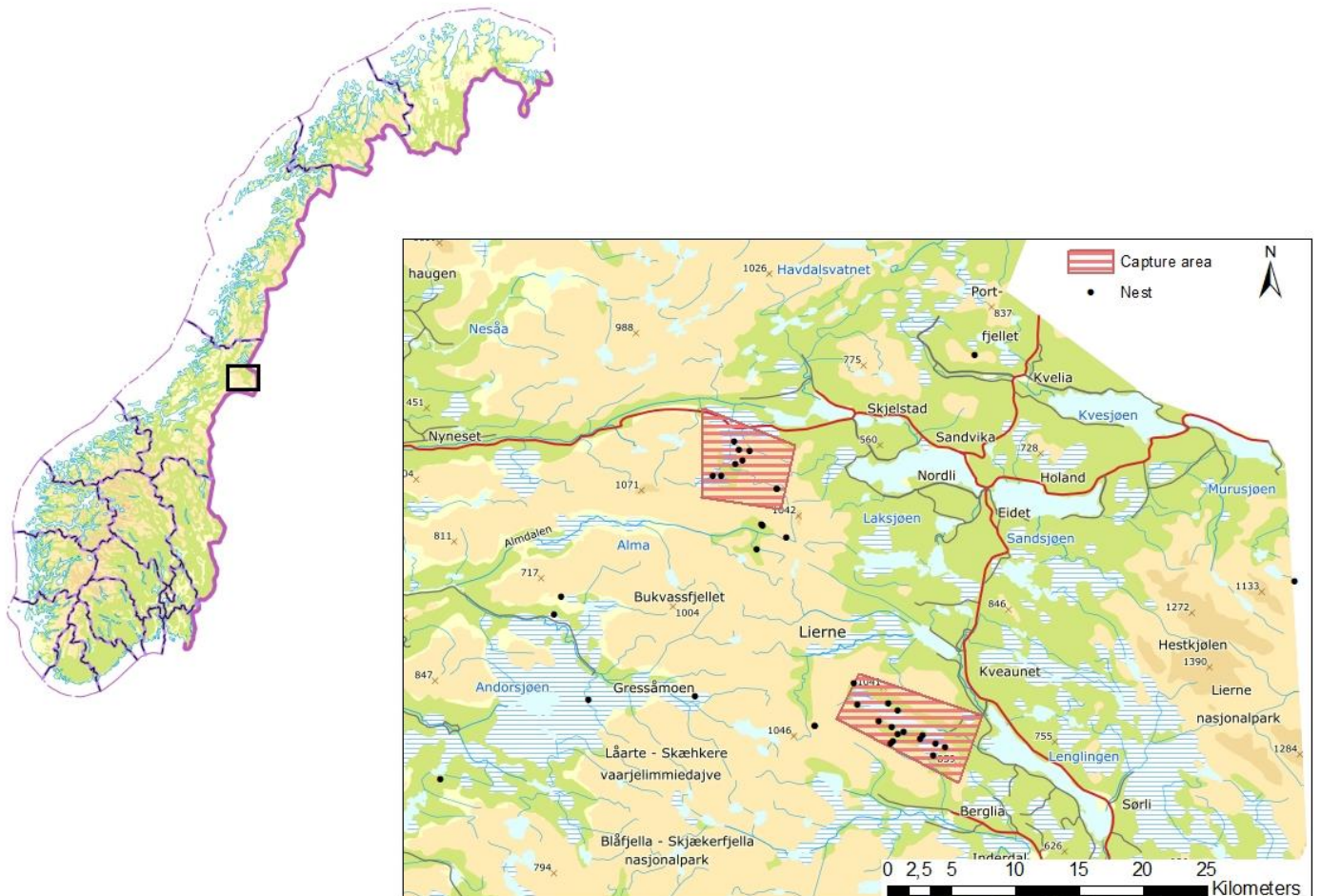


Fig 1. Map of study area indicating the capture areas (red-striped polygons) and the nests (black dots) monitored during the period 2015-17.

Data collection

During the 3-year study period, starting in February 2015, three cohorts of willow ptarmigan were captured. Each cohort consisted of 30-40 individuals, with an intentional equal sex ratio (50:50), whereas no such consideration was made in relation to age, assuming that the age distribution of the sample represented the standing population (Table 1). The total number of individuals that was marked within the study areas during the 3-year study was $n = 110$ (Table 1). Individuals that survived for more than 1 year, were included in the cohort of next year.

Thus, the sample size of 2016 and 2017 comprised 49 and 59 bird-years, respectively, adding up to a total sample size of $n = 138$ bird-years during the 3-year study period.

Table 1. Distribution of age (juvenile <12 months, adult >12 months) and sex (female, male) of the individuals that were radio-tagged each year (2015-17). The total number of radio-tagged birds during the 3-year study was 110. Individuals that survived for more than 1 year, were included in the sample size next year. Thus, the sample size in 2016 and 2017 were 49 and 59 bird-years, respectively, adding up to a total sample size of 138 bird-years during the 3-year study. The sex of 1 radio-tagged juvenile could not be determined in 2016. Total sample size of monitored nests during the study period was 36.

Year	Radio-telemetry				Nest monitoring
	Adult female	Juvenile female	Adult male	Juvenile male	Nests
2015	11	8	8	3	11
2016	8	12	9	10	16
2017	9	9	15	7	9

Capture was conducted during night time in February and March each year. Willow ptarmigan were detected from snowmobiles, using spotlights. When observed by the bright light, the birds were partially paralyzed and could be captured using long-handled dip nets (Brøseth & Pedersen, 2010; Sandercock et al., 2011). The birds were sexed and aged as juveniles (<12 months) or adults (>12 months) at site, based on plumage coloration, size, and patterns of pigmentation in the outer primaries. In cases where the sex of the birds could not be confirmed in the field, a DNA test of a feather sample was used to confirm the sex. Each individual was equipped with a necklace radio-transmitter and a leg ring, with a unique frequency and identification number, respectively. The radio-transmitter has an expected battery time of 24 months and a weight of 15 grams (Holohil R1-2B) which in all cases constituted less than 4% of the body weight of the bird. When the transmitter registered 12 hours of inactivity, a mortality signal was sent. Using radio-transmitters on ptarmigan in survival analyses is a well-established method (Martin & Wiebe, 2004; Novoa et al., 2011; Sandercock et al., 2011; Smith & Willebrand, 1999), and the transmitter have been demonstrated to have little to no effect on the survival or reproduction rate (Cotter & Gratto, 1995; Thirgood et al., 1995).

Status and approximate location of the radio-marked willow ptarmigan were checked approximately once a month through most of the year, but more frequently in the period March to October. During winter, snow- and weather conditions occasionally restricted the access to

the study area and monitoring was therefore more challenging. Monitoring was performed by ground-based radio-tracking combined with quarterly radio-tracking from small aircrafts or helicopters. When mortality signal was detected, the transmitter was retrieved from the field as fast as possible to determine the cause of death based on the carcass and associated signs at the kill place (Sandercock et al., 2011). In many cases few or unclear signs were found, and cause of death could not be determined. Hunters were informed to report it if a radio-marked willow ptarmigan was shot.

In early June each year, when females had just started to lay eggs, the radio-marked females were located using radio-triangulation. The females were flushed on a close distance so that the camouflaged nests could be found. Camera traps (Wingcam II TL, Winge våpen, Norway) to monitor breeding success were set up approximately 1.5 meters from the nests, positioned to minimize predator or human attraction (Ekanayake et al., 2015). Photos were taken every time the motion sensor in the camera was activated. After the breeding season, all photos were analysed to gather information on number of eggs, hatching success, predation of eggs, predation or disappearance of the female, and type of predator. In addition, because the nests were not found by chance, the breeding proportion of females could also be estimated. During the study, a total of $n = 36$ camera traps were installed close by the nests of $n = 32$ different females. Four females were monitored over two breeding seasons.

In addition to the individual based data described above, in August each year population densities were estimated in the study area using distance sampling method from line transect surveys (Buckland et al., 1993). Volunteer personnel used trained pointing dogs to search both sides of specific transect lines. Lines were systematically distributed in advance of the survey, to represent the habitat of the area, with a minimum of 500 meters distance between each line. When willow ptarmigan were observed, cluster size and distance to the observation were recorded by the observer, in addition to sex and age (juvenile or adult) of each individual.

All capturing and handling of willow ptarmigan during the study was approved by the Norwegian Food Safety Authority. Use of snowmobiles in association to the capture was approved by the authorities.

Demographic models

Demographic parameters:

Seven demographic parameters were defined to cover the complete life cycle of the willow ptarmigan, including reproduction in the spring and survival throughout the study year. These parameters were mainly defined to reflect the biology of willow ptarmigan. However, two of the parameters associated to juvenile survival were partially defined to fit the available data. The seven demographic parameters were:

Breeding proportion (BP) was defined as the proportion of females producing eggs in year t .

Clutch size (CS) was defined as the total number of eggs, observed by camera traps on nests of radio-marked females, at the beginning of the incubation period. Renesting events were not always detected, and clutches that were assumed to be renests were excluded.

Proportion hatch (PH) was defined as the observed proportion of clutches that hatched successfully, given that the female had produced eggs. The estimation was based on data from camera traps on nests of radio-marked females, and a clutch was considered successful if at least one egg hatched and produced a chick.

Juvenile summer survival (JS) was defined as the probability of a chick to survive from hatching until the first half of August. The estimation was based on a combination of data from camera traps on nests of radio-marked females and line transect surveys.

Early juvenile winter survival (EJWS) was defined as the probability of survival from early August to 1st of March for juveniles produced in the summer the same year. Estimates were based on combining data from population density estimates and estimates of the other parameters.

Late juvenile winter survival (LJWS) was defined as the probability of a radio-marked juvenile (<12 months of age) to survive from 1st of March to 1st of May.

Adult survival (AS) was defined as the probability of a radio-marked adult individual (>12 months of age) surviving from 1st of May in year t to 1st of May in year $t+1$.

Population model:

When constructing a population matrix model, a definition of the life cycle of the focal population is required (Caswell, 2001). Here, a pre-breeding census was used, implying that the youngest individuals in the population at census time t were 1 year old (yearlings; Fig. 2). The population was divided into two age classes (yearlings: 12-24 months of age, and adults: >24 months of age, respectively) and was assumed to have a net migration rate of zero (closed population model). Following from the pre-breeding life cycle, the recruitment rate results in

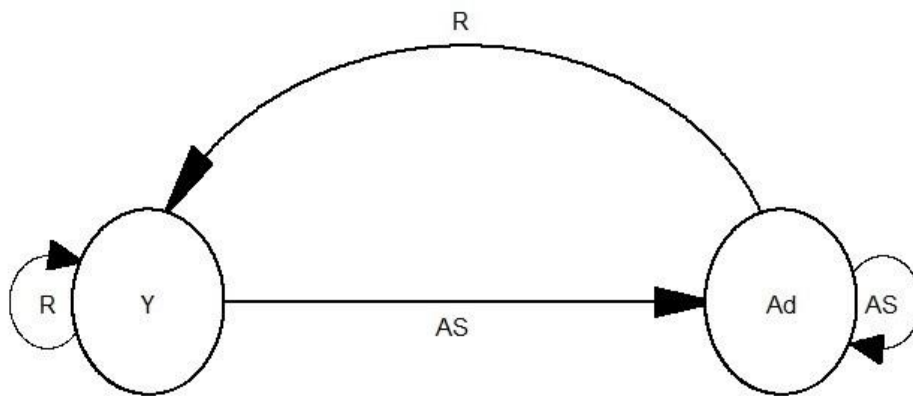


Fig. 2. Life cycle diagram for willow ptarmigan, using a pre-breeding census. The population was distributed into two age classes, yearlings (Y, 12-24 months of age) and adults (Ad, >24 months of age). Adults and yearlings produce juveniles that survive to one year of age (R). AS is the annual survival rate for yearlings and adults.

the production of a yearling bird and thus included both fecundity parameters and juvenile survival. Thus, the recruitment rate (R) was given by the product of the proportion of females breeding in year t (BP), the mean number of female eggs produced in year t (CS; clutch size divided by 2, assuming a balanced sex ratio), the proportion of eggs that successfully hatched in year t (PH), juvenile summer survival (JS), and early and late juvenile winter survival (EJWS, LJWS, respectively):

$$R = BP \times (CS \times 0.5) \times PH \times JS \times EJWS \times LJWS . \quad (1)$$

Based on the demographic parameters presented above, I constructed a stage-structured female only projection matrix with two age classes (yearlings and adults). Previous studies have shown no significant age effect in recruitment rate or survival rate in willow ptarmigan (Sandercock

et al., 2005a), and no significant difference between females and males in survival rate (Sandercock et al., 2011; Smith & Willebrand, 1999). I also tested for age- and sex effects in my data, and I did not detect any differences between first-time breeding females (yearlings) and older females (adults) in neither clutch size ($\chi^2 = 0.51, p = 0.48$) nor proportion hatch ($\chi^2 = 0.31, p = 0.58$), by fitting generalized linear models (GLMs) with a Poisson and a binomial error structure, respectively. Further, I did not detect any difference in the survival rate between females and males (HR = 1.07, CI = [0.68, 1.71], $z = 0.30, p = 0.76$), or between yearlings and adults (HR = 0.88, CI = [0.53, 1.45], $z = -0.51, p = 0.61$), using a Cox-proportional hazard model (see *Statistical analyses* below). Based on these results and previous findings, I assumed that there was no difference between yearlings and adults in recruitment rate or survival rate, and no difference between the sexes in survival rate. Thus, when constructing the projection matrix, I used the same matrix elements in both age classes, and both female and male willow ptarmigan were included in the survival parameter. The population projection matrix (\mathbf{A}) is isomorphic to the life cycle graph (Fig. 2) and is given as

$$\mathbf{A} = \begin{bmatrix} R & R \\ AS & AS \end{bmatrix} \quad (2)$$

, where R expresses the number of female offspring entering the population at time $t+1$ per female alive at the beginning of year t . AS expresses annual adult survival probability, i.e. the probability of an adult to survive from the beginning of year t to the beginning of year $t+1$.

Statistical analyses

All statistical analyses were performed using program R (version 3.4.2; R Core Team 2017), and all tests were considered significant at α -levels ≤ 0.05 . The seven demographic parameters were estimated using different estimation methods, and an overview of the abbreviations and methods are presented in Table 2.

Breeding proportion (BP) was set to a fixed value of 1, indicating that all females of age ≥ 12 months breed every year, an assumption which was supported by previous findings (Sandercock et al., 2005b) and the data in the present study.

The annual variation in clutch size (CS) was analyzed by fitting a GLM assuming a Poisson error structure (Dalgaard, 2008), with number of eggs observed as a function of study year.

The annual variation in hatch probability within nests (PH) was analyzed by fitting a GLM assuming a binomial error structure (Dalgaard, 2008), with fate of the eggs within a nest as a function of study year. I assumed that all eggs resulted in fledglings if hatching was successful, and vice versa, no eggs resulted in fledglings if hatching failed.

Table 2. Estimation methods of the different demographic parameters presented in the study: breeding proportion (BP), clutch size (CS), proportion hatch (PH), juvenile summer survival (JS), early juvenile winter survival (EJWS), late juvenile winter survival (LJWS), and adult survival (AS). See further details in *Methods*.

Demographic parameter	Definition	Estimation method
Breeding proportion (BP)	Proportion of breeding females	Fixed at 1
Clutch size (CS)	Total number of eggs per clutch	GLM; Poisson
Proportion hatch (PH)	Proportion of eggs successfully hatched	GLM; binomial
Juvenile summer survival (JS)	Apparent juvenile survival from hatching to August	Bootstrapping procedure: ratio between mean clutch size after hatching and mean clutch size in August
Early juvenile winter survival (EJWS)	Apparent juvenile survival from August to March	Optimization: minimizing the difference between two estimates of λ by adjusting the value of EJWS
Late juvenile winter survival (LJWS)	Juvenile survival from March to May	Kaplan-Meier
Adult survival (AS)	Adult survival from May in year t to May in year $t+1$	Kaplan-Meier

Direct estimates of juvenile summer survival (JS) based on data from the radio-marked individuals could not be made because the data set contained too few observations of brood sizes at the end of the summer (E. Nilsen, pers. comm.). Therefore, a resampling procedure was used, combining the individual based data with data on population level. First, mean clutch size of successfully hatched eggs (i.e. fledglings; CS_1) was calculated based on the nest monitoring data. Second, mean clutch size of successful clutches (i.e. ≥ 1 chick per clutch; CS_2) from broods observed in August was calculated based on the line transect data. I assumed that observations of adults without clutches in August could be explained by nest predation, a mortality which already had been accounted for in CS_1 . The probability of surviving from hatching until August

was estimated as the ratio between the two mean clutch sizes (i.e. CS_2/CS_1). By making 10 000 random draws from beta distributions representing mean and SD of CS_1 and CS_2 respectively, I obtained a distribution that was used to estimate mean and standard error for JS.

Because we did not capture and radio-tag chicks in August in this study, estimate of early juvenile winter survival (i.e. from October to March, EJWS) could not be calculated from the individual based data. Therefore, an indirect estimate of the parameter was made using an optimizing procedure, combining the individual based data with data on population level. First, because the study period was 3 years, I calculated the population growth rate (λ_1) as the cubic root of the ratio between the population density observed in the last and the first year of the study. The population densities were collected from Hønsfuglportalen (www.honsefugl.nina.no). Second, the population growth rate was also given by the dominant eigenvalue (λ_2) of the projection matrix **A**, which was calculated based on a temporary value of EJWS and fixed values of the rest of the parameters comprising the matrix. Then, as the two estimates of the population growth rate represent the same population, EJWS was optimized to a value which minimized the mean square difference between λ_1 and λ_2 , while the other parameters were kept constant (see R code in Appendix A).

The survival estimate of late juvenile winter survival (LJWS) was based on radio-marked individuals captured in February/March. Juveniles (<12 months of age) were distinguished from adults (>12 months of age) by the brown pigmentation patterns on the outermost parts of the 8-10th primaries (Pedersen & Karlsen, 2007), which contrasts the white feathers of adults. Late juvenile winter survival was calculated using the same procedure as for adult survival presented below.

The cumulative survival of adults throughout the year (AS), and LJWS, was calculated using Kaplan-Meier models (survival package; Crawley, 2013; Therneau & Grambsch, 2013). Potential sex- or age-effects on survival were tested for using Cox-proportional hazard models (Crawley, 2013). The Cox-proportional hazard model assumes proportional hazards, which was tested using the *cox.zph* function (survival package; Therneau & Grambsch, 2013). Encounter histories were constructed for each radio-marked individual to analyze the annual survival on a monthly time step. Four variables were determined in the encounter history of each individual: time of entering the study, time of exiting the study, fate of the bird, and cause of death. Time of entering the study was defined as the marking of a bird, or when a bird re-entered the study if surviving for more than one study year. Independent encounter histories were created for each year a bird survived. Potential lack of independence between encounter histories was accounted

for by including individual as a random effect in the models used. Time of exiting the study was set to the same month as death was reported by the hunter for birds that were harvested, whereas exit time for those who died of other causes was set to the midpoint between last time detected alive and the first time mortality signal was recorded with the radio-telemetry receiver. Birds that disappeared from the study were coded as censored, with exit time equal to the last time when recorded alive. Fate of the bird at exit time was either alive or dead. Cause of death was divided into two categories: “harvest” and “other”. Harvest mortality included birds that were reported shot or snared by hunters, and mortality due to other causes included deaths caused by predation and unknown causes. The *non-parametric cumulative incidence function estimator* (NPCIFE; Heisey & Patterson, 2006) was used to estimate the cause-specific cumulative mortality probabilities owing to harvest and other causes. The estimator arises from the generalized Kaplan-Meier estimator, and obeys the property that causes of mortality are mutually exclusive events (i.e. competing risk of mortality; Heisey & Patterson, 2006).

From the projection matrix (2) many useful properties could be derived. First, the population growth rate (λ) is given by the dominant eigenvalue of the matrix (Caswell, 2001). Second, the matrix was used to calculate elasticities and “lower-level” sensitivities. Elasticities express the effect of proportional changes in matrix element a_{ij} on λ , whereas sensitivities express the effect of an absolute change in matrix element a_{ij} on λ (Benton & Grant, 1999a). Elasticities, and sensitivities of lower-level parameters, were calculated using the *vitalsens* function (popbio package; Stubben & Milligan, 2007).

Last, I calculated the generation time (T) of the willow ptarmigan population in Lierne. Generation time can be defined as the mean age of mothers of newborn individuals when the population has achieved a stable age distribution (Lande et al., 2003), and was calculated as:

$$T = \alpha + [s/(1 - s)] \quad (3)$$

, where α refers to age of females when breeding for the first time (i.e. age of maturity), and s is the expected annual adult survival rate (Lande et al., 2003). My data showed that all females started breeding at 1 year of age, thus $\alpha = 1$.

Standard errors and confidence intervals of all matrix properties were obtained using parametric bootstrapping with 10 000 iterations when constructing the matrix. Parameters that were restricted to a range between 0 and 1 were modelled by making random draws from a beta

distribution, whereas clutch size was modelled by making random draws from a normal distribution. In the results, mean values are presented along with standard errors (mean \pm SE). Uncertainties of estimates in statistical tests are presented as 95% confidence intervals, CI = [lower, upper] (Gerstner et al., 2017).

Results

Demographic parameters

All results reported here are mean values and standard errors (mean \pm SE) of the 3-year study period, whereas annual means are presented in Table 3. On average, females produced 9.1 ± 0.5 eggs per clutch (CS), when reneesting events were not included. The average proportion of eggs that successfully hatched (PH) during the study period was estimated to 0.50 ± 0.08 . JS was estimated to 0.62 ± 0.23 during the study period, and EJWS was estimated to 0.67 ± 0.23 . As expected, the standard error of the latter two parameters were large as they were estimated combining two independent data sets. LJWS was estimated directly from the radio-telemetry data and was more precise with a mean value of 0.86 ± 0.05 . An approximate estimate of the annual juvenile survival probability of 0.36 ± 0.19 was calculated by multiplying the three probabilities of juvenile survival (JS, EJWS and LJWS). There was no significant year-effect in neither of the testable parameters: CS ($\chi^2 = 2.08$, $p = 0.35$), PH ($\chi^2 = 0.20$, $p = 0.90$), and LJWS ($z = -0.39$, $p = 0.70$). The recruitment rate (R) was estimated at 0.81 ± 0.45 .

The annual adult survival rate was estimated to 0.39 ± 0.05 . The steepest drop in the cumulative survival occurred in September (Fig. 3), coinciding with the start of the annual hunting season starting 10th of September. The overall hazard functions did not differ significantly between females and males (HR = 1.07, CI = [0.68, 1.71], $z = 0.30$, $p = 0.76$), and the assumption of proportional hazards was met ($\chi^2 = 2.83$, $p = 0.09$). The effect of age on survival was also considered. Also in this case, the assumption of proportional hazards was met ($\chi^2 = 0.01$, $p = 0.92$), and the overall hazard functions did not differ significantly between the two age-classes (HR = 0.88, CI = [0.53, 1.45], $z = -0.51$, $p = 0.61$). The results supported the assumption made that there is no difference in survival rates between females and males, or between yearlings and adults.

Table 3. Estimated mean values of the vital rates used in the analyses [mean \pm SE (n)]. Proportion of breeding females (breeding proportion, BP), total clutch size (clutch size, CS), proportion of eggs that successfully hatched (proportion hatch, PH), survival of juveniles from hatching to August (juvenile summer survival, JS), survival of juveniles from August to March (early juvenile winter survival, EJWS), survival of juveniles from March to May (late juvenile winter survival, LJWS), and survival of adults from May in year $t+1$ (adult survival, AS).

	Breeding proportion	Clutch size	Proportion hatch	Juvenile summer survival	Early juvenile winter survival	Late juvenile winter survival	Adult survival
2015	1.00 \pm 0.00	8.0 \pm 0.9 (10)	0.55 \pm 0.15 (11)	0.54 \pm 0.37	NA	0.82 \pm 0.12 (11)	NA
2016	1.00 \pm 0.00	9.7 \pm 0.9 (13)	0.50 \pm 0.13 (16)	0.71 \pm 0.52	NA	0.87 \pm 0.07 (23)	NA
2017	1.00 \pm 0.00	9.6 \pm 1.0 (9)	0.44 \pm 0.17 (9)	0.65 \pm 0.38	NA	0.88 \pm 0.08 (16)	NA
Total mean	1.00 \pm 0.00	9.1 \pm 0.5 (32)	0.50 \pm 0.08 (36)	0.62 \pm 0.23	0.67 \pm 0.23	0.86 \pm 0.05 (50)	0.39 \pm 0.05 (129)

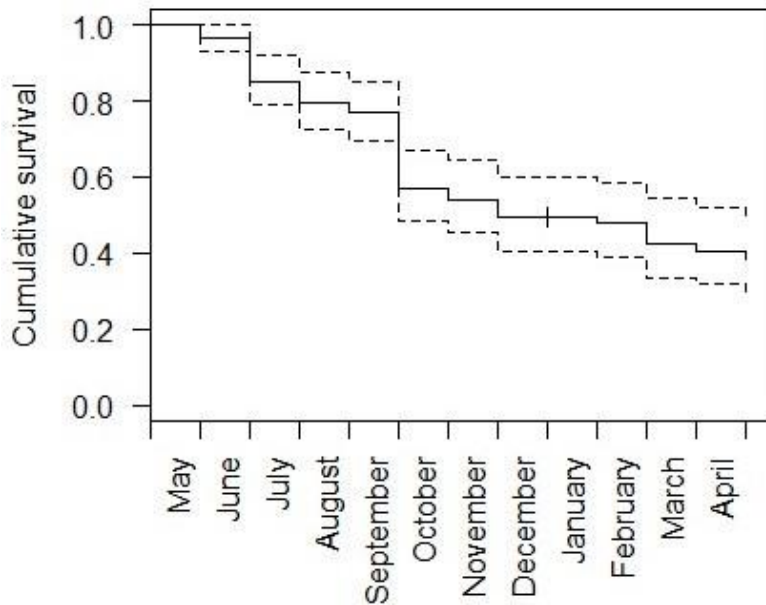


Fig. 3. Kaplan-Meier estimates of cumulative monthly survival (\pm 95% CI) for radio-marked adults (>12 months of age) during the year, starting in May. The estimate includes all individuals across the 3-year study period. Censored individuals are represented by + signs.



Fig. 4. Distributions of cause-specific mortality probabilities owing to harvest and other causes (predation and unknown), based on parametric bootstrapping by making 10 000 random draws from beta distributions representing mean and SD of the mortality probability of harvest and other, respectively. Means and SD were calculated by using the nonparametric cumulative incidence function estimator (NPCIFE). Estimates were based on the faith of radio-marked individuals.

Cause-specific mortality probability due to harvest was estimated to 0.28 (CI = [0.21, 0.35], $n = 22$), whereas the probability of mortality due to other causes, including predation and unknown causes, was estimated to 0.40 (CI = [0.31, 0.49], $n = 51$; Fig. 4).

Matrix parameters

The population growth rate (λ) is given by the dominant eigenvalue of the projection matrix **A**, and confidence intervals were obtained based on parametric bootstrapping. The distribution of λ based on 100 00 iterations predicted an increasing population ($\lambda = 1.20 \pm 0.46$, CI = [0.49, 2.20]). The sensitivity of λ to PH was the highest of all lower-level parameters (Table 4). JS and EJWS had second and third highest sensitivity values. Although it was expected that parameters associated with juvenile survival have high sensitivity values (Sandercock et al., 2005a; Steen & Erikstad, 1996), the sensitivity values of JS and EJWS might be treated with caution. The two parameters could not be empirically estimated based on field data but are instead indirect estimates based on optimization and bootstrapping procedures. The sensitivity value of CS was lowest and will therefore have the least impact on λ per absolute change in the rate. However, it should be taken into consideration that clutch size is on a different scale than the other rates (Manlik et al., 2018).

Elasticity values were higher for recruitment than for adult survival (Table 4), as expected in fast-living species (Sæther & Bakke, 2000). The elasticity values imply that a 10% increase in the recruitment rate will increase λ by 6.3%, whereas a 10% increase in the survival rate will only increase λ by 3.8 %.

Table 4. Sensitivity (mean \pm SE) of lower-level vital rates: breeding proportion (BP), clutch size (CS), proportion hatch (PH), juvenile summer survival (JS), early juvenile winter survival (EJWS), late juvenile winter survival (LJWS), and adult survival (AS), and elasticity (mean \pm SE) of recruitment and adult survival.

	Recruitment						Adult survival
	BP	CS	PH	JS	EJWS	LJWS	AS
Sensitivity	0.81 \pm 0.45	0.18 \pm 0.10	1.62 \pm 0.85	1.32 \pm 0.52	1.20 \pm 0.50	0.94 \pm 0.52	1.00 \pm 0.00
Elasticity	0.63 \pm 0.16						0.37 \pm 0.16

The estimated generation time (T) was 1.64 ± 0.14 (CI = [1.41, 1.94]), which confirms that willow ptarmigan is a fast-living species.

Discussion

The population growth rate (λ) in the study population of willow ptarmigan in Lierne was most sensitive to variation in the recruitment rate. However, the harvest mortality was substantial, and higher than what previously has been implied as a compensatory level of harvest (Sandercock et al., 2011). Accordingly, based on our current knowledge, the observed harvest rate most likely contribute as a limiting factor in the study population. The present study is in alignment with other studies that have demonstrated that willow ptarmigan is a fast-living species with relatively short generation time (Sandercock et al., 2005a), and that top-down factors (i.e. predation and harvest) are the proximate causes of high adult mortality rates (Sandercock et al., 2011). To my knowledge, this is the first study that quantify and parameterizes the complete life cycle of willow ptarmigan based on direct field observations of marked individuals.

Studies based on obtaining high quality demographic data of the whole life cycle in wild bird species are challenging to implement, and relatively few such studies are reported in the literature (Beissinger & McCullough, 2002; Hannon & Martin, 2006). Juvenile survival, in particular, is challenging to estimate empirically as juvenile birds often are cryptic, difficult to capture, and do often emigrate out of the study area due to natal dispersal (Hannon & Martin, 2006; VanderWerf & Young, 2016). In the present study I obtained reliable estimates of vital rates by combining the use of radio-telemetry, camera traps, and line transect data on population level, and thus enabled the incorporation of JS and EJWS in the population model, which were parameters that could not be estimated only based on the individual-based data available (i.e. "hidden" demographic parameters; Tavecchia et al., 2009). This method is quite novel, with similarities to integrated population modelling which jointly analyses population count data and demographic data (Schaub & Abadi, 2011).

As expected for willow ptarmigan, the population in Lierne had a high reproductive potential and low adult survival rate (Table 3), as well as a relatively short generation time, which are typical characteristics of fast-living species. The estimates of breeding success in the present study was partially in accordance with previous studies (Martin & Wiebe, 2004; Sandercock et al., 2005b; Steen & Erikstad, 1996). However, the hatch probability observed in previous studies (0.48-0.63 Sandercock et al., 2005b; 0.70 ± 0.18 ; Steen & Erikstad, 1996) was slightly higher than in the present study (0.50 ± 0.08), which might be explained by sources of bias related to the methods used in these studies. First, estimating clutch size and egg survival in

ground-nesting birds is often based on finding nests by chance (Martin & Wiebe, 2004; Munkebye et al., 2003; Nordström et al., 2003; Steen & Erikstad, 1996; Watson et al., 1998). This method rarely includes nests that already have been predated and therefore will lead to an overestimation of nest success if not explicitly accounted for in the statistical modelling. Accordingly, using radio-tracking will generate less biased estimates of egg survival (Jahren et al., 2016). Second, repeated flushing of birds during laying and early incubation, which also has been a common field practice (Sandercock et al., 2005b; Steen & Erikstad, 1996), can lead to biased results because of increased risk of nest desertion (Connelly et al., 2011). The use of camera traps should decrease this risk because flushing of the female was restricted to a single incident.

The annual adult survival rate of 0.39 ± 0.05 was at the same level as previous estimates of hunted populations in Canada (0.37 ± 0.06 and 0.43 ± 0.03 ; Sandercock et al., 2005b) and Sweden (0.35 ; Smith & Willebrand, 1999). The steepest drop in the cumulative survival occurred during autumn (Fig. 3), which is likely to be associated with the opening of the hunting season 10th of September in Lierne. In addition, high mortality in autumn could potentially be associated with timing of snowfall and migratory movements of raptors, which has been found by Sandercock et al. (2011). The estimate of annual juvenile survival found in the present study (0.36 ± 0.19) was slightly higher than what was found in previous studies (0.30 in hunted area: Smith & Willebrand, 1999; 0.27 ± 0.11 : Steen & Erikstad, 1996). The population growth rate calculated from the line transect surveys was part of the estimation method of EJWS, and the EJWS thus only represents the apparent juvenile survival. Accordingly, if the population growth rate was higher due to net immigration, EJWS would be overestimated, and correspondingly, underestimated if the growth rate was lower due to net emigration in the study area. In contrast to previous studies on willow ptarmigan, where juvenile survival rarely differed significantly from adult survival (Sandercock et al., 2005b; Smith & Willebrand, 1999), the average value of EJWS (0.67 ± 0.23) was higher than the adult survival when AS was scaled down to an equal time span as EJWS (i.e. 7 months; $AS^{7/12} = 0.57 \pm 0.04$). Thus, although EJWS and AS are overlapping due to large standard errors in EJWS, the elevated mean value of EJWS compared to AS might be explained by immigration. To further investigate the effect of my assumptions about population growth on EJWS, I repeated the optimization routine (Appendix A) based on the assumption that $\lambda = 1$. Interestingly, I then found that EJWS would be similar to the adult survival rate (EJWS = 0.57 ± 0.23), which is more likely to be closer to its true value. This suggests that the positive growth rate of the population depended on immigrating individuals.

Immigration has previously been suggested to have an important role in sustaining population size of willow ptarmigan in hunted areas (Smith & Willebrand, 1999), and in other species of birds and mammals (Brommer et al., 2017; Duarte et al., 2016; Wilson et al., 2017). For example in willow tit (*Parus montanus*), immigration by juveniles was demonstrated to have a relative contribution of 22% to λ , despite adults being highly sedentary (Lampila et al., 2006).

The results of the sensitivity and elasticity analysis indicated that λ was most sensitive to variation in PH, followed by JS and EJWS, and that the elasticity of λ to recruitment was higher than to adult survival (Table 4). These results coincided well with the findings of previous studies and current life history theory (Sæther & Bakke, 2000), as juvenile survival has been identified as the parameter with the highest potential influence on λ in willow ptarmigan (Sandercock et al., 2005a; Steen & Erikstad, 1996), and in other fast-living species (Heppell et al., 2000). The actual contribution from a parameter to the observed variation in λ depends however on both its sensitivity value and its temporal variability. Based on the buffering hypothesis one could expect that recruitment should be buffered against environmental variation (Pfister, 1998; Sæther & Bakke, 2000), however, previous studies on willow ptarmigan have demonstrated that the recruitment may exhibit high temporal variability (Hannon & Martin, 2006; Martin & Wiebe, 2004; Steen & Erikstad, 1996). The present study was based on the first 3 years of an ongoing study and was thus too short to perform a formal analysis of the drivers of long-term population fluctuations of willow ptarmigan. To gain a deeper insight into the factors that affected the dynamics of my study population, I therefore compared the observed vital rates in the present study with a long-term study on willow ptarmigan conducted in Tranøy, northern Norway (Steen & Erikstad, 1996). During the 21-year study period on Tranøy, the willow ptarmigan population experienced one phase of quite stable population size (1960-70), and one phase with population decline (1972-80, see demographic data in Table B1). Using a life table response experiment (LTRE, see Appendix B for further description of the method; Caswell 2000, Caswell 2001) I formally assessed the contribution of the vital rates to observed variability in the projected population growth rates ($V(\lambda)$) derived as the dominant eigenvalues from the underlying projection matrices (Table B2). Interestingly, λ of both the stable and the declining phase of the Tranøy population were lower than in the Lierne population (Table B2). The LTRE revealed that the adult survival rate (AS) had a positive contribution to the $V(\lambda)$ in both phases of the Tranøy population, whereas the recruitment rate (R) had a negative contribution, compared to Lierne (Fig 5). This was expected due to observed higher rates of adult survival in both phases in

Tranøy, and a lower rate of recruitment, compared to Lierne (Table B2). The positive contributions of AS to $V(\lambda)$ compared to Lierne might suggest a decrease in adult survival during the last decades. More surprising, the differences between the stable and the declining phase were not substantial (Fig. 5). The magnitude of the negative contributions from R to $V(\lambda)$ were generally larger than the positive contribution from AS, suggesting that R was responsible for the lower λ observed in both phases in Tranøy compared to Lierne (Fig. 5). A potential caveat in this analysis could be that high recruitment rate recorded in Lierne constitute three good years of recruitment by chance, and thus not be representative for the true average recruitment rate in Lierne. However, given that the estimates are valid and representative this is in accordance with other studies that have pointed to reduced reproductive success as a driver of population decline in many bird species (Aldridge & Brigham, 2001; Robinson et al., 2004; Robinson et al., 2014).

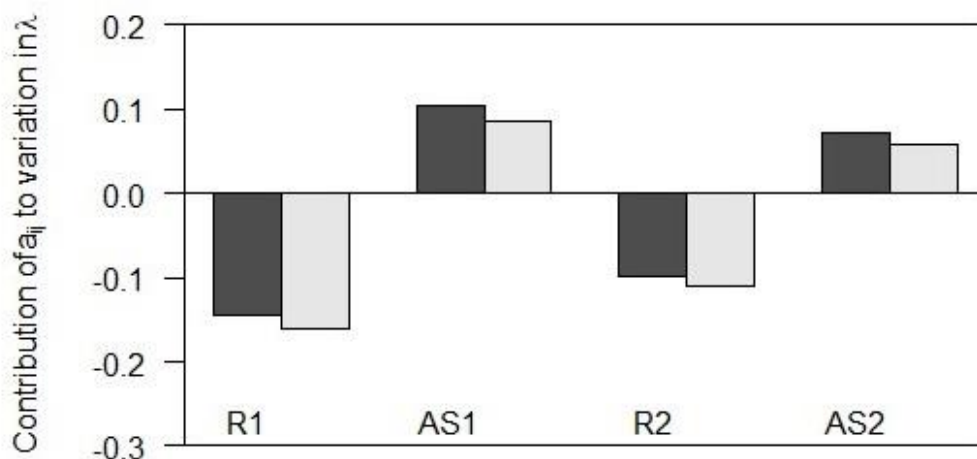


Fig. 5: The contribution of the matrix elements recruitment (R1 and R2: average number of female offspring entering the population at time $t+1$ per female yearling, and adult, respectively, alive at the beginning of year t) and adult survival (AS1 and AS2: the probability of a yearling, and an adult, respectively, to survive from the beginning of year t to the beginning of year $t+1$) to the variability of population growth rates λ of the Tranøy population, compared to the Lierne population (represented by the zero base line; $\lambda = 1.20 \pm 0.46$). Yearlings (12-24 months of age) and adults (>24 months of age) were assumed to have the same recruitment rate and survival rate, thus in the underlying projection matrices I defined $R1 = R2$, and $AS1 = AS2$. The Tranøy population was split into two time-series: stable phase (1966-70, black bars) and declining phase (1972-80, grey bars).

My study generally confirmed that the proximate cause of most mortalities was due to top-down effects from predation and harvest, based on data from the camera traps, observations

from the field and the quantification of cause-specific mortality probabilities (Fig. 4). The exact estimates of cause-specific mortality probabilities should be treated with caution as the sum of the two mortality probabilities (harvest and other causes) was not precisely equal to the inverse survival probability, which is a small violation from the concept of competing risk (Heisey & Patterson, 2006). Harvest was, in contrast to predation and unknown causes, only a potential cause of death during a limited period of time, when the number of birds at risk already had been reduced (Lebreton, 2005), which might have resulted in a small overestimation of the probabilities of both harvest- and predation mortality. Populations of predator species such as red fox and pine marten seem to be increasing, which possibly have a negative effect on willow ptarmigan (Helldin, 2000; Killengreen et al., 2011; Selås & Vik, 2006). Further, previous studies have revealed numerical and functional responses of avian predators to changes in game bird densities (Valkama et al., 2005). For instance, gyrfalcon predation was an essential part of the population cycle of rock ptarmigan in Iceland, and due to a time lag in the population response of gyrfalcons, the predation rate peaked during population declines and low years of rock ptarmigan (Nielsen, 1999). The same inversely density-dependent predation pattern was found between goshawk (*Accipiter gentilis*) and willow ptarmigan populations in Finland (Tornberg, 2001), suggesting that avian predation can be an additive source of mortality in game bird populations.

Fast-living species are demonstrated to show higher ability to compensate for anthropogenic mortality than slow-living species (Peron, 2013). In a field study in central Norway, Sandercock et al. (2011) manipulated the harvest regimes in natural populations of willow ptarmigan into three levels of harvest rates: 0%, 15% and 30%, where the realized risk of harvest mortality was generally 8-12 percentage points higher than the set harvest regimes. The study provided evidence for partial compensation under the 15% harvest rate (harvest mortality: 0.27 ± 0.05) and for additive mortality under the 30% harvest rate (harvest mortality: 0.42 ± 0.06 ; Sandercock et al., 2011). In Sweden, Smith and Willebrand (1999) reported additivity under a risk of harvest mortality of 0.24. Further, populations below their carrying capacity of the environment are found to have less potential for compensation due to weak density-dependence (Peron, 2013). Considering that the population densities recorded in Lierne were generally lower than those presented in Sandercock et al. (2011; 7-32 birds/km²), this indicates that the harvest mortality in Lierne probably was partially or completely additive.

Identifying key demographic parameters is important when constructing management strategies, and lower elasticity values for adult survival suggests that the study population

should be more resistant to factors that affect the mortality rate of adult willow ptarmigan compared to recruitment (Benton & Grant, 1999a). Reduction of predator populations and reduction of harvest pressure are two commonly used management strategies of game bird species (Andersen et al., 2014; Cote & Sutherland, 1997). First, this study, and previous studies on willow ptarmigan, have suggested that predation is likely to be a more important limiting factor of populations than harvest (Sandercock et al., 2011; Smith & Willebrand, 1999). Moreover, a reduction in predator densities would potentially have a large impact on λ considering the high sensitivity of λ to PH, JS and EJWS, which all are highly influenced by predation. However, the actual effect of predator control on prey population performance is complex and not fully understood. Previous studies have demonstrated that reduced predator densities can have a positive effect on post-breeding population size of game birds through enhanced chick production, whereas the effect on the breeding densities the following year was less pronounced (Cote & Sutherland, 1997; Valkama et al., 2005). However, no such positive effects on chick production was measurable in a study on willow ptarmigan in south-central Norway, despite intensive local predator control (Steen & Haugvold, 2009). Thus, predator control might fulfil the aims of game management in some species by increased harvestable population size in autumn (Kauhala et al., 2000), whereas it does not appear as an appropriate management action for populations of willow ptarmigan or for conservational purposes in general. Moreover, previous experiments have indicated that the effect of removing only one predator species is usually small because predators often have high compensatory capacity and reducing the density of one predator species can result in increased predation pressure by another, non-controlled species (Ellis-Felege et al., 2012; Valkama et al., 2005).

In contrast to the effect of predator control, a reduction in the harvest rate would result in an immediate increase in the adult survival rate, considering that harvest mortality is probably partially or totally additive. Further, juveniles have been demonstrated to have a higher risk of harvest mortality than adults (Sandercock et al., 2011), suggesting that the potential impact on λ is large, considering the high sensitivity of λ to juvenile survival. Harvest has previously been pointed to as a contributing factor to population decline, as for instance in a study on northern bobwhite (*Colinus virginianus*) in Florida, where harvest contributed to population decline through a negative impact on production of recruits the following breeding season. This study suggests that a reduction in the harvest pressure would be a more feasible management mitigation to implement compared to the alternative of predator control, due to an immediate impact on the breeding population size.

In conclusion, by using a novel approach where the vital rates of the full life cycle of willow ptarmigan in Lierne, central Norway, was parameterized, the results revealed that the growth rate showed highest sensitivity to changes survival rates at early age, including hatch probability and juvenile survival through summer and autumn. These results may have implications for game bird species with comparable life histories, where variation in the recruitment rate might be a vulnerable part of the life cycle in declining populations of fast-living species. In game birds, juveniles are at least as vulnerable as adults to harvest mortality (Hannon & Martin, 2006; Sandercock et al., 2011). Thus, harvest mortality may result in a substantial negative impact on the population growth rate and the production of recruits the following breeding season. Despite high reproductive output and large intrinsic growth rate, fast-living species can indeed be overexploited with population declines as a consequence.

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Appendices

Appendix A

R code developed to estimate early juvenile winter survival (EJWS):

```
f_find_jws <- function(early.jws_temp) {  
  A <- matrix(NA, nrow=2, ncol=2)  
  A[1,c(1,2)] <- BP*CS*PH*JS*late.JWS*early.jws_temp  
  A[2,c(1,2)] <- SAD  
  
  lam2 <- eigen.analysis(A)$lambda  
  (lam1-lam2)^2  
}  
  
jws_opt <- numeric()  
  
for (i in 1:10000){  
  BP <- betaval(mn=1, sdev = 0)  
  CS <- (exp(rnorm(1, mean = 2.21102, sd = 0.05852)))/2  
  PH <- betaval(mn = 0.5, sdev = 0.08333333)  
  JS <- betaval(mn = 0.6140483, sdev = 0.225538)  
  late.JWS <- betaval(mn = 0.859, sdev = 0.0494)  
  # early.JWS <- (betaval(mn = 0.385, sdev = 0.0498))^(6/12)  
  SAD <- betaval(mn = 0.385, sdev = 0.0498)  
  
  t <- 3  
  D_first <- rnorm(1, 8.3, 1.743)  
  D_last <- rnorm(1, 12, 1.68)  
  lam1 <- pracma::nthroot(D_last/D_first, t)  
  
  jws_opt[i] <- optimize(f_find_jws, interval=c(0, 1))$minimum  
}
```


Appendix B

Table B1. Demographic data extracted from Steen and Erikstad (1996). Values of the demographic parameters used in the analysis: Clutch size (Clutch), survival of eggs from egg laying to hatching (Eg survival), proportion of eggs that hatched (Hatch), proportion of chicks that survived from hatching to four weeks (Chick survival), proportion of juveniles surviving the winter (Juvenile winter survival), proportion of adults surviving the winter (Adult survival), adult survival from arrival at Tranøy until mid May (Adult summer survival), mean value of juvenile and adult apparent winter survival (Pooled winter survival), survival of an egg from egg laying to four weeks after hatching. Standard deviation in the clutch size is based on the total variance and is not weighted as in the other parameters.

Year	Clutch	Egg survival	Hatch	Chick survival	Juvenile winter survival	Adult survival	Adult summer survival	Pooled winter survival	Survival from egg laying to four weeks after hatching
1960	11.37	0.92	0.99	0.39			0.99		0.35
1961	9.89	0.92	0.90	0.32	0.32	0.51	1.00	0.41	0.27
1962	10.00	0.81	0.93	0.45	0.39	0.71	0.99	0.55	0.34
1963	9.79	0.49	0.99	0.43	0.39	0.40	0.99	0.39	0.21
1964	10.00	0.89	0.94	0.46	0.28	0.49	0.92	0.38	0.38
1965	10.21	0.91	0.94	0.75	0.33	0.57	0.99	0.45	0.64
1966	10.00	0.81	0.97	0.69	0.33	0.72	0.99	0.53	0.55
1967	8.00	0.40	0.88	0.56	0.18	0.57	0.99	0.38	0.20
1968	8.95	0.70	0.96	0.58	0.20	0.68	0.99	0.44	0.39
1969	9.89	0.81	0.95	0.58	0.18	0.60	0.99	0.39	0.45
1970	9.89	0.71	0.96	0.63	0.38	0.47	0.98	0.42	0.42
1972	9.89	0.67	0.96	0.53	0.48	0.49	0.97	0.48	0.34
1973	10.74	0.74	0.94	0.53	0.25	0.65	0.98	0.45	0.36
1974	10.00	0.72	1.00	0.49	0.50	0.49	0.99	0.50	0.35
1975	8.74	0.69	0.94	0.20	0.42	0.55	0.91	0.48	0.13
1976	10.21	0.66	0.91	0.31	0.39	0.64	0.98	0.52	0.18
1977	11.89	0.74	0.88	0.51	0.20	0.37	0.98	0.29	0.33
1978	11.89	0.79	0.94	0.57	0.17	0.52	0.94	0.34	0.42
1979	9.68	0.18	0.95	0.31	0.41	0.67	1.00	0.54	0.05
1980	12.21	0.84	0.96	0.61					0.49
Weighted mean	9.80	0.70	0.95	0.54	0.27	0.52	0.97	0.39	0.36
Weighted SD	1.05	0.18	0.03	0.14	0.11	0.10	0.03	0.07	0.14
Min	8.00	0.18	0.88	0.20	0.17	0.37	0.91	0.29	0.05
Max	12.21	0.92	1.00	0.75	0.50	0.72	1.00	0.55	0.64

Further description of the LTRE methods

Starting in 1960, a 21-year study was conducted on a population of willow ptarmigan in Tranøy, an island in northern Norway. The original study was presented in Myrberget (1988) but was later reanalyzed by Steen and Erikstad (1996), where the raw data was presented. The data was mainly based on mark-recapture procedures and population counts. In the period 1960 to 1970, the population size was quite stable. From 1972, the population started to decline in numbers. Thus, the study was naturally divided into two phases; one stable (1960-70) and one of population decline (1972-80). Based on the demographic parameter estimates given in Steen and Erikstad (1996), I constructed one population projection matrix for each of the two phases, using a pre-breeding census. The estimates given were not stage-specific, thus, I assumed there was no difference in the recruitment rate or survival rate of yearlings (<12 months of age) and adults (>12 months of age). The purpose of the analysis was to compare a declining and stable population (i.e. Tranøy) to an increasing population (i.e. Lierne) to quantify the contributions of adult survival and recruitment to variability in the projected λ . Higher contributions imply a combined effect of both high temporal variability and high elasticity. The two matrices were compared to the previously constructed projection matrix of Lierne (see *Methods*) using the *LTRE* function (popbio package; Stubben & Milligan, 2007).

Table B2: Estimates of the matrix elements recruitment (R1 and R2: average number of female offspring entering the population at time $t+1$ per female yearling, and adult, respectively, alive at the beginning of year t [mean \pm SE]), and adult survival (AS1 and AS2: the probability of a yearling, and an adult, respectively, to survive from the beginning of year t to the beginning of year $t+1$ [mean \pm SE]), and the projected population growth rates (λ [mean \pm SE]), of the different ‘treatments’: Lierne (control), stable phase of the Tranøy population (1960-70), and declining phase of the Tranøy population (1972-80). Yearlings (12-24 months of age) and adults (>24 months of age) were assumed to have the same recruitment rate and survival rate, thus in the underlying projection matrices I defined R1 = R2, and AS1 = AS2.

Treatment	R1	AS1	R2	AS2	λ
Lierne (control)	0.81 \pm 0.45	0.38 \pm 0.05	0.81 \pm 0.45	0.38 \pm 0.05	1.20 \pm 0.46
Tranøy (stable, 1960-70)	0.56 \pm 0.35	0.56 \pm 0.16	0.56 \pm 0.35	0.56 \pm 0.16	1.12 \pm 0.39
Tranøy (declining, 1972-80)	0.54 \pm 0.38	0.53 \pm 0.18	0.54 \pm 0.38	0.53 \pm 0.18	1.06 \pm 0.42