

Life-history and demographic variation in an alpine specialist at the latitudinal extremes of the range

Scott Wilson · Kathy Martin

Received: 8 February 2010 / Accepted: 4 January 2011 / Published online: 8 February 2011
© The Society of Population Ecology and Springer 2011

Abstract Alpine environments are unique systems to examine variation in life-history strategies because temperature and seasonality are similar across broad latitudinal gradients. We studied the life-history strategies, demography and population growth of white-tailed ptarmigan *Lagopus leucura*, an alpine specialist, at the latitudinal extremes of the range in the Yukon (YK, studied from 2004 to 2008) and Colorado (CO, 1987–1996). The two populations were separated by 2,400 km of latitude, and the Yukon site was approximately 2,000 m lower in elevation than the Colorado site. Yukon females bred on average 9 days earlier than those in Colorado, but the latter study was conducted 15 years earlier and breeding dates may have advanced over this period. The length of the breeding season was similar between the two populations, and females had comparable probabilities of re-nesting after failure. The two populations differed in how they allocated effort to the first clutch as Yukon females laid larger clutches (7.1 vs. 5.9 eggs) but smaller eggs (18.8 vs.

20.5 g) than those in Colorado. Demographic rates also differed; nest survival was higher in the Yukon (0.40) than in Colorado (0.24), and the resultant annual fecundity was nearly twice as high in the Yukon (3.92 vs. 1.77 chicks/female). In contrast, annual adult survival was higher in Colorado although the confidence intervals overlapped (females: YK = 0.35, CO = 0.44; males: YK = 0.48, CO = 0.59). Estimates of annual population growth (λ) indicated both populations were declining, especially in Colorado ($\lambda_{YK} = 0.83$, $\lambda_{CO} = 0.66$), and thus, dispersal movements are likely key to long-term persistence in both cases. Our findings suggest that breeding-season temperature and seasonality affect measures related to timing of reproduction, but not the costs and benefits of clutch and egg size.

Keywords *Lagopus leucura* · Population growth · Reproductive ecology · Seasonality · Survival · White-tailed ptarmigan

S. Wilson
Smithsonian Migratory Bird Center, 3001 Connecticut Avenue,
National Zoological Park, 20008 Washington, DC, USA

K. Martin
Department of Forest Sciences, University of British Columbia,
2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

K. Martin
Environment Canada, 5421 Robertson Road,
Delta, BC V4K 3N2, Canada

Present Address:
S. Wilson (✉)
Canadian Wildlife Service, 115 Perimeter Road,
Saskatoon, SK S7N 0X4, Canada
e-mail: scott.wilson@ec.gc.ca

Introduction

Understanding how and why species vary in life-history and demography across their range is central to the study of life-history evolution and population ecology. A number of ecological mechanisms are suggested to influence the evolution of avian reproductive traits, including food abundance, seasonality, nest predation and adult survival (reviewed in Ricklefs 2000). Many early studies focused on the role of these mechanisms with respect to specific traits, particularly clutch size, but this approach is limiting when we want to understand how and why life-history strategies vary within and across species. In most cases, multiple traits co-vary and different ecological mechanisms interact

to shape the overall life-history strategy of a particular species (Martin 2004; Sandercock et al. 2005a). Collecting detailed data on a suite of life-history and demographic traits across multiple populations of a species is logistically difficult, and published examples of comparative data from across a species range are relatively rare. However, from such studies, geographic variation in reproductive strategies and age-specific survival is often revealed within species (Frederiksen et al. 2005; Sandercock et al. 2005a; Folk et al. 2007).

Geographic variation in life-history strategies is frequently related to latitude and elevation. At higher latitudes and elevations, the growing season is shorter and individuals typically show a delayed onset of breeding and fewer nesting attempts relative to their southern or lower elevation counterparts (Silverin 1995; Badyaev 1997; Collister and Wilson 2007). Short breeding seasons can mean lower annual fecundity, although individuals may partially offset these effects by investing more in each nest attempt quantitatively and/or by providing greater parental care (Badyaev 1997; Bears et al. 2009; Camfield et al. 2010). An increase in clutch size with increasing latitude is also observed commonly within and among species (Lack 1947; Jetz et al. 2008). Because of limitations in reproductive investment, larger clutches are often balanced with smaller eggs, and thus we expect geographic variation in egg size (Figuerola and Green 2006; Martin et al. 2006). Studies across elevational gradients show similar variation; as elevation increases, clutch sizes typically decline (Krementz and Handford 1984; Lu 2005; but see Dunn et al. 2000), whereas the relationship between elevation and egg size is mixed (Lu 2005; Johnson et al. 2006).

Populations that invest less in reproduction but have higher longevity are typically more sensitive to variation in adult survival, while those with higher reproductive effort are generally more sensitive to changes in the reproductive rates and juvenile survival (Sæther and Bakke 2000; Clark and Martin 2007). As populations differ regionally in their life-history strategies, they will vary in their sensitivity to changes in the demographic rates. Environmental components such as habitat quality, predator and competitor abundance, and climate also vary across a species range, and thus we expect their influence on fecundity and survival to differ geographically (Frederiksen et al. 2005; Wilson et al. 2007; Sæther et al. 2008). These aspects, combined with variation in life-history strategies, should all be considered to understand the dynamics of populations.

We used a comparative approach to study the life-history, demography and population dynamics of white-tailed ptarmigan (*Lagopus leucura*), a grouse specializing in alpine habitats, at the northern and southern extremes of the range in the Yukon (Canada) and Colorado (USA). The

two populations are separated by approximately 3,250 km, including a latitudinal difference of about 2,400 km. Comparable data on life-history and demography were collected at the two sites. Very few studies have addressed variation in life-history strategies among alpine specialists, but alpine environments are unique for comparing life-history patterns because with increasing latitude, there is a decrease in the elevation of the alpine zone. This effect means that some features of the alpine zone, such as temperature and seasonality, vary only slightly across latitude, whereas other aspects such as day length differ considerably. As a result of this pattern, we expect life-history traits that are influenced by seasonality and temperature to be similar among the two populations. In contrast, traits that are primarily influenced by other ecological or environmental factors such as predator communities, day length or hypoxia should differ more strongly. To examine these possibilities we focus on clutch size-egg size tradeoffs and seasonal reproductive investment as indicated by re-nesting propensity and the range of clutch initiation dates. We then examine population differences in fecundity and survival, and construct an age-structured population matrix model to assess the influence of current demographic rates on population growth.

Methods

Study areas and species

White-tailed ptarmigan are precocial, ground-nesting birds within the genus *Lagopus* (family Phasianidae). Most populations, including those at our study sites, are resident year-round, but there is some movement to lower elevations during winter (Braun et al. 1993; Martin et al. 2000). White-tailed ptarmigan occupy breeding areas in April where males establish and defend territories. Pairs are socially monogamous during breeding, although polygyny occurs regularly. Males remain with the female on the territory until approximately mid-incubation, after which they leave and form small flocks with other males and failed female breeders. Females will re-nest following clutch failure, but only produce one brood per year, which the female tends until late August to late September. Because the elevation of the alpine zone generally declines with increasing latitude, breeding elevations for white-tailed ptarmigan are lower in northern populations: 1,219–1,542 m in Alaska, 1,940–3,015 m in southern Alberta, 1,615–2,286 m in Washington, 1,951–2,499 m in Montana and 3,350–4,250 m in Colorado (reviewed in Braun et al. 1993). Nearly all detailed life-history and demographic data for white-tailed ptarmigan come from studies at the southern edge of its range in Colorado

(Braun et al. 1993; Martin et al. 2000; Sandercock et al. 2005a, b).

Population studies of white-tailed ptarmigan were conducted over a 5-year period (2004–2008) on a 10-km² site (Pika Camp) in the Ruby Range Mountains of the Yukon Territory (61°13'N, 138°16'W, Fig. 1) and over a 10-year period (1987–1996) on three mountain areas totaling 22 km² on and near Mount Evans, Colorado (39°62'N, 105°73'W). Habitat structure was similar at the two sites and consisted of alpine tundra with a mixed ground cover of rock, sedges, forbs, dwarf shrubs and lichens (Sandercock et al. 2005a; Wilson and Martin 2008). Sampling effort was similar at the two sites and densities at both ranged from 1 to 3 pairs/km².

Monthly temperature data for Colorado were recorded year-round at the Niwot Ridge Long Term Ecological Research site (Greenland 1989). We used 25 years (1982–2006) of monthly temperature data from the D-1 meteorological station (40°06'N, 105°62'W), approximately 50 km north of our study site at an elevation of 3,739 m. This station is located in an alpine tundra habitat where conditions are similar to those at our study site.

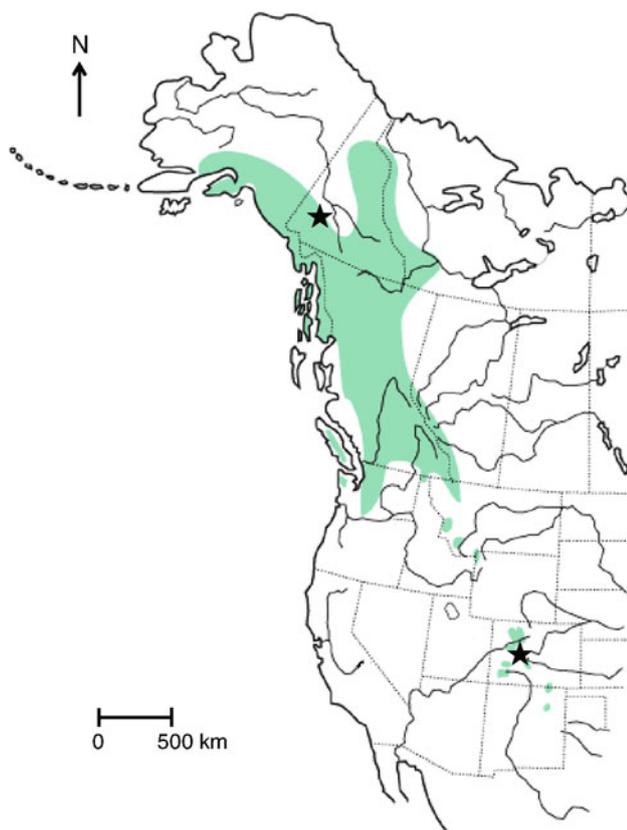


Fig. 1 Distribution of white-tailed ptarmigan in North America with stars showing the location of the study sites in the Yukon and Colorado (map modified from Braun et al. 1993, The birds of North America online, <http://bna.birds.cornell.edu/bna>)

There were no long-term weather stations at the study site in the Yukon, but we used I-button loggers (Maxim Products, Dallas, TX, USA) to collect daily temperature data during the breeding months from 2004 to 2007 and for the winter months in 2004/2005 and 2006/2007. The loggers were located at 1,600–1,700 m elevation. Because only 2 years were available for the winter months we also report 10 years (1988–2007) of monthly temperature data from the nearest high elevation meteorological station located at MacMillan Pass, Yukon Territory (63°2'N, 130°0'W, 1,379 m), approximately 480 km northeast of our study site. Data from this station were obtained from the Environment Canada climate data website: (<http://climate.weatheroffice.ec.gc.ca/climateData>). Throughout the manuscript we discuss seasonality, which for our purposes refers to the change in average monthly temperature throughout the year.

Field methods

Field work was conducted from early May through early August at both sites. Prior to breeding, males and females were caught using ground nets or noose poles, and were color-marked with a numbered aluminum band and 1–3 plastic color bands. We also measured wing length and body mass, and aged them as second-year (SY 9–11 months) or after-second-year (ASY) based on the pigmentation on the outer primaries and primary coverts (Braun et al. 1993). Females were fitted with a 4- or 7-g radio-transmitter (Holohil Inc., Carp, ON, Canada) to locate nests and broods, and to identify movement of individuals between years.

During the laying period, females were located every 1–2 days until the nest was found, after which each was checked every 2–4 days to determine clutch size. For many nests in the Yukon, and during the latter years in Colorado, a temperature logger was placed in the nest. HOBO loggers (HOBOS: Onset Instruments, Massachusetts, USA) were used in Colorado and for the initial year in the Yukon, while Ibutton loggers (Ibutton: Maxim Integrated Products, Texas, USA) were used in the Yukon from 2005 to 2007. These loggers allowed us to determine the time of failure or hatch because the nest temperature changes to match ambient temperatures when the female is no longer incubating. We measured the length and width of eggs for a random sample of clutches, and used these measurements to estimate egg volume. During incubation, nests were checked visually every 3–5 days and more frequently near hatch to determine the number of chicks hatched and when they left the nest. Broods were re-located every 3–7 days to count the number of chicks. If a nest failed, the female was re-located every 1–3 days to determine if she re-nested.

At the start of the following breeding season we conducted extensive surveys of the entire study area and adjacent regions to search for returning adults for estimates of annual survival. Among ptarmigan, dispersal is more likely for females, potentially biasing survival estimates (Braun et al. 1993). At the Yukon site, approximately one third of females kept their radio collars through the winter, allowing us to estimate whether any breeding dispersal had occurred in that portion of the population. Surveys of these birds covered an estimated 100 km² area, but no females were located outside of the 10 km² core study site in the following breeding season. A previous study by Martin et al. (2000) in Colorado estimated breeding dispersal of females and found that 94–98% returned to their previous breeding area. Thus, small amounts of long-distance breeding dispersal may occur, but it is generally rare and unlikely to differ between the two populations.

Because ptarmigan are a game species, they experience some mortality due to hunting. It is unlikely that any of our birds were shot in the Yukon as the remote nature of the site and prevalence of larger game animals results in very low hunting pressure on white-tailed ptarmigan. Some hunting occurred in Colorado (approximately 2%), and any birds shot were removed from subsequent analyses. It is possible that a small number of hunter-killed birds went unreported in both populations, and in this case actual survival estimates may be slightly higher than we report here with a harvest effect more likely in Colorado.

Data analysis

To compare life-history and demography across populations, we estimated values for a range of vital rates described below. For most analyses we used linear or generalized linear models in the statistical environment R (R Development Core Team 2009) and interpret inter-population differences in rates based on non-overlapping 95% confidence intervals and null hypothesis significance tests (based on $\alpha = 0.05$). Other measurements were based on the predictions of a best fit model, and in these cases, we interpret significant differences on the basis of non-overlapping intervals. Some rates were estimated previously in Sandercock et al. (2005a, b) for the CO population or Wilson and Martin (2010) for the YK population, but to be consistent with methodology, all estimates were recalculated here. Estimates for nest, brood, chick and adult survival were calculated using program MARK (White and Burnham 1999). For the population model (see below) we estimated rates for hatched young per female and adult survival for second year and after-second year females.

1. *Initiation and length of the breeding season.* For all females, we estimated mean date of first egg

annually by observing nests during the laying stage, back-dating from date of hatch or floating 2–3 eggs in water to determine the nesting stage if the nest was found after incubation had begun (Westerskov 1950). The duration of clutch initiation was calculated each year for each population as the number of days between the earliest first egg laid and the latest clutch initiation date of the year for all nesting attempts. Values reported in Table 1 were based on annual means ($n = 4$ in the Yukon, $n = 7$ in Colorado).

2. *Clutch size.* Clutch size for first and second attempts was determined as the maximum number of eggs laid per nesting attempt (i.e., completed clutch), defined as those where egg number was constant over two consecutive nest checks. We used a linear regression model to compare the seasonal change in the size of the first nest attempts between the two populations.
3. *Egg mass.* For the first nest attempt, the maximum width and length of a sample of eggs was measured for individual clutches within each population (we lacked sufficient data to compare egg size among second nesting attempts in the Yukon). We first determined the volume for each egg, calculated as $V = kLW^2$ where $k = 0.49$, L = length and W = width (Sandercock et al. 2005a). Egg mass was then calculated as $E = Vg$ where V is egg volume and $g = 1.08$ g/ml, the specific gravity of a chicken egg.
4. *Clutch mass relative to body size.* Average clutch mass of the first attempt was calculated as mean egg mass \times mean first clutch size for each population. We were interested in clutch mass relative to the average non-breeding mass of females but nearly all masses were recorded during the pre-breeding period, a time when females gain mass rapidly for incubation (Braun et al. 1993). As an estimate of non-breeding mass for each population, we conducted a regression of mass against days before the onset of egg laying, which included measurements up to 35 days before egg-laying. We used Akaike's Information Criterion for small samples (AIC_c, Burnham and Anderson 2002) to compare models that allowed for either a linear or curvilinear (quadratic) change in mass over the pre-breeding period and used the top model to estimate female mass at 30 days prior to breeding. We then divided mean clutch mass for the population by the mean early spring body mass of females to derive an estimate of the percent of a female's body mass allocated to the first clutch.
5. *Hatchability.* For each year, we calculated hatchability by dividing the number of eggs that hatched by the number laid in successful nests where at least one young hatched.

Table 1 Body size and breeding traits of white-tailed ptarmigan in the Yukon Territory and Colorado

Trait	Yukon	Colorado	<i>t</i>	<i>P</i>
Pre-breeding mass (g) ^a	352 (336, 367)	394 (387, 402)		
Wing length (mm)	176.6 (169.2, 184.0)	188.0 (187.2, 188.8)	−16.38	<0.001
Mean date of initiation	May 31 (May 22, Jun 9)	June 9 (Jun 5, Jun 14)	−1.98	0.07
Duration of clutch initiation (days)	28.5 (18.6, 38.4)	32.7 (27.6, 37.7)	−0.82	0.43
1st clutch size (no. of eggs)	7.1 (6.8, 7.4)	5.9 (5.7, 6.0)	8.46	<0.001
2nd clutch size	5.3 (4.2, 6.3)	4.7 (4.5, 4.9)	1.78	0.08
Seasonal change in 1st clutch size ^b	−0.04 (−0.06, −0.01)	−0.03 (−0.05, −0.01)		
Egg mass (g)	18.8 (18.4, 19.2)	20.5 (20.2, 20.7)	−5.99	<0.001
1st clutch mass (g)/% investment ^c	134.1/0.380	120.4/0.305		
Hatchability	0.97 (0.93, 1.0)	0.89 (0.85, 0.93)	−3.36	0.007
Incubation length	23.3 (22.5, 24.2)	23.7 (23.5, 24.0)	−1.15	0.26
Re-nesting probability ^d				
Day 2	0.93 (0.70, 1.0)	0.82 (0.69, 0.95)		
Day 8	0.77 (0.39, 1.0)	0.53 (0.38, 0.67)		
Day 14	0.44 (0.16, 0.72)	0.21 (0.07, 0.35)		
Day 20	0.16 (0.0, 0.42)	0.06 (0.0, 0.14)		

Estimates for pre-breeding mass, chick mass at hatch and re-nesting probability are the predicted values from the best fit model. All values in brackets are the 95% confidence intervals. For analyses, Yukon and Colorado individuals were coded 1 and 0, respectively

^a Predicted mass of an individual 30 days before laying her first clutch

^b Slope estimate for first clutch size versus date of first egg

^c Investment refers to the percent of the pre-breeding body mass invested in the first clutch (%)

^d Probability of re-nesting in relation to the age at which the first nest was lost

6. *Renest probability.* Ptarmigan will replace a clutch if their previous clutch is lost prior to hatch, but the probability of re-nesting is dependent on the stage of the nest cycle when the first nest failed (Martin et al. 2011). To examine re-nesting probability, we fit a generalized linear model (binomial distribution, logit link) of whether a female re-nested against the age of the first nest when it was lost.
7. *Chicks hatched/female.* We calculated the average number of young a female hatched in each population (including those females that failed to hatch any chicks) using a generalized linear model with a Poisson distribution.
8. *Nest and chick survival.* We used the nest survival module in program MARK to estimate nest and chick survival. For nest survival estimates, we compared daily nest survival against time of season, but a model with constant survival over time had greater support at both sites (AIC_c constant model $< AIC_c$ time or time²). The constant survival model was then used to compare daily nest survival between populations. Chicks were not individually marked, and instead we used encounters of broods and the number of chicks to build our encounter histories for the nest survival module. This approach requires the assumption that there is no

- movement of chicks between broods. We previously showed that adoption of chicks over the first few weeks after hatch is very rare for white-tailed ptarmigan in the Yukon (0.8% of chicks, Wong et al. 2009) as well as Colorado (0–4%, our unpublished data). We had a priori reasons to believe that chick survival was related to chick age (Braun et al. 1993). Therefore, we first examined models relating survival to chick age (linear and quadratic patterns) and used the best-fit model to predict survival over a 35-day-period. It is likely that the fates of chicks within broods are not independent, and while this does not bias the mean survival estimates, it can lead to an underestimate of the variance (Nichols et al. 1982; Flint et al. 1995). There is currently no suitable goodness-of-fit test for nest survival models in program MARK. Instead, we estimated a variance inflation factor (\hat{c}) as the deviance of the global model/degrees of freedom and used this to correct AIC_c and sampling error.
9. *Adult survival.* We used Cormack-Jolly-Seber models in MARK to estimate apparent annual survival of SY and ASY females and males for each population. At each site we conducted a goodness-of-fit test on the full model (survival and recapture by age) using the median \hat{c} -hat method. Survival estimates are the

product of true survival and the probability that an individual remains in the study area and is available for detection (Sandercock 2006). Our estimates should be considered apparent survival and might be slightly lower than true survival due to emigration.

Population model

To analyze population growth rates, we used female-based matrix models (Caswell 2001; Morris and Doak 2002) constructed in Matlab version 7.1. Variation in the size and age structure of a population from time t to time $t + 1$ can be computed from:

$$n_{t+1} = An_t$$

where n is a vector describing the size structure of the population and A is a population projection matrix. For the projection matrix, we used a two-age pre-breeding model with second-year (SY) and after-second year (ASY) females as the two classes:

$$A = \begin{bmatrix} \text{HY}_1 * S_0 & \text{HY}_2 * S_0 \\ S_1 & S_2 \end{bmatrix}$$

where HY_1 and HY_2 are the number of female young hatched annually by SY and ASY females, respectively, S_0 is the survival rate of juveniles from hatch to the following breeding season, and S_1 and S_2 are the survival rates of adult SY and ASY females. In the same manner as described earlier, we calculated SY and ASY fecundity and survival rates. We incorporated uncertainty in demography by allowing each rate to be drawn from a specified distribution and simulated 10,000 replicates. The number of hatched young were drawn from a stretched beta distribution following Morris and Doak (2002). Stretched beta distributions are suitable for variables that can be described by a beta distribution but do not fall within the 0–1 range. Maximum and minimum values for this distribution were assigned based on likely upper and lower limits for this species (Braun et al. 1993). Annual survival of SY and ASY females was drawn from a beta distribution with mean and variance approximated from field data. We only had juvenile survival estimates for the first 5 weeks after hatch representing the period prior to independence. In a review of juvenile grouse ecology, Hannon and Martin (2006) reported survival rates from independence to the first breeding season for several grouse and ptarmigan species, with an average rate of approximately 0.5. We took our observed values of chick survival multiplied by this estimate to produce a mean juvenile survival rate in each population and assumed the variance in this value to be similar to that for SY adults. Uncertainty in the demographic rates incorporates process

and sampling variation. Therefore, the confidence intervals on the estimate of population growth are conservative and wider than expected based on process variance alone (Gould and Nichols 1998; Sandercock et al. 2005b).

To determine the sensitivity of each population to changes in the demographic rates, we estimated elasticity, the proportional change in λ from a proportional change in a demographic rate (Caswell 2001). Although density-dependent effects and correlations among demographic rates are possible, many years of study are required to identify these relationships, and we do not incorporate them here.

Results

Environmental conditions

The Pika Camp study site in the Yukon was 21 degrees latitude north of the Colorado site (approximately 2,400 km of latitude) and about 2,000 m lower in elevation (Fig. 1; Table 2). Average day length during the pre-breeding period was approximately 3 h longer in the Yukon. Mean temperatures were typically 1–3°C warmer at the Yukon site during the breeding period from May through July, and about 1.5°C colder on average during the winter months (Table 2; Fig. 2). Within the Yukon, temperatures at Pika Camp were very similar to those at MacMillan Pass except during the peak winter months of December and January where they were several degrees warmer, although estimates were based on a small sample size of years (Fig. 2).

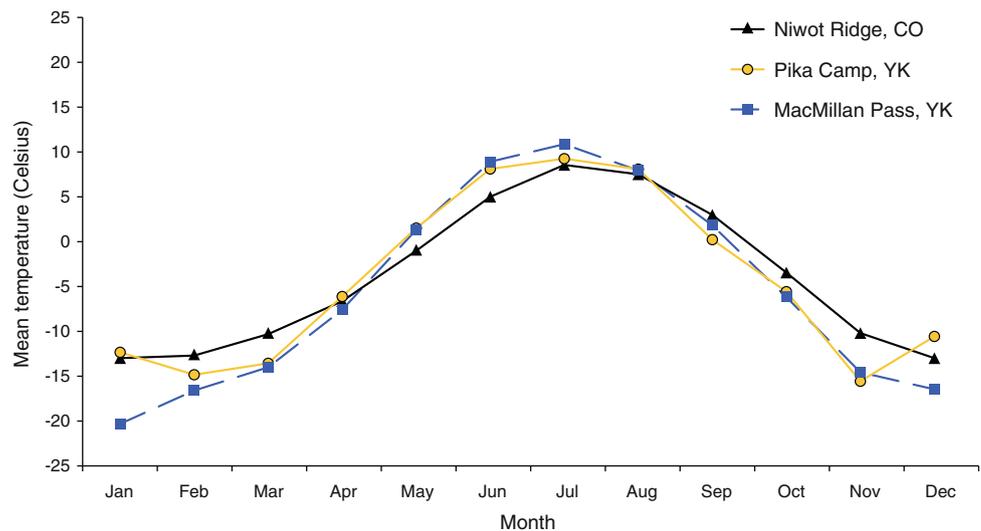
Table 2 Latitude, elevation and environmental conditions at the study sites in the Yukon (2004–2008) and Colorado (1987–1996)

	Yukon	Colorado
Latitude	61.1°N	39.6°N
Elevation (m)	1,475–2,200	3,350–4,250
Average breeding season temperature (°C) ^a		
May	1.8 ± 0.9	−0.9 ± 0.4
June	8.3 ± 1.3	5.2 ± 0.5
July	9.5 ± 0.6	8.8 ± 0.4
Average winter temperature (November–March, °C)	−13.3 ± 3.8	−11.7 ± 0.3
Day length pre-breeding (hours per day)	17.9 ± 0.1	14.8 ± 0.02

Values include the mean and standard error

^a Temperature data for Colorado are based on monthly values at the Niwot Ridge Long-Term Ecological Research site (D-1 Meteorological Station, Greenland 1987) from 1982 to 2006. For the Yukon, temperatures were based on daily temperature loggers at the site and include 4 years for breeding season temperatures (2004–2007) and 2 years for winter temperatures (2004/2005, 2006/2007)

Fig. 2 Mean monthly temperatures in alpine ecosystems at Niwot Ridge, Colorado (39°39'N, 105°35'W, 3,240 m), Pika Camp, Yukon Territory (61°13'N, 138°16'W) and MacMillan Pass, Yukon Territory (63°24'N, 130°04'W, 1,379 m). The MacMillan Pass site was included to provide a second comparison of conditions in the Yukon because of small sample sizes at the Pika Camp study site



Body size and breeding traits

At 30 days prior to breeding, Colorado females were an estimated 37 g (10.4%) heavier than Yukon females and were morphologically larger with wing lengths averaging 11.5 mm (6.5%) longer (Table 1). Clutches were initiated about 9 days earlier in the Yukon, but the overall length of the season was similar between the two populations. Yukon and Colorado ptarmigan showed a significant egg size-clutch size tradeoff for the first nest attempt. First clutches averaged 1.2 eggs larger (20.3% increase) in the Yukon, while the average mass of eggs in those clutches was 1.7 g lower (8.3% decrease, Table 1). The size of the first clutch declined similarly with date of season in both populations. Although there was a tradeoff between egg size and number, females in the Yukon on average allocated 7.5% more of their pre-breeding body mass to the first nest attempt. Incubation lengths for the first nest were approximately 23.5 days for both populations and did not differ significantly. The second nest attempts of Yukon females were 0.5 eggs larger than those for Colorado females, but the sample size was smaller, and there was considerable overlap in the confidence intervals (Table 1). Both populations showed a decline in re-nesting propensity in relation to the age of first nest loss. Yukon females had a higher average probability of re-nesting at all stages of first nest failure at 11% higher in the first week of incubation, 24% at the beginning of the second week and 23% by the third week. However, in all cases the differences were not statistically significant given the wide confidence intervals (Table 1).

Demographic rates

In the Yukon, we monitored the fate of 58 nests from 42 females, while in Colorado we monitored 253 nests from

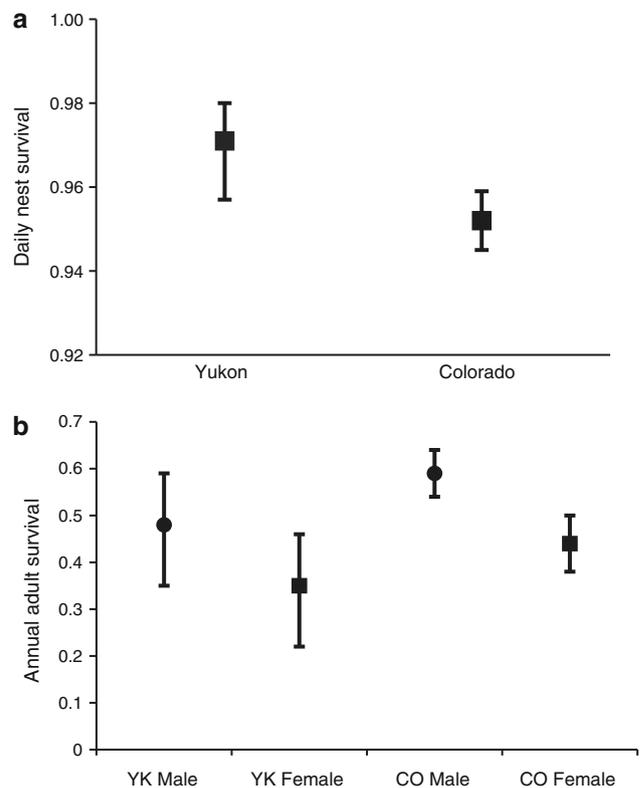


Fig. 3 Estimated mean daily nest survival (a) and annual adult survival (b) for Yukon (YK) white-tailed ptarmigan and Colorado (CO) white-tailed ptarmigan. All estimates were calculated using program MARK. Errors bars represent the 95% confidence intervals

149 females. For analyses of daily nest survival, this represented 839 exposure days for the Yukon and 3,364 for Colorado. Daily nest survival (DNS) for all nests was higher in the Yukon (0.971, 95% CI 0.957–0.980) than in Colorado (0.952, 95% CI 0.945–0.959, Fig. 3a), and the estimates predicted a mean annual nest success of 0.40

(95% CI 0.28–0.56) for Yukon females and 0.24 (0.19–0.30) for Colorado females. The mean number of chicks hatched per female followed a similar pattern. Yukon females produced more than double the number of chicks as Colorado females [generalized linear model, $Z = 8.46$, $P < 0.001$, Yukon 3.92 (3.37–4.47), Colorado 1.77 (1.57–1.97)]. After second year females produced about 42 and 49% more chicks than second year females in the Yukon and Colorado, respectively (Table 3). Hatchability was significantly higher in the Yukon at 97% of eggs compared to 89% in Colorado. Re-nesting contributed 18% of the annual hatched young in the Yukon and 24% in Colorado.

For chick survival, we determined the fates of 146 chicks in the Yukon (2,163 exposure days) and 342 chicks in Colorado (4,711 exposure days). A conservative estimate of over-dispersion was $\hat{c} = 2.29$ for the Yukon and $\hat{c} = 3.12$ in Colorado. Support was greatest for a linear increase in chick survival with age at both sites [Yukon age = 0.105 ± 0.033 (SE), Colorado age = 0.075 ± 0.019]. Using the linear age model we then predicted the survival of chicks to day 35 and estimated a mean rate of 0.52 in the Yukon and 0.38 in Colorado.

To estimate apparent adult survival, we monitored 50 females and 41 males in the Yukon, and 243 females and 257 males in Colorado. There was little evidence of over-dispersion at either site (Yukon $\hat{c} = 1.11$, Colorado $\hat{c} = 1.01$). Adult survival tended to be higher in Colorado, but there was overlap in the confidence intervals for both sexes (Fig. 3b). Annual survival of females was 9% higher in Colorado (0.44, 95% CI 0.38–0.50) compared to the Yukon (0.35, CI 0.24–0.48) and for males was 11% higher in Colorado (0.59, CI 0.54–0.64) than the Yukon (0.48, CI 0.35–0.61). Annual recapture rates were high at both sites

Table 3 Demographic rates and elasticity values for Yukon and Colorado white-tailed ptarmigan for a two age class pre-breeding matrix model

Age group	Yukon		Colorado	
	Rate (\pm SE)	Elasticity	Rate	Elasticity
SY, hatched young	1.59 \pm 0.27	0.267	0.82 \pm 0.16	0.067
ASY, hatched young	2.25 \pm 0.37	0.268	1.22 \pm 0.16	0.214
Juvenile survival	0.26 \pm 0.11	0.536	0.19 \pm 0.05	0.281
SY, survival	0.34 \pm 0.11	0.268	0.42 \pm 0.05	0.214
ASY, survival	0.35 \pm 0.09	0.196	0.46 \pm 0.04	0.505

SY refers to second year females, while ASY refers to after second year females. Juvenile survival was estimated based on observed values during brood-rearing and literature data from Hannon and Martin (2006). Hatched young refers to the number of female young produced per female

(Yukon 0.82, (CI 0.57–0.94), Colorado 0.90, CI 0.85–0.94)).

Population model

Bootstrapped population estimates indicated declining populations at both sites assuming closed populations (Fig. 4). In the Yukon, mean values for λ were 0.83, but the confidence intervals were wide given the error in the demographic rates, and 19% of the simulations predicted stable or growing populations. In Colorado, mean values of λ were 0.66 and individual estimates of λ were <1 for all simulations. The Yukon population was most sensitive to changes in juvenile survival, while survival contributions from SY females were slightly more influential than those from ASY females (Table 3). In contrast, survival of ASY females had the greatest influence on the Colorado population, followed by juvenile survival. Reproductive contributions from ASY females were far more influential than those from SY females in Colorado. Thus, the two populations appear to differ along a life-history continuum with a slower life-history strategy in the southern, high elevation population and a faster strategy in the northern, low elevation population.

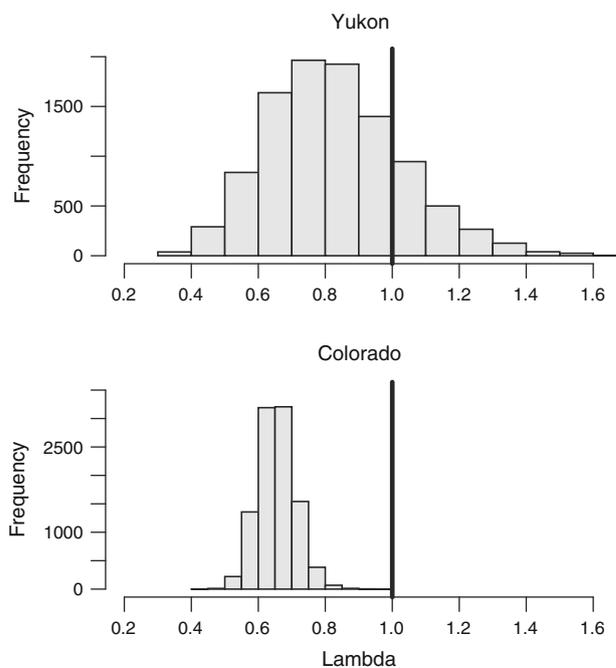


Fig. 4 Frequency distribution for population growth rate estimates of white-tailed ptarmigan in the Ruby Ranges of the southern Yukon Territory (2004–2008) and Mount Evans, Colorado (1987–1996). Estimates were based on 10,000 bootstrapped runs using a pre-breeding two age class matrix model with fecundity and survival data based on field estimates. The **bold line** indicates a stable population with $\lambda = 1$. Smaller sample sizes in the Yukon lead to greater uncertainty in the estimate of λ

Discussion

Life-history variation

Within low-elevation ecosystems, increasing latitude is accompanied by colder temperatures and a shorter breeding season. As a consequence, birds in most northern populations have a delayed onset of breeding to match the delay in spring phenology (Silverin 1995; Dunn 2004), are less likely to re-nest following failure and thus raise fewer broods per season (Collister and Wilson 2007; Camfield et al. 2010), and have a stronger decline in clutch size as the season progresses (Young 1994). Despite a latitudinal difference of over 2,400 km, we did not observe these patterns for white-tailed ptarmigan in alpine environments. The duration of clutch initiation was similar between the two sites (on average 28.5 days in the Yukon and 32.7 in Colorado), as was the likelihood of re-nesting after failure, although it tended to be slightly higher among Yukon females. In comparison with other galliforms, the range of breeding dates observed here approximates those for low-elevation populations at similar latitudes as the Yukon (e.g., Wilson et al. 2007), but is much shorter than those breeding in lower elevations at equivalent latitudes to Colorado, which typically exceed 50 days (e.g., Pitman et al. 2006).

Although the length of clutch initiation differed little between sites, Yukon females initiated breeding 9 days earlier on average than Colorado females. However, the comparison of date of clutch initiation may be somewhat confounded by the study years given that the study in the Yukon occurred 15 years later than the Colorado study and climate change may have led to an advance in breeding dates over that period. Wang et al. (2002) found that median hatch dates of white-tailed ptarmigan in Rocky Mountain National Park, Colorado, advanced by 15 days over the period 1975–1999, and current research on the Mount Evans population indicates that median hatch dates have advanced since 1980 (G. Wann and C.E. Braun, personal communication). Based on these changes, we expect about a 9 day advance in the mean breeding date in Colorado over the past 15 years, and thus timing of breeding may be similar between the two sites. Earlier studies on ptarmigan show a strong relationship between annual breeding date and spring temperature via an influence on timing of snowmelt (Hannon et al. 1988; Martin and Wiebe 2004), and it is very likely that this is the principal ecological mechanism determining the onset of breeding in the two populations studied here.

Most intriguingly, our two populations differed significantly in how they allocated reproductive effort to the first clutch. Mean first clutches in the Yukon were 1.2 eggs larger than those in Colorado (0.056 increase in the number

of eggs per degree of latitude), but mean egg size was 1.7 g lower. Although the larger clutches of Yukon females were partially balanced by smaller eggs, they still allocated a greater proportion of their early spring body mass into the first nest attempt. Clutch size and timing of breeding are often linked (Lack 1968), and thus, if the breeding date has advanced in Colorado, it is possible that clutch sizes are now larger. However, studies have shown that in birds, timing of breeding has responded most strongly to climate warming while other traits such as clutch size respond much less or not at all (Winkler et al. 2002; Torti and Dunn 2005). Thus, while it is possible that mean clutch sizes for the first attempt are now slightly larger in Colorado, it is very unlikely that the sizeable clutch size-egg size tradeoff is only an artifact of the different study periods.

An increase in clutch size with latitude is similar to patterns observed for other species across a range of ecosystems. Among altricial birds, the increase in clutch size per degree of latitude was approximately 0.055 for yellow warblers (*Dendroica petechia*, Salgado-Ortiz et al. 2008), 0.096 for tree swallows (*Tachycineta bicolor*, Dunn et al. 2000) and ranged from 0.003 to 0.299 for seven species of herons (Rubolini and Fasola 2008). Precocial species, including galliforms, appear more variable in clutch size across latitude. Some species have larger clutches at higher latitudes, for example, grey partridge (*Perdix perdix*, 0.267 eggs per degree of latitude, Lack 1947). Other species, including rock (*Lagopus muta*) and willow ptarmigan (*L. lagopus*), are less consistent (Hannon et al. 1998; Holder and Montgomerie 2008), although these two species occur across elevational gradients as well as maritime and continental environments, both of which might confound relationships. For the above studies, we were unable to distinguish between first and subsequent nest attempts and we lacked information on egg size change preventing a full comparison of how investment in first clutches changes with latitude.

Clutch and egg sizes are ultimately adjusted to the maximum number of young that an individual can produce over its lifetime and that survive to reproductive age (Lack 1954; Williams 1966). Because white-tailed ptarmigan are precocial, they are less constrained by the number of young they are able to nourish, a factor strongly limiting investment for altricial species (Lack 1968; Moreno and Carlson 1989). However, they may be restricted by resource acquisition during the pre-breeding period (Lack 1947; Rohwer 1988; Figuerola and Green 2006), the number of young they can care for after hatch (Winkler and Walters 1983) or their ability to effectively cover and incubate a clutch of eggs (Reid 1987), a potentially significant factor for alpine environments where ambient temperatures approach zero nightly during incubation (Wiebe and Martin 2000). Thus, a tradeoff in clutch and egg size is to be

expected, but it is not clear whether the underlying cause of the tradeoff was due to selection for larger clutches further north or larger eggs further south at the higher elevation. As initially proposed by Lack (1947), longer days in the Yukon may allow females to acquire more resources during pre-breeding. However, while this might explain their overall greater investment in the first clutch it does not explain why they lay larger clutches of smaller eggs.

Nest predation is another ecological factor believed to influence clutch size (Slagsvold 1984; Lima 1987). As nest survival declines, individuals are predicted to lay smaller clutches because it shortens the length of the nesting cycle and allows females to maintain reserves for re-nesting should the first attempt fail. Thus, lower nest survival prospects in Colorado may favor smaller clutches, although Colorado females did not appear more likely to re-nest after failure. Also, in a study of two widely separated willow ptarmigan populations, nest survival, re-nesting potential and clutch size were all higher in one population, indicating little relationship between nest predation and re-nesting propensity for a congener in similar habitats (Wilson et al. 2007; Martin et al. 2011). It is also possible that environments with high predation pressure, such as Colorado, select for larger eggs and thus larger chicks at hatch (Grant 1991; Blomqvist et al. 1997). Additional studies across other populations that focused on the effects of predators as well as the influence of hypoxia, severe weather and nutrient limitation would be useful to examine this clutch size-egg size tradeoff further.

Demographic variation and population change

Yukon females produced more than twice as many chicks annually as did Colorado females. This difference was primarily related to the low nest survival rates in Colorado, but was also aided by greater hatchability and first clutch investment in the Yukon. Ground-nesting species like grouse often have low nest success with failure largely driven by avian and mammalian nest predators (Pitman et al. 2006; Moynahan et al. 2007; Wilson et al. 2007). In Colorado, the primary nest predators were coyote (*Canis latrans*), red fox (*Vulpes vulpes*) and long-tailed weasel (*Mustela frenata*), while avian nest predation was less common (Wiebe and Martin 1998). In the Yukon, red foxes and arctic ground squirrels (*Spermophilus parryii*) were the primary mammalian nest predators, while golden eagles (*Aquila chrysaetos*) and short-eared owls (*Asio flammeus*) frequently killed incubating females (Wilson 2008). Nest success of rock ptarmigan (*Lagopus muta*) at the Yukon site averaged 0.32, indicating differences can occur even among sympatric species exposed to the same predator community (Wilson 2008). Elsewhere, apparent nest success of white-tailed ptarmigan in the Sierra Nevada was

0.36 over 6 years (Clarke and Johnson 1992), while mean nest success of willow ptarmigan (*Lagopus lagopus*) was 0.34 at Chilkat Pass, British Columbia, and 0.42 at La Pérouse Bay, Manitoba (Wilson et al. 2007). Thus, our two study populations have nest success rates within the typical range for ptarmigan, but at the low end for Colorado and the high end for the Yukon.

Adult survival showed the opposite pattern and was higher in Colorado, although there was overlap in the confidence intervals. This slight difference in adult survival may have been related to the intrinsic costs of higher reproductive effort (Golet et al. 2004). Not only did Colorado females invest less in the first attempt, but with lower nest survival, fewer females would incur the costs of protecting young after hatch, which remain with them until early fall (Braun et al. 1993). The risk of extrinsic mortality due to factors such as predators, severe weather and disease may also be lower in Colorado. During the breeding season, avian predation appeared to be the principal cause of adult mortality at both sites as it is for grouse generally (Valkama et al. 2005), but because we were unable to follow individuals throughout the year, the causes of mortality are poorly known during the non-breeding period. We previously found evidence for a reproduction-adult survival tradeoff between sympatric white-tailed and rock ptarmigan in the Yukon (Wilson and Martin 2010). Rock ptarmigan invest less in reproduction and produce fewer young than white-tailed ptarmigan, but have approximately 22% higher adult survival. Differing susceptibility to extrinsic sources of mortality may have influenced reproductive investment between the two species in the Yukon and may have been a contributing factor to the differences in survival between Yukon and Colorado white-tailed ptarmigan.

Our estimates of mean population growth (λ) indicated declines for both populations, although more severe in Colorado. Thus, while reproductive rates in the Yukon and survival rates in Colorado were reasonable compared to other ptarmigan populations, the low survival in the Yukon and low fecundity in Colorado meant that insufficient numbers of females were contributing to the population. However, despite the very low estimates of lambda, the Colorado population has persisted for more than 45 years based on detailed studies (Braun et al. 1993; Martin et al. 2000), and breeding records for ptarmigan on Mount Evans extend back to the late 19th century (Lewis 1904). Our estimates of lambda assumed a closed population, but inter-population movement, which is mostly by juveniles, may be frequent and key to population persistence as well as to the recovery of local populations following declines (Martin et al. 2000; Fedy et al. 2009). Thus, the population we studied may be a local sink within a larger, stable meta-population where sources allow for persistence through

immigration. It is also possible that we underestimated some demographic rates. For instance, if dispersal of adult females is more common than expected, our estimates of adult survival may be biased low. Our model was also based on a short number of years, especially in the Yukon, and it is possible that we captured the populations during a declining stage when longer term growth rates were more stable. Ptarmigan populations cycle in many regions with a 5- to 10-year-period (Bergerud and Gratson 1988), and a short window of demographic data may only select one stage of the cycle. The Colorado study likely encompassed a full population cycle, but additional demographic study during years of low density would be valuable in the Yukon.

Our life-history comparison among populations of an alpine specialist allowed us to control for some environmental features of latitude and thus estimate the influence of seasonality on life-history variation within a species. In comparison with species that inhabit lower latitudes, our findings support the idea that annual reproductive effort as reflected in the range of clutch initiation dates and re-nesting propensity was influenced by seasonality. In contrast, seasonality did not appear to influence the allocation of effort to clutch versus egg size as white-tailed ptarmigan displayed patterns that are commonly observed for a range of species. Other factors such as predation pressure may be more plausible mechanisms behind clutch size-egg size tradeoffs in ptarmigan.

Acknowledgments We thank the many able field assistants who helped collect data in the field during these two studies, including D. Chalmers, A. Clason, S. Nouvet, G. Pelchat, A. Wilson and M. Wong for the Yukon study, and T. Artiss, L. Robb, K. Wiebe and many undergraduates for the Colorado study. We thank D.S. Hik, A. and S. Williams, and L. Goodwin for providing logistical support at Pika Camp and the Arctic Institute of North America at Kluane Lake, YK, Canada. C.E. Braun, Colorado Division of Wildlife (Fort Collins, CO, USA) provided critical logistical assistance for the duration of the Colorado study, and M. Mossop and L. Robb provided able technical assistance. Funding for the research on both sites was provided by Natural Sciences and Engineering Research Council of Canada (NSERC; Discovery Grant, Northern Research Supplement, International Polar Year) and Environment Canada support to KM, and NSERC Postgraduate Scholarship, Northern Scientific Training Program, British Columbia Upland Birds Society, Calgary Bird Banding Society, UBC Department of Forestry, and Izaak Walton Killam and University Graduate Fellowships to SW. We thank Cameron Aldridge and an anonymous reviewer for helpful comments in revising this manuscript.

References

- Badyaev AV (1997) Avian life-history variation along altitudinal gradients: an example with cardueline finches. *Oecologia* 111:365–374
- Bears H, Martin K, White GC (2009) Breeding in high elevation habitat results in shift to slower life-history strategy within a single species. *J Anim Ecol* 78:365–375
- Bergerud AT, Gratson MW (1988) Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minnesota
- Blomqvist D, Johansson OC, Götmark F (1997) Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. *Oecologia* 110:18–24
- Braun CE, Martin K, Robb LA (1993) White-tailed ptarmigan (*Lagopus leucura*). In: Poole A (ed) The birds of North America online. Cornell Lab of Ornithology, Ithaca, Retrieved from the birds of North America online: <http://bna.birds.cornell.edu/bna/species/068>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Camfield AF, Pearson SF, Martin K (2010) Life-history variation between high and low elevation subspecies of horned larks *Eremophila* spp. *J Avian Biol* 41:273–281
- Caswell H (2001) Matrix population models: construction, analysis and interpretation. Sinauer Associates, Sunderland
- Clark ME, Martin TE (2007) Modeling tradeoffs in avian life-history traits and consequences for population growth. *Ecol Model* 209:110–120
- Clarke JA, Johnson RE (1992) The influence of spring snow depth on white-tailed ptarmigan breeding success in the Sierra Nevada. *Condor* 94:622–627
- Collister DM, Wilson S (2007) Contributions of weather and predation to reduced breeding success in a threatened northern Loggerhead Shrike population. *Avian Cons Ecol* 2:11
- Dunn PO (2004) Breeding dates and reproductive performance. In: Møller AP, Fiedler W, Berthold P (eds) Birds and climate change. Advances in ecological research, vol 35. Elsevier, San Diego, pp 67–85
- Dunn PO, Thusius KJ, Kimber K, Winkler DW (2000) Geographic and ecological variation in clutch size of tree swallows. *Auk* 117:215–221
- Fedy BC, Martin K, Ritland C, Young J (2009) Genetic and ecological data provide incongruent interpretations of population structure and dispersal in naturally subdivided populations of white-tailed ptarmigan (*Lagopus leucura*). *Mol Ecol* 17:1905–1917
- Figuerola J, Green AG (2006) A comparative study of egg mass and clutch size in the Anseriformes. *J Ornithol* 147:57–68
- Flint PL, Pollock KH, Thomas D, Sedinger JS (1995) Estimating pre fledgling survival: allowing for brood mixing and dependence among brood mates. *J Wildl Manage* 59:448–455
- Folk TH, Holmes RR, Grand JB (2007) Variation in northern bobwhite demography along two temporal scales. *Popul Ecol* 49:211–219
- Frederiksen M, Harris MP, Wanless S (2005) Inter-population variation in demographic parameters: a neglected subject? *Oikos* 111:209–214
- Golet GH, Schmutz JA, Irons DB, Estes JA (2004) Determinants of reproductive costs in the long-lived black-legged kittiwake: a multi-year experiment. *Ecol Monogr* 74:353–372
- Gould WR, Nichols JD (1998) Estimation of temporal variability of survival in animal populations. *Ecology* 79:2531–2538
- Grant MC (1991) Relationships between egg size, chick size at hatching and chick survival in the Whimbrel *Numenius phaeopus*. *Ibis* 133:127–133
- Greenland DE (1989) The climate of Niwot Ridge, Front Range, Colorado, USA. *Arct Alpine Res* 21:380–391
- Hannon SJ, Martin K (2006) Ecology of juvenile grouse during the transition to adulthood. *J Zool* 269:422–433
- Hannon SJ, Martin K, Schieck JO (1988) Timing of reproduction in two populations of willow ptarmigan in Northern Canada. *Auk* 105:330–338

- Hannon SJ, Eason PK, Martin K (1998) Willow ptarmigan (*Lagopus lagopus*). In: Poole A (ed) The birds of North America Online. Cornell Lab of Ornithology, Ithaca, Retrieved from the birds of North America online: <http://bna.birds.cornell.edu/bna/species/369>
- Holder K, Montgomerie R (2008) Rock ptarmigan (*Lagopus muta*). In: Poole A (ed) The birds of North America online. Cornell Lab of Ornithology, Ithaca, Retrieved from the birds of North America online: <http://bna.birds.cornell.edu/bna/species/051>
- Jetz W, Sekercioglu CH, Böhning-Gaese K (2008) The worldwide variation in avian clutch size across species and space. *Plos Biol* 6:2650–2657
- Johnson LS, Ostlind E, Brubaker JL, Balenger SL, Johnson BGP, Golden H (2006) Changes in egg size and clutch size with elevation in a Wyoming population of Mountain Bluebirds. *Condor* 108:591–600
- Krementz DG, Handford P (1984) Does avian clutch size increase with altitude? *Oikos* 43:256–259
- Lack D (1947) The significance of clutch size. *Ibis* 89:302–352
- Lack D (1954) The evolution of reproductive rates. In: Huxley JS, Hardy AC, Ford EB (eds) Evolution as a process. Allen and Unwin, London, pp 143–156
- Lack D (1968) Ecological adaptations for breeding in birds. Methuen and Co, London
- Lewis E (1904) The nesting habits of the white-tailed ptarmigan in Colorado. *Bird Lore* 6:117–121
- Lima SL (1987) Clutch size in birds: a predation perspective. *Ecology* 68:1062–1070
- Lu X (2005) Reproductive ecology of blackbirds (*Turdus merula maximus*) in a high altitude location, Tibet. *J Ornithol* 146:72–78
- Martin TE (2004) Avian life-history evolution has an eminent past: does it have a bright future. *Auk* 121:289–301
- Martin K, Wiebe KL (2004) Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. *Integr Comp Biol* 44:177–185
- Martin K, Stacey PB, Braun CE (2000) Recruitment, dispersal and demographic rescue in spatially structured white-tailed ptarmigan populations. *Condor* 102:503–516
- Martin TE, Bassar RD, Bassar SK, Fontaine JJ, Lloyd P, Mathewson HA, Niklison AM, Chalfoun A (2006) Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution* 60:390–398
- Martin K, Wilson S, Hannon SJ (2011) Mechanisms underlying variation in re-nesting ability of willow ptarmigan. *Stud Avian Biol* (in press)
- Moreno J, Carlson A (1989) Clutch size and the cost of incubation in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scand* 20:123–128
- Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland
- Moynahan BJ, Lindberg MS, Rotella JJ, Thomas JW (2007) Factors affecting nest survival of Greater Sage Grouse in Northcentral Montana. *J Wildl Manage* 71:1773–1783
- Nichols JD, Stokes SL, Hines JE, Conroy MJ (1982) Additional comments on the assumption of homogenous survival rates in modern bird banding estimation models. *J Wildl Manage* 46:953–962
- Pitman JC, Hagen CA, Jamison BE, Robel RJ, Loughin TM, Applegate RD (2006) Nesting ecology of Lesser Prairie Chickens in sand sagebrush prairie of southwestern Kansas. *Wilson J Ornithol* 118:23–35
- R Development Core Team (2009) R: A language and environment for statistical computing, reference index version 2.10.1. R Foundation for Statistical Computing, Vienna Austria. <http://www.R-project.org>
- Reid WV (1987) Constraints on clutch size in the Glaucous-winged Gull. *Stud Avian Biol* 10:8–25
- Ricklefs RE (2000) Density dependence, evolutionary optimization, and the diversification of avian life-history histories. *Condor* 102:9–22
- Rohwer FC (1988) Inter- and intraspecific relationships between egg and clutch size in waterfowl. *Auk* 105:161–176
- Rubolini D, Fasola M (2008) Geographic patterns in reproductive parameters among Nearctic herons (Ardeidae). *Auk* 125:374–383
- Sæther BE, Bakke Ø (2000) Avian life-history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653
- Sæther BE, Lillegård M, Grøtan V, Drever MC, Engen S, Nudds TD, Poduzny KM (2008) Geographical gradients in the population dynamics of North American ducks. *J Anim Ecol* 77:869–882
- Salgado-Ortiz J, Marra PP, Sillett TS, Robertson RJ (2008) Breeding ecology of the Mangrove Warbler (*Dendroica petechia bryanti*) and comparative life-history of the Yellow Warbler subspecies complex. *Auk* 125:402–410
- Sandercocock BK (2006) Estimation of demographic parameters from live encounter data: a summary review. *J Wildl Manage* 70:1504–1520
- Sandercocock BK, Martin K, Hannon SJ (2005a) Life-history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. *Ecology* 86:2176–2186
- Sandercocock BK, Martin K, Hannon SJ (2005b) Demographic consequences of age structure in extreme environments: population models for arctic and alpine ptarmigan. *Oecologia* 146:13–24
- Silverin B (1995) Reproductive adaptations to breeding in the north. *Am Zool* 35:191–202
- Slagsvold T (1984) Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *J Anim Ecol* 53:945–953
- Torti VM, Dunn PO (2005) Variable effects of climate change on six species of North American birds. *Oecologia* 145:486–495
- Valkama J, Korpimäki E, Arroyo B, Beja P, Bretagnolle V, Bro E, Kenward R, Mañosa S, Redpath SM, Thirgood S, Viñuela J (2005) Birds of prey as limiting factors of gamebird populations in Europe: a review. *Biol Rev* 80:171–203
- Wang G, Hobbs NT, Giesen KM, Galbraith H, Ojima DS, Braun CE (2002) Relationships between climate and population dynamics of white-tailed ptarmigan *Lagopus leucurus* in Rocky Mountain National Park, Colorado, USA. *Clim Res* 23:81–87
- Westerskov K (1950) Methods for determining the age of game bird eggs. *J Wildl Manage* 14:56–67
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139
- Wiebe KL, Martin K (1998) Costs and benefits of nest cover for ptarmigan: changes within and between years. *Anim Behav* 56:1137–1144
- Wiebe KL, Martin K (2000) The use of incubation behavior to adjust avian reproductive costs after egg laying. *Behav Ecol Sociobiol* 48:463–470
- Williams GC (1966) Natural selection, the cost of reproduction and a refinement of Lack's principle. *Am Nat* 100:687–690
- Wilson S (2008) Influence of environmental variation on habitat selection, life-history strategies and population dynamics of sympatric ptarmigan in the southern Yukon Territory. PhD dissertation, University of British Columbia Press, Vancouver
- Wilson S, Martin K (2008) Breeding habitat selection of sympatric White-tailed, Rock, and Willow ptarmigan in the southern Yukon Territory, Canada. *J Ornithol* 149:629–637
- Wilson S, Martin K (2010) Variable reproductive effort for two sympatric ptarmigan in response to spring weather conditions in a northern alpine ecosystem. *J Avian Biol* 41:319–326
- Wilson S, Martin K, Hannon SJ (2007) Nest survival patterns in willow ptarmigan: influence of time, nesting stage and female characteristics. *Condor* 109:377–388

- Winkler DW, Walters JR (1983) The determination of clutch size in precocial birds. *Curr Ornithol* 1:33–68
- Winkler DW, Dunn PO, McCulloch CE (2002) Predicting the effects of climate change on avian life history traits. *Proc Nat Acad Sci USA* 99:13595–13599
- Wong ML, Fedy BC, Wilson S, Martin K (2009) Adoption in rock and white-tailed ptarmigan. *Wilson J Ornithol* 121:638–641
- Young BE (1994) Geographic and seasonal patterns of clutch size variation in House Wrens. *Auk* 111:545–555