Articles

Variable reproductive effort for two ptarmigan species in response to spring weather in a northern alpine ecosystem

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Predicting how animal populations respond to climate change requires knowledge of how species traits influence the response of individuals to variation in annual weather. Over a four-year study with two warm and two cold years, we examined how sympatric rock ptarmigan *Lagopus muta* and white-tailed ptarmigan *L. leucura* in the southern Yukon Territory respond to spring weather in terms of breeding phenology and the allocation of reproductive effort. The onset of breeding was approximately synchronous; for each one-degree rise in spring temperature, mean breeding dates of rock and white-tailed ptarmigan advanced by about 2.7 and 4 days respectively. Although onset of breeding was similar, the two species differed in their reproductive effort. As breeding was delayed, average first clutch sizes of rock ptarmigan declined from 9.4 to 5.8 eggs over the breeding period, while those of white-tailed ptarmigan only declined from an average of 7.8 to 6.8. Rock ptarmigan were also less likely to re-nest if their first clutch was lost to predators and as a consequence they had shorter breeding seasons. White-tailed ptarmigan produced about 25% more offspring annually than rock ptarmigan and contributed more young through re-nesting. While white-tailed ptarmigan had higher annual reproductive output, adult rock ptarmigan had a 20–25% higher annual survival rate, which may indicate a reproduction–survival trade-off for the two species. These results show that even within the same location, closely related species can differ in how they allocate effort as environmental conditions fluctuate.

Variation in annual breeding phenology in birds has strong implications for individual fitness. Broad cues, such as photoperiod interacting with endogenous rhythms, typically bring an individual into breeding condition (Dawson et al. 2001). Additional stimuli are then used to fine-tune the actual onset of breeding including environmental conditions, population density, vegetation phenology and social interactions (Wingfield and Moore 1987, Arcese and Smith 1988, Martin and Wiebe 2004). Individual characteristics such as age and previous reproductive experience also influence timing of breeding (Wilson et al. 2007a). For many north-temperate birds, temperature is a key determinant of breeding date (Ludwig et al. 2006, Høye et al. 2007, Visser et al. 2009). Breeding is typically delayed by cold spring temperatures due to a reduction in potential nest sites (Hannon et al. 1988, Madsen et al. 2007), lower food availability (Arcese and Smith 1988, Møller 2008) and increased thermoregulatory costs for adults (Wiebe and Martin 2000). Delayed breeding often lowers annual fecundity because of smaller clutches and less time for re-nesting following either a failed attempt or a successfully raised brood (Martin et al. 1989, Wilson and Arcese 2003).

Mean breeding dates have advanced in many bird populations as spring temperatures have increased over the past few decades (Root et al. 2003), a shift largely attributed to

behavioural plasticity rather than microevolution (Przybylo et al. 2000, Charmantier et al. 2008). However, not all populations respond equally and this has raised questions on what mechanisms interact to influence breeding date and how these constraints will affect the response to further climate change. For instance, many European *Parus* populations vary in their phenological response to rising temperatures, even those within close proximity to one another, suggesting other life history characteristics influence the interaction between temperature and timing of breeding (Visser et al. 2003). Other examples include blue tit *Cyanistes caeruleus* populations in Corsica, which vary in timing of breeding across habitat type (Lambrechts and Dias 1993) and Argentinean *Poospiza* finches, whose breeding dates are influenced by species-specific foraging habits (Mezquida and Marone 2003).

In other cases, sympatric species may respond similarly to spring conditions in determining when to breed, but differ in how they allocate reproductive effort, either to the first attempt or the number of nesting attempts. Adjustment of reproductive effort within a season can be accomplished via changes in clutch or egg size, whether or not they re-nest following failure, the number of broods they raise and the extent of parental care. For example, sympatric western sandpipers *Calidris mauri* and semipalmated sandpipers

C. pusilla breed synchronously in Alaska, but differ in how they adjust egg versus clutch size when breeding is delayed (Sandercock et al. 1999, see also Ligi and Omland 2007). Although greater reproductive effort should enhance annual fecundity, it also raises an individual's energetic costs, which may lower their future reproductive effort or the likelihood of surviving through the non-breeding period (Jacobsen et al. 1995, Nager et al. 2001). The benefits and costs of allocating effort to reproduction under differing environmental conditions may vary among species depending on the overall life history strategy and the constraints imposed by that strategy (Both and Visser 2001, Sæther et al. 2004). However, the extent of interspecific variation in this response and the mechanisms underlying it are poorly known.

Over a five year period (2004–2008), we examined how sympatric rock ptarmigan *Lagopus muta* and white-tailed ptarmigan *L. leucura* in the southern Yukon Territory, Canada responded to annual variability in spring weather in their onset of breeding and allocation of reproductive effort. The two species are resident in the region and share a similar ecology (Braun et al. 1993, Holder and Montgomerie 2008). Females of both species breed at age one and raise a single brood of precocial young, but will re-nest following failure. Incubation and parental care is performed solely by the female. Males defend a territory and remain until mid to late incubation after which they leave and join flocks of other males and failed female breeders.

During the study there were two warm and two cold years during the pre-breeding period; because the two species experienced the same environmental conditions, this allowed for a natural experiment on how each responds to annual variation in those conditions. We first examined how temperature (a surrogate measure for weather including effects of snow melt and vegetation phenology) during the pre-breeding period influenced the onset of breeding. Although only four years were available, we found a significant negative effect of temperature on breeding date for both species. Given this, we asked whether the two species allocated reproductive effort similarly in terms of clutch size, egg mass and the likelihood of re-nesting in relation to date of first nest loss. We examined how reproductive effort influenced annual fecundity and compared annual survival for the two species to examine the potential costs of that effort and to consider whether individuals of each species might differ in susceptibility to the conditions of the region.

Material and methods

Study area and field methods

Field work was conducted from May through July of 2004–2008 on a 10 km^2 alpine site in the Ruby Range Mountains of the southern Yukon Territory, Canada (61°13′N, 138°16′W). Only information on survival was collected in 2008. Rock and white-tailed ptarmigan were distributed throughout the site at densities of about 2–4 and 1–3 pairs km^{-2}, respectively. White-tailed ptarmigan territories tend to occur at higher elevation, on steeper slopes and contain a greater ground cover of rock compared to rock ptarmigan territories (Wilson and Martin 2008). However,

because of heterogeneity in slope and ground cover, territories of the two species were evenly dispersed throughout the study site and they displayed intra- and interspecific territoriality.

Individuals were caught with ground nets or noose poles prior to breeding and then weighed, aged (second-year (SY) or after second-year (ASY)) and colour-banded for individual recognition. Average pre-breeding mass of female rock ptarmigan (411 g ± 21 (SD)) was about 15% greater than female white-tailed ptarmigan (357 g ± 8). Females were fit with a 4 or 7 g radio-transmitter and re-located every 2–3 d until the nest was found. For about two thirds of individuals, the transmitter was removed at the end of the breeding season, while for the remainder it was left on until the start of the following season.

After breeding began, we located all nests using telemetry. Once found, a small I-button temperature logger was placed in the side of the nest, which allowed us to determine onset of incubation and the precise time of failure or hatch. For all nests, we determined date of first egg, maximum clutch size, clutch fate and if successful, the number of young hatched. Date of first egg was estimated by observing nests during laying, back-dating from hatch or floating an egg during incubation following the method of Westerskov (1950). In 2005 and 2006, we measured the width and length of 1 or 2 eggs per nest, which were used to calculate average egg mass for each species. Each year we also conducted extensive surveys of the adjacent regions of the study area to locate individuals for annual survival estimates.

Data analysis

Statistical analyses were performed using general and generalized linear models in R (R Development Core Team 2008). We initially focused on four main questions: 1) how spring temperature affects mean timing of breeding for each species, 2) how an individual's breeding date affects clutch size and the number of hatched young, 3) whether mean egg mass differed in years of early versus late breeding, and 4) how the date at which the first nest was lost affected the probability of re-nesting. The influence of temperature on breeding date was examined with a linear model (normal distribution) of mean date of first egg against spring temperature from 13 April to 13 May. This period was chosen because 14 May was the earliest date of first egg during the study and the month prior to breeding is when females returned to territories and built up body reserves for incubation. Temperature data were obtained from the nearest Environment Canada station at Burwash Landing, 50 km southwest of our site (<http://climate.weatheroffice. ec.gc.ca/climateData>). To address the 2nd and 4th question above, we only used one first nesting attempt per female (randomly selected if she bred in multiple years). We used a linear model with a normal distribution to compare date of first egg and clutch size, and a generalized linear model with a Poisson distribution (log link) to compare date of first egg against number of hatched young. We used a generalized linear model with a binomial distribution and a logit link to examine how date of loss of the first clutch affected the probability of re-nesting for

each species. Because we could not determine the exact date when a particular egg was laid, we compared mean egg mass between years of early (2005) and late (2006) breeding. Following the approach of Sandercock et al. (2005), we first determined egg volume as $V = kLW^2$ where $k = 0.49$, $L =$ length and $W =$ width and then calculated egg mass as $E = Vg$, where V is egg volume and $g = 1.08$ g ml^{-1}, the specific gravity of a chicken egg.

We estimated apparent annual survival of adults using program MARK (White and Burnham 1999) with species and sex as group variables. We conducted a goodness of fit test on the full model but found no evidence of over-dispersion (median ĉ method, ĉ = 0.99). Survival estimates were obtained from models that allowed for a separate recapture estimate for each species. Our aim was to estimate average annual survival, and therefore, we present the results for each species and sex without time.

Results

Spring temperature and date of first egg

Spring temperatures varied markedly during the study with two warm years in 2004–2005 and two cold years in 2006–2007 (Table 1). Average date of first egg for both species showed a strong and significant relationship to temperature from mid-April to mid-May (n = 4 years, rock ptarmigan: $_{temp} = -2.69$ (95% CI: −3.30, −2.08), adj $r^2 = 0.96$, P = 0.01; white-tailed ptarmigan: $_{temp} = -4.05$ (−5.81, −2.89), adj $r^2 = 0.94$, p = 0.02, Fig. 1a–b). The coefficients indicate that for each one degree rise in spring temperature, breeding dates of rock and white-tailed ptarmigan advanced by approximately 2.7 and 4 days respectively. Cessation of breeding showed little relation to spring temperature for either species but was later for white-tailed ptarmigan by 5 to 17 days across years (Table 1).

Interspecific variation in reproductive effort

Over the four years we monitored 86 rock ptarmigan nests from 57 females and 58 white-tailed ptarmigan nests from 42 females (Table 1). Using data from all years, clutch size of the first attempt decreased with later laying for both species (Fig. 2), but the rate of decline was considerably steeper for rock ptarmigan with no overlap in the slope estimate intervals (Rock: $_{dfe} = -0.146$ (95% CI: −0.187, −0.104), adj $R^2 = 0.47$, p < 0.001, n = 54 nests; white-tailed: $_{dfe} = -0.035$ (−0.063, −0.007), adj $R^2 = 0.13$, p = 0.017, n = 37). Based on the regression equation, rock ptarmigan would have a mean clutch size of 9.4 on the earliest date of first egg (day 135, 14 May) and 5.8 on the latest (day 160, 8 June). Over the same time period, the equation for white-tailed ptarmigan predicts a mean change from 7.8 to 6.8. Within years, the slope estimates were also negative for both species, but in every year the intervals overlapped zero. For both species, there were no statistically significant differences between mean egg mass (g) in 2005 (warm, early) compared to 2006 (cold, late) (rock ptarmigan 2005 = 19.6 g (95% CI: 18.8, 20.4), 2006 = 19.2 g (18.3, 20.0), $F_{1,43} = 0.61$, p = 0.43; white-tailed ptarmigan 2005: 19.0 g (18.4, 19.5), 2006: 18.4 g (17.9, 18.9), $F_{1,38} = 2.84$, p = 0.10).

For rock and white-tailed ptarmigan, the probability of re-nesting declined in a sigmoidal pattern as the date of first nest loss increased, however the timing differed (Fig. 3). For rock ptarmigan, re-nesting probability was >80% through 29 May, but declined to less than 20% by 8 June. In contrast, white-tailed ptarmigan maintained a high re-nest probability for approximately 15 days longer before declining after 13 June. The number of hatched young declined significantly with later laying for both species (rock ptarmigan: $_{dfe} = -0.035$ (SE = 0.012), p = 0.003, n = 55; white-tailed ptarmigan: $_{dfe} = -0.026$ (SE = 0.009), p = 0.004, n = 40). Rock ptarmigan hatched fewer young annually (mean = 2.96, SE = 0.47) than white-tailed ptarmigan (mean = 3.88, SE = 0.51, $_{white-tailed} = 0.27$ (SE = 0.11), p = 0.01) and contributed fewer young through re-nest attempts (8% of hatched young vs 18% for white-tailed ptarmigan). Fewer young were produced overall in 2006, but there was little evidence that white-tailed ptarmigan hatched more young than rock ptarmigan in colder years (Table 1).

Interspecific variation in annual adult survival and between year breeding dispersal

For females and males respectively, rock ptarmigan annual survival rates averaged 22 and 24% higher than for

Table 1. Pre-breeding temperature and timing of breeding for rock and white-tailed ptarmigan in the southern Yukon Territory. Pre-breeding temperature refers to the average daily temperature (°C) from 13 April to 13 May (earliest date of first egg on 14 May). Date of last attempt refers to the last date a clutch was initiated each year including re-nests.

|	2004	2005	2006	2007
Pre-breeding temperature (mean)	3.74	5.14	0.23	1.46
Rock ptarmigan				
Mean date of first egg for the first attempt (95% CI in brackets)	144.2 (142.3, 146.0)	142.1 (139.4, 144.7)	154.3 (153.1, 155.6)	152.5 (146.2, 159.0)
Date of last attempt	162	159	160	168
Total nests	24	28	27	7
Mean hatched young year^{-1} (SE in brackets)	3.20 (1.36)	3.28 (0.85)	2.29 (0.69)	4.00 (1.34)
White-tailed ptarmigan				
Mean date of first egg	146.3 (137.4, 155.1)	140.4 (138.9, 141.9)	158.9 (156.8, 160.9)	158.3 (148.1, 168.1)
Date of last attempt	170	176	174	173
Total nests	6	23	22	7
Mean hatched young year^{-1} (SE in brackets)	6.67 (0.67)	4.43 (0.84)	2.94 (0.76)	4.00 (1.70)
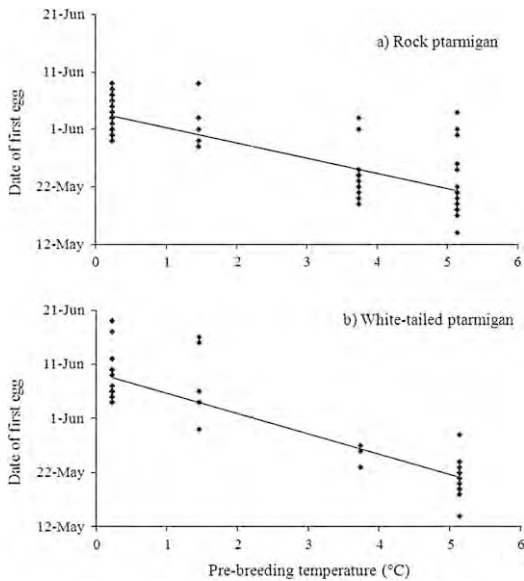
Figure 1. Date of first egg in relation to pre-breeding temperature for (a) rock and (b) white-tailed ptarmigan in the southern Yukon Territory. Each point represents an observation for a single female. Pre-breeding temperature refers to the mean daily temperature from mid-April (13 Apr) to mid-May (13 May).

white-tailed ptarmigan (Table 2). Within species, survival rates of males were higher than for females, 14% for rock ptarmigan and 13% for white-tailed ptarmigan, respectively. During the study, 20 female rock ptarmigan and 13 female white-tailed ptarmigan had radio-collars through the non-breeding period, allowing us to search over approximately 100 km^2 the following season for evidence of long-distance breeding dispersal. Of these individuals, 14 rock and 6 white-tailed ptarmigan were re-located the following spring and all returned to the study area, typically the same breeding territory as in the previous year. Thus, the higher apparent survival of rock ptarmigan females does not appear to be related to a greater tendency for long-distance breeding dispersal among years.

Discussion

Warmer spring temperatures lead to earlier breeding

Over four years, mean onset of breeding was similar in rock and white-tailed ptarmigan, but varied by about 2–3 weeks over the latter half of May and early June. Synchrony in breeding phenology of each species suggests they are responding to the same environmental cues. Onset of egg-laying occurred earlier when spring temperatures in the month prior to breeding were warmer, similar to findings for other temperate zone birds including grouse (Root et al. 2003, Ludwig et al. 2006). Females may be encouraged to lay eggs earlier if warmer temperatures advance snowmelt, which would increase available nesting and foraging habitat, and stimulate vegetative growth and insect activity (Martin and Wiebe 2004, Høye et al. 2007). Cotter (1999) found that rock ptarmigan in the Canadian Arctic began breeding shortly after snow cover declined to less than 50% of the territory area. Similar effects of snow
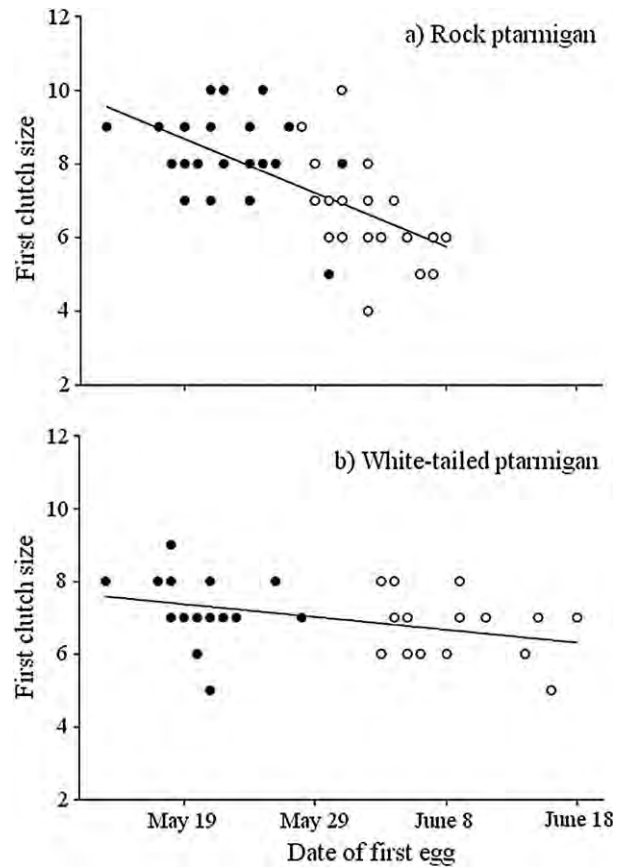

Figure 2. Change in clutch size in relation to date of first egg of the first nest attempt for rock (n = 54) and white-tailed ptarmigan (n = 37) in the Yukon Territory, Canada. Solid and open circles refer to breeding attempts during the two warm (2004–2005) and two cold (2006–2007) seasons, respectively.

cover were noted for white-tailed ptarmigan in the Sierra Nevada of California (Clarke and Johnson 1992) and for willow ptarmigan *Lagopus lagopus* in the same region as our study site (Hannon et al. 1988). Onset of breeding for other tundra breeding species including shorebirds (Høye et al. 2007) and waterfowl (Madsen et al. 2007) are also influenced by the timing of snowmelt. Temperature might also influence females directly through effects on
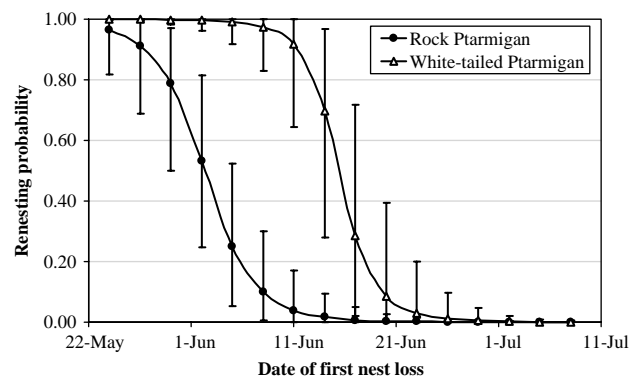

Figure 3. Probability of re-nesting in relation to date of first nest loss for rock and white-tailed ptarmigan in the Yukon Territory. Error bars show the 95% intervals for predictions of the logistic regression model.

Table 2. Average annual survival of rock and white-tailed ptarmigan in the Yukon Territory, Canada. The 95% confidence interval for survival rate is shown in brackets. Effective sample size refers to the number of times an individual had the potential to survival from year x to year x+1.

Sex	Species	No. of individuals	Effective sample size	Survival rate
Female	rock	67	126	0.57 (0.48, 0.66)
	white-tailed	50	70	0.35 (0.24, 0.48)
Male	rock	53	123	0.71 (0.63, 0.79)
	white-tailed	41	60	0.48 (0.35, 0.61)

thermoregulation. Prior to incubation, females add up to 25% of their body mass and colder temperatures may lead to a delay in breeding if the increased energetic costs lower the available energy that can be devoted to reproduction (Wiebe and Martin 2000).

Interspecific variation in reproductive effort in warm and cold springs

Although both species tracked spring temperature similarly in determining when to breed, they differed in their allocation of reproductive effort. White-tailed ptarmigan maintained larger clutches as breeding was delayed, showed a greater propensity to re-nest following failure and as a consequence had longer breeding seasons and higher reproductive output. A decline in clutch size with delayed breeding is common in birds (Perrins 1970). This may be related to individual quality such that lower quality individuals initiate breeding later in the season and tend to lay smaller clutches (Price et al. 1988). While this may explain differences among individuals within a season, a population level shift in clutch size between years as breeding is delayed is more likely related to an environmental influence on the costs and benefits of continued effort. In this case, clutch sizes might decline over time either because the survival prospects for young decrease with later hatch or because maintaining high effort has costs for female survival or future reproductive effort (Winkler and Allen 1996). Because rock ptarmigan displayed a greater reduction in reproductive effort as breeding was delayed (via smaller clutches and fewer re-nests), it appears that the perceived costs and benefits of continued effort differed between the two species even though they experienced the same environmental conditions.

Larger clutches can result in higher annual reproductive output, although change in clutch size tends to be less influential for reproduction than nest survival or the number of nesting attempts (Martin et al. 1989, Nagy and Holmes 2004). White-tailed ptarmigan allocated more effort to reproduction and on average produced more young than rock ptarmigan, but the difference in reproductive output between species was not greater in the two colder years as might have been expected. This might simply be due to the small sample size of years or it may reflect the fact that other aspects of reproduction that are largely outside an individual's control (e.g. nest predation) may have an over-riding influence on annual reproductive output (Wilson et al. 2007b). Warm years with early

breeding would also give more opportunities for re-nesting, which white-tailed ptarmigan were more likely to engage in and this may have helped to contribute to their relatively greater reproductive output under those conditions. We have previously shown that re-nesting efforts contributed between 2–27% to annual fecundity of willow ptarmigan (Martin et al. 1989). With the added physiological costs of laying and incubating another clutch, and the associated predation risks of raising young if successful, re-nesting may actually be one of the strongest measures of reproductive effort for terrestrial birds.

Potential mechanisms behind interspecific variation in reproductive effort

Given that rock and white-tailed ptarmigan experience the same environmental conditions and are similar in many aspects of their ecology, it is intriguing that one species would expend less effort on reproduction when there are clear benefits for productivity and fitness. The difference in survival between the two species may indicate a reproduction–survival trade-off. Adult survival of white-tailed ptarmigan was 20–25% less than rock ptarmigan and they would therefore have a lower likelihood of future breeding opportunities, raising the value of current breeding attempts. Theoretical models as well as comparative and experimental studies on a range of taxa have shown how age-specific survival can influence the allocation of reproductive effort (Partridge and Harvey 1988, Reznick et al. 1990, Ghalambor and Martin 2001, Bears et al. 2009). In our study, this might have operated in two directions. Differences in body size, defence behaviour, physiology or winter habitat selection might result in differing susceptibility of white-tailed and rock ptarmigan to sources of mortality within the region, including predators, severe weather or disease (Keith and Bloomer 1993, Thomas et al. 1995). With a lower likelihood of survival, white-tailed ptarmigan may have evolved a strategy to persist in their reproductive effort even under less favourable breeding conditions. Among grouse, re-nesting rates are typically higher across and within species with lower adult survival, consistent with our results (Bergerud and Gratson 1988). We have also observed that the reproductive effort of white-tailed ptarmigan in Colorado tends to be lower than in the Yukon, while adult survival is slightly higher (Sandercock et al. 2005). This observation suggests that reproductive-survival strategies of ptarmigan may vary across populations depending on the environmental conditions as observed for other taxa (Frederiksen et al. 2005, Folk et al. 2007).

If white-tailed ptarmigan have a higher likelihood of successfully raising offspring, selection may also favour greater reproductive effort even though it may lower survival or future reproductive potential (Jacobsen et al. 1995, Nager et al. 2001). White-tailed ptarmigan tend to have higher nest survival than rock ptarmigan, which appears to be driven by their different nest habitat preferences and possibly stronger nest defence behaviour (Wilson 2008). A study on songbirds found that experimentally reducing the risk of nest predation led to greater parental investment in the form of egg size, clutch mass

and provisioning rate, although clutch size did not vary (Fontaine and Martin 2006).

Food is another important driver of reproductive effort and higher food abundance has been linked with larger clutches and more nesting attempts per year (Hussell and Quinney 1987, Rodenhouse and Holmes 1992). Thus, the effects of food might also contribute to the interspecific differences in our study. Because they are sympatric and exposed to the same range of food types, this would only operate if the two species differ in food preferences during early spring and summer. Early studies in the region showed that all three species of ptarmigan differed in winter diet and this was believed to influence the degree to which they co-exist during the non-breeding season (Weeden 1967, 1969). Rock and white-tailed ptarmigan have similar diets during the pre-breeding period (S. Wilson unpubl.), but further studies on the effects of food abundance on reproductive effort in this system would be valuable. Temperatures at the nest site might also influence reproductive investment. For many species, higher ambient temperatures at the nest result in larger eggs (Hargitai et al. 2005, Cucco et al. 2009) or clutches (D'Alba et al. 2009). In a rare example of a negative relationship between temperature and investment, Williams and Cooch (1996) showed that female snow geese *Chen caerulescens* lay larger eggs during colder temperatures and suggested that this may be related to their use of exogenous resources for breeding. White-tailed ptarmigan nest on steeper slopes and at higher elevations (mean = 99 m a.s.l.) where temperatures average approximately 1 degree colder. This difference is slight compared to day-to-day variation, but if temperature was positively related to investment, we should have observed higher investment for rock ptarmigan, and this was not the case. However, ptarmigan are well adapted to the cold conditions of northern alpine and arctic ecosystems, and it is not clear that they would be impacted by cold temperatures in the same manner as other species (e.g. passerines) breeding at their environmental limits.

Interspecific variation in reproductive effort may also be related to the effects of phylogenetic constraint (Partridge and Harvey 1988). The influence of phylogeny on life histories is most pronounced when comparing across higher level taxa (Owens and Bennett 1995), but it is still possible that rock and white-tailed ptarmigan tend to have slower and faster life history strategies, respectively, regardless of the environmental conditions at a particular location. With only two species, we cannot confirm the mechanisms underlying the patterns in reproductive effort we observed, but our results appear to be most consistent with the effects of age-specific mortality as predicted by life-history theory (Partridge and Harvey 1988). Additional research, perhaps through meta-analyses, would be useful to explore this possibility further.

In conclusion, our results show how two congeneric, sympatric species can differ in their allocation of reproductive effort even when exposed to the same environmental conditions. While both species allocated similar effort to first clutches when breeding began early, white-tailed ptarmigan were more persistent in maintaining that effort when breeding was delayed by unfavourable spring weather. They also had longer breeding seasons, due to a higher re-nest propensity. This variation may be related to how species- or population-specific demographic traits influence the relationship between individuals and their environment, and how that, in turn, affects the allocation of reproductive effort. Our findings add to previous research showing how characteristics of populations or species such as age structure (Wilson et al. 2007a) and migratory status (Both and Visser 2001) influence the manner by which individuals respond to weather variation.

References

Arcese, P. and Smith, J. N. M. 1988. Effects of population density and supplemental food on reproduction in song sparrows. – J. Anim. Ecol. 57: 119–136.

Bears, H., Martin, K. and White, G. C. 2009. Breeding in high elevation habitat results in shift to slower life-history strategy within a single species. – J. Anim. Ecol. 75: 365–375.

Bergerud, A. T. and Gratson, M. W. 1988. Adaptive strategies and population ecology of northern grouse. – Univ. of Minnesota Press.

Both, C. and Visser, M. E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. – Nature 411: 296–298.

Braun, C. E., Martin, K. and Robb, L. A. 1993. White-tailed ptarmigan Lagopus leucurus. – In: Poole, A. and Gill, F. B. (eds), The birds of North America, no. 68. Academy of Natural Sciences, American Ornithologists' Union.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B. and Sheldon, B. C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. – Science 320: 800–803.

Clarke, J. A. and Johnson, R. E. 1992. The influence of spring snow depth on white-tailed ptarmigan breeding success in the Sierra Nevada. – Condor 94: 622–627.

Cotter, R. C. 1999. The reproductive biology of rock ptarmigan Lagopus mutus in the central Canadian Arctic. – Arctic 52: 23–32.

Cucco, A., Guasco, B., Ottonelli, R., Balbo, V. and Malacarne, G. 2009. The influence of temperature on egg composition in the grey partridge Perdix perdix. – Ethol. Ecol. Evol. 21: 63–77.

D'Alba, L., Monaghan, P. and Nager, R. G. 2009. Thermal benefits of nest shelter for incubating female eiders. – J. Therm. Biol. 34: 93–99.

Dawson, A., King, V. M., Bentley, G. E. and Ball, G. F. 2001. Photoperiodic control of seasonality in birds. – J. Biol. Rhythms 16: 365–380.

Frederiksen, M., Harris, M. P. and Wanless, S. 2005. Inter-population variation in demographic parameters: a neglected subject? – Oikos 111: 209–214.

Folk, T. H., Holmes, R. R. and Grand, J. B. 2007. Variation in northern bobwhite demography along two temporal scales. – Popul. Ecol. 49: 211–219.

Fontaine, J. J. and Martin, T. E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. – Ecol. Lett. 9: 428–434.

Ghalambor, C. K. and Martin, T. E. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. – Science 292: 494–497.

Hannon, S. J., Martin, K. and Schieck, J. O. 1988. Timing of reproduction in two populations of willow ptarmigan in northern Canada. – Auk 105: 330–338.

Hargitai, R., Torok, J., Toth, L., Hegyi, G., Rosivall, B., Szigeti, B. and Szollosi, E. 2005. Effects of environmental conditions and parental quality on inter and intra-clutch size variation in the collared flycatcher Ficedula albicollis. – Auk 122: 509–522.

Holder, K. and Montgomerie, R. 2008. Rock ptarmigan Lagopus muta. – In: Poole, A. and Gill, F. (eds), The birds of North America, no. 51. Academy of Natural Sciences, American Ornithologists' Union.

Høye, T. T., Post, E., Meltofte, H., Schmidt, N. M. and Forchhammer, M. C. 2007. Rapid advancement of spring in the high arctic. – Curr. Biol. 17: R449–R451.

Hussell, D. J. T. and Quinney, T. E. 1987. Food abundance and clutch size of tree swallows Tachycineta bicolor. – Ibis 129: 243–258.

Jacobsen, K. O., Erikstad, K. E. and Sæther, B. E. 1995. An experimental study on the costs of reproduction in the kittiwake Rissa tridactyla. – Ecology 76: 1636–1642.

Keith, L. B. and Bloomer, S. E. M. 1993. Differential mortality of sympatric snowshoe hares and cottontail rabbits in central Wisconsin. – Can. J. Zool. 71: 1694–1697.

Lambrechts, M. M. and Dias, P. C. 1993. Differences in the onset of laying between island and mainland Mediterranean blue tits Parus caeruleus: phenotypic plasticity or genetic differences. – Ibis 135: 431–435.

Ligi, S. and Omland, K. 2007. Contrasting breeding strategies of two sympatric orioles: first documentation of double brooding by orchard orioles. – J. Field Ornith. 78: 298–302.

Ludwig, G. X., Alatalo, R. V., Helle, P., Lindén, H., Lindström, J. and Siitari, H. 2006. Short and long-term population dynamical consequences of asymmetric climate change in black grouse. – Proc. R. Soc. Lond. B 270: 1461–1466.

Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F., Nyegaard, H. and Cottaar, F. 2007. Effects of snow cover on the timing and success of reproduction in high arctic pink-footed geese Anser brachyrhynchus. – Polar Biol. 30: 1363–1372.

Martin, K., Hannon, S. J. and Rockwell, R. F. 1989. Clutch size variation and patterns of attrition in fecundity of willow ptarmigan. – Ecology 70: 1788–1799.

Martin, K. and Wiebe, K. L. 2004. Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. – Int. Comp. Biol. 44: 177–185.

Mezquida, E. T. and Marone, L. 2003. Comparison of the reproductive biology of two Poospiza warbling finches of Argentina in wet and dry years. – Ardea 91: 251–262.

Møller, A. P. 2008. Climate change and micro-geographic variation in laying date. – Oecologia 155: 845–857.

Nager, R. G., Monaghan, P. and Houston, D. C. 2001. The cost of egg production: increased egg production reduces future fitness in gulls. – J. Avian Biol. 32: 159–166.

Nagy, L. R. and Holmes, R. T. 2004. Factors influencing fecundity in migratory songbirds: is nest predation the most important. – J. Avian Biol. 35: 487–491.

Owens, I. P. F. and Bennett, P. M. 1995. Ancient ecological diversification explains life history variation among living birds. – Proc. R. Soc. Lond. B 261: 227–232.

Partridge, L. and Harvey, P. H. 1988. The ecological context of life history evolution. – Science 4872: 1449–1455.

Perrins, C. M. 1970. The timing of birds' breeding seasons. – Ibis 112: 242–255.

Price, T., Kirkpatrick, M. and Arnold, S. J. 1988. Directional selection and the evolution of breeding date in birds. – Science 240: 798–799.

Przybylo, R., Sheldon, B. C. and Merilä, J. 2000. Climatic effects on breeding and morphology: evidence of phenotypic plasticity. – J. Anim. Ecol. 69: 395–403.

R Development Core Team. 2008. R: a language and environment for statistical computing, reference index version 2.7.0. R Foundation for Statistical Computing, Vienna Austria.

Reznick, D. A., Bryga, H. and Endler, J. A. 1990. Experimentally induced life-history evolution in a natural population. – Nature 346: 357–359.

Rodenhouse, N. L. and Holmes, R. T. 1992. Results of experimental and natural food reductions for breeding black-throated blue warblers. – Ecology 73: 357–372.

Root, T. R., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. and Pounds, A. 2003. Fingerprints of global warming on wild animals and plants. – Nature 421: 57–59.

Sæther, B. E., Sutherland, W. J. and Engen, S. 2004. Climate influences on avian population dynamics. – Adv. Ecol. Res. 35: 185–209.

Sandercock, B. K., Lank, D. B. and Cooke, F. 1999. Seasonal declines in the fecundity of arctic-breeding sandpipers: different tactics in two species with an invariant clutch size. – J. Avian Biol. 30: 460–468.

Sandercock, B. K., Martin, K. and Hannon, S. J. 2005. Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. – Ecology 86: 2176–2186.

Thomas, F., Renaud, F., Rousset, F., Cezilly, F. and De Meeûs, T. 1995. Differential mortality of two closely related host species induced by one parasite. – Proc. R. Soc. Lond. B 260: 349–352.

Visser, M. E., Adriaensen, F., van Balen, J. H., Blondel, J., Dhondt, A. A., van Dongen, S., du Feu, C., Ivankina, E. V., Kerimov, A. B., de Laet, J., Matthysen, E., McCleery, R., Orell, M. and Thomson, D. L. 2003. Variable responses to large-scale climate change in European Parus populations. – Proc. R. Soc. Lond. B 270: 367–372.

Visser, M. E., Holleman, L. J. M. and Caro, S. P. 2009. Temperature has a causal effect on avian timing of reproduction. – Proc. R. Soc. Lond. B 276: 2323–2331.

Weeden, R. B. 1967. Seasonal and geographic variation in the foods of adult white-tailed ptarmigan. – Condor 69: 303–309.

Weeden, R. B. 1969. Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. – Auk 86: 271–281.

Westerskov, K. 1950. Methods for determining the age of game bird eggs. – J. Wildl. Manage. 14: 56–67.

White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – Bird Study 46: S120–S139.

Wiebe, K. L. and Martin, K. 2000. The use of incubation behavior to adjust avian reproductive costs after egg laying. – Behav. Ecol. Sociobiol. 48: 463–470.

Williams, T. D. and Cooch, E. G. 1996. Egg size, temperature and laying sequence: why do snow geese lay big eggs when it's cold? – Funct. Ecol. 10: 112–118.

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 thesis. – Univ. of British Columbia.

Wilson, S. and Arcese, P. 2003. El Niño drives timing of breeding but not population growth in the song sparrow *Melospiza melodia*. – Proc. Natl. Acad. Sci. USA 100: 11139–11142.

Wilson, S., Norris, D. R., Wilson, A. G. and Arcese, P. 2007a. Breeding experience and density affect the ability of a songbird to respond to future climate variation. – Proc. R. Soc. Lond. B 274: 2539–2545.

Wilson, S., Martin, K. and Hannon, S. J. 2007b. Nest survival patterns in willow ptarmigan: influence of time, nesting stage and individual characteristics. – Condor 109: 377–388.

Wilson, S. and 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.

Wingfield, J. C. and Moore, M. C. 1987. Hormonal, social and environmental factors in the reproductive biology of free-living male birds. – In: Crews, D. E. (ed.), Psychology of reproduction: an evolutionary perspective. Prentice-Hall, pp. 148–175.

Winkler, D. W. and Allan, P. E. 1996. The seasonal decline in tree swallow clutch size: physiological constraint or strategic adjustment. – Ecology 77: 922–932.