Ecology, 86(8), 2005, pp. 2176–2186

LIFE HISTORY STRATEGIES IN EXTREME ENVIRONMENTS: COMPARATIVE DEMOGRAPHY OF ARCTIC AND ALPINE PTARMIGAN

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Abstract. Arctic and alpine habitats are extreme environments characterized by short breeding seasons, cold temperatures, limited food availability, and potentially high predation rates. Stringent ecological conditions are likely to have important consequences for the evolution of life history traits, but direct empirical tests are few. We compare the demography of three populations of ptarmigan on an environmental gradient spanning alpine, subalpine, and arctic habitats. Female Willow Ptarmigan (*Lagopus lagopus*) and White-tailed Ptarmigan (*L. leucurus*) breeding at subalpine and alpine sites had smaller clutches and lower probabilities of nesting success, fledging success, and renesting than Willow Ptarmigan nesting at a low-elevation arctic site. Annual fecundity, measured as female fledglings per breeding female, did not overlap among the three populations and was ranked: alpine (0.40 ± 0.08, mean ± SE, 95% CI = 0.26–0.58) < subalpine (1.33 ± 0.10, 1.13–1.54) < arctic (2.04 ± 0.18, 1.68–2.39). There was a nonsignificant trend for apparent survival rates (ϕ) of breeding females to vary in the opposite direction: alpine (0.46 ± 0.04) > subalpine (0.43 ± 0.03) > arctic (0.37 ± 0.06). Population growth rates predicted significant declines for the alpine population ($\lambda = 0.65 \pm 0.07$, 95% CI = 0.52–0.79), but not the subalpine ($\lambda = 1.00 \pm 0.07$, 0.86–1.14) or arctic populations ($\lambda = 1.13 \pm 0.20$, 0.78–1.54). The adjusted estimates of survival necessary to sustain a stationary population indicated that actual variation in female survival was more pronounced than the observed rates: alpine (0.71) > subalpine (0.43) > arctic (0.33). Together, the fecundity and survival values provide evidence that even congeneric populations can exhibit a continuum between high reproductive and survivor life history strategies. Variation in ptarmigan life history traits was consistent with population differences in predation rates on eggs and breeding females, and it was not related to duration of the breeding season, climatic conditions, or food availability. Ptarmigan demography also covaried with body size, but not in the predicted pattern. Overall, the life history strategies of ptarmigan are consistent with our current understanding of the impacts of environmental factors upon life history variation in passerine songbirds.

Key words: *avian demography; bet-hedging, fecundity; fecundity–survival trade-offs; grouse;* Lagopus lagopus; Lagopus leucurus; *lambda; life history strategies; survival; White-tailed Ptarmigan; Willow Ptarmigan.*

INTRODUCTION

A central goal of evolutionary ecology is to understand why life history traits vary among populations and species. Three major life history strategies can be observed in iteroparous organisms: *high-reproductive* species that have early maturity, high fecundity, and low survival; *survivor* species with late maturity, low fecundity, and high survival; and *bet-hedging* species with late maturity, high fecundity, and low survival (Sæther et al. 1996). Although the general patterns of life history variation are well-established, the underlying causes of such variation are often unclear. Studies seeking ecological correlates of life history variation have focused on four major environmental factors: food limitation, predation, climatic conditions, and duration of the breeding season (Krementz and Handford 1984, Jönsson et al. 1991, Martin 1995, Badyaev 1997, Conway and Martin 2000). Evaluating the relative importance of different environmental factors and their impact on life history traits is a long-standing challenge, but one that might be effectively addressed by comparative studies of the demography of organisms living in extreme environments.

Interspecific comparisons of life history traits need to consider phylogenetic relationships, because differences could reflect the disparate evolutionary history of unrelated lineages, whereas similarities might be the result of phylogenetic inertia. One possible solution is to use comparative methods that map traits onto phy-

Manuscript received 24 March 2004; revised 30 December 2004; accepted 17 January 2005. Corresponding Editor: C. W. Fox.

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logenetic data, and this approach is most robust if it entails sampling across a broad array of species. To ensure a large sample of species, however, comparative methods may be restricted to life history traits that are easily measured, such as clutch size. Other demographic rates, especially survival, are often difficult to compare among studies because the estimates can be sensitive to variation in capture methodology, spatial scale of study plots, and analytical technique (Sandercock and Jaramillo 2002).

In this paper, we investigate patterns of life history variation in ptarmigan (*Lagopus* spp.), a group of small-bodied grouse resident in arctic and alpine habitats throughout the holarctic region. We compared the demography of two closely related species across an environmental gradient that includes arctic, subalpine, and alpine habitats. We examined only three study populations, and our conclusions would be stronger if we had examined a larger sample of species. However, one advantage of studying a restricted sample of populations was that we were able to estimate seven demographic rates from a combined total of 26 years of intensive fieldwork. Direct comparisons of demographic parameters among our study populations were feasible because the same standardized protocols were used at all three of our field sites. Finally, we used known environmental differences among our three sites to investigate the importance of ecological factors in explaining variation in ptarmigan life history strategies. Female ptarmigan start breeding as yearlings and rarely fail to produce a clutch (Martin et al. 1989, Hannon and Martin 1996). Because ptarmigan are relatively short-lived birds, changes in annual fecundity (the number of female offspring produced per breeding female per year) and recruitment rates should have the greatest effect on fitness (Wisdom and Mills 1997). We will make exclusive predictions for the optimal fecundity of female ptarmigan at three sites that differ in five ecological factors.

1. *Body size*.—Correlations between demographic variables and body size are ubiquitous in terrestrial vertebrates. Small-bodied species tend to mature earlier, have higher fecundity and lower survival than large-bodied species (e.g., north temperate birds, Western and Ssemakula [1982], Sæther [1989], Martin [1995]; marsupials, Fisher et al. [2001]; eutherian mammals, Read and Harvey [1989]). The mechanisms responsible for these patterns are incompletely understood, but may include physiological constraints, such as the allometry of field metabolic rates and their effect on the energy requirements of homeotherms (Nagy 1987), or perhaps the effects of selection on other correlated life history traits. We observed a 1.5-fold difference in body mass of female ptarmigan among our three study sites (Table 1). If life history variables are affected by body mass in ptarmigan, annual fecundity should be lowest at the arctic site and greatest at the alpine site (Fig. 1).

2. *Duration of breeding season and day length*.—Annual fecundity is determined by the number of nesting attempts per year that can be made by a breeding pair (Martin et al. 1989, Martin 1995). The timing and duration of breeding were similar at our three study sites (Table 1). Female White-tailed Ptarmigan could have less time to forage because of shorter day lengths at the low-latitude alpine site. However, female White-tailed Ptarmigan compensated for shorter day length by foraging throughout the day, whereas Willow Ptarmigan were most active in the early morning and late afternoon (Hannon and Martin 1992, Braun et al. 1993). Hence, we predict that annual fecundity should be similar at all three sites (Fig. 1).

3. *Climate*.—Adult ptarmigan are well-adapted to coping with cold temperatures (Martin 2001, Martin and Wiebe 2004). Severe winter conditions increase the mortality rates of songbirds, but have little effect on ptarmigan (Peach et al. 1999, Hannon et al. 2003), possibly because ptarmigan are large-bodied and have greater flexibility in managing their energy reserves. Climatic conditions are most likely to affect grouse demography through the impacts of inclement weather on the growth and survival of young (Erikstad and Andersen 1983, Jørgensen and Blix 1985), although warm or variable temperatures may pose problems for adult ptarmigan in the future (Wang et al. 2002). Our arctic field site had the lowest mean temperatures, the most degree-days $<18^{\circ}$C, and received the least precipitation of the three sites, followed by the alpine site, and then the subalpine site (Table 1). If climatic conditions affect life history strategies of ptarmigan by reducing juvenile survival, then females at the subalpine site should have the highest fecundity, followed by those at the alpine and then the arctic site (Fig. 1).

4. *Food*.—Grouse are income breeders that derive most of their resources for egg production and incubation from exogenous nutrients at nesting areas (Meijer and Drent 1999, Wiebe and Martin 2000). Ptarmigan feed predominantly on the buds and leaves of ericaceous shrubs (e.g., *Salix*, *Betula*, and *Vaccinium* spp.), and the annual net primary productivity of these plants is lower in arctic and alpine areas than in subalpine habitats (Billings and Mooney 1968, Bliss 1971). Food is thought to be of minor importance to life history evolution in songbirds (Martin 1995, 2002). In ptarmigan, fecundity could be related to food availability if nutrient constraints influence the energy allocation of females to reproductive or somatic effort (Martin 1987). Shrub cover and ptarmigan densities were lowest at the alpine site and highest at the subalpine site (Table 1). If nutritional constraints impact egg production, then fecundity should be greatest at the subalpine site, followed by the arctic and alpine sites (Fig. 1).

5. *Predation*.—The impact of predation on life history evolution is mediated through impacts on age-specific demographic rates: predation on juveniles se-

TABLE 1. Environmental and ecological conditions at the three study sites; data are means ± SE (with sample size *n* in parentheses).

Variable	Willow Ptarmigan		White-tailed Ptarmigan
	Arctic	Subalpine	Alpine
Location	Manitoba	British Columbia	Colorado
Latitude	58.4° N	59.8° N	39.6° N
Elevation (m a.s.l.)	1	890	3350–4250
Spring body mass of females (g/female)	622 ± 9 (50)	513 ± 2 (318)	418 ± 3 (154)
Egg volume (mL/egg)	20.0 (22)	19.9 ± 0.01 (343)	18.9 ± 0.1 (227)
Egg mass/spring body mass (%)	3.5	4.2	4.9
Clutch mass/spring body mass (%)	37.5	34.4	28.3
Duration of breeding season			
Mean date of clutch initiation (d/yr)	3 June ± 3.2 (4)	2 June ± 1.2 (12)	9 June ± 2.2 (9)
Duration of clutch initiation (d/yr)	34.3 ± 3.5 (4)	31.3 ± 1.8 (9)	31.7 ± 2.6 (9)
Day length during pre-laying (h/d)	17.6 ± 0.06 (14)	18.0 ± 0.11 (14)	14.8 ± 0.02 (14)
Climatic conditions			
Mean temperature (°C)			
May	−0.7	7.5	2.2
June	6.6	11.7	7.6
July	12.0	14.2	10.6
Degree days <18°C (d/mo)			
May	579.6	324.5	501.8
June	344.8	188.6	322.2
July	194.2	119.0	240.6
Precipitation (mm)			
May	31.9	47.2	88.4
June	44.3	35.0	55.8
July	56.0	41.5	75.4
Food			
Extent of shrub cover	moderate	abundant	sparse
Density (no. females/km^2)	5–10	20–46	1–2
Predator sightings			
Foxes and coyotes (no./100 h afield per yr)	···	3.0 ± 0.6 (11)	4.6 ± 1.6 (10)
Raptors (no./100 h afield per yr)	···	9.8 ± 0.8 (11)	3.8 ± 0.7 (10)
Predation rates			
Eggs and young	low	moderate	high
Breeding females	high	moderate	low

Notes: Female body mass was based on birds captured in early spring; least-square means are corrected for days prior to clutch initiation (ANCOVA: for site, $F_{2,516} = 209.2$, $P < 0.001$; for days, $F_{1,516} = 50.6$, $P < 0.001$; for the interaction, $F_{2,516} = 0.5$, $P = 0.58$). Egg volume (V) was calculated as $V = kLB^2$ where $k = 0.49$, L is egg length, and B is egg breadth from measurements reported by Hannon et al. (1998) and Braun et al. (1993). It differed significantly between the subalpine and alpine sites ($t_{568} = 13.7$, $P < 0.001$). Only a summary mean was available for the arctic site. Egg mass (E) was calculated as $E = Vg$ where V is egg volume and $g = 1.08$ g/mL, the specific gravity of chicken eggs. Clutch mass (M) was calculated as $M = \text{TCL}_1E$ where TCL_1 is the average total clutch laid in first nests (Table 2). Mean date of clutch initiation was calculated for first nests within each year; global means differed among sites (Watson-Williams F test, $F_{2,22} = 5.2$, $P = 0.01$). Duration of the clutch initiation period was calculated as the difference in initiation dates between first- and last-laid clutch of the year (first nests and renests combined); it did not differ among sites (Kruskall-Wallis test, $\chi^2_2 = 0.59$, $P = 0.74$). Day length during pre-laying was calculated for the 14-day period preceding the site-specific mean annual date of laying, and it differed among sites (ANOVA: $F_{2,39} = 538.7$, $P < 0.001$). Climatic conditions are based on 30-year normals, 1971–2000. Data from weather stations at the arctic (Churchill A, Manitoba) and subalpine sites (Pleasant Camp, British Columbia) were from Environment Canada (2003); data for the alpine site (Mt. Evans Research Station, Colorado) were from the National Oceanic and Atmospheric Administration (2003); all were accessed 20 July 2003. Female densities are from Martin et al. (1989) and Hannon and Martin (1996). Predator sightings were recorded during the breeding season (May–July) at two of three study sites (Hannon et al. 2003; K. Martin, *unpublished data*). Sighting frequency of raptors (Northern Harriers and falcons, $t_{19} = -5.7$, $P < 0.001$) but not canid predators (coyote, red fox, and arctic fox, $t_{19} = 1.0$, $P = 0.33$) differed between the two sites. Predation rates were taken from this study (Table 2).

lects for reduced fecundity, whereas predation on adults selects the opposite (Martin 2002). Ptarmigan are prey for an array of vertebrate predators. Loss of eggs and young is common; the seasonal mortality rate of females is also greatest during the breeding season (Hannon et al. 2003). Foxes and coyotes were the main predators of ptarmigan eggs and young at our study sites (Martin et al. 1989, Schieck and Hannon 1993), whereas the main predators of adult females were Northern Harriers (*Circus cyaneus*) and falcons (Hik et al. 1986, Braun et al. 1993, Hannon et al. 2003). The relative abundance of predators at the arctic site was unknown, but canid predators were common at the alpine site and raptors were abundant at the subalpine

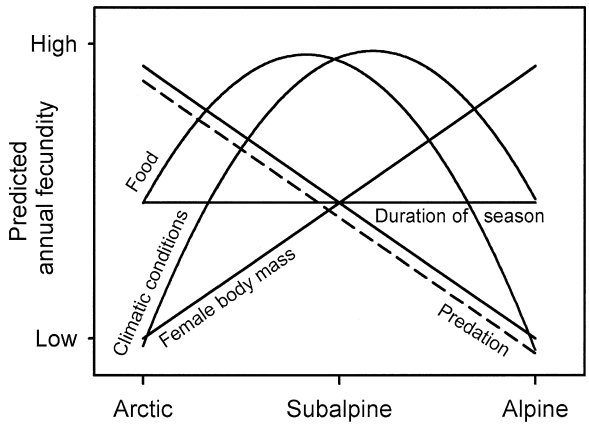

FIG. 1. The predicted fecundity of ptarmigan across a gradient of extreme environments. Solid lines indicate the optimal fecundity predicted by population differences in female body mass and four environmental conditions. The dashed line indicates the empirical pattern observed in our three study populations of Willow and White-tailed Ptarmigan.

site. Results of predator activity differed among our study sites: nest predation was lowest at the arctic site and highest at the alpine site; annual predation rates of breeding females showed the opposite pattern (Table 1). Predation rates on eggs and female ptarmigan predict the same result: fecundity should be greatest at the arctic site, followed by the subalpine and alpine sites (Fig. 1).

METHODS

Study sites and study species

Population studies of Willow Ptarmigan (*Lagopus lagopus*) were conducted in a four-year study (1981–1984) at La Perouse Bay, 40 km east of Churchill, Manitoba (58.40° N, 94.40° W) and a 12-year study (1979–1981 and 1984–1992) at Chilkat Pass in northwestern British Columbia, Canada (59.83° N, 136.50° W; Martin and Cooke 1987, Hannon and Martin 1996). White-tailed Ptarmigan (*L. leucurus*) were studied for 10 years (1987 and 1989–1997) at four areas in the vicinity of Mt. Evans, Colorado, USA (39.62° N, 105.73° W; Martin et al. 2000). The dominant habitats at the three sites were: arctic tundra at La Perouse Bay, subalpine tundra dominated by willow shrubs (*Salix* spp.) at Chilkat Pass, and alpine meadows and screes slopes at Mt. Evans (hereafter: arctic, subalpine, and alpine sites). Size of the study plots differed among the arctic (10 km^2), subalpine (2.5–4.5 km^2), and alpine study sites (22 km^2), because densities of ptarmigan varied (Table 1). Sampling effort was similar and ~50–100 territories were monitored annually at each location (Martin et al. 1989, Hannon and Martin 1996).

Comparative studies must control for the effects of common ancestry, either by examining closely related taxa or by applying comparative methods. In the present study, we would have preferred to make comparisons across three populations of one species in different environments. We proceeded with a mixture of intra- and interspecific comparisons for four reasons. First, phylogenetic analyses based on molecular data show that Willow and White-tailed Ptarmigan are closely related (Gutiérrez et al. 2000). Second, the two species share similar ecology: both are herbivorous and live year-round in tundra habitats. Ptarmigan are territorial and form socially monogamous pair bonds during the breeding season, then segregate into sex-specific flocks in winter (Braun et al. 1993, Hannon et al. 1998). Third, interspecific differences in the duration of reproductive events are small. The two species differ in their egg-laying rates (Willow: 1 egg/day vs. White-tailed: 0.7 egg/day) and duration of incubation (21–23 days vs. 24–26 days for Willow and White-tailed, respectively; Martin et al. 1993, Sandercock 1993, Wiebe and Martin 1995), but variation in clutch size results in nesting attempts of similar duration (30–33 days for Willow vs. 34 days for White-tailed, based on modal clutch size). Finally, differences in parental care have a negligible impact on reproductive success. Males regularly attend broods and defend young from predators in Willow Ptarmigan, but not White-tailed Ptarmigan (Braun et al. 1993, Hannon et al. 1998). However, male presence is not essential in Willow Ptarmigan: removal of males has no negative effects on fledging success or female survival (Martin and Cooke 1987, Hannon and Martin 1992). Defense of young by males may be a salvage strategy for the rare occasions when females are killed during brood-rearing (Martin and Cooke 1987).

Demographic rates of ptarmigan

Field methods were similar for all study populations (Martin and Hannon 1987, Martin et al. 1989, Wiebe and Martin 1998); one of us (K. Martin) worked at each study site for 3–10 years. In spring, >90% of resident birds were captured with ground nets and noosing poles, and were individually marked with colored leg-bands. Females were readily identified by vocalizations and plumage coloration. We found pairs, nests, and broods with the help of dogs, taped calls, radiotelemetry, or a combination of these techniques. We directly estimated seven demographic rates for breeding female ptarmigan, and used indirect estimates for one additional parameter.

1) Total clutch laid (TCL) was the number of eggs laid in the ground nest. The sample was restricted to nests found during laying or early incubation (≤3 days), because partial clutch loss sometimes occurred during incubation and before hatching.

2) Nest success (NEST) was the probability that at least one egg hatched and produced a chick that departed the nest. Mayfield estimators of nest success were not used because most nests were found during laying or early incubation. Nests were visited 2–3 times

per week during incubation, and every 1–2 days near the expected hatch date. Nests were considered *successful* if we captured hatching chicks at the nest or soon after departure. For those nests where we did not capture chicks, we also considered the nest to have hatched if eggshells were left in the nest cup after the young had left the nest. Nest predators either removed the entire clutch or damaged the eggs, and we classified empty nests and those containing smashed eggs as *unsuccessful*.

3) Renesting rate (RENEST) was the probability of a female producing a replacement clutch if her previous clutch was lost. Renesting rates are higher if clutches are lost early in incubation (Robb et al. 1992), but stage of clutch loss did not differ among females of different age classes or at different study sites (K. Martin and S. J. Hannon, *unpublished data*). Although females frequently renested after failure and laid up to four clutches, females produced a maximum of one brood per breeding season (Martin et al. 1989).

4) Chicks per egg laid (C/E) was the proportion of eggs laid that eventually hatched and produced chicks that left the nest. We calculated C/E, FLED, and F/C only for successful nests ($\geq$1 egg hatched). Values of C/E $<$ 1 included losses of eggs that disappeared during incubation and eggs that survived incubation but failed to hatch.

5) Fledging success (FLED) was the probability that at least one chick survived until 15–25 days after hatching. Total brood loss was readily detected because ptarmigan activity changed markedly: parents immediately left brood-rearing areas, became more secretive, and often joined flocks of failed breeders in late summer. In our analyses, we included data from lone females in polygynous pairbonds and in male removal treatments because male accompaniment did not affect fledging success. Data from experimental broods where females were removed at hatching were discarded (Martin and Cooke 1987, Hannon and Martin 1996).

6) Fledglings per chick hatched (F/C) is the proportion of hatched chicks that left the nest and survived until fledging at 15–25 days. F/C was calculated only for successful broods ($\geq$1 chick fledged). Ptarmigan young are self-feeding and nidifugous, develop homeothermy at ~6 days of age, and fly at 10–12 days of age (Braun et al. 1993, Hannon et al. 1998). Broods were relocated and flushed while the young were 15–25 days old, until at least three good brood counts were obtained; the highest count was taken as the number of young fledged.

7) Apparent survival of adults (ϕ_A) was the annual probability that a female ptarmigan survived and returned to the study area. We surveyed ptarmigan populations each spring when the birds were conspicuous in courtship and territorial defence. Mark–recapture analyses based on resighting data were used to calculate apparent survival, corrected for the probability of resighting (p). Hunting pressure was low for Willow Ptarmigan populations, but ~6% of female White-tailed Ptarmigan were harvested each year (K. Martin, *unpublished data*).

8) Apparent survival of juveniles (ϕ_J) was the probability that juvenile ptarmigan survived from postfledging until their first breeding season, and returned to the study area. Direct estimates of juvenile survival were unavailable for all of our study populations because return rates of young birds marked with patagial tags to natal areas were low in all years, especially among females (5–11%; Martin and Hannon 1987, Martin et al. 2000). In our population model, we set ϕ_J equal to ϕ_A because radiotelemetry studies elsewhere have found that overwinter survival rates are similar between juvenile and adult ptarmigan (Smith and Willebrand 1999).

Our field methods could have resulted in underestimates of some demographic rates. Four rates (TCL, C/E, FLED, and F/C) were determined by regular checks of nests and broods, and it is unlikely that additional sampling would have changed our estimates of these parameters. RENEST was determined by relocating individual females throughout the breeding season, and would be a minimum estimate if nests were overlooked. Nests were located by searching with dogs at the arctic site; here, renests could have been missed because female ptarmigan give off little scent while incubating (Hudson 1986). Renests were found by tracking radio-marked birds at the subalpine and alpine sites, but predation rates on eggs were higher in these populations than at the arctic site, and some renests may have been destroyed before they were located by observers. We reject the possibility that our estimates of nest success (NEST) are lower than the success rates of undisturbed nests because the timing of nest predation was not associated with observer visits to ptarmigan nests (Hannon et al. 1993, Wiebe and Martin 1997).

We are confident that most components of reproduction were estimated with relatively little bias, and were comparable across populations. Our estimates of apparent survival for females (ϕ_A) are not true survival, but are the product of true survival and site fidelity. Movement data from our study populations indicated that natal dispersal is greater than breeding dispersal, and that White-tailed Ptarmigan are more likely to disperse than Willow Ptarmigan (Martin and Hannon 1987, Schieck and Hannon 1989, Giesen and Braun 1993, Martin et al. 2000; S. J. Hannon and K. Martin, *unpublished manuscript*). Thus, field estimates of apparent survival are likely to be a conservative index of true survival, particularly for juveniles and for White-tailed Ptarmigan living in patchy habitats.

Estimation and analyses of demographic rates

We opted to pool multiple years to examine site differences in the demographic rates because our data would not allow examination of annual variation for

all parameters. One complication was that some females were observed in multiple years. For analyses of clutch size, nest success, and renesting rates, we randomly selected one year of reproductive data for each female and treated first and subsequent nesting attempts separately. Nest predation limited the number of successful nests, so we pooled first nests and renests to estimate the proportion of eggs hatched, fledging success, and the proportion of chicks fledged. Here, we selected one clutch at random from any successful nesting attempt for each female.

We analyzed reproductive data with Program SAS Version 8.1 (SAS Institute 2000). Continuous response variables were tested for normality and equality of variances prior to application of parametric tests. Proportions were normalized by the arcsine square-root of x transformation before ANOVA was conducted. For the nonparametric Kruskall-Wallis test, we used the χ^2 approximation of Proc NPAR1WAY. Contingency tests were used if response variables were categorical. All tests were two-tailed and were considered significant at $\alpha < 0.05$.

To estimate apparent survival rates, we used Program Mark Version 3.1 (White and Burnham 1999) to analyze mark–recapture histories based on live encounter data. Capture histories were constructed for female ptarmigan where 0 = not detected and 1 = detected by physical capture or by resighting. Birds known to have died as a result of hunting, experimental removals, or handling were treated as not released at last capture. A parametric bootstrap goodness-of-fit test was used to assess the fit of a global model (ϕ_t, p_t) with time dependence in apparent survival (ϕ) and the probability of encounter (p) to the mark–resighting data. A distribution of expected deviances was generated from 1000 random simulations of the capture histories, under the assumptions of equal catchability and full independence. A variance inflation factor ($\hat{c}$) was calculated as the observed deviance divided by the mean deviance of the bootstrap distribution. To correct for overdispersion, $\hat{c}$ was used to inflate the confidence intervals of apparent survival (Burnham and Anderson 1998). Post hoc comparisons of survival rates were conducted using χ^2 statistics in Program Contrast (Sauer and Williams 1989). Reproductive and survival rates are reported as means ± SE.

Estimation of annual fecundity and population growth rates

The expected number of eggs laid that survived until hatching was summed across successful nesting attempts as:

$$\begin{aligned}\text{EGGS} &= (\text{TCL}_1 \times \text{NEST}_1) \\ &\quad + [(1 - \text{NEST}_1) \times \text{RENEST}_1 \times \text{TCL}_2 \times \text{NEST}_2] \\ &\quad + [(1 - \text{NEST}_1) \times \text{RENEST}_1 \times (1 - \text{NEST}_2) \\ &\qquad \times \text{RENEST}_2 \times \text{TCL}_3 \times \text{NEST}_3]\end{aligned}$$

where subscripts 1, 2, and 3 on the different components of reproduction indicate first, second, or third nests, respectively. Annual fecundity (F) was then calculated as the expected number of female fledglings produced per adult female:

$$F = \text{EGGS} \times \text{C/E} \times \text{FLED} \times \text{F/C} \times 0.5.$$

We then combined our estimates of annual fecundity with survival rates to calculate the average finite rate of population growth (λ) from the following population model:

$$\lambda = F\phi_J + \phi_A.$$

To evaluate potential bias in our estimates of apparent survival, we constrained survival rates to be equal for juveniles and adults, and estimated the minimum survival rate (S) necessary to obtain a stationary population growth rate ($\lambda = 1$) for the observed rates of annual fecundity (F) as:

$$S = 1/(F + 1).$$

Parametric bootstrapping was used to obtain confidence intervals for annual fecundity and population growth rates. All modeling was performed with Program MATLAB Version 6.1 (MathWorks 2000). The total clutch laid (TCL) was modeled as random draws from a normal distribution; all other demographic rates were modeled as random draws from beta distributions to bound probabilities within the range 0 to 1. Estimates of variance were taken directly from the sampling distributions for each demographic rate, with the exception of the probabilities of nest success, renesting, and fledging success. For these three demographic rates, the variance of a probability was estimated as:

$$V(p) = p(1-p)/N$$

where p is the probability and N is the total sample size. Because years were pooled, it was not feasible to separate sampling and process variance for the demographic rates. For each bootstrap replicate, we drew a set of demographic rates at random and used them to parameterize these formulae. We generated bootstrap distributions for the annual fecundity and population growth rate of each ptarmigan population by repeating these steps for 10 000 iterations. To adjust for slight discrepancies between the observed means and means of the bootstrap distributions, we calculated bias-corrected 95% confidence intervals as:

$$\text{bias-corrected 95\% percentiles} = \Phi[2\Phi^{-1}(F) \pm 1.96]$$

where Φ is the normal cumulative distribution, Φ^{-1} is the inverse normal cumulative distribution, F is the fraction of bootstrap values smaller than the observed mean, and 1.96 is the critical value for 95% confidence intervals (Caswell 2001).

RESULTS

Reproductive rates differed among the three populations of ptarmigan. Clutch size in both first nests and

TABLE 2. Demographic rates of female Willow Ptarmigan at arctic and subalpine sites, and White-tailed Ptarmigan breeding at an alpine site; data are means ± SE or proportions (with *n* in parentheses).

Demographic rate	Nesting attempt	Willow Ptarmigan	
		Arctic	Subalpine
Total clutch laid (no. eggs)	1	10.8 ± 0.2 (60)	8.2 ± 0.1 (177)
	2+	7.4 ± 0.3 (16)	5.8 ± 0.2 (44)
Probability of nest success	1	0.632 (87)	0.475 (282)
	2+	0.786 (42)	0.628 (86)
Probability of renesting	1	0.641 (117)	0.495 (204)
	2+	0.200 (10)	0.143 (35)
Chicks per egg laid (%)	all	85.9 ± 2.2 (73)	89.1 ± 1.4 (171)
Probability of fledging success	all	0.922 (51)	0.880 (83)
Fledglings per chick hatched (%)	all	62.3 ± 3.3 (47)	69.3 ± 3.1 (73)
Apparent survival of females ($\hat{\phi}$)	···	0.372 ± 0.061 (187)	0.429 ± 0.025 (599)

renests was significantly larger for Willow Ptarmigan at the arctic site, intermediate for Willow Ptarmigan at the subalpine site, and smallest for White-tailed Ptarmigan at the alpine site (Table 2). The probability of nest success for first nesting attempts and renests differed significantly among populations and showed the same pattern as clutch size, ranging from highs of 0.632 and 0.786 for first nests and renests at the arctic site, to lows of 0.292 and 0.333 at the alpine site. Nesting success was higher among renesting attempts at all three sites. The probability of renesting after loss of the first clutch was significantly different among sites and was highest among Willow Ptarmigan nesting at the arctic site. A similar trend was observed for rates of renesting after loss of the second clutch, but interpopulation differences were not significant. Variation in the probability of fledging success matched that of nesting success, and ranged from a high of 0.92 at the arctic site to a low of 0.65 for alpine White-tailed Ptarmigan. The three populations did not differ significantly in the number of chicks produced per egg (expressed as a percentage, C/E, 84–89%), or the number of fledglings produced per hatched chick (F/C, 62–69%).

Estimates of annual fecundity based on these reproductive rates differed significantly among the three study sites, with no overlap in the 95% confidence intervals. The expected numbers of female fledglings produced per breeding female were 2.04 ± 0.18 (mean ± SE; bias-corrected 95% CI = 1.70–2.40) and 1.33 ± 0.10 (1.13–1.53) for Willow Ptarmigan at the arctic site and subalpine sites, respectively, and 0.40 ± 0.08 (0.26–0.58) for White-tailed Ptarmigan at the alpine site.

Variance inflation factors ($\hat{c}$) based on a parametric bootstrapping goodness-of-fit test detected only minor overdispersion, indicating that the global model ϕ_t, p_t was a good fit to the mark–recapture data from the arctic ($\hat{c}$ = 1.94), subalpine ($\hat{c}$ = 1.22), and alpine populations ($\hat{c}$ = 1.10). Overall survival rates were calculated from a reduced model ϕ_{con}, p_t with constant apparent survival and time dependence in the probability of encounter. This model was one of the most parsimonious models at both the arctic and alpine sites ($\Delta QAIC_c \leq 2$), but not at the subalpine site, where the global model was the best fit ($\Delta QAIC_c = 9$). The overall apparent survival rates of breeding females showed a nonsignificant trend opposite to the variation in annual fecundity (Table 2): ϕ_A was lowest at the arctic site (ϕ = 0.37), moderate at the subalpine site (0.43), and highest at the alpine site (0.46). The probability of encounter (p, from ϕ_{con}, p_{con}) was high at all sites: arctic ($\hat{p}$ = 0.95 ± 0.07), subalpine (0.83 ± 0.05), and alpine (0.87 ± 0.06).

Finite population growth rates based on our estimates of annual fecundity and apparent survival predicted an increasing population at the arctic site (λ = 1.13 ± 0.20, bias-corrected 95% CI = 0.78–1.54), a stationary population at the subalpine site (λ = 1.00 ± 0.07, 0.86–1.15), and a declining population at the alpine site (λ = 0.65 ± 0.07, 0.52–0.79). To evaluate the potential bias in our estimates of apparent survival, we calculated the minimum survival rates needed for population growth rates to be stationary. Our observed estimates of apparent survival would have to be adjusted by −11.5% (to S = 0.33) for the arctic site, by +0.3% (to S = 0.43) at the subalpine site, and by +54.1% (to S = 0.72) at the alpine site to obtain a λ value equal to 1.0.

DISCUSSION

This study provides demographic data for three ptarmigan populations and links variation in life history traits to the ecological conditions found in extreme environments. Our results extend previous interspecific comparisons of birds (Martin 1995, Sæther et al. 1996) to show that a continuum between high-reproductive and survivor life history strategies can also be found among congeneric populations of closely related birds, and not just different species. We first examine the evidence for life history trade-offs between annual fecundity and survival of breeding females, and then consider whether the population differences in ptarmigan demography are consistent with predictions based on variation in female body mass and four environmental factors.

TABLE 2. Extended.

White-tailed Ptarmigan	Statistic			
Alpine	*F*	df	χ^2	*P*
5.8 ± 0.1 (120)	416.6	2, 354		0.001
4.7 ± 0.1 (42)	43.7	2, 99		0.001
0.292 (96)			21.5	0.001
0.333 (51)			20.9	0.001
0.549 (113)			6.4	0.041
0.029 (34)			3.7	0.16
84.4 ± 3.8 (41)	1.5	2, 282		0.23
0.649 (37)			3.7	0.002
63.3 ± 6.2 (24)	0.9	2, 139		0.39
0.464 ± 0.042 (156)			1.6	0.46

Life history trade-offs in ptarmigan demography

The three populations of ptarmigan exhibited striking differences in their demographic rates. Clutch size, probability of renesting, and probabilities of nesting and fledging success were all ranked: arctic > subalpine > alpine (Table 2). The net result of differences in the components of reproduction was that annual fecundity showed no overlap among the three populations. Population differences in apparent survival were not significant, but were ranked in the opposite direction: alpine > subalpine > arctic, suggesting a trade-off between annual fecundity and adult survival in ptarmigan. Our results for ptarmigan are consistent with a trade-off between clutch size and annual survival found in seven species of forest grouse (Jönsson et al. 1991).

Interpreting estimates of apparent survival (ϕ) can be challenging because this parameter is not true survival (*S*), but is the product of *S* and site fidelity (ψ), albeit corrected for the probability of encounter (*p*). Similarly, our estimates of projected population growth rates (λ) are likely to underestimate realized population growth rates because our population model included potential losses to permanent emigration, but not gains from immigration. Our population model predicted major declines among White-tailed Ptarmigan in Colorado, but population numbers remained stable for the duration of the field study (Martin et al. 2000). If true survival were similar to our observed rates of apparent survival (Table 2), then our study population could have been maintained by regional immigration. Alternatively, if true survival were similar to adjusted survival, then breeding dispersal must be confounded with mortality.

Movement data favor the latter explanation. In both species of ptarmigan, >75% of females returned to the same or a neighboring territory (Schieck and Hannon 1989, Hannon and Martin 1996). Breeding dispersal movements were relatively short at the arctic and subalpine sites (up to 2 km), but were much greater among White-tailed Ptarmigan at the alpine site (up to 30 km; Hannon and Martin 1996, Martin et al. 2000). Densities of Willow Ptarmigan were high and breeding habitat at arctic and subalpine sites was continuous. Movements >2 km probably led to population losses among White-tailed Ptarmigan because densities were lower and the alpine habitat was patchily distributed. Indeed, dispersal is probably critical for maintaining stable population numbers in alpine vertebrates that occur in naturally fragmented habitats (Giesen and Braun 1993, Martin et al. 2000, Martin 2001, Beever et al. 2003). If our adjusted survival rates are close to the true survival rates of female ptarmigan, then a trade-off between annual fecundity and female survival would be evident among our study populations.

Environmental factors affecting life history strategies of ptarmigan

We considered body size and four ecological factors as potential explanations for life history variation among ptarmigan populations. Demographic rates of ptarmigan covaried with body size across our three populations: small-bodied populations of White-tailed and Willow Ptarmigan had the smallest clutches, the lowest annual fecundity, and the highest adult survivorship (Table 2). However, our results were exactly opposite to the patterns that would be predicted from interspecific comparisons of birds and mammals (Fig. 1). It is possible that a more favorable surface area to volume ratio may have reduced energetic losses for large-bodied ptarmigan, allowing females to invest more energy in reproduction. Future studies should explore the effects of body size among birds in extreme environments. The duration of the breeding season was about one month at all sites, despite differences in habitat, latitude, and altitude (Table 1). This factor cannot explain life history variation in ptarmigan, because population differences in reproductive output were pronounced, even though duration of breeding predicted similar levels of fecundity (Fig. 1).

Site differences in climatic conditions and food availability predicted that annual fecundity should be greatest at the subalpine site (Fig. 1). Both climate and food can be rejected as explanatory factors because the subalpine environment had the mildest temperatures and greatest density of food plants (Table 1), yet the subalpine population of Willow Ptarmigan had inter-

mediate demographic rates (Table 2). Climate and food may contribute to some differences between our two study species. If a hypoxic atmosphere poses additional energy demands at the alpine site, it could explain the slower rates of egg-laying and longer incubation periods among White-tailed Ptarmigan (Martin et al. 1993). This possibility could be tested by examining nesting White-tailed Ptarmigan at low-elevation sites in the arctic. Last, nutritional constraints could explain the smaller clutch size of White-tailed Ptarmigan (Table 2), but they are not consistent with differences in fecundity between arctic and subalpine populations of Willow Ptarmigan.

Of the five factors that we examined, population differences in ptarmigan demography were most consistent with the predicted effects of predation (Fig. 1). Clutch size and mortality rates of female ptarmigan varied inversely with rates of nest and brood failure across the three sites (Table 2). At the arctic site, an environment with low predation of nests, greater investment in egg production could have lowered female survival through a cost of reproduction. Conversely, the reproductive rates of White-tailed Ptarmigan at the alpine site can be viewed as a bet-hedging strategy in response to relatively high numbers of canid nest predators. A small clutch size, coupled with relatively high rates of renesting, would spread risk among multiple nesting attempts. Laying fewer eggs reduces exposure by minimizing the duration of a nesting attempt, and laying a clutch of relatively lower mass would facilitate renesting by reducing the foraging costs associated with egg production. A trade-off between clutch size and relative egg size indicates that White-tailed Ptarmigan also have a greater investment per egg (Tables 1 and 2). A lack of difference in absolute egg size across the three populations may indicate that precocial neonates of ptarmigan must be of a minimum body size to elude predators or to be viable in an extreme environment. Nest predation is the most important source of reproductive failure in open-cup and ground-nesting birds (Ricklefs 1969, Martin et al. 1989, Schieck and Hannon 1993), and is one of the most important environmental factors leading to diversification of life history traits among passerine songbirds with altricial young (Martin 1995, Conway and Martin 2000, Remeš and Martin 2002). Our results for ptarmigan are intriguing because they show that a similar model of life history evolution may be operating in one of the most basal lineages of birds: galliform species with precocial young.

Raptors are important predators of breeding females throughout the geographic range of ptarmigan (Nielsen 1999, Smith and Willebrand 1999, Thirgood et al. 2000). Apparent survival rates of breeding females did not differ among our three study sites (Table 2). Adjusted survival rates that controlled for losses due to breeding dispersal were highest at the alpine site and lowest at the arctic site. We lacked data on predators from the arctic site, but both raptor abundance and female mortality rates were higher at the subalpine site than the alpine site. As predicted by life history theory, female ptarmigan made a greater investment in annual fecundity when exposed to higher mortality rates in both the arctic and subalpine environments. Seasonal patterns of raptor predation at the subalpine site are also consistent with a cost of reproduction: female Willow Ptarmigan incur the highest seasonal mortality rates during nesting and brood-rearing, and females accompanying young have lower survival than broodless females (Hannon et al. 2003). Overall, our results suggest that predation of breeding females also may be an important determinant of life history variation in ptarmigan, as has been suggested previously for forest grouse (Jönsson et al. 1991) and passerine songbirds (Sæther 1988, Martin 2002).

Conclusions

Investigations of life history strategies usually examine life history traits for one species in detail, or compare a few demographic parameters across an extensive sample of species. Most comparisons of birds in extreme environments primarily have considered variation in clutch size (Krementz and Handford 1984, Badyaev 1997, Sanz 1998). Only a few studies have presented data on age at first breeding or adult survival (Gratto and Cooke 1987, Francis et al. 1992). Our results demonstrate that intensive study of congeneric populations can be a useful approach for the study of life history strategies. Our conclusions must be qualified because we examined only three populations, but our ability to estimate seven vital rates and to develop synthetic metrics of annual fecundity and population growth allowed us to make stronger inferences about life history strategies.

Early workers predicted that harsh, unpredictable climatic conditions, low population densities, and limited food availability might favor a high-reproductive life history strategy among species living in those environments (Cody 1966, Boyce 1979). The demography of Willow Ptarmigan at the arctic site conformed to a high-reproductive strategy: this population had high fecundity and low adult survival. On the other hand, alpine populations of White-tailed Ptarmigan followed a survivor, or possibly a bet-hedging, life history strategy. Thus, our results show that the life history traits of closely related species can vary tremendously among extreme environments. Overall, variation in ptarmigan demography agrees with comparative studies of terrestrial vertebrates along elevational gradients, which show that alpine populations generally have low fecundity and adult mortality, consistent with a survivor strategy (Berven 1982, Innes and Millar 1990, Dobson 1992). Two challenges for the future will be to examine age-specific variation in the demography of organisms in extreme environments, and to identify those life his-

tory parameters that have the greatest impact on rates of population change.

Acknowledgments

We thank the many field assistants and graduate students who worked hard to collect the 26 years of demographic information under challenging field conditions. C. E. Braun and the Colorado Division of Wildlife provided logistical assistance for the White-tailed Ptarmigan population study. Field research was financed by grants from the Canadian Circumpolar Institute (NSTG and BAR grants), Canadian Wildlife Service, Natural Sciences and Engineering Research Council of Canada (to F. Cooke, S. J. Hannon, and K. Martin), Queen's University, and the Universities of Alberta, British Columbia (UBC), Sherbrooke, and Toronto. We thank G. Gauthier and C. K. Ghalambor for reviewing our manuscript twice and for their many constructive comments. H. H. Bears, E. Cam, J. M. Reid, D. W. Roberts, S. Wilson, and one anonymous reviewer reviewed earlier versions of the manuscript. B. K. Sandercock received financial support from a postdoctoral fellowship from the Killam Foundation (UBC) and the Division of Biology at Kansas State University.

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