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Demographic consequences of age-structure in extreme environments: population models for arctic and alpine ptarmigan

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Abstract Organisms living in arctic and alpine environments are increasingly impacted by human activities. To evaluate the potential impacts of global change, a better understanding of the demography of organisms in extreme environments is needed. In this study, we compare the age-specific demography of willow ptarmigan (*Lagopus lagopus*) breeding at arctic and subalpine sites, and white-tailed ptarmigan (*L. leucurus*) breeding at an alpine site. Rates of egg production improved with age at the alpine and subalpine sites, but the stochastic effects of nest and brood predation led to similar rates of annual fecundity among 1-, 2-, and 3+-year-old females. All populations had short generation times ($T < 2.7$ years) and low net reproductive rates ($R_0 < 1.2$). Stable age distributions were weighted towards 1-year-old females in willow ptarmigan (>59%), and to 3+-year-old females in white-tailed ptarmigan (>47%). High damping ratios ($\rho > 3.2$) indicated that asymptotic estimates were likely to match natural age distributions. Sensitivity and elasticity values indicated that changes in juvenile survival would have the greatest impact on the finite rate of population change (λ) in willow ptarmigan, whereas changes to the survival of 3+-year-old females would have a greater effect in white-tailed ptarmigan. High survivorship buffers white-tailed ptarmigan in alpine environments against the potential effects of climate change on annual fecundity, but may make the species

more sensitive to the effects of pollutants or harvesting on adult survival. Conversely, processes that reduce annual fecundity would have a greater impact on the population viability of willow ptarmigan in arctic and subalpine environments. If these same demographic patterns prove to be widespread among organisms in extreme environments, it may be possible to develop general recommendations for conservation of the biological resources of arctic and alpine ecosystems.

Keywords Conservation · *Lagopus* · Life history · Population model · Projection Matrix

Introduction

Arctic and alpine ecosystems are among the most pristine environments worldwide but are increasingly impacted by human activities. One of the greatest potential threats to the biota of these regions is global climate change (Chapin and Körner 1994; Krajick 2004). Regional deposition of air-borne pollutants and the local impacts of mining and recreational activities are also of concern (Blais et al. 1998; Larison et al. 2000; Kelly and Gobas 2003, Watson and Moss 2004). Plant and animal populations have responded to warming climates by breeding earlier or by shifting their biogeographic range (Walther et al. 2002; Parmesan and Yohe 2003). A better understanding of the demography of organisms in extreme environments will aid conservation measures by identification of the demographic parameters or life stages that are likely to have the greatest influence of population viability.

Arctic and alpine environments are characterized by extreme climatic conditions, short growing seasons, low primary productivity, and variable predation rates (Sandercock et al. 2005). Arctic and alpine organisms cope with extreme environments with specialized life history strategies, and a suite of other biochemical, morphological, and behavioral adaptations (Martin 2001; Martin and Wiebe 2004). Studies along environ-

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mental gradients have shown that offspring number, offspring size, and adult survival often covary with latitude or altitude in plants (Eriksen et al. 1993; Gugerli 1998), invertebrates (Mani 1968; Blanckenhorn 1997; Baur and Baur 1998), and terrestrial vertebrates (Berven 1982; Dobson 1992; Kremetz and Handford 1984). Arctic and alpine organisms are often long-lived and may be some of the most effective sentinel species for detecting biological responses to environmental change (Morris and Doak 1998; Inouye et al. 2000; Barbraud and Weimerskirch 2001; Cooch et al. 2001; Derocher et al. 2004).

Ptarmigan are small-bodied herbivorous birds that live year round in arctic and alpine habitats (Hannon et al. 1998; Martin and Wiebe 2004). Willow ptarmigan (*Lagopus lagopus*) and red grouse (*L.l. scoticus*), white-tailed ptarmigan (*L. leucurus*), and rock ptarmigan (*L. mutus*) are closely related species that share similar ecology (Gutiérrez et al. 2000). Both sexes are territorial and form socially monogamous pair bonds during the breeding season, then segregate into sex-specific flocks in winter. Female ptarmigan lay and incubate their clutch in a ground nest, attend the precocial young alone or with the assistance of their mate, and produce a maximum of one brood per season. The life-history strategies of ptarmigan are strongly influenced by predation rates, and form a continuum between the high-reproductive strategy of willow ptarmigan and the survivor strategy of white-tailed ptarmigan (Sandercock et al. 2005). Timing of breeding, clutch size, and other demographic rates vary with age in ptarmigan (Hannon and Smith 1984; Wiebe and Martin 1998a), and in other grouse (Willebrand 1992; Caizergues and Ellison 2000; Hagen et al. 2005). Population models for grouse indicate that the finite rate of population change (λ) is likely to be sensitive to age-specific variation in fecundity and survival rates (Steen and Erikstad 1996; Wisdom and Mills 1997; Johnson and Braun 1999).

Identifying the life history components that have the greatest effect on λ is an important prerequisite for management of species in a changing environment. In this study, we summarize 26 years of field data and examine the age-specific demography of an arctic and a subalpine population of willow ptarmigan and an alpine population of white-tailed ptarmigan. Our objectives were: (1) to compare age-specific variation in the fecundity and survival rates among populations, (2) to develop a matrix population model to identify the age-classes and demographic parameters that have the greatest potential impact on the finite rate of population change (λ), and (3) to explore the possible effects of climate change and other anthropogenic perturbations on the population viability of ptarmigan.

Methods

Population studies of willow ptarmigan were conducted in a 4-year study (1981–1984) at La Perouse Bay, 40 km east of Churchill, Manitoba (1 masl, 58.40°N, 94.40°W)

and a 12-year study (1979–1981 and 1984–1992) at Chilkat Pass in northwestern British Columbia (890 masl, 59.83°N, 136.50°W, Martin et al. 1989; Hannon and Martin 1996; Hannon et al. 1998). White-tailed ptarmigan were studied for 10 years (1987 and 1989–1997) at four areas in the vicinity of Mt. Evans, Colorado (3,350–4,250 masl, 29.62°N, 105.73°W, Wiebe and Martin 1998a, b; 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 scree slopes at Mt. Evans (henceforth: arctic, subalpine, and alpine sites).

We could make direct comparisons among our study populations because field methods were similar at all three sites. In spring, more than 90% of resident birds were captured with ground nets and noosing poles, and individually marked with colored leg bands. Pairs, nests, and broods were found by locating birds throughout the breeding season with the use of dogs, taped calls, radio-telemetry, or a combination of these techniques. The sexes were distinguished by differences in vocalizations and plumage coloration. Age-class was determined by comparing pigmentation patterns of the two outermost primaries (9 and 10) to adjacent remiges. Yearlings (1-year-old) retained pigmented feathers, whereas adults (2+ -year-old) had white feathers. Patagial wing-tags were also used to age ptarmigan that were philopatric and returned to the study site after their natal year. Resightings after the year of first capture were subsequently used to calculate female age. After the first year of field work at each site, ca. 77% of breeding females each year were of known age; the remainder were first captured as immigrating adults and assigned a minimum relative age.

We estimated seven demographic parameters 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 or models for known fate data were not necessary because the sample was restricted to nests found early in the nesting cycle. Nests were visited 2–3 times per week during incubation, and every 1–2 days near the expected hatch date. Chicks leave the nest within 24 h of hatching. 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 successful if pipped 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 the 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. C/E, FLED, and F/C (see below) were calculated only for successful nests (≥ 1 egg hatched). Values of $C/E < 1$ included losses of eggs that disappeared during incubation and from 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. We included data from lone females in polygynous pair-bonds and male removal treatments because male accompaniment did not affect fledging success. Data from experimental broods where females were removed at hatching were discarded (Hannon and Martin 1996).
6. Fledglings per chick hatched (F/C) was the proportion of hatched chicks that left the nest that survived until fledging at 15–25 days. F/C was calculated only for successful broods (≥ 1 chick fledged). 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_1 to ϕ_{3+}) 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. Site fidelity of breeding females was high; $> 75\%$ returned to the same or a neighboring territory (Schieck and Hannon 1989; Hannon and Martin 1996). Hunting pressure was low for willow ptarmigan populations, but about 6% of female white-tailed ptarmigan were harvested each year (K. Martin, unpublished data).
8. Survival of juveniles (S_0) was the probability that juvenile ptarmigan survived from post-fledging until their first breeding season. Direct estimates of juvenile survival were unavailable for our study populations because return rates of young marked with patagial tags to natal areas were low, especially among females (5–11%, Martin and Hannon 1987; Martin et al. 2000). Natal dispersal is likely to lead to permanent emigration because dispersal movements are greater among juvenile than adult ptarmigan

(Giesen and Braun 1993; Martin et al. 2000, Pedersen et al. 2004). Thus, indirect estimates of S_0 were used in our population model (see below).

Estimation of demographic parameters

To estimate demographic parameters for three age-classes of female ptarmigan, we restricted our analyses to birds of known age. To increase the sample size of birds in the oldest age-class, we included female immigrants that were first banded as 2+-year-olds but had survived for one or more years and were a minimum age of ≥ 3 years. We opted to pool multiple years to examine age-specific variation in ptarmigan demography because our data would not allow examination of annual variation if we retained age-structure in all seven parameters. Clutch size, nest success, and renesting rates were estimated separately by female age-class and nesting attempt. High rates of nest predation limited the number of successful nests. Thus, the proportion of eggs hatched, fledging success, and the proportion of chicks fledged were estimated separately by female age-class but were pooled across first nests and renesting attempts. Apparent survival rates were estimated for three female age-classes (see below). In total, 30 demographic parameters were estimated for each of the three study populations (Table 1).

The components of reproduction were estimated and compared using statistical procedures of Program SAS (SAS Institute 2000). Site and age-class were treated as categorical variables in all analyses. Clutch size and other continuous response variables were tested for normality and equality of variances prior to application of parametric tests. The proportions of eggs hatched and chicks fledged were normalized by the arcsin \sqrt{x} transformation before analysis of variance was conducted. Probabilities of nest success, renesting, and fledging success were categorical variables and analyzed with contingency tests. Tests were two-tailed and considered significant at α -levels < 0.05 . Means are reported with standard errors.

To estimate apparent survival rates, analyses of mark-recapture data were conducted with the Program Mark (ver. 3.1, White and Burnham 1999). Encounter histories were constructed for adult females (≥ 1 -year old) where 0 is not detected and 1 is detected by capture or by resighting. Birds that died as a result of hunting, experimental removals, or handling were treated as not released at last capture. The global model for the mark-recapture models was: $\phi_{yr-3ac}, \phi_{ad-2ac}, p_t$. This model included three (3ac) and two age-classes (2ac) in apparent survival (ϕ) for birds first captured as yearlings (yr) and adults (ad), respectively, and time-dependence (t) in the probability of encounter (p). The terminal age-class represented 3+-year-old birds and was pooled between females first captured as yearlings and adults. We used the parametric bootstrap procedure of Program Mark to calculate a variance

Table 1 Age-specific demographic parameters for female willow ptarmigan breeding at the arctic and subalpine sites, and female white-tailed ptarmigan breeding at an alpine site. Means \pm 1 SE (n) or frequency (n)

Age of female							
Demographic parameter	Nesting attempt	Study site	1 year	2 years	3+ years	Statistic	$P^{\text{adj}} \leq$
Total clutch laid (TCL)	1	arctic	10.8 \pm 0.2 (37)	10.6 \pm 0.2 (10)	11.1 \pm 0.3 (20)	$F_{2,64} = 0.8$	0.449
		subalpine	8.0 \pm 0.1 (146)	8.5 \pm 0.1 (58)	8.4 \pm 0.2 (47)	$F_{2,248} = 4.0$	0.020*
		alpine	5.6 \pm 0.1 (92)	6.1 \pm 0.1 (39)	6.3 \pm 0.2 (35)	$F_{2,163} = 11.0$	0.001***
	2+	arctic	7.2 \pm 0.3 (10)	7.5 \pm 1.5 (2)	8.0 \pm 1.0 (3)	—	—
		subalpine	5.8 \pm 0.2 (22)	5.8 \pm 0.3 (16)	6.7 \pm 0.2 (19)	$F_{2,54} = 5.7$	0.006**
		alpine	4.7 \pm 0.2 (24)	4.8 \pm 0.2 (12)	5.0 \pm 0.2 (16)	$F_{2,49} = 0.9$	0.409
Probability of nest success (NEST)	1	arctic	0.630 (54)	0.733 (15)	0.633 (30)	$\chi^2_2 = 0.6$	0.746
		subalpine	0.512 (217)	0.388 (80)	0.542 (72)	$\chi^2_2 = 4.5$	0.104
		alpine	0.324 (74)	0.400 (35)	0.324 (37)	$\chi^2_2 = 0.7$	0.713
	2+	arctic	0.889 (27)	0.800 (5)	0.750 (8)	$\chi^2_2 = 1.0$	0.593
		subalpine	0.682 (44)	0.440 (25)	0.690 (29)	$\chi^2_2 = 4.8$	0.093
		alpine	0.387 (31)	0.333 (12)	0.318 (22)	$\chi^2_2 = 0.3$	0.863
Probability of renesting (RENEST)	1	arctic	0.636 (66)	0.467 (15)	0.591 (22)	$\chi^2_2 = 1.5$	0.476
		subalpine	0.400 (150)	0.482 (56)	0.679 (53)	$\chi^2_2 = 12.3$	0.002**
		alpine	0.417 (84)	0.414 (29)	0.690 (29)	$\chi^2_2 = 6.9$	0.031*
	2+	arctic	0.000 (4)	0.000 (1)	0.000 (2)	—	—
		subalpine	0.087 (23)	0.083 (12)	0.375 (8)	$\chi^2_2 = 4.5$	0.103
		alpine	0.000 (18)	0.000 (7)	0.250 (12)	$\chi^2_2 = 6.8$	0.033*
Chicks per egg laid (C/E,%)	all	arctic	85.1 \pm 2.7 (58)	79.9 \pm 6.6 (15)	80.6 \pm 4.5 (25)	$F_{2,95} = 0.8$	0.438
		subalpine	88.9 \pm 1.5 (141)	92.9 \pm 1.5 (42)	82.4 \pm 3.1 (60)	$F_{2,240} = 4.0$	0.020*
		alpine	85.2 \pm 4.1 (36)	86.0 \pm 3.6 (18)	80.0 \pm 5.5 (19)	$F_{2,70} = 0.2$	0.830
Probability of fledging success (FLED)	all	arctic	0.921 (38)	0.818 (11)	1.000 (17)	$\chi^2_2 = 3.2$	0.205
		subalpine	0.859 (71)	0.842 (19)	0.889 (27)	$\chi^2_2 = 0.2$	0.890
		alpine	0.667 (33)	0.611 (18)	0.778 (18)	$\chi^2_2 = 1.2$	0.546
Fledglings per chick hatched (F/C,%)	all	arctic	61.9 \pm 3.4 (35)	56.6 \pm 9.8 (9)	68.8 \pm 4.9 (17)	$F_{2,69} = 0.5$	0.592
		subalpine	71.5 \pm 3.7 (61)	67.4 \pm 5.9 (16)	65.6 \pm 5.4 (24)	$F_{2,96} = 0.6$	0.565
		alpine	62.8 \pm 5.3 (22)	56.2 \pm 10.1 (11)	64.5 \pm 9.3 (14)	$F_{2,44} = 0.2$	0.789
Apparent survival of breeding females (ϕ) ^b	—	arctic	0.355 \pm 0.097	0.409 \pm 0.207	0.590 \pm 0.193	$\chi^2_2 = 1.8$	0.553
		subalpine	0.405 \pm 0.040	0.446 \pm 0.069	0.384 \pm 0.052	$\chi^2_2 = 0.5$	0.771
		alpine	0.423 \pm 0.059	0.643 \pm 0.105	0.465 \pm 0.087	$\chi^2_2 = 3.3$	0.188
Adjusted survival rates ^c	—	arctic	0.290	0.334	0.482		
		subalpine	0.396	0.436	0.376		
		alpine	0.581	0.884	0.639		

^a $P < 0.05$, ^{**} $P < 0.01$, ^{***} $P < 0.001$.

^b Age-specific estimates of apparent survival rates were taken from the global model $\phi_{\text{juv-3ac}}, \phi_{\text{ad-2ac}}, P_t$. Statistical comparisons based on χ^2 -test of Program Contrast (Hines and Sauer 1989).

^c Adjusted age-specific survival rates of breeding females that would yield a stationary population ($\lambda = 1$) if combined with observed age-specific variation in components of fecundity.

inflation factor (\hat{c}), where \hat{c} equals the observed deviance of the global model divided by the mean expected deviance of the bootstrap distribution ($N = 1,000$ iterations). Values of $\hat{c} \leq 3$ indicate that the global model structure is acceptable but minor overdispersion is present (Burnham and Anderson 1998). We controlled for overdispersion by using \hat{c} to adjust the confidence intervals of the parameter estimates. Post hoc comparisons of survival rates were conducted using Program Contrast (Hines and Sauer 1989).

Population model

To synthesize age-dependent variation in the 30 demographic parameters for each of the three populations, we developed an age-structured matrix model based on the sequence of events in a life cycle with prebreeding censuses. The model had three nodes for female ptarmigan

where subscripts $i = 0$ to $3+$ indicate hatch year, 1-, 2-, and 3+ -year-old birds.

$$\mathbf{A} = \begin{bmatrix} F_1 S_0 & F_2 S_0 & F_{3+} S_0 \\ S_1 & 0 & 0 \\ 0 & S_2 & S_{3+} \end{bmatrix}$$

Our projection matrix was linear and did not incorporate the potential effects of density-dependence on ptarmigan demography. We parameterized the model with field estimates of age-specific fecundity and survival. The expected number of eggs laid (EGGS_{ij}) was calculated separately for each age-class (i), and across multiple nesting attempts where subscripts $j = 1, 2$, and 3 on the different components of reproductive performance indicate first, second, or third nests, respectively. For example, the expected number of eggs laid by yearling females was calculated as:

$$\text{EGGS}_{11} = 1 \times \text{TCL}_{11}$$

$$\text{EGGS}_{12} = (1 - \text{NEST}_{11}) \times \text{RENEST}_{11} \times \text{TCL}_{12}$$

$$\text{EGGS}_{13} = (1 - \text{NEST}_{11}) \times \text{RENEST}_{11} \\ \times (1 - \text{NEST}_{12}) \times \text{RENEST}_{12} \times \text{TCL}_{13}$$

The total number of eggs laid per female per year (egg production, E) was summed across all nesting attempts as:

$$E_i = \sum_{j=1}^3 \text{EGGS}_{ij}$$

Age-specific estimates of annual fecundity or the expected number of female fledglings produced per adult female (F) were calculated by multiplying egg production by the attempt-specific estimates of nest success, and by the transition probabilities that determined survival until fledging. For example, the annual fecundity of yearling females was calculated as:

$$F_1 = [(\text{EGGS}_{11} \times \text{NEST}_{11}) + (\text{EGGS}_{12} \times \text{NEST}_{12}) \\ + (\text{EGGS}_{13} \times \text{NEST}_{12})] \times C/E_1 \times \text{FLED}_1 \times F/C_1 \\ \times 0.5$$

Age-specific estimates of the annual survival of females (S_1, S_2, S_{3+}) were taken as the estimates of apparent survival (ϕ) from the mark-recapture analyses (see below). We calculated the net reproductive rate (R_0) for each population as:

$$R_0 = \sum_i F_i \prod_{k=1}^{i-1} S_k$$

where $k = 3$ age-classes.

The matrix model required five assumptions. First, age of first breeding was set at 1 year and the probability of breeding at unity because <1% of female ptarmigan fail to produce a clutch during the breeding season (Hannon and Martin 1996). Second, we truncated our fecundity estimates at three nesting attempts because fourth nesting attempts were rare (Martin et al. 1989). We did not have adequate data to estimate clutch size and nesting success separately for third nesting attempts, and set these values equal to second nests. Third, we used an adjustment factor of 0.5 to calculate the number of female offspring. We lack data for our study populations, but natal sex ratios are 1:1 in other precocial birds (Blums and Mednis 1996; Co-och et al. 1997). Fourth, the survival rates of juvenile ptarmigan (S_0) were set equal to the apparent survival rates of 1-year-old females (S_1). The total combined duration of the nesting and brood-rearing periods was approximately 2 months in all three populations (Sandercock et al. 2005). Thus, juvenile survival for the remaining 10 months of the year was calculated as $S_0 = (zS_1)^{10/12}$, where z was a weighting factor that reduced juvenile survival relative to the survival of 1-year-olds. Defining juvenile survival as a function of 1-year-old female survival implies that the study

populations are closed at some larger spatial scale, and that local estimates of yearling survival are representative of regional variation in this rate. We initially set $z=1$ because radio-telemetry studies have shown that winter survival rates are similar between juveniles and adults in ptarmigan (Hudson 1992; Smith and Willebrand 1999) and other grouse (Caizergues and Ellison 1997; Moss et al. 2000). However, we also modeled the sensitivity of this assumption by varying the weighting factor z from 0.2 to 1.0. Last, true survival rates were set equal to apparent survival rates ($S=\phi$). As a result, the population model included losses due to mortality and emigration, and gains from fecundity but not immigration. Thus, the asymptotic estimates of the finite rate of population change (λ) are an index of population viability in the absence of demographic rescue.

Matrix properties were calculated using algorithms of Program Matlab (ver. 6.1, Mathworks 2000) and formulae presented by Caswell (2001). We first calculated the finite rate of population change (λ_1 , the dominant eigenvalue), the subdominant eigenvalue (λ_2), the stable age distribution (\mathbf{w} , the right eigenvector), and the weighted reproductive value (\mathbf{v} , the left eigenvector). We then combined these variables to calculate the damping ratio (ρ), convergence time (t_{20}), and generation time (T):

$$\rho = \frac{\lambda_1}{|\lambda_2|} \quad t_{20} = \frac{\ln(20)}{\ln(\rho)} \quad T = \frac{\ln(R_0)}{\ln(\lambda_1)}$$

Elasticities of the matrix elements are not reported because they comprised multiple rates and were therefore difficult to interpret. Instead, the ‘lower-level’ sensitivity (s_x) and elasticity (e_x) of λ to instantaneous changes in the age-specific fecundity and survival rates were calculated as:

$$s_x = \sum \frac{vw}{\langle \mathbf{w}, \mathbf{v} \rangle} \frac{\partial a}{\partial x} \quad e_x = \frac{x}{\lambda} s_x$$

where x = an age-specific fecundity or survival rate (i.e., F_i or S_i), vw is the product of the left and right eigenvectors v and w , $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of the same eigenvectors, $\partial a/\partial x$ is the partial derivative of each matrix element (a) with respect to x (i.e., the product of rates other than x , in all terms that contain x), and x/λ is the age-specific demographic rate divided by the rate of population change λ .

We used parametric bootstrapping to obtain confidence intervals for all matrix properties. Total clutch laid was modeled as random draws from a normal distribution; all other demographic parameters were modeled as draws from a beta distribution to bound probabilities within the range 0 to 1. Estimates of variance were taken directly from the sampling distributions for each demographic parameter, with the exception of the probabilities of nest success, renesting and fledgling success. For these three demographic parameters, variance was estimated as:

$$\text{Var}(\hat{p}) = \frac{\hat{p}(1 - \hat{p})}{N}$$

where p is the probability and N is the total sample size.

For each bootstrap replicate, a set of 30 demographic parameters was drawn at random, the parameters were combined to parameterize the projection matrix, and the asymptotic properties were calculated for that random matrix. We did not consider covariances among demographic parameters because years were pooled to examine age-specific variation in demography. In simulation studies, inclusion of covariance structure may increase confidence intervals for stochastic rates of population change (μ , Fieberg and Ellner 2001). We generated distributions for each of the matrix properties by repeating the three steps for 100,000 random matrices. Variances were taken directly from the bootstrap distributions. To compensate for slight discrepancies between the mean matrices and the means of the bootstrap distributions, we calculated bias-corrected 95% confidence intervals as:

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

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 value from the mean matrix, and 1.96 is the critical value for 95% CI. Comparisons of the 95% CI are a conservative test of significance because the confidence intervals of the underlying demographic parameters were based on total and not process variance (Gould and Nichols 1998).

Results

Fecundity

Female ptarmigan in the three populations exhibited varying degrees of age dependence in the six components of reproduction. Willow ptarmigan at the arctic site exhibited no significant age-specific variation in the reproductive parameters (Table 1), including total egg production (Fig. 1a). At the subalpine and alpine sites, female ptarmigan that were 2 or 3+ years of age produced first clutches that were 0.5 eggs larger on average than 1-year-old birds (Table 1). At the subalpine site, 3+-year-old birds produced renests that were almost an egg larger than the renest clutches of younger birds. In addition, a greater proportion of 3+-year-old birds renested after loss of first and second clutches in both the subalpine and alpine populations. These differences led to the age-specific variation in egg production (E) for the alpine and subalpine populations (Fig. 1a). In both populations, 3+-year-old females laid more eggs per year than yearlings, and 2+-year-old females were intermediate. Site differences in egg production were consistently ranked: alpine < subalpine < arctic. The 95% confidence intervals for E did not overlap between the

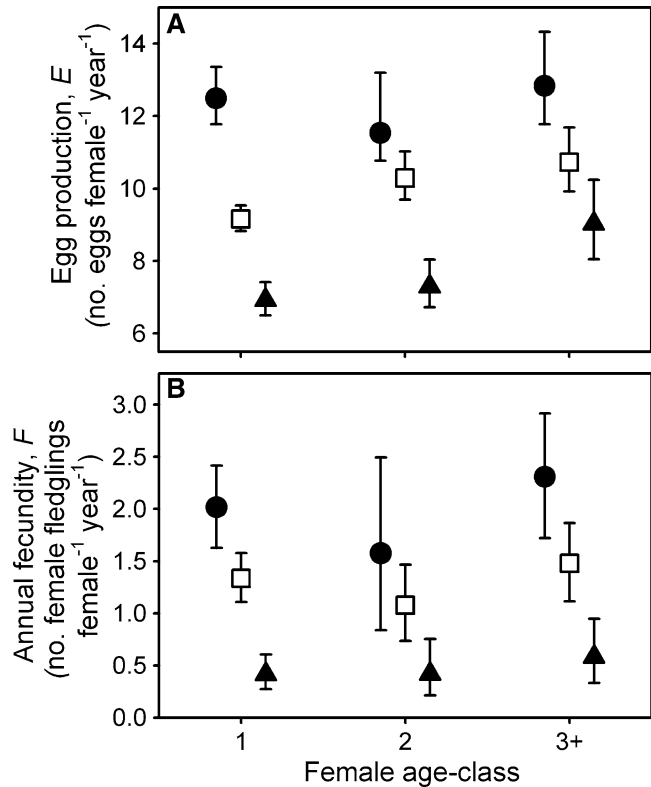


Fig. 1 Age- and site-specific variation (mean \pm 95% CI) in **a** egg production (E , total number of eggs laid per breeding female per year), and **b** annual fecundity (F , female fledglings per breeding female per year) for arctic (●) and subalpine populations (□) of willow ptarmigan, and an alpine population (▲) of white-tailed ptarmigan

alpine and arctic sites, but the subalpine site was intermediate to the other sites.

Within each population, female ptarmigan of all three age-classes had similar rates of nesting and fledging success, and produced similar numbers of chicks per egg and fledglings per chick (Table 1). Despite the age-specific differences in egg production (Fig. 1a), annual fecundity (F) was not significantly different among 1-, 2- and 3+-year-old females for any population (Fig. 1b). The population differences in annual fecundity were consistent with the geographic variation in rates of egg production. The expected number of female fledglings per breeding female among white-tailed ptarmigan at the alpine site did not overlap with estimates for willow ptarmigan in any age-class (Fig. 1b). In willow ptarmigan, yearlings at the arctic site had significantly higher annual fecundity than yearlings at the subalpine site, but the differences among 2- and 3+-year-old females at the two sites were not significant.

Apparent survival

Estimates of apparent survival were based on encounter histories for $n=187$ females at the arctic site, $n=599$ females at the subalpine site, and $n=156$ females at the

alpine site. Estimates of the overdispersion factor (\hat{c}) from the parametric bootstrap procedure showed that the global model $\phi_{yr-3ac}, \phi_{ad-2ac}, p_t$ was a good fit to the encounter histories of ptarmigan at all three sites: arctic ($\hat{c} = 2.56$), subalpine ($\hat{c} = 1.35$), and alpine ($\hat{c} = 1.02$). The average probability of encounter (p) for female ptarmigan was high at all study sites: arctic ($\hat{p} = 0.951 \pm 0.027SE$), subalpine (0.757 ± 0.067), and alpine (0.818 ± 0.075). Apparent survival rates were highest for 3+-year-old females at the arctic site and for 2-year-old females at the other two sites, but the age-specific variation in apparent survival was not significant for any population (Table 1).

Finite rate of population change and matrix parameters

Estimates of the finite rate of population change for the arctic and subalpine populations were not significantly different from a stationary population ($\lambda = 1$), whereas the alpine population would be predicted to decline without immigrants (Table 2). If the populations were effectively closed, the four annual survival rates (S_0 to S_{3+}) would have to be adjusted by -18% in the arctic, -2% in the subalpine, and $+38\%$ in the alpine population to obtain a λ -value of one (Table 1). Damping ratios were high for all three populations ($\rho > 3.2$) and all three populations of ptarmigan would be expected to converge rapidly to a stable age distribution ($t_{20} < 2.6$ years). The net reproductive rate for a fledgling female ptarmigan was generally low ($R_0 < 1.5$), and significantly below replacement ($R_0 = 1$) at the alpine site (Table 2). All populations were short-lived with generation times (T) ranging from 1.8 to 2.6 years. Nonetheless, non-overlapping confidence intervals indicated that willow ptarmigan at the subalpine site had a significantly higher net reproductive rate and a shorter generation time than white-tailed ptarmigan at the alpine site. Neither of these two populations differed from birds at the arctic site.

Stable age distributions (\mathbf{w}) were significantly different between willow and white-tailed ptarmigan (Table 3). The stable age distributions of the arctic and subalpine populations were weighted towards 1-year-old females ($> 59\%$), and the proportions of 2- and 3+-

year-old birds were low ($< 24\%$ each, Table 3). In contrast, the stable age distribution of the alpine population had a greater proportion of 3+-year-old females ($> 47\%$) and significantly fewer yearlings ($< 34\%$). The reproductive value (\mathbf{v}) of female ptarmigan tended to increase with age-class but differences among age-classes and populations were not significant. The 95% CI of the age-specific reproductive values consistently included one (Table 3).

Sensitivity and elasticity analyses

In the arctic and subalpine populations of willow ptarmigan, the sensitivity of λ to juvenile survival (S_0) was considerably higher ($s_x > 1.0$) than any other age-specific fecundity or survival rate (Fig. 2a). In the subalpine population, the sensitivity of age-specific fecundity and survival were significantly higher among yearlings than 2- and 3+-year-old females. The arctic population exhibited a similar pattern but age-specific differences were not significant because confidence intervals for the sensitivity estimates overlapped substantially. The pattern among alpine white-tailed ptarmigan was somewhat different: all of the age-specific fecundity and survival rates had relatively low sensitivity values ($s_x < 0.5$), and the confidence intervals of most rates overlapped. Overall, survival of juveniles (S_0), yearlings (S_1), and 3+-year-old females (S_{3+}) had the highest sensitivity values in white-tailed ptarmigan.

The elasticity values of the subalpine and alpine populations differed significantly for several age-specific fecundity and survival rates. The subalpine population of willow ptarmigan had significantly higher elasticity values for survival of juveniles (S_0) and fecundity of 1-year-olds (F_1), whereas the alpine population of white-tailed ptarmigan had significantly higher elasticity values for survival of 3+ year-olds (S_{3+} , Fig. 2B). There were no significant differences between these two populations in the elasticity values of the four remaining age-specific rates. Mean elasticity values were similar for willow ptarmigan at the arctic and subalpine sites, but the confidence intervals of elasticity values for the arctic population were wide, and spanned the range of values calculated for the other two populations.

Table 2 Five asymptotic properties of projection matrices for three populations of ptarmigan: the finite rate of population change (λ), damping ratio (ρ), time to convergence to stable age distribution (t_{20} , years), net reproductive rate (R_0) and generation time (T). Point estimates were based on the mean matrices. The \pm ISD and bias-corrected 95%CI (in brackets below means) were taken from bootstrap distributions based on 100,000 replicates

Matrix property	Willow ptarmigan		White-tailed ptarmigan
	Arctic	Subalpine	Alpine
λ	1.22 \pm 0.25 (0.78, 1.78)	1.02 \pm 0.09 (0.86, 1.20)	0.73 \pm 0.08 (0.58, 0.88)
ρ	5.92 \pm 3.07 (3.43, 53.72)	4.77 \pm 3.94 (3.13, 15.11)	3.21 \pm 3.07 (2.04, 10.64)
t_{20}	1.68 \pm 1.40 (0.75, 2.43)	1.92 \pm 0.39 (1.10, 2.62)	2.57 \pm 0.75 (1.27, 4.20)
R_0	1.43 \pm 0.77 (0.62, 3.50)	1.03 \pm 0.15 (0.78, 1.37)	0.43 \pm 0.11 (0.26, 0.71)
T	1.77 \pm 3.30 (1.29, 3.73)	1.70 \pm 0.10 (1.53, 1.92)	2.62 \pm 0.40 (2.05, 3.62)

Table 3 Stable age distributions (\mathbf{w}) and weighted reproductive values (\mathbf{v}) for $i=1, 2$ and $3+$ -year-old female ptarmigan. Point estimates are based on the mean matrices; the \pm 1SD and bias-corrected 95%CI (in brackets below means) were taken from bootstrap distributions based on 100,000 replicates

Matrix property	Willow ptarmigan		White-tailed ptarmigan
	Arctic	Subalpine	Alpine
w_1	0.677 ± 0.047 (0.567, 0.745)	0.598 ± 0.020 (0.557, 0.634)	0.333 ± 0.041 (0.250, 0.407)
w_2	0.196 ± 0.032 (0.121, 0.247)	0.237 ± 0.013 (0.212, 0.261)	0.194 ± 0.033 (0.129, 0.256)
w_{3+}	0.126 ± 0.075 (0.026, 0.317)	0.166 ± 0.026 (0.118, 0.221)	0.474 ± 0.069 (0.351, 0.617)
v_1	1.00	1.00	1.00
v_2	1.05 ± 0.41 (0.59, 2.06)	0.97 ± 0.11 (0.77, 1.20)	1.24 ± 0.20 (0.91, 1.70)
v_{3+}	1.53 ± 1.72 (0.87, 4.31)	1.09 ± 0.16 (0.81, 1.45)	1.09 ± 0.30 (0.63, 1.82)

High elasticity values for juvenile survival might be viewed with caution because S_0 was the only demographic parameter for which we lacked empirical estimates based on field data. In our population model, S_0 was calculated as a function of the survival of 1-year-old females (S_1) by $S_0 = (zS_1)^{10/12}$. We found that the relative rankings of the age-specific elasticity were largely unchanged if the weighting factor (z) was reduced from 1.0 to 0.2 by increments of 0.2. In the alpine population, the elasticity value of S_{3+} remained highly ranked, regardless of the value of z (Table 4). In the arctic and subalpine populations, juvenile survival retained the highest elasticity value if S_0 was set between 40% and 100% of S_1 ($z \geq 0.4$, Table 4). The elasticity value of S_{3+} became highly ranked only if S_0 was 20% of S_1 ($z=0.2$,

Table 4). Finally, the high elasticity of S_{3+} in the alpine population could have been due to a λ -value < 1 (Table 2). The values of the age-specific elasticity values were unchanged if z was set to 1 and if adjusted survival rates were used to obtain $\lambda=1$ for each population of ptarmigan (Table 1).

Discussion

In this study, we synthesized 26 years of field data to compare the demography of three populations of two species of ptarmigan breeding at arctic, subalpine, and alpine sites. The demographic and population parameters of ptarmigan showed moderate variation with female age-class and large differences among the three extreme environments. In addition, rates of population change were sensitive to different age-specific fecundity and survival rates in willow and white-tailed ptarmigan. We develop the implications of our demographic analyses for conservation of ptarmigan and other organisms associated with arctic and alpine ecosystems.

Age-specific variation in demography

Age-specific variation in ptarmigan demography was primarily due to components of fecundity related to egg production: clutch size and the probability of reneating increased with female age, leading to age-specific increases in total egg production. Reneats are an important component of fitness in ptarmigan, contributing up to 27% of total annual production (Martin et al. 1989). Annual survival of female ptarmigan tended to increase with age-class but the differences were not significant, presumably because confidence intervals for our estimates were large. Overall, our analyses confirm that patterns of age-dependence in demographic parameters can be complex, even in short-lived species of birds (Møller and de Lope 1999; Orell and Belda 2002).

Probabilities of nest and fledging success did not vary with female age-class, indicating that female experience with nest site selection or predators did not improve annual fecundity. Loss of eggs and chicks to predators appear to be unpredictable events in ptarmigan populations (Schieck and Hannon 1993; Wiebe and Martin 1998b), which had the net effect of masking the effects of age-specific variation in rates of egg production. As a

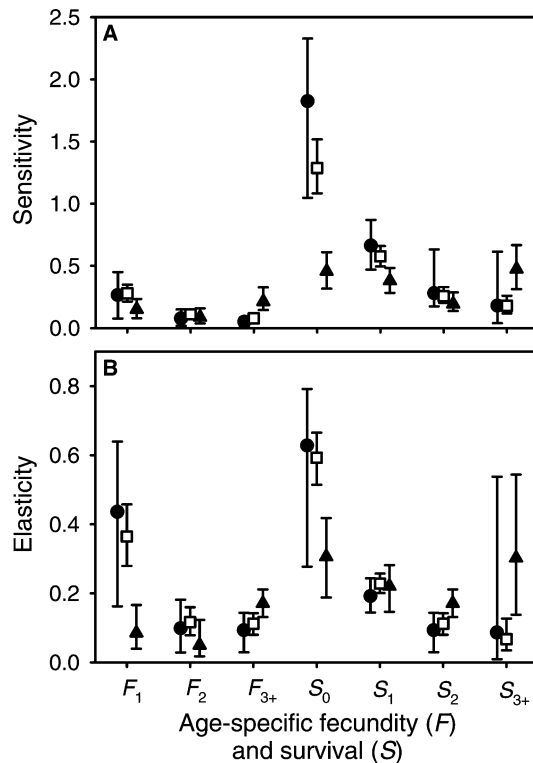


Fig. 2 a Sensitivity (means \pm 95%CI), and b elasticity of age-specific fecundity (F_i) and survival (S_i) rates of arctic (\bullet) and subalpine populations (\square) of willow ptarmigan, and an alpine population (\blacktriangle) of white-tailed ptarmigan. Subscripts (i) indicate female age-class, where 0 to 3+ = hatch year to 3+-year-old females

Table 4 Elasticity values of age-specific fecundity (F_i) and survival (S_i) in relation to the weighting factor (z) used to calculate juvenile survival (S_0). Juvenile survival (S_0) for the 10 month period from fledging until the next spring was calculated as a function of the annual survival of yearlings: $S_0 = (zS_1)^{10/12}$. Survival rates of juveniles and yearlings are equal if $z = 1.0$. The highest elasticity value is indicated in boldface type

	Weighting factor (z)				
	0.2	0.4	0.6	0.8	1.0
<i>Arctic</i>					
F_1	0.063	0.170	0.274	0.363	0.436
F_2	0.025	0.056	0.079	0.092	0.099
F_{3+}	0.116	0.134	0.125	0.109	0.093
S_0	0.204	0.360	0.477	0.564	0.628
S_1	0.140	0.190	0.203	0.201	0.192
S_2	0.116	0.134	0.125	0.109	0.093
S_{3+}	0.540	0.316	0.195	0.127	0.087
<i>Subalpine</i>					
F_1	0.085	0.173	0.247	0.310	0.364
F_2	0.049	0.081	0.099	0.110	0.117
F_{3+}	0.161	0.158	0.142	0.126	0.112
S_0	0.295	0.411	0.489	0.547	0.593
S_1	0.210	0.238	0.242	0.237	0.228
S_2	0.161	0.158	0.142	0.126	0.112
S_{3+}	0.333	0.193	0.128	0.091	0.067
<i>Alpine</i>					
F_1	0.013	0.031	0.049	0.068	0.085
F_2	0.010	0.022	0.033	0.042	0.050
F_{3+}	0.111	0.144	0.160	0.167	0.171
S_0	0.135	0.197	0.242	0.277	0.306
S_1	0.122	0.166	0.192	0.209	0.221
S_2	0.111	0.144	0.160	0.167	0.171
S_{3+}	0.632	0.492	0.406	0.347	0.302

result, annual fecundity did not differ among the three female age-classes in any of our study populations of ptarmigan. Age-specific variation in demography may be greater in other grouse. Differential rates of nest and brood loss can lead to 7- to 10-fold differences in annual fecundity between yearling and adult black grouse (*Tetrao tetrix*, Willebrand 1992; Caizergues and Ellison 2000), and age-specific changes in male survival are common in many grouse populations (Hagen et al. 2005).

Matrix parameters

Estimates of the rate of population change for arctic and subalpine populations ($\lambda = 1$) indicated that willow ptarmigan numbers would be stationary with our observed demographic rates and no immigration. The alpine population was predicted to decline ($\lambda < 1$), but numbers of white-tailed ptarmigan were maintained by regional immigration during our study (Martin et al. 2000; Sandercock et al. 2005). Unlike our arctic and subalpine field sites, our alpine study area was naturally fragmented into small, isolated patches of habitat. Demographic rescue via dispersal was an important feature of the white-tailed ptarmigan population, and is probably important for maintaining the population

viability of most alpine vertebrates (Martin 2001; Franken and Hik 2004a).

All three ptarmigan populations were short-lived ($T \leq 2.7$ years) with low net reproductive rates ($R_0 \leq 1.2$), as might be expected for gamebird species. However, the two species differed markedly in their demography, with the greatest differences between the subalpine and alpine populations. Willow ptarmigan had a shorter generation time, a higher net reproductive rate, and a stable age distribution strongly skewed towards yearling females, whereas white-tailed ptarmigan had the opposite pattern, including age distributions dominated by 3+-year-old females. The asymptotic stable age distributions are likely to be a good indication of natural age distributions in ptarmigan populations because damping ratios were high ($\rho \geq 3.2$) and convergence times were short ($t_{20} \leq 2.6$ years). Comparative data for other grouse are limited: stable age distributions had equal number of juvenile and adult birds in greater sage-grouse (*Centrocercus urophasianus*, Johnson and Braun 1999), but were not reported in matrix models for other grouse populations (Steen and Erikstad 1996; Wisdom and Mills 1997).

Sensitivity and elasticity analyses

The sensitivity and elasticity values predicted that absolute or proportional increases in juvenile survival (S_0) would have the greatest influence on λ for willow ptarmigan, followed by improvements to the fecundity of yearlings. Elasticity of juvenile survival was also high in white-tailed ptarmigan, but changes to the survival rates of 3+-year-old females would have a greater effect on λ . Juvenile survival was the only parameter for which we lacked field estimates. However, our conclusions were robust because elasticity values for S_0 remained highly ranked if S_0 was set to be 40% to 80% of S_1 . Elasticity rankings changed only if S_0 was set to be 20% of S_1 , a value that telemetry studies suggest would be unlikely for ptarmigan (Hudson 1992; Smith and Willebrand 1999).

High elasticity values for S_0 are consistent with the current understanding of ptarmigan population dynamics: spring numbers are often correlated with the survival and recruitment of young birds (Watson et al. 1984; Martin et al. 2000; Moss and Watson 2001), although correlations with annual fecundity can also be strong (Bergerud et al. 1985; Watson et al. 1998). Land management practices applied to moorlands in Scotland, including prescribed burning of heather and predator control, are primarily aimed at increasing the annual fecundity of red grouse but may impact juvenile survival as well (Tharme et al. 2001). Relatively few studies of grouse have presented accurate estimates of the post-fledging survival of juveniles (S.J. Hannon and K. Martin, unpublished manuscript), and this stage of the life cycle deserves greater attention in the future.

In general, high elasticity of juvenile survival is often a feature of population models for short-lived verte-

brates, including grouse (Steen and Erikstad 1996; Wisdom and Mills 1997; Johnson and Braun 1999), lizards (Blomberg and Shine 2001), and small mammals (Haydon et al. 1999). In contrast, adult survival usually has the highest elasticity value in studies of long-lived organisms (Crone 2001). White-tailed ptarmigan are interesting as a possible intermediate case: a relatively short-lived bird species where survival of the oldest females had the highest elasticity value. This result might be explained, in part, by a negative relationship between the elasticity values and λ (Meats 1971). However, our conclusions were unchanged if we adjusted all survival rates by a constant proportion to obtain a stationary population (Table 1).

Implications for conservation and management

The ecological conditions of extreme environments play an important role in determining the life-history strategies of ptarmigan, and other arctic and alpine organisms (Sandercock et al. 2005). In the future, understanding the demographic consequences of age-specific variation in population structure will be important in evaluating the potential effects of a changing environment. Relatively high elasticity values for fecundity suggest that factors impacting reproduction would have the greatest impact on the population viability of willow ptarmigan. The seasonal phenology of winter snowfall and spring melt has strong effects on the annual fecundity of ptarmigan (Clarke and Johnson 1992; Martin 2001; Martin and Wiebe 2004), and other arctic and alpine vertebrates (Van Vuren and Armitage 1991; Franken and Hik 2004b). Some models of climate change predict more variable conditions and a greater frequency of extreme events (Wang et al. 2002). Climate events, such as the atmospheric effects of volcanic activity, can cause widespread breeding failure among arctic-breeding birds (Ganter and Boyd 2000). Reductions in habitat quality or changes in predator activity can also impact annual fecundity. For example, at our arctic field site, foraging activities of an expanding population of snow geese (*Anser caerulescens*) have degraded habitat quality, leading to population declines in ptarmigan and other arctic-breeding birds (Hitchcock and Gratto-Trevor 1997; Cooch et al. 2001). In Scotland, increases in corvid nest predators following development of a ski resort led to lower breeding success and population declines among rock ptarmigan (Watson and Moss 2004). Low elasticity values for survival of older birds, however, suggest that the population viability of willow ptarmigan should be resistant to factors that affect mortality rates of breeding females.

White-tailed ptarmigan may be buffered against potential effects of perturbations on reproduction by their high survival rates. High elasticity values for survival of 3+ -year-old females indicate that perturbations affecting older birds would have the greatest impact on the alpine population of white-tailed ptarmigan. White-

tailed ptarmigan are well adapted to the alpine environment, and extreme variation in climatic conditions has little effect on survival rates of females (Martin and Wiebe 2004). However, mortality rates of older females could be increased by warmer winter temperatures (Wang et al. 2002), by differential hunting pressure on older females (e.g., if hunters are more likely to detect and harvest older females attending successful broods, Smith and Willebrand 1999; Pedersen et al. 2004), or by accumulation of heavy metals and other contaminants in female body tissues (Myklebust and Pedersen 1999; Larison et al. 2000).

It is not clear whether our results for ptarmigan can be generalized to other organisms in extreme environments. Our population model was a prospective analysis and our analyses could be extended in three directions in the future. First, if estimation of process variance is feasible, one could examine the relationship between process variance and elasticity values of the demographic parameters (Morris and Doak 2004). Second, if multiple projection matrices were available, the methods of life-table response experiments (LTRE) could be used to retrospectively examine the contributions of variation in the demographic parameters to variation in the rate of population change (Caswell 2001; Cooch et al. 2001). Last, our inferences were based on the asymptotic properties of our projection matrices. Temporal symmetry models for mark-recapture data relax this assumption, and could be used to investigate environmental factors affecting realized rates of population change (Nichols and Hines 2002). These alternative modeling approaches could be applied to ptarmigan and other organisms in extreme environments. If the demographic parameters of arctic and alpine organisms are found to vary in predictable ways, general recommendations could be developed for conservation of the biological resources of extreme environments.

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