

Coping Mechanisms of Alpine and Arctic Breeding Birds: Extreme Weather and Limitations to Reproductive Resilience¹

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SYNOPSIS. As ground nesting homeotherms, alpine and arctic birds must meet similar physiological requirements for breeding as other birds, but must do so in more extreme conditions. Annual spring snowfall and timing of snow melt can vary by up to 1 month and daily temperatures near the ground surface vary from below freezing to over 45°C in alpine and arctic habitats. Species breeding in these environments have various behavioral, physiological, and morphological adaptations to cope with energetically demanding conditions. We review the ways birds cope with harsh and variable weather, and present data from long term field studies of ptarmigan to examine effects of spring weather on reproduction. In variable but normal spring conditions, timing of breeding was not influenced by snow melt, snow depth or daily temperatures in the alpine, as breeding did not commence until conditions were generally favorable. Arctic ptarmigan tended to vary breeding onset in response to spring conditions. Generally, birds breeding in alpine and arctic habitats suffer a seasonal reproductive disadvantage compared to birds at lower latitudes or elevations because the breeding window is short and in late years, nest failure may be high with little opportunity for re-nesting. Coping mechanisms may only be effective below a threshold of climactic extremes. Despite strong resilience in fecundity parameters, when snowmelt is extremely delayed breeding success is greatly reduced. Alpine and arctic birds will be further challenged as they attempt to cope with anticipated increases in the frequency and severity of weather events (climate variability), as well as general climate warming.

INTRODUCTION

Terrestrial animals in the alpine and arctic experience more stochasticity and extreme variation in abiotic parameters such as temperature, wind, precipitation, and snow cover than those in many other habitats. Climate variation increases with elevation and latitude so that these areas may experience years of exceptionally harsh conditions during which it is difficult to breed in the short time window available (Mayfield, 1978; Wingfield, 1984; Martin *et al.*, 2000; Morton, 2002). When daily conditions vary between wide extremes, the structurally simple tundra habitats offer little protection from inclement weather. However, alpine and arctic birds must provide the same buffered, thermal regime to incubate eggs and rear young as other birds (Webb, 1987; Carey, 2002). Thus, parent birds in these habitats must expend more energy to close the gap between ambient conditions and those required for normal embryonic development compared to birds breeding at lower elevations or latitudes (Piersma *et al.*, 2003).

Alpine and arctic birds have a variety of physiological, behavioral, and morphological adaptations to cope with the usual range of climate variability (Martin *et al.*, 1993; Martin, 2001). Phenotypes with the greatest capacity to buffer harsh conditions and maintain a constant reproductive output will have superior mean fitness (Boyce, 1979). The effectiveness of ad-

aptations for reproductive resilience (ability of species to experience disturbance and maintain normal processes) may be limited so that variation in weather may impose annual variation in timing of breeding, breeding condition, or patterns of reproductive investment (Barry, 1962; Hannon *et al.*, 1988; Badyaev and Ghalambor, 2001). Table 1 outlines several non-exclusive mechanisms that alpine and arctic birds may use to cope with variable and extreme weather. One strategy may be to opt out of breeding entirely. Opting out, frequently cited as an option for longer-lived species (*e.g.*, Ganter and Boyd, 2000) is rarely documented because it is very difficult to detect. For example, Mayfield (1978) reported years with no phalaropes nesting at an arctic study site, but he was unable to determine whether the unmarked individuals failed to breed, or bred elsewhere.

Other coping mechanisms may be to delay arrival on breeding sites or to delay egg laying by up to one month if necessary (Martin *et al.*, 2000). Alpine residents or migrants may wait on the breeding grounds, but also have the option of lingering in adjacent habitats until conditions ameliorate higher up (Morton, 2002). Predicting the timing of local spring conditions and snow melt may be more challenging for arctic birds that travel to distant breeding sites. Some songbirds modify their sensitivity to the usual photoperiodic cues that control breeding onset, such that photoperiod response thresholds differ between populations at different latitudes (Silverin, 1995). Birds in habitats with unpredictable spring conditions can use more supplementary information to determine breeding onset (Wingfield *et al.*, 1992; Svensson, 1995). For arctic geese, that import resources for breeding, delays

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TABLE 1. Potential coping strategies for alpine and arctic birds breeding in extreme environmental conditions.

A. Short-term (individual) responses
1. Do not breed. Save resources for a more benign year.
2. Maintain fecundity but sacrifice body condition or maintenance, possibly lowering adult survival
3. Reduce investment in current breeding attempt by reducing the number or quality of eggs or offspring raised
B. Long-term adaptations (behavioral/physiological)
1. Arrival biology/clutch initiation
– delay departure from winter areas, stopover enroute or in adjacent habitats with cover and food
– use supplementary cues to photoperiod that reflect local conditions to determine breeding onset
– place nests in locations/aspects where snow melts first, and are sheltered from storms and with upslope cover from prevailing winds
– develop flexible nest site placement (shrub, on or under ground)
– construct better insulated nests
2. Egg laying and incubation
– develop cold tolerance of unincubated eggs and of embryos during incubation recesses
– develop high tolerance by adults to physiological stress to avoid abandonment of eggs/offspring
– adjust incubation constancy to compensate for low body reserves
– develop a large thermal neutral zone to cope with weather extremes
– increase the number of developed follicles and development rate in order to facilitate rapid nesting/renesting
– extend egg laying period in late years
– develop bi-parental care and/or increased male provisioning to distribute energetic costs between both parents

in breeding imposed by weather may be costly because their energy reserves are drained for somatic maintenance. Hence, body condition at the start of breeding may be sacrificed (Cooke *et al.*, 1995).

In general, alpine and arctic birds have developed a variety of mechanisms to adjust or delay reproductive effort during storms, without forgoing or abandoning the breeding attempt. However, these often reduce reproductive output (Wingfield, 1988; Nol *et al.*, 1997; Bears, 2002). Birds might invest less total energy by producing fewer and/or smaller, lower quality offspring (Table 1). Another strategy may be to initiate breeding with low energy reserves, but to recoup those reserves as soon as the weather allows. Birds that feed during incubation, such as arctic and alpine ptarmigan, may increase the length or frequency of recesses to recoup energy deficits (Erikstad, 1986; Wiebe and Martin, 2000). In comparison, birds that rely only on stored energy during incubation such as common eiders (*Somateria mollissima*) may be forced to abandon clutches completely in harsh periods (Bottitta *et al.*, 2003). At high elevations, songbirds shift investment from offspring number to offspring quality, and many show increased male care and provisioning compared to related species at lower elevations (Badyaev and Ghalambor, 2001).

Mechanisms to cope with variable weather may be species-specific, yet few studies have compared responses between alpine or arctic species, or examined the range of responses within generalist species that breed across elevational or latitudinal gradients. Also rare are multi-annual studies that examine the success of coping mechanisms in maintaining reproductive resilience across wide fluctuations in weather conditions (but see Skinner *et al.*, 1998; Morton, 2002). Here, we present data for two tundra grouse species, white-tailed ptarmigan (*Lagopus leucurus*) in the alpine and arctic breeding willow ptarmigan (*L. lagopus*). We look for patterns of reproduction in response to the normal range of annual variation and for compromises and

constraints in response to extreme weather events, as the latter are predicted to increase with climate change (Diaz and Bradley, 1997). In particular, we examine the effect of spring weather on timing of breeding in ptarmigan as phenology generally has a strong influence on reproductive success (Rowe *et al.*, 1994).

FIELD METHODS

We studied white-tailed ptarmigan breeding at four high alpine sites at 3,350–4,250 m a.s.l. in the Colorado Rocky Mountains (39°34–40'N, 105°35–53'W) from 1987 to 1996, and arctic willow ptarmigan in La Perouse Bay, Manitoba (58°24'N, 94°24'W) from 1981–1985. The life history, breeding biology and field methods are described elsewhere for white-tailed ptarmigan (Braun *et al.*, 1993; Martin *et al.*, 2000) and willow ptarmigan (Martin *et al.*, 1989; Hannon *et al.*, 1998). After birds had settled on territories in spring, they were located using playbacks of male territorial calls or with dogs, captured, and individually color-marked. We classified birds as yearlings (≤ 1 yr old) or adults (> 1 yr) (Braun *et al.*, 1993). To monitor annual breeding success, we used radio-telemetry to locate alpine ptarmigan females (3.4 g necklace design transmitters, Holohil Ltd, Carp, Ontario, Canada) and dogs to locate arctic ptarmigan.

Over 90% of birds were of known-age and marked, with the exception of first study years. We obtained data on clutch initiation dates, clutch size, nesting success, and annual production of fledglings (juveniles ≥ 25 days) for about 95% of females. White-tailed ptarmigan produced an average clutch of 6 eggs and incubated for 23–26 days (Braun *et al.*, 1993; Wiebe and Martin, 2000). Willow ptarmigan in Manitoba had a mean clutch of 10.8 eggs and an incubation period of 22 days (Martin *et al.*, 1993). Females raised only one brood per season, but older females that failed in early to mid incubation produced replacement clutches (renests; Braun *et al.*, 1993; Martin *et al.*, 1989).

We treated years individually in most statistical

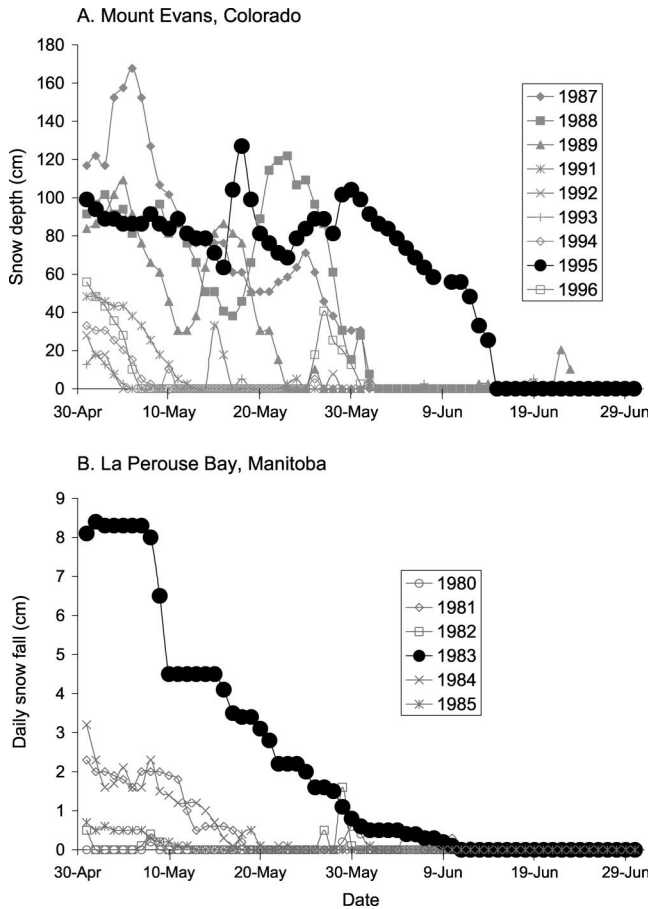


FIG. 1A. Snow depth during May and June near alpine ptarmigan breeding sites in Colorado measured in an open non-drifted area at Mount Evans High Altitude Research Station (3,243 m a.s.l., Station # 055797, Atmospheric Sciences Center, Desert Research Institute, Reno, Nevada). B. Daily snow fall at Churchill airport, Manitoba, 40 km from arctic ptarmigan site (<1 m a.s.l., Environment Canada Weather Station # 5060600).

tests, but these indicated that the “harsh” year, 1995, was a statistical outlier in the alpine study. Therefore, we also summarized some reproductive parameters by comparing the harsh year to pooled means for the other years considered “normal” to examine resilience patterns. With respect to weather, we envision a “harsh” year, as one with conditions that only occurs once every few decades, such as the persistent snow-fall in 1995 that caused the latest snowmelt in 30 years at our alpine site (C. E. Braun, personal communication). Mean values are presented with \pm SE. Statistical significance is reported for two-tailed tests ($P < 0.05$) using log likelihood chi-square tests, ANCOVA and ANOVA. Sample sizes vary for different parameters.

RESULTS

Snow depth and snow fall showed significant annual variation in both the alpine and arctic studies (Fig. 1). In Colorado, mean snow depth in May ranged in normal years from 1.9–82.3 cm with snowmelt date varying from 4–31 May (7 yr, Mt. Evans Weather Station

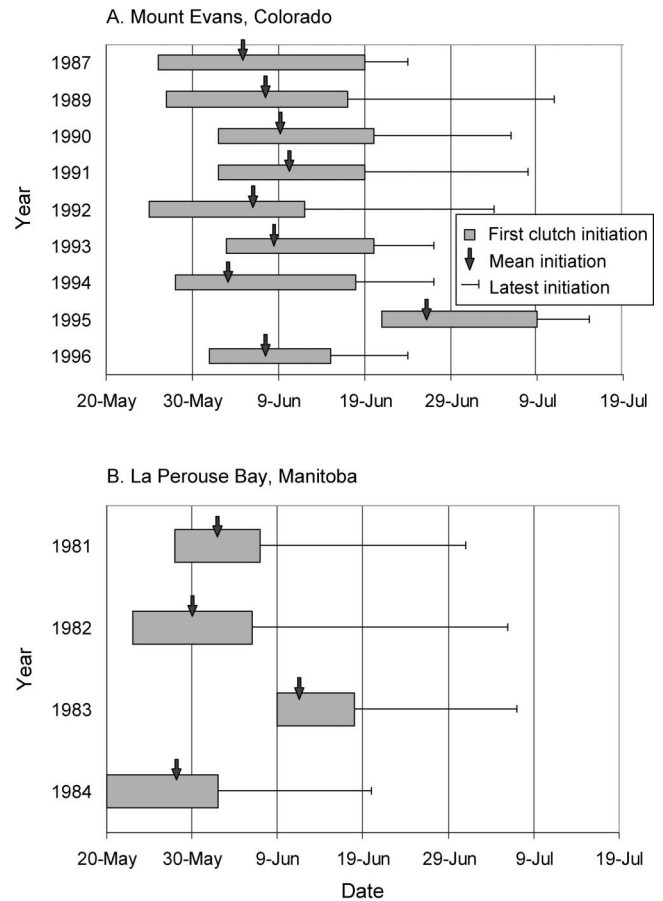


FIG. 2. Clutch initiation dates for nesting attempts of (A) white-tailed ptarmigan in Colorado and (B) willow ptarmigan in Manitoba. Shaded bars indicate the range of initiation dates and arrows above the bars the annual means for first clutches. Lines to the right of the bars indicate the range of initiation dates each year, including re-nests. Note no overlap in initiation dates for first clutches in 1995 and 1983 compared to all other years in Colorado and Manitoba, respectively (ANOVA: mean annual variation in first clutch initiation date—Colorado: $F = 65.93, P = 0.0001$, Fishers Protected LSD Posthoc test, 1995 differed from all 8 other study years; La Perouse Bay: $F = 256.87, P = 0.0001$ (similar value for LPB in Hannon *et al.*, 1988), Posthoc tests: 1983 was later than 3 other years and 1984 earlier than 1981 (all $P < 0.0001$).

#055797). In 1995, mean snow depth in May was relatively high (87.3 cm), but persisted much longer than normal, throughout most of June (mean June snow depth of 27.4 cm compared to 0.0–1.4 cm for other years; Fig. 1A). Since the Mt. Evan’s weather station was located 100–1,000 m below alpine, snow melt on our study sites was at least one week later (*i.e.*, late June) than indicated in Figure 1A. At La Perouse Bay, similar patterns of annual variability in spring conditions occurred, with persistent snow fall until mid June in one year (1983, Fig. 1B).

Initiation of first clutches for alpine ptarmigan varied by 10 days in earliest dates (25 May–3 June) and mean dates (3–12 June) for normal years (Fig. 2A). In 1995, the first egg was laid 18 days later than the study mean of 7 June for normal years, but the latest clutch (July 15) was initiated only 4 days later than any other

year. Thus, 1995 was a very short season as both the earliest and mean clutch initiation dates were significantly later than all other years (Dixon's test for outliers; earliest: r [critical value] = 0.69, $P < 0.01$; mean initiation: $r = 0.71$, $P < 0.01$), but laying was not prolonged as the latest clutch initiation date in 1995 was not an outlier ($r = 0.19$, ns; Sokal and Rohlf, 1995). With fewer years of data, arctic ptarmigan showed similar annual variation in first egg dates in normal years of 8 days and a spread of 9 days for mean initiation dates (Fig. 2B). Mean initiation date in 1983 tended to be later than the other three years ($r = 0.72$, $0.10 > P > 0.05$), but the earliest and latest initiation dates in 1983 were not outliers.

Timing of breeding activities and the influence of weather

We expected the extensive annual variation in the timing of environmental variables (snow melt and spring temperatures) to correlate with timing of breeding as reported earlier for willow ptarmigan (Hannon *et al.*, 1988). We observed positive correlations between snow melt and clutch initiation for alpine ptarmigan when including the outlier year (1995), but not with only normal years included (Fig. 3A). Egg laying in the arctic was significantly positively correlated with snowmelt (Fig. 3B).

To examine influences of spring temperatures on breeding phenology, we calculated Warmth-Sum values (monthly sum of means of daily maximum and minimum temperatures) for April, May and June for each site across years. We present patterns for May as only May Warmth-Sum values showed a potential trend for breeding onset to be related to temperature (earlier clutch initiation dates with warmer temperatures. May Warmth-Sum temperatures in normal years ranged from 568–707.5°C (Mean 641.9°C) in the alpine and from –22.7–70.8°C in the arctic (in sub-zero conditions, negative daily values are subtracted from positive values). In the alpine site, the May Warmth-Sum in the outlier year was below average, but was not unusually cold. Timing of breeding was not correlated with spring temperatures in normal years or extreme years in the alpine, but there was a trend with arctic ptarmigan (Fig. 4).

Although weather parameters had only a modest influence on timing of breeding, phenology had a strong influence on fecundity in the alpine (1987, 1989–1996: 1 Factor ANCOVA with year as factor, initiation date and first clutch size in Colorado— $F = 35.02$, $n = 211$, $P = 0.0001$, slope = –0.04). In normal years, clutch size of first nests declined with laying date ($n = 184$, slope = –0.05, $R^2 = 0.10$, $F = 19.7$, $P = 0.0001$), and also in 1995 ($n = 27$, slope = –0.11, $R^2 = 0.32$, $F = 11.96$, $P = 0.002$). However, the rate of decline in clutch size with date did not differ between harsh and normal years (no interaction of year type and initiation date on first clutch size: $F_{1,8} = 1.02$, $P = 0.42$). First clutches in 1995 were laid on the same dates as renests in other years. If the smaller clutches in 1995

reflected simply a later initiation date, 1995 clutches should have been similar in size to renests from other years. In 1995, females invested more in clutches than would be “expected” based on calendar dates as first clutches were 0.68 eggs larger than renests from other years (ANCOVA: $F_{1,91} = 11.7$, $P = 0.0009$). In extreme years, females might maintain clutch sizes by compromising egg size or quality, but mean egg volume or egg shell thickness did not differ in harsh and normal years (Table 2). Since mean chick mass per brood also did not differ in harsh (1995) and normal years (Table 2), alpine ptarmigan reduced the number, but not the quality, of offspring in the harsh year.

Timing of breeding had a much more modest influence on ptarmigan fecundity in the arctic, despite significant annual variation in clutch initiation (Fig. 2B). Generally, clutch size of first nests declined with laying date (1 Factor ANCOVA: $n = 123$, slope = –0.03, $R^2 = 0.03$, $F = 4.95$, $P = 0.03$), but this relationship was not significant in 1983 ($n = 34$, slope = –0.12, $R^2 = 0.05$, $F = 1.68$, $P = 0.21$). There was no interaction of year and initiation date on first clutch size: $F_{1,3} = 0.99$, $P = 0.40$). Furthermore, the lowest clutch size was in 1982, the second earliest year.

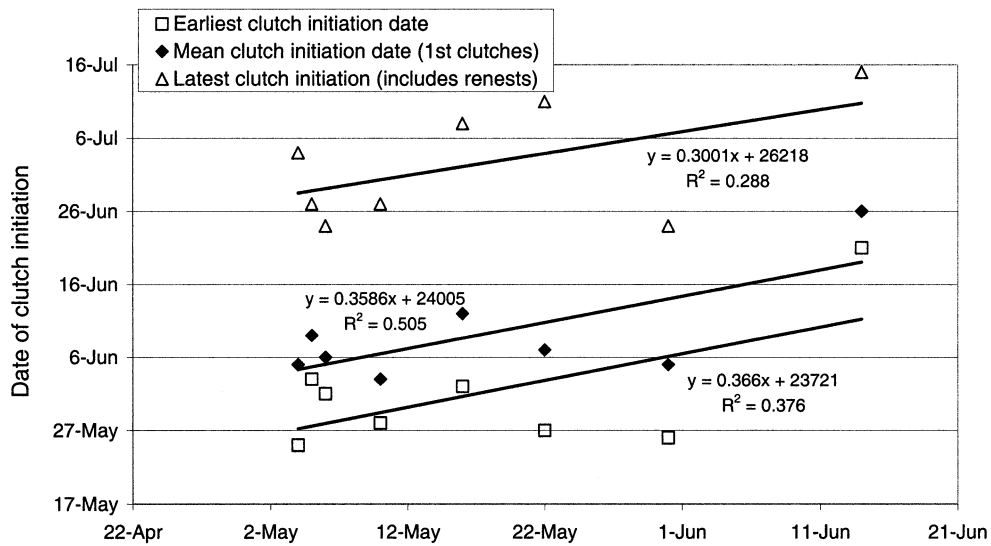
Previously, we showed that incubating alpine ptarmigan took more incubation recesses in 1995 compared with 1994, an early spring with low snow (Wiebe and Martin, 1997). Reduced nest attentiveness in 1995 was associated with longer incubation periods, but embryo viability remained high (Table 2A). Depredation of first clutches was high in 1995, and few birds renested after failure in contrast with other years, but renest clutch size was normal relative to date (Table 2B).

Breeding under extreme conditions may result in tradeoffs between energy still required for reproduction and that required for post-breeding maintenance and survival. Although laying was not protracted in 1995 relative to other years (Fig. 2A), primary molt of alpine females was initiated later in 1995 (ANCOVA, date controlled as a covariate: $F_{1,205} = 14.5$, $P < 0.001$) suggesting that energy limitation persisted to the post-breeding period. Survival of females during the harsh breeding season and over the following winter was normal (Table 2C; Martin and Wiebe, 2004).

Age-structured reproduction in extreme years

Alpine ptarmigan, unlike arctic ptarmigan, show strong age-specific variation in body condition and fecundity (Wiebe and Martin, 1998). Thus, we investigated the influence of the harsh year on age-related reproduction in Colorado. In the harsh year (1995), females initiated egg laying with fewer body reserves compared with females at the same stage in other years (Table 2), but the pattern of age-related variation in body condition at breeding onset did not change between normal years and the harsh year (Fig. 5A). In normal years, older females laid eggs earlier than two yr olds and yearlings (2-way ANOVA: $F_{2,200} = 3.2$, P

A. Mount Evans, Colorado



B. La Perouse Bay, Manitoba

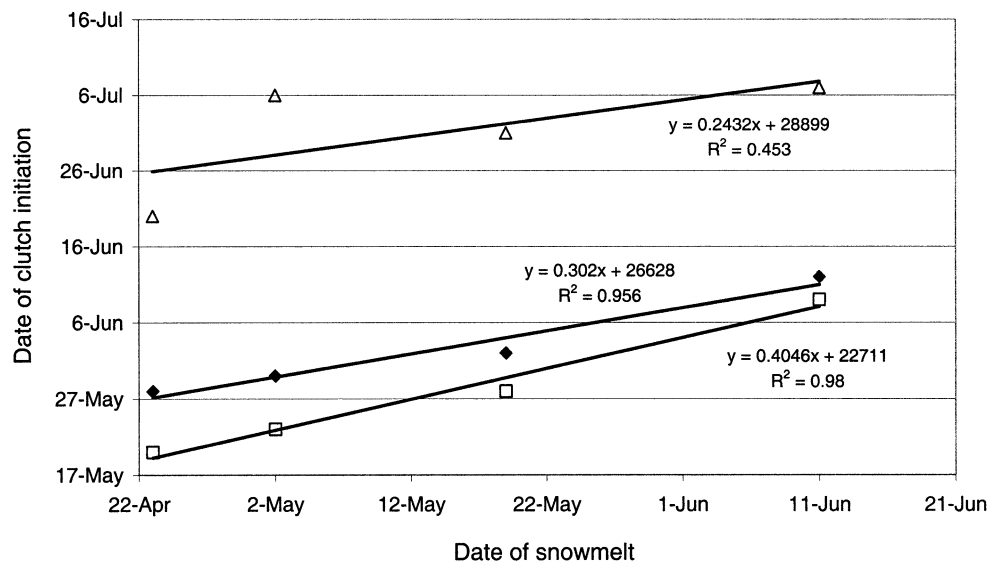


FIG. 3A. Correlations between annual snow melt dates and clutch initiation for alpine ptarmigan. Including all years, mean first clutch initiation dates were significantly delayed in late snow melt years ($R^2 = 0.51$, $P = 0.048$), and a trend for earliest initiation dates ($R^2 = 0.38$, $P = 0.11$). However, with 1995 (outlier year) removed, regression slopes did not differ from zero for mean and earliest initiation dates ($R^2 = 0.001$ and $R^2 = 0.15$; both ns respectively). B. Correlations between snow melt (date snow disappeared or only a trace remained at Churchill airport) and clutch initiation for arctic ptarmigan. Despite only 4 yr, mean initiation dates of first clutches were delayed significantly in late snow melt years ($R^2 = 0.96$, $P = 0.02$), and earliest laying dates ($R^2 = 0.98$, $P < 0.01$), but egg laying was not extended in late years (latest clutch initiation dates; $R^2 = 0.45$, $P = 0.33$).

= 0.04) and the size of first clutches increased with female age (2-way ANOVA: $F_{2,182} = 6.5$, $P = 0.002$). Similar age-related reproductive patterns were also maintained in the harsh year for laying dates (Fig. 5B) and clutch size (Fig. 5C). For example, the reduced size of first clutches observed in 1995 (Table 2) was

apparent in all age classes (0.77 fewer eggs for yearlings, 0.89 for 2 yr olds and 0.64 fewer for females ≥ 3 yr; Fig. 5C). Despite significant effects of the harsh year on body condition, laying dates and size of first clutches, the usual female age-related investment patterns were maintained (Fig. 5).

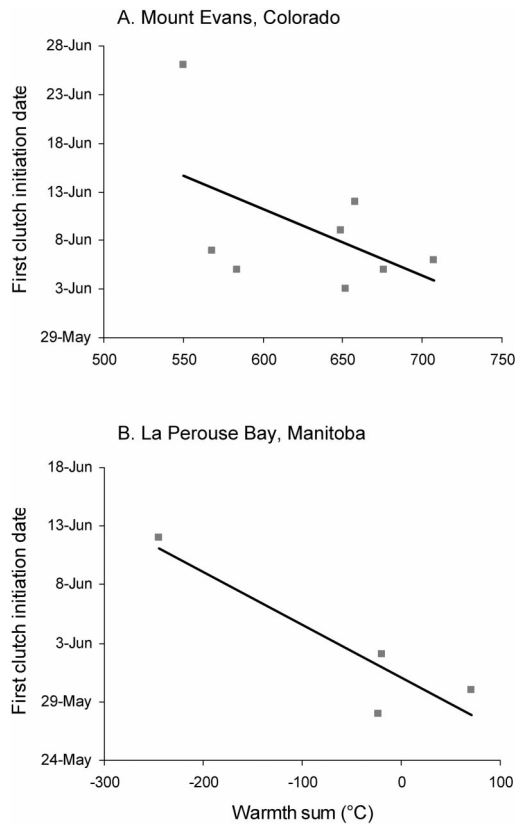


FIG. 4. Relationship between May Warmth-Sum values (see text for explanation) and mean initiation dates of first clutches for alpine and arctic ptarmigan. Even with outlier years included, variation in initiation dates was not related to May temperatures (Alpine, Colorado: $R^2 = 0.27$, $P = 0.18$; Arctic, Manitoba: $R^2 = 0.82$, $P = 0.09$).

DISCUSSION

Alpine and arctic birds clearly assess a variety of risks before reproducing in their stochastic habitats. Birds initiating too early incur high risks of losing clutches to storms, yet early initiation increases annual fecundity (Bollmann *et al.*, 1997). The fitness costs to poorly-timed reproduction are largest in single-brooded species with restricted breeding seasons. Thus, alpine and arctic birds should base their decisions to commence breeding on several reliable cues as each breeding attempt represents a proportionately high fraction of the seasonal reproductive success (Svensson, 1995). Our 13 study-years of breeding activities for congeneric species in alpine and arctic environments found that these habitats normally showed considerable annual variation in spring conditions (Fig. 1). Our exceptionally harsh study year (1995) in the alpine and fairly harsh year (1983) in the arctic provided insight for constraints on ability of birds to cope with weather fluctuations. Alpine ptarmigan avoided egg laying until late May even if snow pack was low earlier, and must cope with a short breeding season. After breeding onset however, they showed strong resilience in maintaining fecundity during years of normal weather variation (breeding parameters uncorrelated

with snow melt), and especially so in the outlier harsh year. There may be a threshold of environmental extremes beyond which alpine females are unable to cope effectively. In the harsh year, females compromised body condition to initiate breeding, and suffered the lowest breeding success in the study. However, survival of adult birds was normal during the harsh spring and over the following winter (Martin *et al.*, 2000). An earlier study of willow ptarmigan found significant positive correlations between hatch date and snow melt date and negative correlations with maximum May temperatures in NW British Columbia, and a trend for later clutch initiation with more days of snow in May for ptarmigan at La Perouse Bay (Hannon *et al.*, 1988). Thus, arctic ptarmigan appear to track local conditions and began breeding earlier in years of early snow melt, and similar to alpine ptarmigan, show strong resilience for fecundity parameters after breeding onset.

Since most alpine and arctic birds are ground nesters, they require some snow-free ground to initiate laying, and thus must be flexible in reproductive timing. The variety of coping mechanisms available to birds (Table 1) may be used to greater or lesser extent by species depending on their ecology and life histories. After arrival, the ability to adjust breeding schedules to local conditions is critical in these unpredictable environments (Bollmann and Reyer, 2001; Morton, 2002). Snow depth and spring temperatures in April and May had little impact on breeding phenology of alpine ptarmigan, but delayed snowmelt in June 1995 caused hardship. In normal years, birds may be able to select nesting sites that are snow-free despite considerable annual variation in snow cover, but when snow cover is nearly 100% as it was in 1995, delayed nesting may be the only option. Flexible nest site choice allowed white-crowned sparrow (*Zonotrichia leucophrys*) to minimize breeding delays in high snow years as they switched from ground nests to nesting in trees or shrubs (Morton, 2002); however, this strategy was not available to ptarmigan.

Storms and other stressful environmental stimuli activate adrenal tissues that release plasma corticosterone; increased levels of this steroid sometimes results in birds entering an emergency life history state (individuals cease reproduction and focus on survival; Wingfield, 1985). However, alpine and arctic breeders such as white-crowned sparrow and dark-eyed junco (*Junco hyemalis*) have reduced adrenocortical responses and release less corticosterone in response to stressors. Thus, they can resist clutch abandonment during inclement weather (Wingfield *et al.*, 1995; Bears *et al.*, 2003).

Faced with breeding delays, females may compromise in one or more reproductive parameters. White-tailed ptarmigan in the extremely harsh year initiated laying with poorer body condition compared with other years, yet recouped condition by the end of incubation with increased time off the nest (Wiebe and Martin, 2000). This strategy allowed larger clutches than expected for the calendar date. In late years,

TABLE 2. *Effects of weather on reproduction and survival of alpine ptarmigan.*

	Harsh year	Normal year	F/X ² (P)
(A) Egg quality			
shell thickness/clutch ^a (mm ± SE)	0.178 ± 0.004 (14 clutches)	0.183 ± 0.012 (2 clutches)	F = 0.14 (0.72)
egg volume/clutch ^b (cm ³ ± SE)	19.56 ± 0.3 (15 clutches)	19.62 ± 0.1 (54 clutches)	F = 0.09 (0.77)
% eggs hatched (viability)	100 (25 eggs/5 clutches)	88 (323 eggs/61 clutches) ^c	X ² = 2.3 (0.13)
clutch size ± SE – first nest	5.38 ± 0.19 (24)	5.94 ± 0.07 (160)	F = 8.65 (0.0004)
clutch size ± SE – re-nest	4.5 ± 0.22 (6)	4.7 ± 0.09 (72)	F = 0.37 (0.54)
chick mass/brood ± SE (g)	13.2 ± 0.08 (4 broods)	13.1 ± 0.14 (41 broods)	F = 0.67 (0.80)
(B) Nesting			
spring body mass ^d (g)	398.7 ± 5.0 (28 hens)	428.1 ± 2.7 (185 hens)	F = 14.66 (0.0002)
spring condition ^d (residual)	-14.15 ± 5.16 (28 hens)	+2.25 ± 1.94 (176 hens)	F = 9.64 (0.002)
mean incubation period ^e (days)	25.2 (4 clutches)	24.2 (53 clutches)	
% success – first nests	9.4 (32 clutches)	38 (177 clutches)	X ² = 9.9 (0.002)
% re-nesting probability ^f	38 (8 clutches)	83 (46 clutches)	X ² = 7.59 (0.006)
% hens producing broods ^g	16 (32 hens)	50 (164 hens)	X ² = 12.8 (<0.0003)
(C) Adult survival			
breeding season ^h (%)	88 (32 hens)	88.4 (147 hens)	X ² = 0.02 (0.88)
over winter ^g (%)	41 (32 hens)	43 (233 hens)	X ² = 0.06 (0.81)

^a Means of three thickness measurements per egg were taken by one observer using Starrett micrometer calipers on an air dried fragment from the largest diameter of each egg with the inner membrane removed. Eggs were collected after hatch or depredation.

^b Calculated by Volume (mm³) = K × (length × width²), where K = 0.51 for ptarmigan; Hoyt 1979). Data from clutches in the harsh (1995—n = 15) and other years (1990–1992, 1994—n = 54).

^c From Braun *et al.* (1993).

^d Female Mass: 1-Factor ANCOVA with days before date of clutch initiation (dci) as a covariate. Female spring condition: An index of spring body condition was calculated using the residuals of a regression of mass on wing chord length and dci corrected for age class (yearlings, 2 yrs and ≥3 yrs; Wiebe and Martin, 1998).

^e Normal years (1987–1994, 1996): mode of 24 days (54% of 53 clutches, range 23–25 days; Wiebe and Martin, 2000); harsh year: 24, 25, 26 and 26 days (this study).

^f For adult hens (≥2 yrs) that lost first nests ≤15 days into incubation in both year types; none of 6 yearlings that lost clutches after ≤8 days of incubation re-nested in 1995.

^g From Martin *et al.* 2000. Data on over winter returns of breeding birds closely approximated local survival as probability of detection was ≥95% for birds on study sites (mark-recapture analyses).

^h From Martin and Wiebe (2004).

white-crowned sparrows laid smaller eggs (Morton, 2002), thus potentially decreasing offspring quality (Table 1), but this did not seem to occur in ptarmigan (Table 2). Small eggs may jeopardize survival for precocial grouse chicks that rely extensively on nutrient stores after hatching. Egg size in many birds may not vary if there is a threshold egg size for viability (Wiebe and Bortolotti, 1995), or if egg size has high heritability (Cooke *et al.*, 1995).

Reproductive success may be lower in harsh years because of smaller clutches or poorer egg or offspring survival, and often nest depredation is higher (Ganter and Boyd, 2000). Predators may locate nests more easily on the smaller patches of snow-free ground (Byrkjedal, 1980). Often, there is less time or lower propensity for re-nesting (Bollmann and Reyer, 2001; Morton, 2002; this study). Breeding seasons for alpine and arctic birds are generally not extended in late years, perhaps because late-hatching offspring often have low recruitment to natal areas (Cooke *et al.*, 1984; Martin and Hannon, 1987). Thus, delayed years are usually short seasons with low production.

Specific impacts of climate change in alpine and arctic systems are difficult to predict. Animals need to cope with both warming (mean temperatures) and stochastic weather events (variance). Some species may initiate breeding earlier in response to a mean increase

in spring temperatures (Crick and Sparks, 1999), but potential increases in fecundity from larger clutches can be eliminated by stochastic weather events at later breeding stages as reported for pied flycatchers (*Ficedula hypoleuca*) in Finland (Jarvinen, 1994). Other difficulties may arise if advancing laying date causes a mismatch with timing of hatch and peaks in food supply (Visser *et al.*, 1998). The larger the scale of the extreme weather, the more devastating the impact on population sizes. The 1991 eruption of Mt. Pinatubo, Philippines, caused circumpolar cooling, delayed snowmelt, and resulted in global reductions in productivity of arctic waterbirds in 1992 (Ganter and Boyd, 2000).

We predict several traits may decrease the ability of birds to cope with variable spring weather. Migrants may be less resilient than residents because they have a less well cold-adapted physiology and because they are less able to predict local conditions from distant wintering grounds. Although capital breeding is considered a beneficial tactic for resource acquisition for reproduction under unpredictable or limited time or foraging conditions (Jonsson, 1997), capital breeders may be more susceptible to extreme delays than income breeders if they are unable to recoup energy losses quickly. Finally, dependence on certain food sources, such as insects, may be more risky than herbivory.

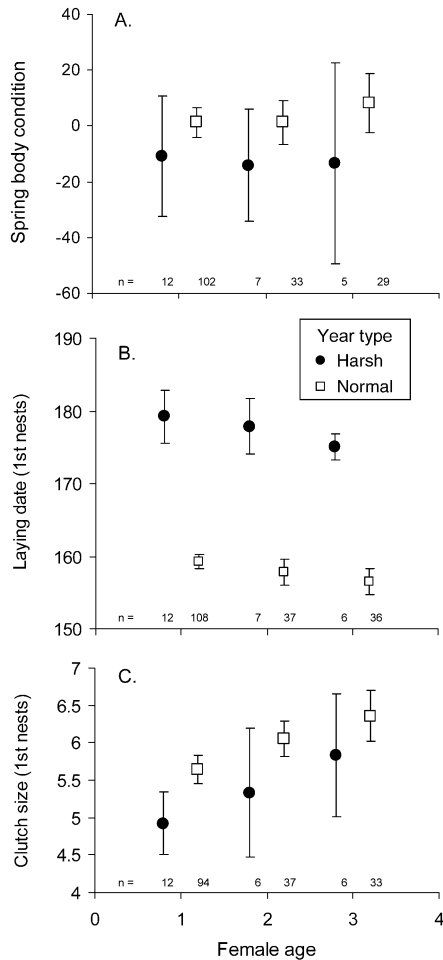


FIG. 5. Harsh weather in Colorado and age related patterns of A) spring body condition, B) initiation dates for first clutches and C) clutch size for alpine ptarmigan (means \pm 95% CI). Two-way ANOVAs were used to compare parameters in Harsh (1995) and Normal years (1987, 1989–1994, 1996). Number of females (n) given for each age class and year type. Spring body condition residuals (see Wiebe and Martin, 1998) were lower in the harsh year for all ages ($F_{1,182} = 6.9$, $P = 0.009$; No interaction between female age and year type). For all age classes, egg laying was later in the harsh year ($F_{1,200} = 270.9$, $P < 0.0001$; No interaction between female age and year type— $F_{2,200} = 0.15$, $P = 0.86$), and clutches were smaller ($F_{1,182} = 10.9$, $P = 0.001$; No interaction between female age and year type— $F_{2,182} = 0.095$, $P = 0.91$).

Deep snow may increase food availability for herbivores by allowing access to the upper branches of plants; however, low temperatures and snow may reduce food abundance and/or foraging ability for insectivores (Bollmann *et al.*, 1997).

On a longer time scale, natural selection should lead to increased ability to cope with stochastic and harsh years by various mechanisms (Table 1). However, alpine and arctic animals often have low productivity and long generation times that slow rates of adaptive change (Krementz and Handford, 1984). Elevational or latitudinal generalists such as juncos, horned larks (*Eremophila alpestris*) or savannah sparrows (*Passerculus sandwichensis*) may have more difficulty refin-

ing adaptations to harsh conditions, particularly if alleles are mixing between populations to slow local adaptations. To predict how life histories are likely to evolve in variable environments, it is necessary to identify the nature of tradeoffs (fixed, multiple optima) between adult survivorship and reproduction (Benton and Grant, 1999; Orzack and Tuljapurkar, 2001). Future studies should examine patterns of weather-related reproduction to determine limits to reproductive resilience. Then, we can assess whether these thresholds are likely to be exceeded with predicted climate change patterns.

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