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S08-3 Impacts of extreme climate events on alpine birds

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Abstract With climate change, the frequency and severity of extreme environmental events such as heavy snow fall are expected to increase in north temperate and alpine areas. In a 9-year field study, we evaluated impacts imposed on reproduction in white-tailed ptarmigan (*Lagopus leucurus*) by a year of heavy and persistent snow cover. Under extreme conditions in 1995, all females attempted nesting, but timing was so delayed (mean 18 days) that it did not even overlap with other years. Breeding success in 1995 was the lowest for the study, but survival of adults was normal. Quantifying impacts of extreme climate events on fitness allows refinement of predictions for avian responses to climatic change.

Key words Extreme climatic events, Reproductive success, White-tailed ptarmigan, Quantified impacts

1 Introduction

Patterns of wildlife responses to climate change are emerging from long term monitoring and population data (Crick and Sparks, 1999). A proportion of migratory birds and resident vertebrates now arrive on territories and initiate breeding 1 to 4 weeks earlier than several decades ago (Inouye et al., 2000). Earlier arrival and breeding can result in ecological mismatches if the phenology of different components of food chains do not advance at the same rate (Visser et al., 1998). For example, earlier arrival dates for pied flycatchers (*Ficedula hypoleuca*) in Finland were associated with earlier laying dates, and increases in egg size, clutch size and hatching success over the past two decades (Järvinen, 1994). However, such reproductive investment did not result in improved reproductive success, due to weather events during brood-rearing period later in the season. Thus, potential fitness gains resulting from climate warming need not be realized due to differential changes in climate at different times of the year.

Terrestrial animals in temperate systems regularly experience stochasticity in temperature, wind, precipitation or snow cover that impose seasonal variation in timing of breeding with reproductive consequences (Wingfield, 1984; Hannon et al., 1988). Climate change models predict a general increase in the frequency of extreme weather (IPCC, 2001), with warmer winter temperatures and greater spring snow fall already experienced in western North American and European alpine areas (Diaz and Bradley, 1997).

Ptarmigan are ground-dwelling, herbivorous, tundra grouse with morphological, physiological and behavioral adaptations to survive and reproduce in harsh and unpredictable weather conditions (Braun et al., 1993). In a 9 year study of alpine white-tailed ptarmigan (*Lagopus leucurus*), we recorded one year (1995) with unusually heavy and persistent snow cover. Here, we evaluate responses and fitness costs imposed on ptarmigan breeding in such extreme conditions, and evaluate the potential impact of increases in the frequency of such events on alpine birds.

2 Materials and methods

We studied white-tailed ptarmigan at 4 alpine habitats in the Colorado Rocky Mountains (3 350–4 250 m a.s.l., 39°34–40'N, 105°35–53'W) from 1987 to 1996. The life history and breeding biology of the ptarmigan, and the field methods used, are detailed in Martin et al. (2000). We located birds using dogs or playbacks of male territorial calls, and captured them with noose poles or nets. All females were taken after they had settled on a territory, and were affixed with radio tags to monitor survival and breeding success. Birds were aged as yearlings (≤ 1yr) or adults (> 1yr) based on pigmentation on primaries 8 and 9, after Braun et al. (1993). We recorded survival of breeding birds by thorough checks of study sites and adjacent mountains for marked birds through the summer and the next year.

Data on snow depth were obtained from the Atmospheric Sciences Center, Desert Research Institute, Reno, Nevada, USA. Here we defined a “harsh year” as one of extreme conditions that occurs less frequently than the average life span of individuals that have reached adulthood; such a life span for white-tailed ptarmigan is 3–4 years. Because the timing of snowmelt and laying phenology in 1995 were well outside the normal range of variation for our study, we felt justified in calling it an unusually harsh year (Fig. 1). Thus, we pooled data from the 8 normal years for

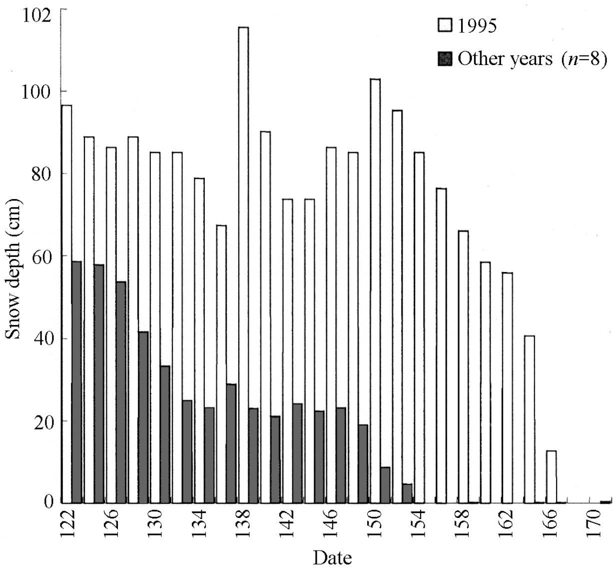

Fig. 1 Snow depths (cm) in May and June (averaged for 2 day periods) near ptarmigan study sites in 1995 (harsh year) compared to average snow depths for other years (normal years: 1987–1989, 1991–1994, 1996)
Depths are averaged for two day periods and measured in an open, non-drifted area at Mount Evans High Altitude Research Station (Stn. # 055797), Colorado, 3 243 m a.s.l. January1=day 1.

comparison with the harsh year. Statistical significance is reported for two-tailed tests ($P < 0.05$).

3 Results

The spring snow depth in May 1995 was approximately double that in other study years, and snow fall and a deep snow pack persisted until late June, a month later than in "normal" years (Fig. 1). Snow fall was deeper and melted at least 1 week later on our study sites than recorded on Fig. 1, as the Mt. Evan weather station, from which the recordings came, was located several hundred meters below. Leaf-out in willow (*Salix* spp.), the main spring food of ptarmigan, was also delayed by about 3 weeks in 1995 (pers. obs). Excessive snow fall and delayed melt occurred in all study areas (Martin et al., 2000) and elsewhere in Colorado in spring that year (Inouye et al., 2000).

3.1 Survival and breeding propensity

Virtually all females on our sites obtained mates and bred annually. We determined survival, egg laying dates, clutch size and annual production for about 95% of hens. We expected higher predation on birds in 1995 given that the development of dark nuptial plumage reduced their crypsis in a white landscape prolonged by delayed snow melt. During summer 1995, 5 females (15.6%) died, compared to 11.6% on average in normal years (n=147 hens; Braun et al., 1993). Over winter survival of adults after the harsh year was normal (Martin et al., 2000). We expected yearling females to opt out of breeding in 1995 because breeding was delayed beyond the date of re-nest initiation. In 1995, all 32 hens located and radio-tagged on our study sites (including 12 yearlings) initiated clutches. We might have failed to detect birds that had opted out of breeding had they left our sites; but, if this were so, we would then expect fewer breeding pairs in 1995. Breeding densities in that year, however, were above the norm of 26 hens/year. Thus, we have direct and indirect evidence that all female ptarmigan attempted breeding in the harsh year.

3.2 Timing and success of breeding activities

In 1995, first clutches were initiated 18 days later than 7 June, the mean date across all study years (Fig. 2). First clutches in 1995 (5.38±0.19 *SE* eggs, n=24 clutches) were also smaller than across other years (5.94±0.07, n=160; $F_{1,210}$=8.65, P=0.0004). Reproductive success in 1995 was

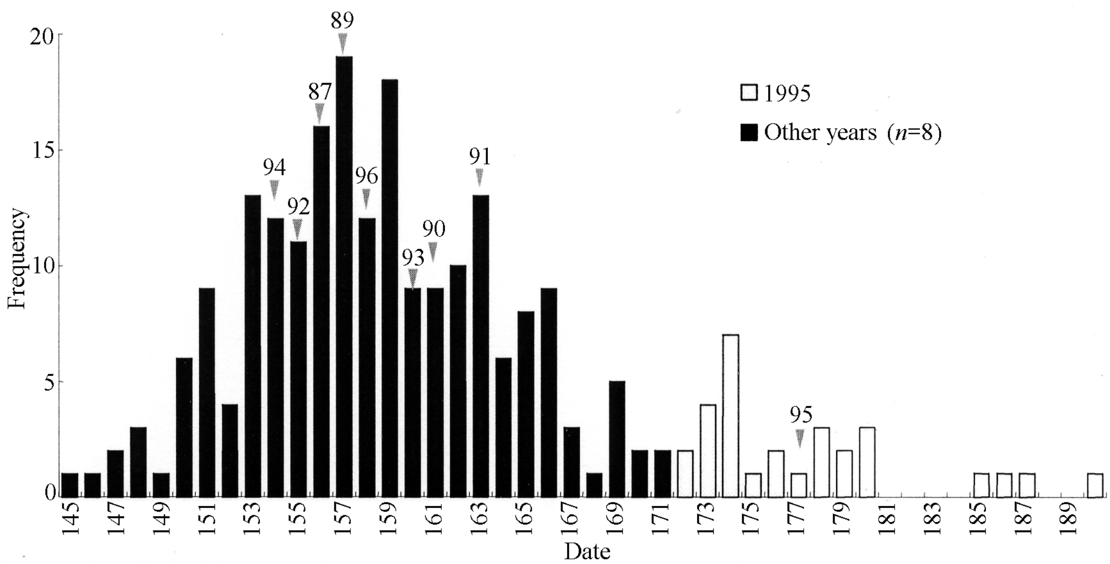

Fig. 2 Initiation dates for first clutches of Colorado white-tailed ptarmigan in harsh (1995) and normal years (1987, 1989–1994, 1996); $F_{1,200}$ = 270, P < 0.0001
Triangles with year above bar indicate mean annual clutch initiation dates. January 1=day 1.

the lowest of all years, as more than 70% of first clutches failed. Only 3 of 8 adult hens renested compared to 83% in other years. No yearlings renested.

4 Discussion

It is instructive to examine impacts from the extreme year because increased frequency and severity of extreme events is one predicted consequence of climate warming, especially for high elevation habitats. Despite exceptional delays, no birds opted out of breeding. Proximate responses by ptarmigan to extreme conditions involved adjustments in timing of breeding and fecundity. Over our 8 "normal" years, mean clutch initiation dates varied by 10 days; but in 1995, mean clutch initiation was 14 days later than that in the latest normal year. The harsh year breeding season was also considerably shorter than in normal years. Although they experienced the lowest production recorded, the ptarmigan suffered no increase in mortality in the harsh season or over the next winter. Ground-feeding herbivores may generally resist such extreme weather events, as deeper snow fall in spring may increase access to higher parts of plants. This may differ for insectivorous and granivorous birds, for which harsh conditions often reduce food availability or foraging capacity, so reducing survival of young and adults.

4.1 Impacts of climate variability on avian populations

Reproductive success for birds is often low in harsh years, due to smaller clutches and reduced renesting in late years. Delayed snow melt physically constrains nest building for ground nesting birds, and the patches of available bare ground are fewer and smaller, helping predators to detect nests more readily (Martin, 2001). Recruitment of late hatching offspring to natal areas is often lower (Martin and Hannon, 1987). Thus, the consequences of breeding in harsh years may be fewer and poorer quality offspring. It is unclear why female ptarmigan attempted to breed in the harsh year, given their extremely low success. With few survival costs, birds may risk breeding with low benefits, or they may be unable to predict the persistence of harsh conditions.

Increases in climate warming (mean temperature) and extreme weather events may affect animal populations differently, depending on patterns of resource availability and life history traits (Martin, 2001). Their interactive effects are especially complex in sites with strong biophysical gradients, such as alpine or arctic habitats. Food for alpine herbivores may increase with predicted increases in moisture, but advancing treelines will result in smaller, more isolated patches of habitat that may impede dispersal. In some cases, extreme events later in the spring-summer season may remove potential fitness gains due to advances in breeding phenology associated with climate warming. There may even be a loss of fecundity.

Studies of the impacts of climate variability yield important insights into proximate mechanisms that animals may use to cope with climate change; and they can be used to predict longer term effects of environmental change on behavior, demography and life history. Given their strong biophysical gradients, alpine habitats provide a good system for studying the effects of changing frequencies in extreme climatic events, and alpine animals may function as "canaries" in such research.

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