

## MOVE, ADAPT, OR DIE: *LAGOPUS LEUCURA* CHANGES IN DISTRIBUTION, HABITAT, AND NUMBER AT GLACIER NATIONAL PARK, MONTANA

DAVID BENSON AND MATTHEW CUMMINS

*School of Mathematics and Sciences, Marian University, 3200 Cold Spring Road, Indianapolis, IN 46222, USA. E-mail: dbenson@marian.edu*

**ABSTRACT.**—Because of the “montane island” effect and relative rates of climate change, alpine species may be particularly affected by changing climate. White-tailed Ptarmigan (*Lagopus leucura*) are adapted to life in the alpine cold, but may be less well-adapted to hot summer temperatures. In 1996 and 1997, ptarmigan living in Glacier National Park (GNP) were closely associated with remnant snow and free water in the late summer, a resource that is rapidly changing in distribution and extent as climate changes. We examined White-tailed Ptarmigan distribution, habitat, and numbers in 2009–2010 for comparison with 1996–1997 data. Briefly, five areas within GNP were searched for ptarmigan during August. Habitat data including microclimate were collected at flock locations. Microclimate at ptarmigan flock locations differed from other areas nearby. Flocking ptarmigan appeared to be less numerous than described in 1996 and 1997, and mean flock locations on Logan Pass moved 335 m upslope between the 1990s and 2009 and 2010. Ptarmigan in 2009 and 2010 chose habitat that had the same coverage of vegetation and rock as 1996 and 1997, but contained less snow and water, was farther from snow and water, contained lower soil moisture content, was higher in elevation, and steeper in slope. Our study demonstrates that White-tailed Ptarmigan in GNP have changed distribution, altered habitat preferences, and perhaps on a local scale, experienced declining population numbers in late summer. *Received 1 March 2011, accepted 20 June 2011.*

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**Key words:** *Lagopus leucura*, White-tailed Ptarmigan, climate, habitat, distribution, water.

AS CLIMATE CHANGES (IPCC 2007), species' distributions, habitat and demography are being affected (see reviews: McCarty 2001, Parmesan and Yohe 2003, Crick 2004, Parmesan 2006, Visser 2008). Some of these effects may be more pronounced in mountain systems. Several researchers have uncovered elevational changes attributable to climate

change. Parmesan (1996) documented a shift of 124 m upward in elevation in the Edith's Checkerspot butterfly (*Euphydryas editha*) in the Sierra Nevada Mountains of California. Montane plant species in the Swiss Alps have shifted upward 4–9 m per decade (Grabherr et al. 1994), while treeline in the Canada Rockies has moved significantly upslope (Luckman

and Kavanagh 2000). Montane birds have the potential to be affected, too. Pounds and others (1999, 2005) found a significant increase in elevation in the distribution of bird species using montane cloud forest habitat. A modeling study of Snow Bunting (*Plectrophenax nivalis*) distribution suggested that breeding range will decrease or disappear in the Grampians of Scotland under some predicted climate change scenarios (Berry et al. 2001).

Implicit in such studies are changes in a species' habitat. Rather than, or in addition to changes in distribution, species may adapt to changes in habitat by modifying behavior. Thus far, the behavioral changes in response to climate most often recorded are phenological (Bradley et al. 1999, Parmesan and Yohe 2003). For example Dunn and Winkler (1999) used Tree Swallow (*Trachycineta bicolor*) nest records from across its range to document a 5–9 day advance in breeding date between 1959 and 1991. Inouye et al. (2000) revealed a phenological disjunction between arrival and emergence dates of American Robin (*Turdus migratorius*) and Yellow-bellied Marmots (*Marmota flaviventris*) and the first date of bare ground. Species may also adapt by changing what habitat they select or exploiting different aspects of their preferred habitat (Martin 2001).

Local extinctions, such as of Pika (*Ochotona princeps*) in the Great Basin, have also been attributed to changing climate. Parmesan and Galbraith (2004) found that extinct populations of Pika were from significantly lower elevations than those still present. A similar result was found in Checkerspot Butterflies; local extinction rates were found to be greater at the southern end of the species range and at lower elevations (Parmesan 1996).

White-tailed Ptarmigan (*Lagopus leucura*) are the only bird species in North America to spend their entire lives in the alpine (Braun et al. 1993), and the effects of changes in winter

and spring alpine climate on ptarmigan have begun to emerge. In Colorado, median hatch dates have moved ahead by approximately 15 days during 1975–1999 (Wang et al. 2002). Wang et al. (2002) also found that higher minimum winter temperatures retarded the growth rate of a White-tailed Ptarmigan population. Martin and Wiebe (2004) found White-tailed Ptarmigan breeding success was greatly reduced when spring snow melt was delayed by two weeks.

Lesser known are how changes in summer climate may affect these alpine specialists. Ptarmigan at the northernmost end of the Rocky Mountains in the lower 48 states, USA, in Glacier National Park (GNP), Montana were found to be very closely tied to snow and water in the late summer (Choate 1963a, Benson 1999), possibly due to the cool microclimate which that habitat provides (Johnson 1968). GNP has experienced a mean average temperature increase of 1.6°C in the past 150 years, approximately three times the global average (Hall and Fagre 2003). Although precipitation has increased near the park over the past century, and winter snowpack within the park and summer temperatures have remained relatively stable (Selkowitz et al. 2002), glaciers and perennial snow cover within the park have decreased from 99 to 27 km<sup>2</sup> during the past 150 years (Key et al. 2002). The number of glaciers has declined from 150 to 27 since the late 1800s and all are predicted to be gone by 2030 (Hall and Fagre 2003).

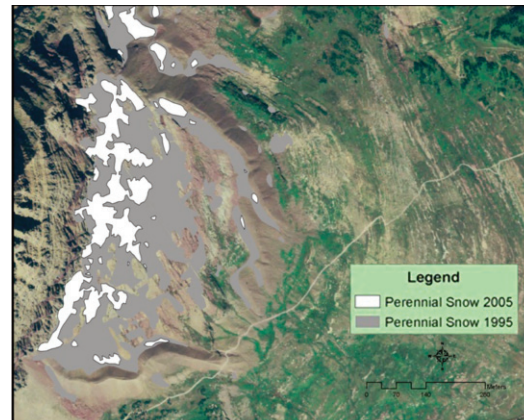
Ptarmigan in GNP choose habitat closely associated with snow and water (Choate 1963a, Benson 1999), a resource that rapidly changed in distribution from year to year as perennial snow has decreased. Our study examines how White-tailed Ptarmigan in GNP have responded to the rapid changes in the distribution of perennial snow and water in terms of alterations in late summer flock locations, habitat preferences, and local population numbers.

## METHODS

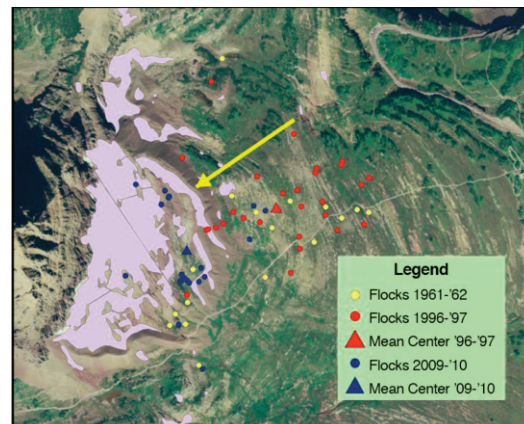
**Study Area.**—The primary study area encompassed approximately 2.5 km<sup>2</sup> southeast of Logan Pass in Glacier National Park, MT, USA, as described by Choate (1963a) and consisted of large, glacially-carved alpine hanging valleys and cirques, with meadows transected by long benches of sedimentary rock. Much of the study area was treeless, with stunted Subalpine Fir (*Abies lasiocarpa*) and Whitebark Pine (*Pinus albicaulis*) occurring sporadically throughout. Snow covered much of the study area until mid-July, after which the meadows became snow free and relatively dry. The distribution of perennial snow on Logan Pass has changed over the past century from the 1930s when Clement's glacier was the principal source of late summer water and snow, to the 1950s when it was downgraded to a permanent snowfield, to the 2000s when that permanent snowfield was almost completely melted by late August (Figure 1).

We searched five other areas for ptarmigan flock sites: Lunch Creek, Piegan Pass, Grinnell Glacier, Reynolds Mountain, and Bear Hat Mountain. Previous searches of each of these areas were reported by Benson (1999). These areas were similar in character to Logan Pass, described above.

**Habitat Analysis.**—After the breeding season (approximately mid-July–late September), ptarmigan males and unsuccessful females form flocks of 2–20+ birds (Braun et al. 1993). Flocking individuals are sedentary or slowly moving and are generally found within 2 m of another individual. Flocks leave behind obvious sign, including fresh droppings and multiple feathers in approximately 20-cm-diameter circles where each bird was sitting (pers. obs.). We centered habitat plots on flock locations found between 9 August and 7 September 2009 and 2010. These flock locations were defined as areas with either two or more ptarmigan within 2-m of each other or with more than two piles of fresh (not dried out)



**Figure 1.** Distribution of perennial snow on 22 August 1995 (231,499 m<sup>2</sup>) versus 27 August 2005 (35,283 m<sup>2</sup>) on Logan Pass in Glacier National Park (USDA 2005; USGS 2001). The majority of the snow is on the site of the former Clement's glacier.



**Figure 2.** White-tailed Ptarmigan flock sites in 1961–62, 1996–97, and 2009–10 on Logan Pass in Glacier National Park, MT (Choate 1963a; USDA 2005). The arrow indicates the direction of increasing slope.

droppings and fresh (still fluffy; not wet and matted) feathers. Several sites with dry droppings, matted feathers, or feathers with mud or dirt splashed on them were not used in the analysis because they were assumed to be more than one week old.

We measured habitat variables (Benson 1999 following Frederick and Gutiérrez 1992) in 177-m<sup>2</sup> circular plots (15-m diameter) centered on the estimated middle of the flock location. Vegetation and abiotic components of the habitat plot were sampled along two 15-m transects on random compass bearings intersecting at the point where the bird was observed, totaling 100 equally spaced line intercepts (Benson 1999). We took five surface samples of soil on each transect totaling approximately 150 g wet mass. Each soil sample was weighed to the nearest 0.1 g on an electronic balance, oven-dried at 50°C, and re-weighed to give percent soil moisture content.

*Microclimate.*—We collected microclimate data at three of the five study sites from 9–28 August 2010. Ambient temperature and humidity were collected with a data logger housed in a radiation shield. We took black globe temperature with a thermometer in the center of a six-inch copper globe painted matte black. An apparatus was placed in the noted location of two individuals in each flock. We placed three other apparatuses in semi-random locations with a similar light regime to the flock location at or near a random distance within 50-m along a random compass bearing. We left these microclimate collectors in place an average of four days, then moved to another flock location for a total of 12 flock locations.

*Ptarmigan Population Size and Distribution.*—Birds in 2009 and 2010 were not banded. Population sizes were estimates based on the number, size, and location of flocks. We used GPS (2-m accuracy) to obtain flock location coordinates and ArcView 9.2 to map and find the average center-point of flock locations near

the Hidden Lake Nature Trail in the Logan Pass study area. We obtained 1961 and 1962 flock location data from hand-drawn maps in Choate (1963a).

*1996 and 1997 Data.*—Habitat data from Benson (1999) was used to compare with those from 2009–2010 on the number of individuals and flock locations on Logan Pass and habitat preferences in the five study areas combined. A consumer-grade GPS unit was used to obtain flock coordinates in 1996 and 1997 with selective availability corrupting locations in random directions by about 50 m horizontally. While each individual point may not be as precise as recorded in 2009, the average center point of all flocks on Logan Pass in 1996 and 1997 is assumed to be accurate because each individual location is incorrect in a random direction and because the GPS locations match one of the authors' (Benson) descriptive notes and maps of flock locations.

*Statistical Analysis.*—T-tests were used to compare nine variables from 2009–2010 and 1996–1997 habitat data with a Bonferroni-corrected significance level of  $\alpha < 0.006$ . One-way ANOVA was used to compare five microclimate variables between random and flock locations in 2010. The Bonferroni-corrected significance level was  $\alpha < 0.01$ . Non-normally distributed data were transformed using square root or log transformation. The values reported are means  $\pm$  SE.

## RESULTS

In 2009–2010, we found flocks in four of the five locations extensively searched. The largest flock contained five individuals, although three flocks in close proximity (within 30 m) were found on Logan Pass totaling seven birds (Table 1). On Logan Pass, the one-day highest total number of individuals found was 11. However, no other flocks were found on that day, and no search in prior days yielded more than 11 individuals (Table 1).

**Table 1.** Flocking individuals and flock sizes from 1959 (Choate 1963a), 1997 (Benson 1999), 2009, and 2010. Individuals in 1959 and 1997 were individually marked. “Big day” indicates the number of flocks and total birds seen on one day of searching the Logan Pass study area.

	1959	1997	2009	2010
Total Flocking Individuals	55	18	10 (unmarked est.)	11 (unmarked est.)
Largest Flock	17	10	4	11
Average Flock	5.0	5.1	3.0	5.0
“Big day” on Logan Pass	4 flocks; 33 birds	2 flocks; 12 birds	3 flocks; 7 birds	1 flock; 11 birds

The distance between the mean center of the late 1990s flock locations ( $n = 20$ ) and the 2009–2010 flock sites ( $n = 20$ ) on the Logan Pass study area was 335.2 m horizontally (Figure 2).

In 2009–2010, ptarmigan ( $N = 49$ ) chose habitat significantly farther from snow and marginally farther from water, with higher soil moisture and a steeper slope than ptarmigan in 1996 and 1997 ( $N = 26$ , Figures 3 and 4). Coverages and elevation were similar, although 2009–2010 had fewer flock sites with snow or over 20% water (Figures 5 and 6).

Compared to random sites, ptarmigan flock locations tended toward lower average high ambient temperatures, lower black globe temperatures, and lower average high black globe temperatures, although none of these comparisons had a P-value below the Bonferroni corrected alpha (Figure 7). Mean ambient temperature (Figure 7) and humidity (random mean = 58.1 +/- 15.7; flock mean = 65.2 +/- 14.7;  $df = 51$ ,  $F = 2.74$ ,  $P = 0.1$ ) did not differ between random and ptarmigan flock locations.

## DISCUSSION

In this study, we found fewer total individuals than 13 years prior at Logan Pass and much fewer than encountered in a study done in the same location during 1958–1962 (Table 1; Choate 1963a, Benson 1999). The decline apparent among these three studies could be

due either to the difficulty in finding flocks in the late summer or to an actual decline in late summer numbers in this location. Ptarmigan are cryptically-colored throughout the year and are especially difficult to find in the late summer because they do not respond as readily to recorded calls. This characteristic, however, should affect studies equally.

A decline in the number of individuals using Logan Pass in the late summer does not necessarily mean there was a change in breeding numbers. In fact, between the late 1950s and the late 1990s there was a large change in the number of late summer individuals on Logan Pass, but little change in breeding numbers (Choate 1963a, Benson 1999). For 2009–2010 we had no data from the breeding season. Other researchers have found ptarmigan moving among alpine valleys in the late summer (May and Braun 1972), presumably because they could not find suitable late-summer habitat at higher elevations at their breeding locations (Herzog 1977). Our findings suggest that Logan Pass may have been less suitable for flocks in 2009–2010 than in the past; however, if ptarmigan moved to a more suitable location, we were unable to find that location despite searching potential habitat surrounding the area. We did not find large numbers of ptarmigan in any of the areas searched in 2009–2010.

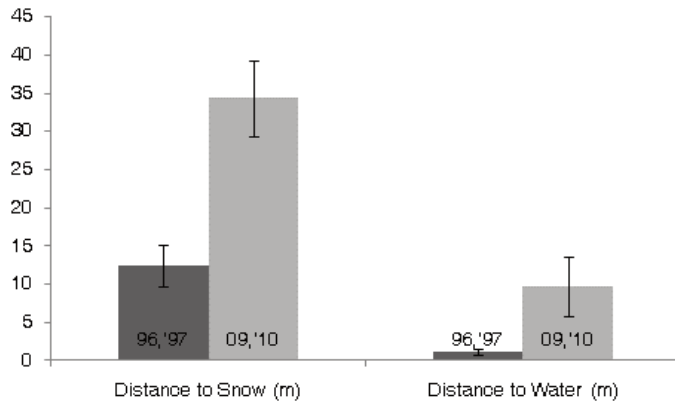
We found ptarmigan in GNP in the late summer 2009–2010 in close proximity to both

water and snow, though not as close to these resources as ptarmigan were in the late '90s (Figure 3). The 1961–1962 distribution of flocking locations on Logan Pass changed in 1996–1997, and again in 2009–2010, following the horizontal and elevational movement of perennial snow melt-off (Figs. 1 and 2). These elevation shifts are similar to those reported for lowland bird species in Costa Rica (Pounds et al. 1999), Edith's Checkerspot Butterfly in North America (Parmesan 1996), and Pika in the Great Basin (Beever et al. 2003).

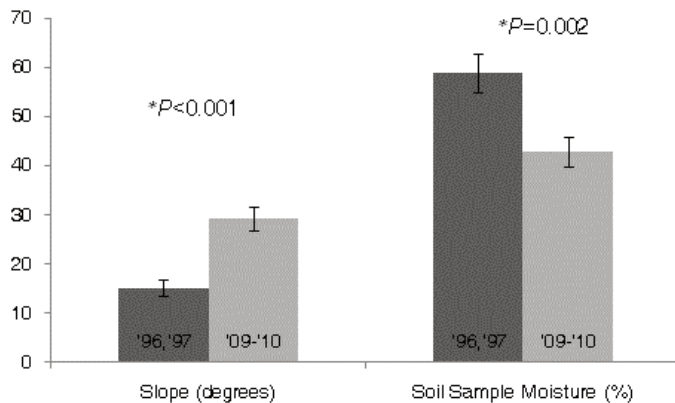
Summer diet of White-tailed Ptarmigan consists of leaves and seeds of herbaceous plants such as clovers, sedges (*Carex* spp.), *Poly-*

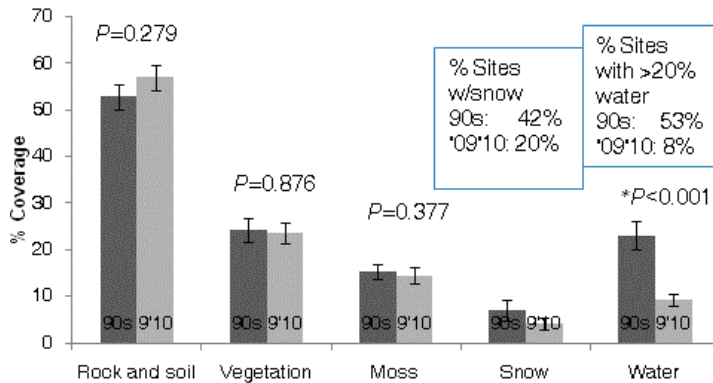
*gonum* spp., *Ranunculus* spp., and *Mimulus* spp. (Weeden 1967, May and Braun 1972, Clarke 1989). It has been suggested that the close relationship between ptarmigan and water and snow in the late summer is primarily due to the availability of this young, lush vegetation in those areas (Choate 1963b, Braun 1971, Herzog 1977, Scott 1982). A further explanation for the association of late summer flocking habitat with snow, water and related variables may be the cooler microclimate they provide (Johnson 1968). Indeed, we found that locations chosen by ptarmigan tended to have lower average high temperatures than random areas nearby. Snow and water have a moderating effect on local environment, and the pres-

**Figure 3.** Distance to snow ( $P = 0.001$ ) and distance to water ( $P = 0.014$ ) from White-tailed Ptarmigan flock sites in 1996–97 ( $N = 26$ ) vs. 2009–10 ( $N = 49$ ) in Glacier National Park, Montana. Error bars are  $\pm$  SE.



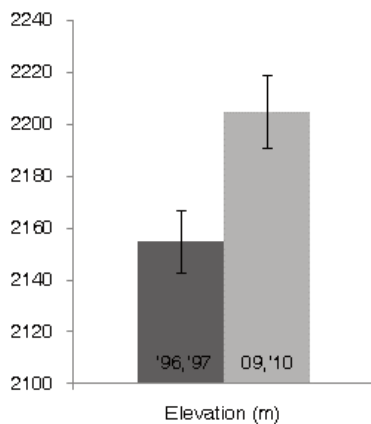
**Figure 4.** Soil moisture content and slope at White-tailed Ptarmigan flock sites in 1996–1997 ( $N = 26$ ) vs. 2009–2010 ( $N = 49$ ) in Glacier National Park, Montana. Error bars are  $\pm$  SE.



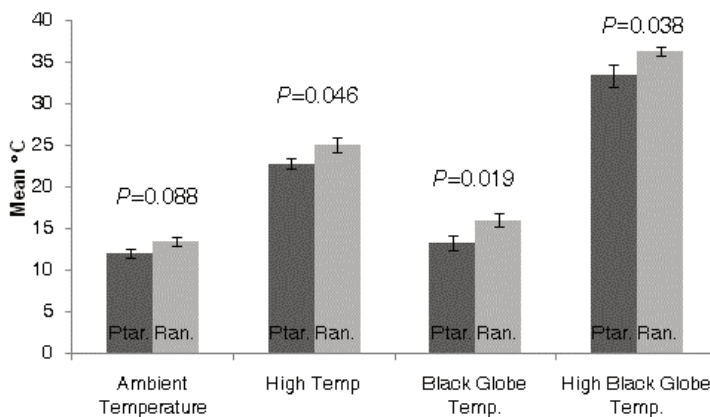


**Figure 5.** Coverages of habitat variables at White-tailed Ptarmigan flock sites in 1996–1997 (N = 26) vs. 2009–2010 (N = 49) in Glacier National Park, Montana. “Rock and soil” includes the cover categories: gravel, rock, boulder, and soil. “Vegetation” includes forbs, grasses, ericaceous shrubs, and *Salix nivalis*. Error bars are +/- SE.

Inset boxes show the percentage of White-tailed Ptarmigan flock sites with snow (w/snow) and with over 20% water coverage (>20% water) in 1996–97 (90s) and 2009–10 (09'10).



**Figure 6.** Elevation at White-tailed Ptarmigan flock sites in 1996–1997 (N = 26) vs. 2009–2010 (N = 49; P = 0.009) in Glacier National Park, Montana. Error bars are +/- SE.



**Figure 7.** Microclimate comparisons at White-tailed Ptarmigan flock locations (N = 25) and random (N = 27) locations within 50 m with similar sunlight characteristics for 4-day-average periods. “High Temp.” and “High Black Globe Temp.” refer to the mean of the daily high ambient and Black Globe temperatures. Error bars are +/- SE.

ence of snow and water at a location in the late summer is likely due to other environmental characteristics such as shade and shelter from wind resulting in a cool “airshed” at that location. Choosing habitat based on thermal characteristics is not unique to ptarmigan. Other species may base nest site selection (Wachob 1996), roost selection (Barrows 1981), and location of daily activities (Walsberg 1993, Wolf et al. 1996, Patten et al. 2005) on thermal needs. As the only birds in North America to spend their entire lives in the alpine environment, White-tailed Ptarmigan are very well adapted to cold, but are less well adapted to high summer temperatures. Johnson (1968) found that White-tailed Ptarmigan had a very low evaporative cooling efficiency as well as a low upper critical temperature. At the southern end of their range, in Colorado and New Mexico, ptarmigan find thermal refugia in the shade of large boulder fields on hot summer days (C. E. Braun pers. comm., Wolfe 2011). Perhaps ptarmigan in GNP take refuge near snow because, unlike Colorado and New Mexico, snow is still available in the late summer in GNP.

Thus, White-tailed Ptarmigan in GNP seem to have responded to changing habitat by shifting the habitat they chose. Ptarmigan still selected habitat that was very close to water and snow in the late summer, but not to the same degree as in the 1990s. With the rate of long-term snow loss, areas near perennial snow that are exposed by late summer have been under snow for at least the last several thousand years. Further, some of those areas have had soil removed by recent glaciation and remain completely devoid of vegetation. Change in the proximity of White-tailed Ptarmigan in late summer to water and snow might thus be due to a tradeoff between thermal needs and the need for food at flocking locations. Further studies should explore whether GNP ptarmigan, like ptarmigan in more southern portions of their range, begin to use boulder fields as thermal refugia as perennial snow becomes less and less common.

As the alpine environment changes with continuing warming, alpine species like ptarmigan are afforded three scenarios: (1) follow their preferred habitat, (2) change their habitat preference, or (3) become less prevalent in their former range all year or during certain seasons. In the case of White-tailed Ptarmigan in GNP, it appears as if all three may have occurred at once. The fact that ptarmigan are able to move long distances, and appear able to adjust their behavior in response to altered thermal regimes, bodes well for their long-term prospects in a changing climate.

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#### LITERATURE CITED

- BARROWS, C. W. 1981. Roost selection by Spotted Owls: An adaptation to heat stress. *Condor* 83:302–309.
- BEEVER, E. A., P. F. BRUSSARD, AND J. BERGER. 2003. Patterns of apparent extirpation among isolated populations of Pikas (*Ochotona princeps*) in the Great Basin. *Journal of Mammalogy* 84:37–54.
- BENSON, D. P. 1999. Causes and consequences of the evolution of monogamy in White-tailed Ptarmigan. Ph.D. dissertation, Washington State University, Pullman, Washington, USA.
- BERRY, P. M., D. VANHINSBERG, H. A. VILES, P. A. HARRISON, R. G. PEARSON, R. J. FULLER, N. BUTT, AND F. MILLER. 2001. Impacts on terrestrial environments. Pages 43–150 in P. A. Harrison, P. M. Berry, and T. P. Dawson (Eds.). *Climate Change and Nature Conservation in Britain and Ireland: Modelling Natural Resource Responses to Cli-*



- mate Change (the MONARCH Project). UKCIP Technical Report, Oxford, UK.
- BRADLEY, N. L., A. C. LEOPOLD, J. ROSS, AND H. WELLINGTON. 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences, USA* 96:9701–9704.
- BRAUN, C. E. 1971. Habitat requirements of Colorado White-tailed Ptarmigan. *Proceedings of the Western Association of State Game and Fish Commissioners* 51:284–292.
- BRAUN, C. E., K. MARTIN, AND L. A. ROBB. 1993. White-tailed Ptarmigan (*Lagopus leucurus*). In A. Poole and F. Gill (Eds.). *The Birds of North America*, no. 68. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, DC, USA.
- CHOATE, T. S. 1963a. Ecology and population dynamics of White-tailed Ptarmigan (*Lagopus leucurus*) in Glacier National Park, Montana. Ph. D. dissertation, University of Montana, Missoula, Montana, USA.
- CHOATE, T. S. 1963b. Habitat and population dynamics of White-tailed Ptarmigan in Montana. *Journal of Wildlife Management* 27:684–699.
- CLARKE, J. A. 1989. White-tailed Ptarmigan (*Lagopus leucurus*) in the Sierra Nevada: A comparative study of an introduced population. Ph.D. dissertation, Washington State University, Pullman, Washington, USA.
- CRICK, H. Q. P. 2004. The impact of climate change on birds. *Ibis* 146(s.1):48–56.
- DUNN, P. O., AND D. W. WINKLER. 1999. Climate change has affected the breeding date of Tree Swallows throughout North America. *Proceedings of the Royal Society of London, Series B.* 266:2487–2490.
- FREDERICK, G. P., AND R. J. GUTIERREZ. 1992. Habitat use and population characteristics of the White-tailed Ptarmigan in the Sierra Nevada, California. *Condor* 94:889–902.
- GRABHERR, G., M. GOTTFRIED, AND H. PAULI. 1994. Climate effects on mountain plants. *Nature* 369:448.
- HALL M. H. P., AND D. B. FAGRE. 2003. Modeled climate-induced glacier change in Glacier National Park, 1850–2100. *Bioscience* 53:131–140.
- HERZOG, P. W. 1977. Summer habitat use by White-tailed Ptarmigan in Southwestern Alberta. *Canadian Field Naturalist* 91:367–371.
- INOUE, D. W., B. BARR, K. B. ARMITAGE, AND B. D. INOUE. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences, USA* 97:1630–1633.
- IPCC. 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller (Eds.). Cambridge University Press, Cambridge, UK, and New York, USA.
- JOHNSON, R. E. 1968. Temperature regulation in the White-tailed Ptarmigan, *Lagopus leucurus*. *Comparative Biochemistry and Physiology* 24:1003–1014.
- KEY, C. H., D. B. FAGRE, AND R. K. MENICKE. 2002. Glacier retreat in Glacier National Park, Montana. Pages J365–J376 in R. S. Williams, Jr. and J. G. Ferrigno (Eds.). *Satellite Image Atlas of Glaciers of the World.* US Geological Survey Professional Paper 1386J. US Government Printing Office, Washington, DC, USA.
- LUCKMAN, B., AND T. KAVANAGH. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio* 29:371–380.
- MARTIN, T. E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: Climate change impacts? *Ecology* 82:175–188.
- MARTIN, K., AND K. L. WIEBE. 2004. Coping mechanisms of alpine and arctic breeding birds: Extreme weather and limitations to reproductive resilience. *Integrative and Comparative Biology* 44:177–185.
- MAY, T. A., AND C. E. BRAUN. 1972. Seasonal foods of adult White-tailed Ptarmigan in

- Colorado. *Journal of Wildlife Management* 36:1180–1186.
- MCCARTY, J. P. 2001. Ecological consequences of recent climate change. *Conservation Biology* 15:320–331.
- PARMESAN, C. 1996. Climate and species' range. *Nature* 382:765–766.
- PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Evolutionary Systematics* 37:637–669.
- PARMESAN, C., AND H. GALBRAITH. 2004. Observed ecological impacts of climate change in North America. Pew Center for Global Climate Change, Arlington, Virginia, USA.
- PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- PATTEN, M. A., D. H. WOLFE, E. SHOCHAT, AND S. K. SHERROD. 2005. Effects of microhabitat and microclimate selection on adult survivorship of the Lesser Prairie-chicken. *Journal of Wildlife Management* 69:1270–1278.
- POUNDS, J. A., M. P. L. FOGDEN, AND J. H. CAMPBELL. 1999. Biological response to climate change on a tropical mountain. *Nature* 398:611–615.
- POUNDS, J. A., M. P. L. FOGDEN, AND K. L. MASTERS. 2005. Responses of natural communities to climate change in a highland tropical forest. Case study. Pages 70–74 in T. Lovejoy and L. Hannah (Eds.). *Climate Change and Biodiversity*. Yale, New Haven, Connecticut, USA.
- SCOTT, M. D. 1982. Distribution and habitat use of White-tailed Ptarmigan in Montana. *Proceedings of the Montana Academy of Science* 41:57–66.
- SELKOWITZ, D. J., D. B. FAGRE, AND B. A. REARDON. 2002. Interannual variations in snowpack in the Crown of the Continent Ecosystem. *Hydrological Processes* 16:3651–3665.
- USDA (UNITED STATES DEPARTMENT OF AGRICULTURE). 2005. Farm Services Agency Aerial Photography Field Office, Montana 2005 Color NAIP Orthophotos, 12-km Tiles, Montana State Library, Helena, Montana, USA.
- USGS (UNITED STATES GEOLOGICAL SURVEY). 2001. Digital Orthophoto Quadrangles for Montana, Montana State Library, Helena, Montana, USA.
- VISSER, M. E., C. BOTH, AND M. M. LAMBRECHTS. 2008. Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research* 35:89–110.
- WACHOB, D. G. 1996. A microclimate analysis of nest-site selection by Mountain Chickadees. *Journal of Field Ornithology* 67:525–533.
- WALSBERG, G. E. 1993. Thermal consequences of diurnal microhabitat selection in a small bird. *Ornis Scandinavica* 24:174–182.
- WANG, G., N. T. HOBBS, K. M. GIESEN, H. GALBRAITH, D. S. OJIMA, AND C. E. BRAUN. 2002. Relationships between climate and population dynamics of White-tailed Ptarmigan *Lagopus leucurus* in Rocky Mountain National Park, Colorado, USA. *Climate Research* 23:81–87.
- WEEDEN, R. B. 1967. Seasonal and geographic variation in the foods of adult White-tailed Ptarmigan. *Condor* 69:303–309.
- WOLF, B. O., K. M. WOODEN, AND G. E. WALSBERG. 1996. The use of thermal refugia by two small desert birds. *Condor* 98:424–428.
- WOLFE, D. H., L. C. LARSSON, J. R. OLDENETTEL, H. A. WALKER, AND M. A. PATTEN. 2011. Status of populations of the White-tailed Ptarmigan at the southern edge of its range. In R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov (Eds.). *Gyrfalcons and Ptarmigan in a Changing World*. The Peregrine Fund, Boise, Idaho, USA. <http://dx.doi.org/10.4080/gpcw.2011.0122>