J. Field Ornithol., 63(3):331-338

EFFECTS OF A SEVERE SNOWSTORM ON SUBALPINE AND ALPINE POPULATIONS OF NESTING AMERICAN PIPITS

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Abstract.—The effect of a midsummer snowstorm on nesting success of two populations of American Pipits (*Anthus rubescens*) in the Beartooth Mountains, Wyoming is described. An alpine population (3200 m) suffered 79% nestling mortality during the storm, whereas a subalpine population (2900 m) experienced 7% nestling mortality. All nestlings of the alpine population at least 11 d old ($n = 44$) survived burial by snow for 24 h, whereas younger nestlings ($n = 36$) had only 11% survivorship. This age effect corresponds to the age of endothermy; younger nestlings apparently died of exposure. Snow covered the ground for an additional 36 h after nests were excavated; older nestlings experienced high (73%) mortality, probably from starvation, during this period. The observed survivorship pattern was apparently unrelated to brood size. Implications of severe storms for alpine populations of breeding birds are discussed.

EFECTO DE UNA TORMENTA SEVERA EN POBLACIONES SUBALPINAS Y ALPINAS DE *ANTHUS RUBESCENS*

Sinopsis.—En este trabajo se discute el efecto de una tormenta veraniega en el éxito de anidamiento de dos poblaciones de *Anthus rubescens* en las montañas Beartooth de Wyoming. Como efecto de la tormenta de nieve, la población alpina (3200 m) sufrió un 79% de mortalidad entre sus pichones, mientras que la población subalpina (2900 m) experimentó un 7% de mortalidad. Todos los pichones de la población alpina de al menos 11 d de edad ($n = 44$) sobrevivieron a la cobertura por la nieve por espacio de 24 h, mientras que los pichones de menor edad ($n = 36$) tuvieron una supervivencia de 11%. El efecto relacionado con la edad se debe al desarrollo de la endotermia; los pichones más jóvenes murieron aparentemente por exposición. La nieve cubrió los suelos nuevamente por espacio de 36 h luego de haber sido excavados los nidos; los pichones de mayor edad sufrieron una mortalidad de 73% probablemente debido a falta de alimentación durante este período. La supervivencia observada probablemente no estuvo relacionado al tamaño de las camadas. Se comentan en el trabajo las implicaciones de tormentas severas sobre poblaciones reproductivas de aves alpinas.

Inclement weather during late spring and summer can have severe effects on the survival and nesting success of breeding bird populations (e.g., Eckhardt 1977, Jehl and Hussell 1966, Norment 1985, Pulliainen 1978, Sutton and Parmelee 1954). These consequences may be particularly serious for arctic and alpine species, which often must begin breeding activities without delay if they are to reproduce successfully. Although

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temperate alpine habitats may experience frequent cyclonic storms and sudden changes in weather conditions (Barry et al. 1981), the impact of severe storms on alpine bird populations has been poorly documented. Here we describe and compare the effects of a severe snowstorm on breeding populations of American Pipit (*Anthus rubescens*) in alpine and nearby subalpine habitats, and speculate on the significance of severe storms on the dynamics of alpine populations of this species.

STUDY AREA AND METHODS

During summer 1987 we observed nesting activities of American Pipits at two sites in the Beartooth Mountains, Park County, Wyoming: near Beartooth Pass in alpine habitat at an average elevation of 3200 m (site described by Pattie and Verbeek 1966) and the Chain Lakes area, 6.4 km SW of the pass, in subalpine meadows at about 2900 m elevation.

Nests were checked daily, or nearly so, to follow incubation and nestling development. Ambient temperatures at the pass site were recorded on a Taylor Maximum-Minimum thermometer; snow depth was measured with a meter stick. Statistical analyses follow Sokal and Rohlf (1981), with level of significance set at 0.05.

WEATHER CONDITIONS

Weather conditions in the Beartooth Mountains vary considerably from summer to summer. Snow is rare or absent in some years and precipitation is primarily associated with thunderstorms; in other years cyclonic storms lasting for several days may bring snow, hail and sleet to higher elevations (Johnson and Billings 1962, Verbeek 1970). Weather was unsettled during Jun. and Jul. 1987, with frequent rain or snow storms (24 of 39 d at the pass had measurable precipitation). Daily mean ambient temperature at the pass averaged 8.8 C in June, 8.6 C in July. Respective average maxima and minima were 16.0 C and 1.6 C in June, and 15.0 C and 2.1 C in July. Comparable measurements are not available from the Chain Lakes site in 1987, but 15 multi-day measurements in Jul.–Aug. 1989 gave temperature maxima that averaged 2.7 C warmer, and minima 1.5 C cooler, at Chain Lakes than at the pass site.

A low pressure system moved over the Beartooth Mountains on 10 Jul. bringing snowfall to higher elevations. A steady fall of wet snow at the pass lasted 24 h, ceasing at about 0915 hours on 11 Jul. The area was 100% snow covered, with a maximum depth of 30 cm. At Chain Lakes, rain preceded snowfall that began during the evening of 10 Jul. and continued until early in the morning of 11 Jul. Snow cover was 100%, with a maximum accumulation of 15 cm. The pass remained 85% snowcovered on 12 Jul., with 18 cm on the ground, and did not become snowfree until the afternoon of 13 Jul., 72 h after the storm began. At Chain Lakes most of the accumulated snow had melted by 1400 on 11 Jul., less than 24 h after snowfall began.

At the pass ambient temperature remained above freezing (maxima of 8.0 C and 6.5 C on 10 and 11 Jul., respectively, with an overnight low of 3.0 C) until early morning of 12 Jul. when it cleared and the temperature decreased to −4.5 C. High temperatures for 12 and 13 Jul. were 13.5 C and 18.5 C, respectively, with an overnight low of −0.5 C. The two nights with sub-freezing temperatures turned the wet snow into a hard crust.

RESULTS

At the start of the storm, most pairs of American Pipits were tending nestlings (Table 1), but young had fledged from a few nests. The data pertain to active nests at the time of the storm; we found no dead fledglings or adults.

Storm effects on nestlings at the two sites.—For the two sites combined, 138 nestling pipits were alive at the start of the storm (Table 1). Total mortality attributable to the storm (not counting predation) was high (49%), but mortality at the pass (79%) was significantly higher (G_{adj} = 88.249, df = 1, $P \ll 0.001$) than at the lower Chain Lakes site (7%). Not included in this calculation was one six-egg clutch destroyed at the pass (all eggs had well-developed embryos).

All nests at the pass were excavated by us and checked by noon on 11 Jul. At this time 48 nestlings (60%) were still alive. By the time the pass became mostly snowfree on 13 Jul., however, 31 of these nestlings had died of starvation or exposure related to the storm (and one brood of five was depredated). Without excavation most nests would not have been accessible to adults until 60 h after the storm began (evening of 12 Jul.). All mortality at Chain Lakes attributable to the storm occurred prior to 1500 hours on 11 Jul.

Effect of nestling age on survivorship.—Nestling age had an important effect on survivorship of young pipits buried by the storm, especially during the first 24 h. At the pass, nestlings >10 d old on the day the storm began, showed 100% survivorship (n = 44) through the first day of the storm, whereas nestlings ≤10 d old had only 11% survivorship (n = 36) for the same period; the difference was significant (G_{adj} = 79.952, df = 1, $P \ll 0.001$). The 12 nestlings at the pass that survived the storm to fledging were >10 d old when the storm began. At least two of four nestlings that died during the storm at Chain Lakes were also in this age group, however. At the onset of the storm only 7–9 of 58 nestlings at Chain Lakes were ≤10 d old. This may have contributed to the extreme difference in survivorship between the two sites (Table 1).

Effect of brood size on survivorship.—Although sample sizes were small, there was no difference (G = 0.254, df = 2, $P > 0.5$) between nestling survivorship in broods of different sizes at the pass for the first 24 h after the storm began. The number of broods with no nestling mortality, for brood-size categories of <5, 5 and >5, were two, five and two, respectively. Respective numbers of broods experiencing nestling mortality were two, three and two; for these broods, all nestlings were dead except four in two broods of four young. Extremes in brood size at the onset of the storm were three and seven nestlings. All nestlings in the brood of three (12 d old) were alive at the time nests were excavated, in contrast to the brood of seven (9 d old) in which all nestlings were dead. The 12 nestlings that

TABLE 1. Effects of the 10–11 Jul. 1987 snowstorm on nesting American Pipits at two sites, Beartooth Mountains, Park County, Wyoming.

	Beartooth Pass	Chain Lakes
Elevation (m)	3200	2900
Accumulated snow (cm)	30	15
Duration of snow cover (h)	60	<24
Active nests at start of storm	17	12
Nestlings alive at start of storm	80	58
Nestlings died as result of storm	63[a]	4
Eggs being incubated at start of storm	6	—
Eggs destroyed by storm	6	—

[a] Not including 5 nestlings depredated by red fox (*Vulpes vulpes*) following observer tracks.

fledged were all >10 d old at the start of the storm, and came from broods of three, five, five and six nestlings. Fledging success of the older age group in the three brood sizes mentioned above was two of seven nestlings (28.6%), seven of 25 nestlings (28.0%), and three of 12 nestlings (25.0%), respectively.

DISCUSSION

Survival of adults and young.—Death of nestling and/or adult pipits (*Anthus* spp.) and nest abandonment resulting from severe weather during the breeding season have been reported previously (Eckhardt 1977, Ojanen 1979, Pulliainen 1978, Sutton and Parmelee 1954). Adult pipits are susceptible to unseasonal cold and extensive snowcover because they feed on ground-dwelling arthropods (Hendricks 1987, Verbeek 1970) and they nest on the ground.

We found no dead adult American Pipits, but Eckhardt (1977) documented the impact of a severe snowstorm on a high montane insectivorous bird community in the Rocky Mountains of Colorado, and adult American Pipits were included in the list of species found dead. Possibly some adult pipits may have perished during the storm at the pass, and at other high elevations in the Beartooth Mountains. Much of the alpine was snow-covered for 60 h or more, limiting access to food.

Our observations show the impact of a storm on nests and young can be extreme at higher elevations (Table 1). The difference in nestling mortality between the alpine and subalpine populations was probably due to the duration of snowcover at the respective sites. If nests at the pass had not been dug out by us after 24 h, we think mortality would have been 100%, because most nests would have been inaccessible to adult pipits until almost 60 h after the storm began. As it turned out, 31 of 43 nestlings died after their nests were excavated, suggesting that the survivors were already in a weakened condition after 24 h of burial.

There was a striking pattern in the ability of nestlings of different ages to survive the first 24 h of the storm. All nestlings 11 d old or older were alive at this time, while only four of 36 nestlings 10 d old or younger were still alive; these latter four nestlings were in two nests with siblings that had already died. Eleven days of age is about the stage of development when American Pipits (Conry 1978, Miller 1988) and Water Pipits (*A. spinoletta*) (Verbeek 1988) reach the physiological age of endothermy (Dunn 1975). Thus, lower mortality of older nestlings during the first 24 h was probably related to their greater thermoregulatory capabilities.

Although effective endothermy is reached by pipit broods a few days before individuals reach the physiological age of endothermy (Dunn 1975, Verbeek 1988), brood size had no apparent effect on nestling survival in the first 24 h. Clearly, larger brood size did not aid survivorship of younger nestlings through the first 24 h of the storm. The four surviving nestlings ≤10 d old were in the smallest broods. Perhaps younger birds, with poorly developed plumage, became wet early in the storm, which would have reduced any potential physiological advantage held by larger broods of young nestlings.

Nest site characteristics could also affect survivorship irrespective of brood size or nestling age. Most American Pipit nests are protected by overhanging rock, sod, or vegetation (Verbeek 1970, 1981), but some are placed in exposed sites (Verbeek 1970, Hendricks and Norment, unpub. data) where eggs and nestlings may be more vulnerable to inclement weather. Differences in nest placement may explain the deaths of two nestlings older than 10 d that died at Chain Lakes in a nest only minimally protected by a small, sparse clump of rush (*Juncus* sp.).

We believe that most nestlings <11 d old died from exposure. Most older nestlings probably starved to death, due to continued snowcover and the inability of adults to deliver sufficient food to them. Unfortunately, we did not examine the stomachs of the dead nestlings, which could have resolved the alternative hypotheses. Our 24-h results appear to contradict Sutton and Parmelee's (1954) suggestion that younger nestlings are more likely to survive than older nestlings during inclement weather, due to a smaller demand for food. Perhaps we would have seen this pattern if females had been able to brood their nestlings throughout the duration of the storm.

Importance of storms for alpine breeding bird populations.—Abiotic factors, especially unfavorable climatic conditions, have been implicated in determining the abundance and distribution of arctic birds (Järvinen 1984, Jehl and Hussell 1966, Myers and Pitelka 1979). This may apply to breeding populations of alpine birds as well.

The onset of breeding by birds in high mountain environments is often contingent upon the timing of snowmelt, which is influenced primarily by the depth of winter snowpack in late Spring. An early snowmelt is especially important for ground-nesting species, because it may allow birds time to raise a second brood (Morton 1978, Smith and Andersen 1985), or, in the case of alpine passerines, to renest successfully.

Severe storms during the breeding season can cause considerable mortality of eggs and nestlings of montane passerines (King and Mewaldt 1987, Mewaldt and King 1985, Morton et al. 1972, this study), and even of adults (Eckhardt 1977). There can be some compensation for losses of clutches and broods through successful renesting. Renesting has been documented following nest destruction due to severe weather (King and Mewaldt 1987, Morton et al. 1972), but such attempts are not always successful (Mewaldt and King 1985). American Pipits will renest within a week following loss of nests (Hendricks 1991), but for the week following the storm we detected no evidence of attempted renesting. At least some pairs continued to defend their destroyed nests for several days after they had been free of snow. We believe there was insufficient time remaining in the breeding season to raise successfully a brood before the onset of autumn (late August) storms. Further, male American Pipits are becoming reproductively refractory by mid-July (Verbeek 1970). Therefore, reproductive success for the pipits breeding at Beartooth Pass was particularly low in 1987.

An occasional year of low reproductive success may not be a problem for maintaining alpine bird populations where extensive habitat is available, and populations are large and inhabit a relatively broad range of elevations, as is the case with American Pipits in the Beartooth Mountains of Montana and Wyoming. Extensive areas of suitable pipit breeding habitat are present below the upper limit of trees, at elevations from 2800 to 3100 m, particularly to the south and west of Beartooth Pass. Low nesting success in high elevation (alpine) populations during "poor" summers could be offset by recruitment from nearby low alpine/high subalpine populations, such as at Chain Lakes, where nesting mortality due to inclement weather is lower. A similar pattern of recruitment, from lower to higher elevations, has been proposed for bird populations in Sierra Nevada fir forests (Hejl et al. 1988, but see DeSante 1990).

Severe weather may have serious consequences for small, insular populations at the limits of their distributions. King and Mewaldt (1987) suggested that severe weather, coupled with predation, occurred frequently (about every 5 yr) in an isolated population of White-crowned Sparrows (*Zonotrichia leucophrys*) in Oregon, depressing recruitment to the extent that the population could go extinct. This is a plausible scenario for populations of American Pipits breeding in small, isolated patches of alpine habitat, such as in the mountains of the Great Basin. For example, a snow storm in the Snake Range of Nevada in Jul. 1987 left up to 10 cm of snow and ice on the ground for about 36 h (R. E. Johnson, pers. comm.). A storm of this severity could cause significant mortality in the small pipit population there if it occurred at the proper period of breeding. Ehrlich et al. (1972) documented the impact of a June snowstorm in the subalpine of Colorado, which caused extinction of a butterfly population and 100% loss of first broods of White-crowned Sparrows. Ehrlich et al. (1972) concluded that this random environmental event caused the downward trends in a variety of animal populations at their study site.

We conclude that severe climatic conditions have an important role in the population dynamics of alpine breeding birds, especially where populations inhabit small, insular alpine sites. It remains to be determined how frequently inclement weather depresses reproductive success to any significant extent (Weatherhead 1986), but if King and Mewaldt's (1987) study is typical for many isolated montane and alpine populations in marginal habitat, the frequency of such events may be greater than is currently appreciated.

ACKNOWLEDGMENTS

We appreciate the thoughtful comments of C. E. Braun, D. J. T. Hussell, R. E. Johnson, M. L. Morton and an anonymous reviewer on an earlier draft of this paper (although the conclusions expressed are our own), and thank G. Schleger for advice on statistical analysis of some of our data. C. Pidgeon helped locate pipit nests at the pass in 1987.

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Received 17 Sep. 1990; accepted 25 Oct. 1991.