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THE INFLUENCE OF SPRING SNOW DEPTH ON WHITE-TAILED PTARMIGAN BREEDING SUCCESS IN THE SIERRA NEVADA[1]

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Abstract. The relationship between spring snow depth and breeding success of an introduced population of White-tailed Ptarmigan (*Lagopus leucurus altipetens*) in the Sierra Nevada, California, was studied from 1982 through 1987. Yearly spring snow depth varied from 50.8 cm to 424.2 cm. Hatch dates were later in years of deep snow ($P < 0.05$) but brood size showed no relation to snow depth. Nesting success, chick survival, and brood success (all of which contribute to breeding success) were negatively correlated with snow depth as was breeding success ($P < 0.05$). The number of paired ptarmigan in the study area varied from 22 (in 1987) to 46 in 1985 which was the year with the least snow; however, no significant relationship existed between breeding numbers and snow depth. Successful reproduction of White-tailed Ptarmigan in the Sierra Nevada appears to be strongly affected by snow, potentially due to its influence on the availability of resources such as nest sites, food, and cover.

Key words: White-tailed Ptarmigan; Lagopus leucurus; *snow; breeding success; Sierra Nevada.*

INTRODUCTION

Climate exerts an indirect influence on the breeding seasons of birds through changes in vegetation and food supply (Immelmann 1971). This is true especially in alpine areas, where snow may cover nesting and foraging areas. Snow depth has been observed to influence the breeding biology of various ground nesting birds in high altitudes in North America. White-crowned Sparrows (*Zonotrichia leucophrys*) in the Sierra Nevada delay breeding in years with late-lying snow (Morton 1976) and Dark-eyed Juncos (*Junco hyemalis*) in the Bear River Mountains of Utah exhibit a later average hatch date in years of deep snowpack and late snowmelt (Smith and Andersen 1985); both species typically nest on the ground in these mountain ranges.

Little information is available concerning the relationship between snow depth and the breeding biology of North America's three primary species of alpine breeding birds, the American Pipit (*Anthus rubescens*), the Rosy Finch (*Leucosticte arctoa*) and the White-tailed Ptarmigan (*Lagopus leucurus*). American Pipits nest on alpine meadows and snow accumulation areas, whereas Rosy Finches usually nest on high cliffs well above the snow and sometimes on low cliffs, rock slides and moraines. Limited correlative evidence for both species (except those Rosy Finches on high cliffs) suggests that snow depth may influence both timing of nesting and nest site selection (Dawson 1923; Shaw 1934, 1936; Verbeek 1970; Conry 1978), but the subject has never been examined carefully.

Snow depth has been suggested as a factor that affects nest site selection, timing of reproduction, breeding success and spacing of White-tailed Ptarmigan (Weeden 1959; Choate 1960, 1963a, 1963b; Braun 1969; Braun and Rogers 1971; Schmidt 1969; Giesen et al. 1980); however, these relationships have not been quantified. Snow cover has been linked to later annual dates of reproduction in Willow Ptarmigan (*Lagopus lagopus*) (Hannon et al. 1988) and phenologically late years delay reproductive events of Rock Ptarmigan (*L. mutus*) (Weeden 1959, Weeden and Theberge 1972). Among paleartic populations, similar relationships between snow and breeding schedules and success have been observed in Rock Ptarmigan (Gardarsson 1988), Willow Ptarmigan (Slagsvold 1975, Jorgensen and Blix 1985, Myrberget 1988), and Red Grouse (*L. l. scoticus*) (Jenkins et al. 1963).

In this six-year study of a population of White-

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TABLE 1. Values for reproductive variables (defined in the Methods section) of a population of White-tailed Ptarmigan in the Sierra Nevada from 1982 to 1987 and Spearman Rank correlation coefficients between these reproductive variables and spring snow depth.

Year	Snow depth (cm)	Nesting success %	Chick survival %	Brood success %	Breeding success %	Chick numbers	Juvenile numbers
1982	284.5	19	64	19	17	11	7
1983	424.2	25	45	16	15	9	4
1984	170.2	45	54	27	54	24	13
1985	50.8	61	93	52	80	40	37
1986	203.2	29	67	21	21	9	6
1987	124.5	36	75	36	55	16	12
Corr. Coeff.		−0.89	−0.83	−1.00	−1.00	−0.84	−0.89
P value		<0.05	<0.05	<0.005	<0.001	<0.05	<0.05

tailed Ptarmigan in the alpine region of the Sierra Nevada, we investigated the influence of snow depth on annual reproductive variables (hatch dates; nesting success; chick survival; brood size; breeding success; and total numbers of chicks, juveniles and breeding birds) of this ground nesting species. This was also the first long-term study of the breeding biology of White-tailed Ptarmigan in the Sierra Nevada, where, prior to this introduction two decades ago, this species is not believed to have existed (Clarke and Johnson 1990).

METHODS

The study area in the Harvey Monroe Hall Natural Area of the Inyo National Forest, Mono County, California (37°58′N, 119°18′W) encompassed 7 sq km and ranged in elevation from 3,050 to 3,660 m. The vegetation has been described by Clausen (1969) and Taylor (1984). Field work was conducted during spring and summer (mid June to late August) from 1982 through 1987. The study population consisted of the progeny of 72 White-tailed Ptarmigan that were introduced in 1971–1972 from the Rocky Mountains of Colorado. Ptarmigan were captured using a short pole (1 m) and noose (modified from that of Zwickel and Bendell 1967) or caught by hand. In total, 80 birds (approximately 95% of the population) were banded, each with a unique combination of plastic color bands and an aluminum U.S. Fish and Wildlife Service band. Chicks were banded in late August with only an aluminum band, when they were considered juveniles (Braun and Rogers 1971).

Hatch dates were recorded from known nests (no renests were observed) or were estimated using measures of chick size (Choate 1960) and behavior. Definitions of reproductive variables for the population are: *brood size*—number of chicks per brood; *nesting success*—percentage of hens hatching at least one egg; *chick survival*—percentage of chicks surviving to juvenile age; *brood success*—percentage of hens producing at least one juvenile; *breeding success*—ratio of juveniles to paired adults in fall; *numbers of chicks*—all chicks counted; *numbers of juveniles*—chicks which were counted that survived to mid-late August; *numbers of breeding birds*—females present in the spring plus their mates.

Indices of *spring snow depth* were obtained using measures of snow on the ground in the last week of March from U.S. Climatological Records of the nearby Twin Lakes Weather Station, CA. from 1982–1987 (2,426 m elevation, 38°42′N, 120°2′W). This was the nearest weather station which had snow conditions similar to the conditions in the study site and the only station which had complete records for all six years.

Data were analyzed using the SAS statistical programs package. The nonparametric tests used in analyzing data were Kruskal-Wallis one-way analyses of variance and Spearman rank correlation. Nonparametric tests were employed because the data did not exhibit normal distributions (hence the use of median values). Differences were considered significant when $P \leq 0.05$.

RESULTS

During 1982–1987, spring snow depth varied widely, ranging from 50.8 cm to 424.2 cm (Table 1, Fig. 1). Hatch dates were positively correlated with snow depth ($P < 0.01$). Median hatch dates were earliest in the year of least snow (3 July 1985) and latest in the year with the deepest snow (24 July 1983). Brood size (median and mode =

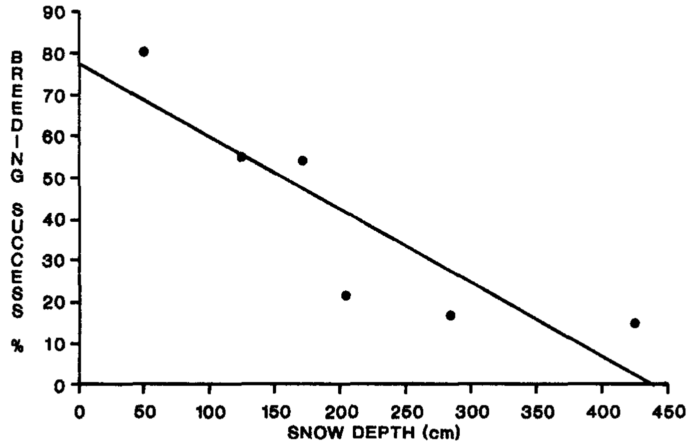

FIGURE 1. Relationship between breeding success of White-tailed Ptarmigan in the Sierra Nevada and spring snow depth from 1982 to 1987 (Spearman Rank $R = -1.00$, $P < 0.001$).

4 chicks) did not appear to be related to snow depth or hatch date ($P > 0.05$). Nesting success, chick survival, brood success, and total numbers of chicks and juveniles were all negatively correlated with spring snow depth ($P < 0.05$, Table 1). The year with the least spring snow (1985, 50 cm) was also the year with the highest nesting success (61%), chick survival (93%), and brood success (52%). The year with the most snow (1983, 424.2 cm) was also the year with the lowest chick survival (45%) and brood success (16%) and the second lowest nesting success (25%). Numbers of chicks and juveniles were also highest when spring snow depth was the least and lowest when snow depth was greatest (Table 1). Nesting success, chick survival, brood success and total numbers of chicks and juveniles are all reproductive variables which directly contribute to breeding success. Consequently, breeding success was also negatively correlated with snow depth ($P < 0.05$, Table 1, Fig. 1) and ranged from 15% in the year with the deepest snow (1983) to 80% in the year with the least snow (1985). Breeding success in years of snow depths exceeding approximately 200 cm varied little from one another (21%, 17%, and 15%). This indicates that the negative effect of snow on breeding success appears to reach a "maximum" at 200 cm depth.

Numbers of breeding birds varied from 22 to 46 in the six years of study (Table 2) while total numbers of adult and yearling birds ranged from 28 to 46, with males in the majority in five out of six years. The highest number of breeding pairs (23 pairs) inhabited the study site in 1985, the year of least snow (50 cm). No significant correlation existed between any of the numbers of potentially breeding birds (numbers of females, males, or females plus males) and snow depth, between any of the values of potentially breeding birds and breeding success, nor between the number of breeding birds and snow depth the previous spring ($P > 0.05$).

DISCUSSION

Spring snow depth is a primary determinant of when ptarmigan nesting and foraging areas are snowfree in the Hall Natural Area of the Sierra Nevada, although other factors may contribute to snowmelt rate (e.g., air temperature and snow water content [Morton 1978]). Wind action has a minor effect on the availability of snow-free areas in the Hall Natural Area due to the bowl-

TABLE 2. Numbers of adult and yearling White-tailed Ptarmigan in the Hall Natural Area in the Sierra Nevada.

Year	Breeding birds	Birds ≥ 1 yr old	
		Females	Males
1982	42	21	22
1983	26	13	15
1984	24	12	17
1985	46	23	23
1986	28	14	24
1987	22	11	21

like terrain; this contrasts sharply with the wind conditions in ptarmigan breeding areas in the Rocky Mountains where wind action is often a major factor in producing snow-free areas (pers. obs.). Judging from the late hatch dates in years of deep snow, snow-free areas appear to be an important determinant affecting the timing of ptarmigan nesting in the Sierra Nevada. We suggest that hens may require snow-free sites for nesting, in part due to food and cover availability in these areas. The major summer food of adult ptarmigan in the Sierra Nevada is dwarf alpine willow (*Salix anglorum*) (Clarke, in prep.), which rarely exceeds 6 cm in height and is readily covered by snow. Deep snow reduces food availability; therefore, a hen's time off the nest while foraging may be increased as would the time the eggs are exposed to weather and predation. Additionally, Keppie and Towers' (1990) data indicate that the timing of plant development affects commencement times for egg-laying in Spruce Grouse (*Dendragapus canadensis*). Also, areas where snow has melted provide cover in the form of rock and krummholz for a nesting or foraging hen. In years of deepest spring snow, we found few nests in exposed sites on ridges where wind decreased snowcover; we also observed that forage and cover were scarce in these areas as compared to less windblown sites in which the birds nested. These windblown areas were uninhabited by ptarmigan in years of low snow. Note that the breeding areas were never entirely snow-free in any year.

Numerous factors may contribute to low breeding success in years of deep, late-lying snow. Food availability and quality may be a major factor influencing chick survival. White-tailed Ptarmigan chicks forage on a variety of plant species, plant parts, and insects (Choate 1960; Schmidt 1969; May 1975; Clarke, in prep.) and late-lying snow delays the development of alpine plants (Weaver 1974, Owen 1976). Extremely late snowmelt in the Sierra Nevada may reduce the quantity of forage and produce differences in the quality of the plants on which chicks feed (see Slagsvold 1975, Myrberget 1988). Spidsø (1980) proposed that differences in chick production are due to variation in food quality and Jorgensen and Blix (1985) found that reductions in availability of high-quality food negatively affected growth and survival of Willow Ptarmigan chicks. Insects, which are important in chicks' diets, may also be less available when snow is deep and spring is late (Slagsvold 1975, Erikstad and Spidsø 1982, Erikstad 1985, Smith and Andersen 1985).

Predation may influence breeding success; however, the greatest number of predators was recorded in the study area in the year with the least snow and highest breeding success. In 1985, the presence of four species of avian predators (Prairie Falcon, *Falco mexicanus*; Golden Eagle, *Aquila chrysaetos*; Red-tailed Hawk, *Buteo jamaicensis*; and Great Horned Owl, *Bubo virginianus*) was recorded eight times. Long-tailed weasels (*Mustela frenata*) were sighted twice and two coyotes (*Canis latrans*) were seen above timberline. This is twice the average number of sightings of these predators for the other five years. Corvid species, potential predators of ptarmigan eggs and chicks, were not recorded above timberline in the study area.

Although our primary conclusions that late-lying snow delays hatch dates and negatively affects ptarmigan reproduction in the Sierra Nevada are based on correlative data, late snow cover is clearly an important determinant of the population's annual breeding success. Interestingly, snow does not appear to influence reproduction negatively in the species' natural range. We compared breeding data from Braun and Rogers' (1971) and Choate's (1963a, 1963b) studies of ptarmigan in the Rocky Mountains with U.S. Climatological Records of spring snow depth data for these study sites and found no significant correlations. This may be due to wind action in these locations causing snow-free areas in spite of high snowfall. The specific proximal causes of the negative effects of snow on ptarmigan breeding in the Sierra Nevada have yet to be identified. As Cody (1971) noted, a particular new environment rapidly produces new values of reproductive characteristics that are independent of the original states. We are observing novel responses by the ptarmigan to climatic conditions in the alpine region of the Sierra Nevada which would not have been predicted based on data from natural populations.

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