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SNOW CONDITIONS AND THE ONSET OF BREEDING IN THE MOUNTAIN WHITE-CROWNED SPARROW

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Since the summer of 1968, my students and I have been studying the breeding biology of the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in the Mono Basin of the Sierra Nevada of California, especially at Tioga Pass. This bird summers in high mountain meadows of western North America and winters in the southwestern United States and northern Mexico. Earlier we reported on reproductive schedule and success of *oriantha* during the consecutive seasons of 1968 through 1970 (Morton et al. 1972). Of all environmental factors affecting the reproductive efforts of this bird, snow conditions seem to be most important. In many years snowpack seems to determine arrival and occupancy schedules at breeding grounds. Duration of snowpack and rate of disappearance affect the availability and suitability of habitat throughout much of the breeding season.

The 1969 season of our study followed a winter with the heaviest snowpack ever recorded in the Mono Basin and the 1976 season followed a winter with one of the lightest snowpacks recorded. Herein I compare data from these seasons, and others, in order to provide insight as to how migratory birds are adapted for breeding under the range of conditions found in high mountains.

Most of our study was conducted at Tioga Pass Meadow, a 0.5 × 1.0 km subalpine meadow that extends northward from Tioga Pass (elev. 9,500–10,300 ft).

RESULTS

SNOW CONDITIONS

Beginning in 1927, and for all but three years since, snow depth has been measured, usually several times a year, at Tioga Pass Meadow by State and private agencies. Snowpack is usually deepest about 1 April but measurements on that date have varied greatly during the past 50 years (Fig. 1).

In terms of snow depths during this study, 1968 and 1976 (especially 1976) were dry years and 1969 was extremely wet. 1970 was intermediate (compare Table 1 with Fig. 1) and closest to the long-term average snow depth of 161.5 cm on 1 April. The rate at which snowpack disappears each spring depends on many factors including pack depth, water content, and the weather. During our study, snow disappeared earliest in the year of least snowpack (1976) and latest in the year of greatest snowpack (1969). Snowcover, the percent of ground covered by snow, expresses this variation in snow disappearance (Fig. 2). The percent of snowcover indicates the quality and availability of habitat for nesting.

The date when egg laying began each year in our study population varied according to snowpack, but not to the extent one might have predicted (Table 1 and Fig. 2). In fact, egg laying began on the same date, 4 June, in 1968 and in 1970. It began five days later in 1969 and seven days earlier in 1976, thus it

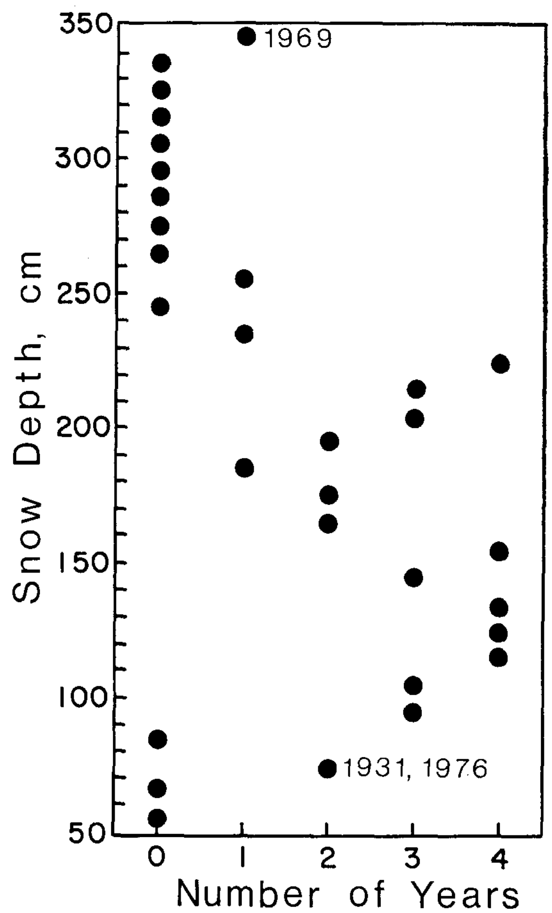

FIGURE 1. Frequency of snow depths measured on or about 1 April at Tioga Pass, Mono Co., California, 1927–1976. Data taken from State of California, Bull. 120.

TABLE 1. Measurements of snow and habitat conditions, nesting phenology, nest placement, and number of breeding pairs of *Zonotrichia leucophrys oriantha*. Data taken from Tioga Pass and adjacent areas of Lee Vining Creek watershed in Mono Basin, Mono Co., California.

	1968	1969	1970	1976
SNOW CONDITIONS				
Snowpack, 1 April (cm)	113.5	342.1	176.3	79.0
Date of 25% snowcover	9 June	4 July	14 June	17 May
NESTING PHENOLOGY				
Number of clutch starts	42	46	51	62
Date of first clutch start	4 June	9 June	4 June	28 May
Date of last clutch start	9 July	23 July	24 July	15 July
Mean date of clutch starts	16 June	28 June	24 June	11 June
Span of clutch starts (days)	36	45	51	49
HABITAT CONDITIONS				
Date willows were leafed out	5 June	12 July	25 June	20 June
Date onions bloomed	7 July	30 July	17 July	7 July
Date of peak mosquito abundance	25 June	10 July	24 June	25 June
NEST PLACEMENT				
Numbers of nests measured	41	55	76	73
Percent on ground	61	22	62	86
Percent above ground	39	78	38	14
Mean nest height (cm)	15.5	38.4	18.2	11.1
PAIRS ON TIOGA PASS MEADOW	28	23	25	27

had a range of 12 days. The end of egg laying, first egg of the last clutch, including renests and second clutches, ranged over 15 days (9 July in 1968–24 July in 1970, see Table 1). In 1976, egg laying continued until 15 July but clutches begun in July were located in only a few hillside areas kept green by ground water.

Snowcover varied greatly from year to year at the time when egg laying began: near 100% in 1969 but less than 10% in 1976. Melting was prolonged in 1969, as expected from pack depth, and also in 1970. A week-long storm in early June 1970 brought more snow, and relatively cool temperatures tended to preserve the pack and prolong the melt period.

The timing of vegetational development differed the most between 1968 and 1969. The approximate dates of two conspicuous vegetational changes—when willows (*Salix* spp.) finished leafing out and when swamp onion (*Allium validum*) began flowering—are given in Table 1. Growth of willows and other vegetation seemed to be retarded by the extremely dry conditions of 1976. This did not inhibit nesting, however, because in the absence of snowcover, many *Z. l. oriantha* nested on the ground in patches of old grass, usually at the base of small, scraggly willows.

Mosquitos became most abundant about seven to ten days after they began emerging in all years. This date was about 25 June every year except 1969, when it was 15 days later (Table 1).

Snow conditions seemed to affect the sparrows' nesting in at least three ways:

1. *Timing.* Assuming that the temporal progress of the breeding cycle was best indicated by mean date of all clutch starts, the nesting schedule varied only 17 days among years, whereas snow conditions, as calculated from date of 25% snowcover, varied by 48 days (Table 1). These ranges were calculated by comparing 1969 and 1976 seasons.

2. *Nest site.* If thick, dry grass was available, most females built their nests on the ground. If the grass was wet or covered by snow, the birds often nested above ground in pines or willows, even unleafed willows. This adaptability is shown most clearly by comparing data on location and average height of nests in 1969 and 1976 (Table 1).

3. *Number of breeding pairs.* If the birds were present during the main period of thaw, patches of emerging vegetation, particularly willows, formed foci for establishment of territories. The first clutches of the season were started in these first patches of open vegetation. If snowcover persisted through the last half of June, as in 1969 and 1970, some meadow areas that provided territories in other years were not used. This had the effect of reducing total numbers of breeding pairs because there was no apparent compensatory decrease in territory size. For example, in 1968 and 1976, years when snow melted early, Tioga Pass Meadow supported 28 and 27 pairs of White-crowned Sparrows, respectively (Table 1). In 1969 and 1970, years when snow melted late, 23 and 25 pairs were present.

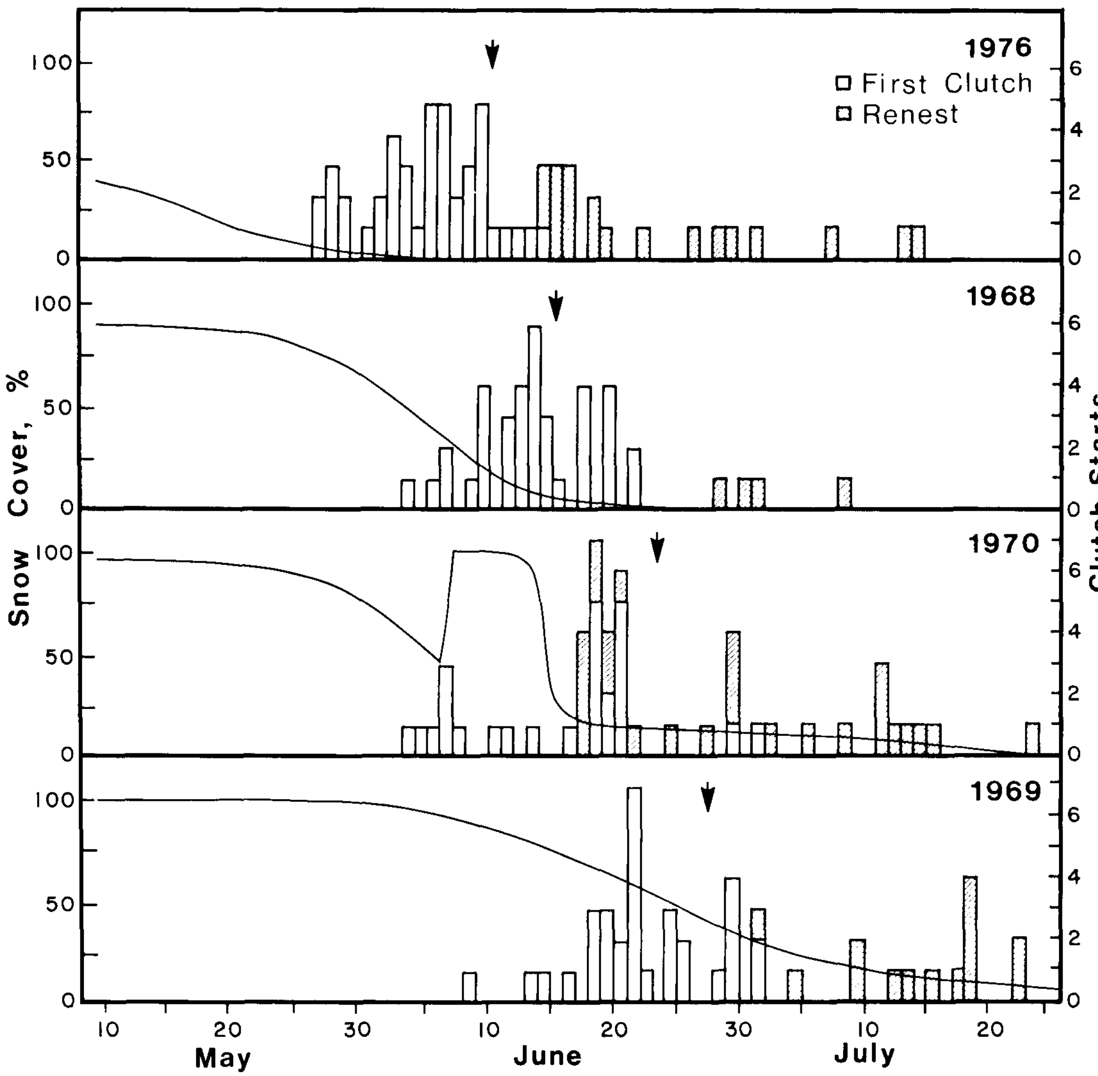

FIGURE 2. Snowcover at Tioga Pass and schedule of clutch starts in *Zonotrichia leucophrys oriantha*. Arrows mark mean date when clutches were started, including renests.

AIR TEMPERATURE

Air temperature was measured daily by the U.S. Park Service at Tioga Pass with a maximum-minimum thermometer. Daily oscillations in temperature formed no definable pattern in spring and early summer with respect to snowpack conditions. Minimum and maximum temperatures rose from mid-May through June (Table 2). Frost-free conditions generally prevailed from late June through August although freezing temperatures might occur at any time during the summer.

TABLE 2. Mean daily low and high air temperature (°C) at Tioga Pass, 1968–1970 and 1976.

	Low	SD	High	SD
May 11–20	–1.6	1.7	8.9	4.2
21–31	0.4	2.7	12.7	3.8
June 1–10	0.7	3.1	11.4	4.6
11–20	1.3	3.2	14.6	4.9
21–30	6.4	3.3	18.4	3.1
July 1–10	8.6	2.7	19.4	2.6
11–20	8.6	2.3	20.3	2.5
21–31	7.7	2.6	18.8	3.1

Daily temperature was typically coldest in early morning, the time of egg laying. During the laying period minimum temperatures were often at or near freezing. In one extreme instance, 5–7 June 1968, three clutches were started when daily highs were 2 to 4°C and lows were –12 to –13°C.

DISCUSSION

WEATHER AND ONSET OF BREEDING

Gonadal growth in *Zonotrichia leucophrys* is primarily controlled by day length (see reviews by Farner and Follett 1966, Farner and Lewis 1973) although social interactions (Lewis and Orcutt 1971) and air temperature (Farner and Mewaldt 1952, 1953, Lewis and Farner 1973) may additionally affect it.

In *Z. l. oriantha* considerable gonadal growth occurs after arrival at the breeding grounds (Morton, Horstmann and Osborn 1972, Morton 1976). Environmental conditions prevailing at that time might be expected to affect growth of the gonads. Weather modifies the birds' breeding schedule indirectly through effects on vegetation and such crucial factors as availability of cover, nesting sites, and food supply. Snowpack seems to be the most important of all weather-related conditions that affect the annual cycle of plant growth at high altitude (Weaver 1974, Owen 1976). The earlier developmental phases of plants in subalpine meadows are delayed up to eight days for every 10% increase in snowpack above the long-term average. In years of greatest snowpack herbaceous plants may grow and mature as much as six weeks later than normal. The growing season may be shortened appreciably at such times because cessation of plant growth is regular from year to year (Owen 1976).

Male White-crowned Sparrows usually appear and begin establishing territories at Tioga Pass in mid-May (Morton 1976), but in 1976 several singing males were present on 2 May (Paul Sherman, pers. comm.). This suggests that some birds may arrive in lowland valleys at the latitude of the breeding ground in late April or earlier. They may then ascend to breeding areas as soon as habitat becomes available, but retreat if storms in the mountains close the areas.

Although males tend to arrive before females at Tioga Pass, there are a few females among the vanguard (Morton 1976). Therefore, in a dry year, nesting can begin as soon as gonadal maturation is complete.

These sparrows are omnivorous and feed in various ways. This increases their ability to lay and incubate eggs while much snow is still present, although storms of several days duration may interrupt nesting (Morton et al. 1972). *Z. l. gambelii* nesting in Alaska can also endure considerable bad weather while laying eggs (Oakeson 1954).

Birds arrive at the breeding grounds with substantial fat stores that they are usually able to maintain (Morton et al. 1973, Morton 1976). Thus they have an energetic reserve for surviving poor weather and for vitellogenesis.

Habitat becomes available unevenly because of differences in snowmelt. South-facing knolls clear first. Sparrows in snow-free areas proceed with nesting while those in adjacent snow-covered areas must wait.

WEATHER AND PRODUCTIVITY

The effects of weather on productivity of a *Z. l. oriantha* population are difficult to evaluate. Deep snow can delay the nesting season and alter the choice of nest sites, possibly resulting in increased predation. Storms during the nesting season can cause considerable mortality in both eggs and chicks (Morton et al. 1972). These adverse effects are offset by some unknown margin, however, because the birds routinely renest if eggs or chicks are lost, several times if necessary. I believe that they are physiologically able to breed, and do so, as long as conditions in their territories are favorable. Toward the end of the breeding season, favorable conditions are highly localized, seeming to depend on the presence of sumps and springs that maintain areas with growing grass. The birds nest and forage in such places as long as they exist. Melting snow from a heavy pack may keep the meadow wet and green until late July, as happened in 1969 and 1970. Some double-brooding occurred in those years but rarely otherwise.

If snow on the ground reduces the amount of habitat available while territories are being established, fewer pairs will be able to breed. Hence, it seems that, on the average, productivity of the population should decrease after winters of heavy snow.

SUMMARY

Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) migrate to and breed in montane areas that sustain large variations in snowfall. Hence, they encounter considerable annual variation in environmental conditions upon arrival at their breeding grounds. At Tioga Pass, breeding is delayed in years of deep snowpack. However, individual pairs will occupy patches of habitat as soon as they are snow-free. Furthermore, under such conditions, many females alter an apparent preference for nesting in dense grass on the ground, instead, they nest in small pine trees, willows, and elsewhere. Once the birds are ready to breed and habitat is available, nesting proceeds relatively unaffected by temperature extremes or storms.

In years of heavy snow, some habitat is unavailable until late in the summer. This reduces the number of breeding pairs in a given area and may decrease breeding success or productivity for the population. The birds re-

nest readily but usually cease breeding after a brood is fledged. Suitable breeding habitat is patchily distributed at the end of the season, wherever surface water continues to sustain wet-green conditions. In such areas efforts at renesting are prolonged and double-brooding may occur.

Owing to their schedule of arrival, modes of foraging, management of energy reserves, flexibility in nest placement, renesting capabilities, and ability to withstand brief spells of bad weather, these sparrows are able to reproduce successfully in subalpine areas despite large annual variations in environmental conditions.

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LITERATURE CITED

Farner, D. S., and B. K. Follett. 1966. Light and other environmental factors affecting avian reproduction. J. Anim. Sci. Suppl. 25:90–155.

Farner, D. S., and R. A. Lewis. 1973. Field and experimental studies of the annual cycles of White-crowned Sparrows. J. Reprod. Fertil. Suppl. 19:35–50.

Farner, D. S., and L. R. Mewaldt. 1952. The relative roles of photoperiod and temperature in gonadal recrudescence in male *Zonotrichia leucophrys gambelii*. Anat. Rec. 113:612.

Farner, D. S., and L. R. Mewaldt. 1953. The relative roles of diurnal periods of activity and diurnal photoperiods in gonadal activation in male *Zonotrichia leucophrys gambelii* (Nuttall). Experientia 9:219–221.

Lewis, R. A., and D. S. Farner. 1973. Temperature modulation of photoperiodically induced vernal phenomena in White-crowned Sparrows (*Zonotrichia leucophrys*). Condor 75:279–286.

Lewis, R. A., and F. S. Orcutt, Jr. 1971. Social behavior and avian sexual cycles. Scientia 65: 447–472.

Morton, M. L. 1976. Adaptive strategies of *Zonotrichia* breeding at high latitude or high altitude. Proc. 16th Int. Ornithol. Congr. (1974):322–336.

Morton, M. L., J. Horstmann, and J. Osborn. 1972. Reproductive cycle and nesting success of the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in the central Sierra Nevada. Condor 74:152–163.

Morton, M. L., J. Horstmann, and C. Carey. 1973. Body weights and lipids of summering Mountain White-crowned Sparrows in California. Auk 90:83–93.

Oakeson, B. B. 1954. The Gambel's Sparrow at Mountain Village, Alaska. Auk 71:351–365.

Owen, H. E. 1976. Phenological development of herbaceous plants in relation to snowmelt date, p. 323–341. *In* H. W. Steinhoo and J. D. Ives [eds.], Ecological impacts of snowpack augmentation in the San Juan Mountains, Colorado. San Juan Ecology Project, Final Report. Colorado State Univ. Publ., Fort Collins.

State of California. Water conditions in California. Dept. Water Resources, Bull. 120.

Weaver, T. 1974. Ecological effects of weather modification: Effect of late snowmelt on *Festuca idahoensis*, Elmer meadow. Am. Midl. Nat. 92: 346–356.

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