

# REPRODUCTIVE CYCLE AND NESTING SUCCESS OF THE MOUNTAIN WHITE-CROWNED SPARROW (*ZONOTRICHIA LEUCOPHRYS ORIANTHA*) IN THE CENTRAL SIERRA NEVADA

MARTIN L. MORTON,  
JUDITH L. HORSTMANN,<sup>1</sup>

AND

JANET M. OSBORN<sup>2</sup>

Department of Biology  
Occidental College  
Los Angeles, California 90041

The Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) breeds in the high-mountain meadows of the western United States and southwestern Canada and winters in the southwestern United States and northern Mexico (AOU 1957). Apparently, the Rocky Mountains and the Sierra Nevada provide the greatest amount of habitat suitable for reproduction, but the Cascades and small ranges within the Great Basin also harbor breeding populations (Banks 1964).

The habitat elements essential for reproductive success include grass, bare ground, dense shrubs or scrub conifers, water, and on the periphery, tall conifers (DeWolfe and DeWolfe 1962). These elements are contained in certain mountain meadows that are often very small and widely separated and which may change in terms of suitability from year to year. This results in a disjunct distribution of breeding birds with as few as one pair at a given locale. Naturally, this has made it difficult to study the breeding biology of these birds and even to describe with accuracy the breeding range.

In early June 1968, we looked for *Z. l. oriantha* in known breeding areas in the Sierra Nevada and found them in substantial numbers near Tioga Pass, Mono County, California. We then began a 3-year study of their breeding biology. Herein we report on various aspects of the reproductive cycle in this population.

## METHODS

Sex was determined during the breeding season in adults by the presence of a cloacal protuberance or brood patch. In immatures and in adults beyond the breeding season, sex was determined by laparotomy.

All released birds were banded with Fish and Wildlife Service bands. Following sex determination, a blue plastic band was placed on males above their

service band. A red plastic band was placed on females.

Cloacal protuberances were measured with a millimeter ruler. Gonads of collected birds were fixed in Bouin's solution and later weighed to the nearest 0.1 mg on a torsion balance.

Birds were captured with mist nets or with four-celled Glenhaven Standby traps baited with mixed seed. Netting was done mostly when we wanted to identify positively a particular bird. Sometimes it was necessary to catch certain females by flushing them from their nest into the net after dark.

To observe activities at nests we watched with binoculars from a nearby vantage point if possible. If not, we erected a burlap-covered blind 2–3 m from the nest and observed from within.

## THE STUDY AREA

The study area lies just outside the eastern boundary of Yosemite National Park where it is entered at Tioga Pass by State Highway 120. It has an altitude of 9500–10,300 ft. *Zonotrichia leucophrys oriantha* occupied subalpine meadows around Ellery and Tioga Lakes and along the streams within the watershed drained by Lee Vining Creek. Typically, the meadows were wet with standing and running water. They were 25–60% covered with willows (*Salix* spp.) interspersed here and there with scrub lodgepole (*Pinus murrayana*) and Jeffrey pine (*P. jeffreyi*). Tall lodgepoles were usually on the periphery. Areas of bare ground were present along road banks and on knolls, especially where they contained the burrow systems of Belding ground squirrels (*Spermophilus beldingi*). The rest of these meadows were covered primarily by grasses, sedges, and flowering annuals. Typically, this area has a heavy snowpack during winter, but there is a lot of variation as to when the last of it melts away each spring. We first got into the study area in early June 1968 and 1969 and in late May 1970. Upon our arrival in 1968, there was no snow except for a few drifts. The willows were well leafed out and the grass was 5–10 cm high. Highway 120 into Yosemite had been opened on 3 May. In 1969, there was an exceptionally heavy snowpack and it still covered much of the breeding habitat to a depth of 0.5–1.0 m in early June. A few areas of bare ground could be seen but only on the southern slopes. The willows did not leaf out until mid-July and Highway 120 was not opened until 2 June. In 1970, the season was not quite as late as in 1969. The highway was opened on 15 May and by 7 June about half of the habitat was snow-free. However, there was a

<sup>1</sup> Present address: Department of Biology, University of Oregon, Eugene, Oregon.

<sup>2</sup> Present address: Department of Zoology, University of Washington, Seattle, Washington 98105.

late season storm, and it snowed every day from 7 to 14 June; the total accumulation of snow was 7–10 cm. This slowed considerably the opening of the habitat. The willows, for example, did not leaf out until late June.

## RESULTS AND DISCUSSION

### TIME OF ARRIVAL

Nearly all of the birds arrived ahead of us in 1968 and 1969, so there is little to be said about their arrival schedule in those years. In 1970, we surveyed the study area on 21 and 22 May and found 21 *Z. l. oriantha*. As near as we could tell, these consisted of seven pairs plus seven lone males. All the males were singing. Within 10 days there were about four times this many birds in the area, nearly all paired. This suggests that the birds arrive during the last half of May, with the males probably tending to arrive before the females. It is common among migratory passerines for the males to arrive at the breeding ground ahead of the females. This behavior has been documented in *Z. l. gambelii* by Oakeson (1954) and by King et al. (1965). However, Oakeson (1954) also observed both sexes of *Z. l. puge-tensis* arriving on the same day.

### TERRITORIES

After arrival, the males establish themselves on areas of snow-free meadow and attract a mate. If no open areas are available, they maintain singing perches in the tall conifers edging the meadows until they can move out onto the breeding habitat. They may become paired during this period. As soon as a patch of thawed habitat appears, the lone male or the pair, as the case may be, move onto it and defend it. A pair may occupy their territory for a full 2 weeks before nest building occurs if environmental conditions are retarded. The thaw pattern of a meadow has a great influence on the specific location and shape of a territory. This became especially clear to us in 1969 and 1970 when the birds were establishing themselves as the habitat opened up. The defended area tended to conform to the thawed area despite its fluctuating size and shape. Adjacent pairs foraged for insects on the same snow patches between their territories during this time. Once the snow was gone, an overlap in feeding areas persisted but its extent varied according to the vegetation. Most of the foraging took place on patches of open (grassy or bare) ground. In large meadows that had 70–80% open ground, there was little or no overlap in feeding areas and a pair sometimes occupied 15,000–20,000 m<sup>2</sup> although they actively defended only within a

TABLE 1. Per cent of banded adult *Zonotrichia leucophrys oriantha* recaptured in subsequent years at Tioga Pass meadow.

	Total present		Returned from 1968		Returned from 1969		% previously banded	
	♂	♀	♂	♀	♂	♀	♂	♀
1968	48	33						
1969	47	37	20	6			42.6	16.2
1970	43	37	11	5	11	16	51.2	56.8

radius of about 50 m of the nest. This distance could be much less because the nests were seldom centrally located in the territory and we have seen them placed with no apparent conflict only 13 m apart near the edges of adjacent territories. In habitat where there was only 20–30% open area available for foraging, the territories were as small as 1500 m<sup>2</sup>. Under such circumstances, adjacent pairs commonly foraged on the same small grassy plots and we have seen as many as four pairs utilizing concurrently the same 450 m<sup>2</sup> plot.

### RETURN OF BANDED BIRDS AND SEX AND AGE DISTRIBUTION

During all 3 years of the study, we routinely collected *Z. l. oriantha* with gun, net, and trap. Most of the netting and trapping was done on a large rectangular meadow about 1,000 × 400 m that extends from the southern tip of Tioga Lake south to the park boundary right at Tioga Pass. We named this Tioga Pass meadow. Our capture records on this meadow show that the same individuals tend to return to it each year to breed (table 1). For example, 51.2% (22 of 43) of the males and 56.8% (21 of 37) of the females taken in 1970 had been captured on the meadow during 1968 or 1969. There seems to be high fidelity to breeding locale, since these recaptured birds probably represent nearly all of the survivors from previous years.

We constructed an accurate map of Tioga Pass meadow, with 10-m coordinates, in the first summer of the study for use in fixing capture location. From this we are able to show that if a bird returns, it occupies the same part of the meadow as it did previously. This means, of course, that if both members of a pair return, they are likely to mate again. We know definitely of three cases wherein the same birds were mated two consecutive years.

Table 2 shows that we captured more males than females, both adult and immature, every year. The ratio of males to females in adults and in immatures is nearly identical (1.29:1 and 1.27:1). Results of a  $\chi^2$  test of these differences in sex distribution are significant at the

TABLE 2. Sex and age distribution and number of captures of *Zonotrichia leucophrys oriantha* at Tioga Pass meadow.

	Adults		Immatures	
	♂	♀	♂	♀
1968				
Individuals	48	33	69	46
No. of captures	142	66	253	159
1969				
Individuals	47	37	77	68
No. of captures	164	104	510	385
1970				
Individuals	43	37	38	34
No. of captures	192	111	127	101
Total				
Individuals	138	107	184	148
No. of captures	498	281	890	645
Sex ratio, all years	1.29:1.00		1.27:1.00	
Capture ratio, all years	1.77:1.00		1.38:1.00	

0.05 level. We cannot find a bias in our methods that favors the capture of males. From our experience in the laboratory with many hundreds of birds, we estimate that our method of laparotomy for identification of sex is better than 95% accurate. We conclude that more male than female *Z. l. oriantha* are hatched and that this disparity in sex distribution persists through adult life.

We do not know the fate of the extra adult males during the breeding season. In the three summers of the study, we captured only one male that had collapsed testes and no cloacal protuberance during the breeding season. This male was lean and had one foot missing. We accidentally killed a paired male in June 1970 on Tioga Pass meadow. Within a week we were certain that his female was paired with a new male. Perhaps, then, some of the extra males do not come into reproductive condition and some are ready to breed but do not have a mate. We do not know of or suspect any cases of polyandry.

King et al. (1965) found that there were more males than females in both adult and immature *Z. l. gambelii* killed on their central Alaska breeding grounds. They felt, however, that this was due to their intentional selection of larger birds since they were trying to collect principally males. Sex was not determined in released birds.

In our study it is apparent that, beside being present in greater numbers, males are also easier to catch than females (table 2). The ratio of the total number of captures of males versus those of females is 1.77:1 in adults and

1.38:1 in immatures. In adults this ratio differs significantly ( $P < 0.05$ ) from the determined sex ratio.

The data in tables 1 and 2 include birds that did not breed on Tioga Pass meadow nor were they hatched there. We know from our banding records that at least some of these birds came onto the meadow from nearby breeding areas. New adults began to appear near the end of the period of postnuptial molt and we began to capture new immatures shortly after they had fledged. Three of these immatures had been banded as nestlings about 6 km NW of Tioga Pass meadow.

In 1970, our take of immatures, but not of adults, was greatly reduced from previous years. In 1970, we retained in captivity immatures when they were captured initially or upon a subsequent recapture. This mostly prevented their occurrence in flocks, as seen in previous years from the first half of August onward. Perhaps under normal circumstances, flocks on the meadow attracted and retained wandering or migrating immature birds.

#### THE REPRODUCTIVE CYCLE

Upon their arrival, the females had 30–60 mg ovaries and the combined testes of males weighed 200–400 mg (fig. 1). Gonadal maturation, as judged by size, continued in both sexes for about 2 weeks after their arrival. A maximum in gonadal size was maintained for about 2 weeks in the females and for 6 weeks in the males. A prolonged maintenance of testicular activity was seen also in *Z. l. gambelii* on their breeding grounds in Alaska (King et al. 1966). Obviously it is important for the males to be fertile for a long period in case renesting is attempted.

Compared to testicular weight, the decrease in ovarian weight occurred slowly. Actually, ovarian weights are probably deceptive in terms of functional state. Females with nestlings often had only 30–40 mg ovaries, but we know that they could be ready to lay again in a week or less if their brood was lost (see beyond).

The cloacal protuberance is caused by the enlarged seminal glomera or seminal vesicles. The protuberance may facilitate intromission during copulation and may also function as a site for sperm storage in a manner analogous to the mammalian scrotum since protuberance temperatures are 1.5–4.5° C cooler than deep body temperatures (Wolfson 1954a,b). The seminal glomera have been found to be under endocrine control and their size varies directly with testes size in starlings, *Sturnus vulgaris*

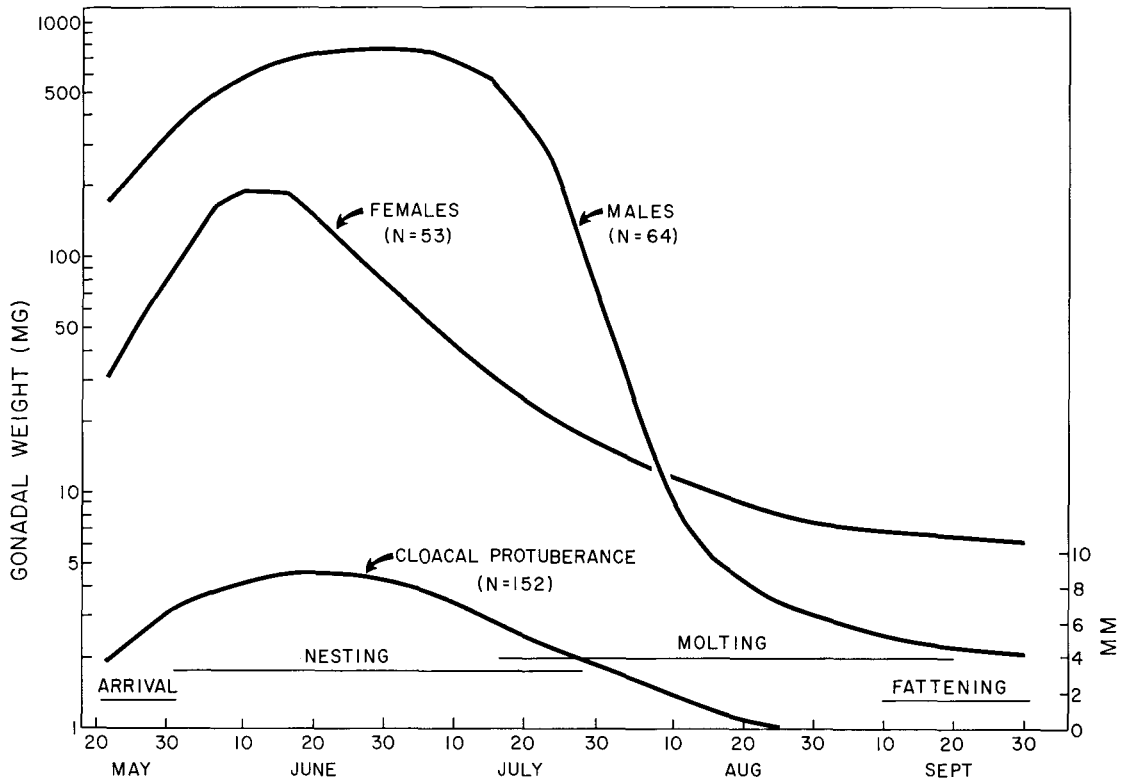


FIGURE 1. Gonadal cycle and schedule of events in *Zonotrichia leucophrys oriantha* on their breeding grounds in the central Sierra Nevada.

(Hilton 1968). In *Z. l. oriantha* there is also a close parallel between the size of the glomera and the functional state (size) of the testes.

The postnuptial molt began in the population in mid-July and carried through into the period of premigratory fattening.

#### NEST CONSTRUCTION AND LOCATION

As in other races of White-crowned Sparrows, only the female *Z. l. oriantha* builds the nest, usually in 2-4 days. The base and main cup are made from a variety of materials including small sticks, grass stems, moss, or shreds of bark. As the final step in construction, the cup is lined with fine dry grass or sedge. The completed nest has a cup that is about 6.5 cm wide and 5.0 cm deep. By the time a brood leaves the nest, the cup has been stretched to a diameter of 8.0-8.5 cm.

The site selected by the female for placement of the nest is influenced greatly by the condition of the habitat. In 1968 and 1970, just over 60% of the nests were built on the ground (fig. 2). In 1969, only 22% were built on the ground. Obviously, this happened because at the time of nest building much of the ground was still covered with snow and thawed areas had opened so recently that the

grass was often not high enough for hiding a nest. Apparently, many of those birds that would normally have built on the ground moved their nests up into the first limbs suitable for nest placement in willows and scrub pine. This is the zone 21-40 cm above the ground. There are very few suitable sites present between 1 to 20 cm and only a few nests were placed in that zone in any year. The height of 41-60 cm corresponds to the dense crown area of the willows used for nesting. In 1968 and 1969, 22% of the nests were built in that area. In 1969, this was done when the willows had not yet leafed out and the nests were exposed and easy to find. In 1970, most of the nests constructed early in the season were placed above ground because there was still a lot of snow. The thaw proceeded very swiftly, however, and most of the later nests were built on the ground. Others have noted marked changes in nest site selection with change in vegetative cover and growth. Usually, however, nest height increased as the season progressed (compare Nice 1937; Walkinshaw 1939, 1944).

There was a greater tendency in the 2 late years (1969) and 1970) to build nests above 60 cm. These nests were usually located in pines

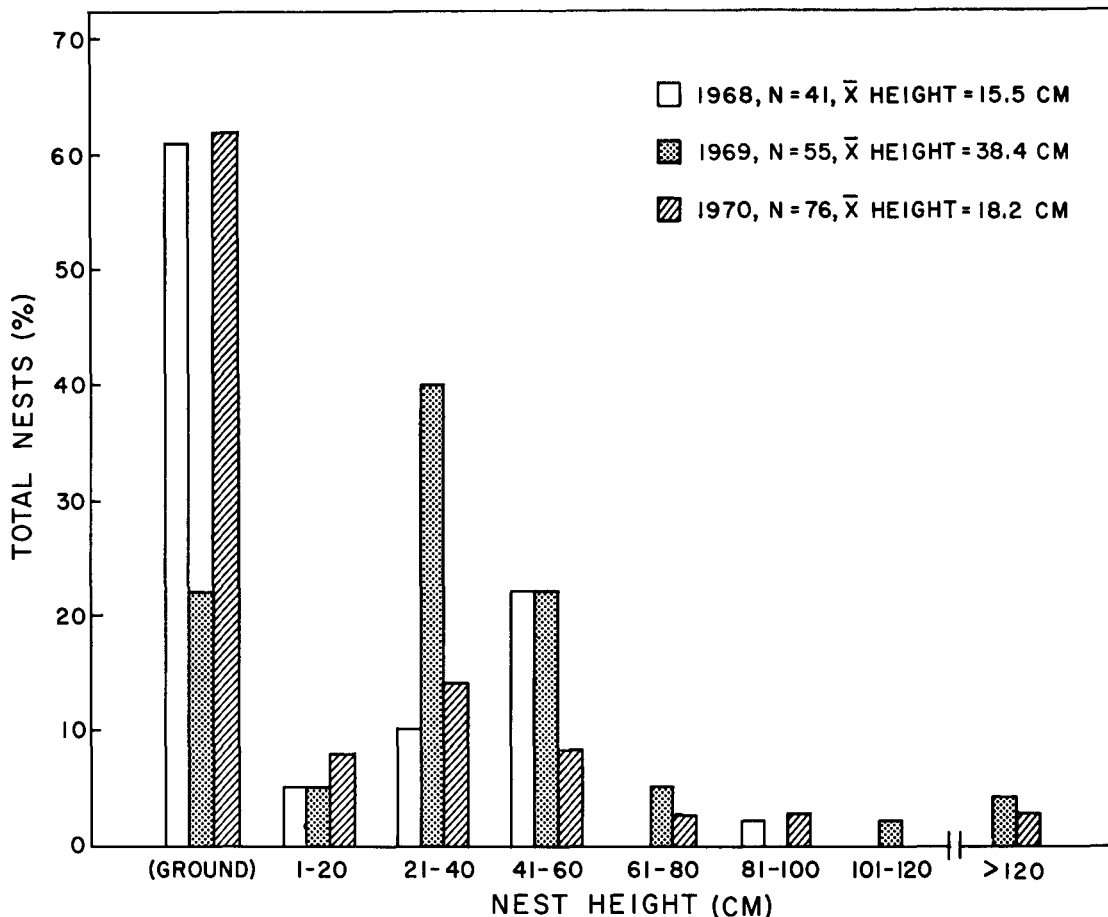


FIGURE 2. Height at which nests of *Zonotrichia leucophrys oriantha* were found.

at the periphery of the meadows. They probably represent secondary choices for nest location. The picture seems to be that *Z. l. oriantha* prefer to build on the ground in thick grass clumps and at the base of shrubs and in the crowns of willows, especially if they are leafed out. If insufficient sites of this type are available, they will build on fairly wet, open ground in willows that are not leafed out, and at the edge of the preferred habitat relatively high up in pine trees.

#### LAYING SCHEDULE

Eggs were laid singly on consecutive mornings until the clutch was complete. We noted only two exceptions to this. Each time a lapse of an extra day occurred between a second and third egg. Laying took place in the early morning when it was first becoming light. As close as we could determine, this was between 04:10 and 05:30.

We weighed and measured 42 eggs of various ages. They weighed an average of  $3.04 \pm 0.25$  g and were  $2.26 \pm 0.06$  cm long and

$1.63 \pm 0.04$  cm wide at the widest point. The eggs were blue with brown spots. The brown usually covered about half of the surface but in a few clutches it was almost completely lacking.

In 22 cases we observed the completion of nest construction followed by laying. The average interval between these two events was  $2.5 \pm 2.4$  days (range, 1-12 days). The 12-day interval was very unusual since the next longest interval was 5 days. It occurred in 1970 when a female constructed her nest on the ground under a small willow in the very same spot as in 1969. She completed the nest on 7 June, only hours before the onset of the week-long snowstorm. During the storm, the nest became filled with snow. On 19 June, she laid in this nest the first egg of a four-egg clutch. All other recently completed empty nests and many of those with eggs were abandoned during this storm (see beyond). Apparently a predilection for a specific nest site was involved in this unusual case.

The chronology of egg-laying was different

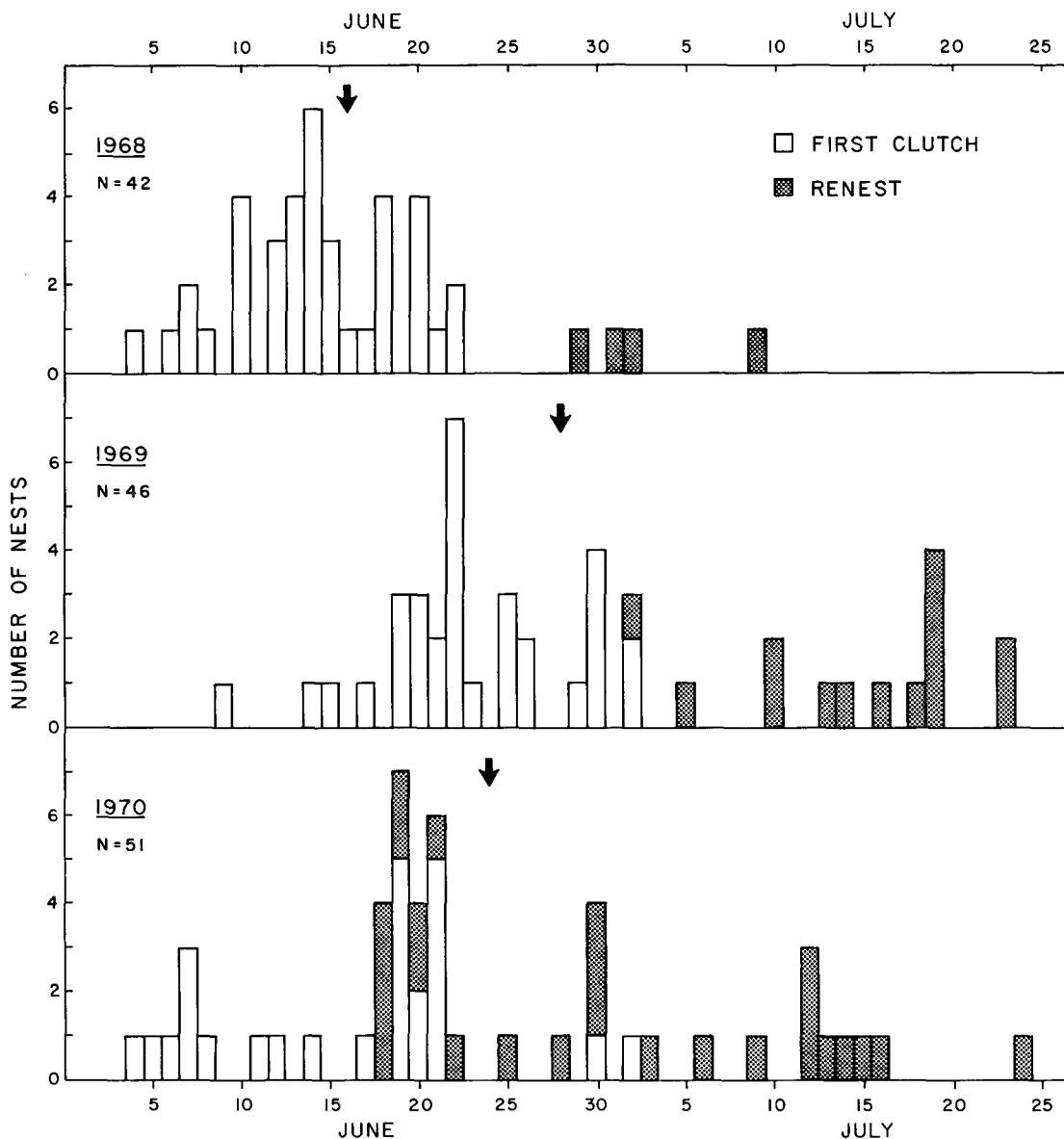


FIGURE 3. Time of clutch starts for *Zonotrichia leucophrys oriantha* in the central Sierra Nevada. Arrows indicate mean date for all starts in a given year.

every summer and obviously greatly influenced by immediate edaphic and climatic conditions. In 1968, when the habitat opened early, laying started on 4 June (fig. 3). The number of clutch starts (date of first egg) increased until 14 June and declined thereafter. The last start was on 9 July. This is a total of 35 days over which clutches were started. The mean date for all clutch starts was 16 June. The renests were second attempts following loss of the first clutch or brood. The 1968 data typify early nesting activity unhindered by snowcover or storms. Late nesting was undoubtedly hampered, however, by the dry conditions.

In 1969, when the habitat opened late, the mean date for all clutch starts was 28 June, 12 days later than in 1968. At least three of the renests in 1969 were second broods. We documented these by catching the banded female in a mist net as she was flushed off the nest. Despite the late beginning of the breeding season, conditions were favorable for raising young much later in the summer than in 1968 and there was a total of 44 days over which clutches were started. The runoff from melting snow kept the meadows wet and green well into August; therefore insect adults and larvae were readily available for feeding the nestlings.

TABLE 3. Clutch size in *Zonotrichia leucophrys oriantha* at Tioga Pass.

Year	n	Clutch Size			$\bar{x}$
		3	4	5	
1968	40	9	30	1	3.80
1969	47	5	41	1	3.91
1970	56	5	44	7	4.04
Total	143	19	115	9	3.93

Although the breeding habitat was not opened completely in early June 1970, egg-laying began on 4 June and might well have proceeded on a schedule similar to that of 1968 except for the week-long storm already mentioned. At the time the storm began on 7 June, we knew of 12 nests: six newly constructed and without eggs and six with eggs. Of these, five without eggs and three with eggs were abandoned during the storm. Only four starts were recorded from 8 June to the storm's end on 14 June. Obviously, the adverse weather inhibited nest construction and laying during this time. An end effect of the storm was that it synchronized the female population such that 42% of the clutch starts that we observed in 1970 occurred between 18 and 21 June. As in 1969, renesting occurred until late in the summer (24 July) due to the favorable conditions preserved by snow-melt and clutches were started over a span of 50 days. The mean date for all clutch starts was 24 June. Most of the renesting efforts were made by females that had been thwarted in their previous attempts but we did observe two known instances of double brooding.

#### CLUTCH SIZE

The clutch size of *Z. l. oriantha*, as determined from 154 museum records, has been reported to range from two to seven eggs, with a mean of  $4.0 \pm 0.03$  (DeWolfe and DeWolfe 1962). Four-egg clutches constituted 88% of the total. Among our 143 records (table 3) from Tioga Pass, the clutches varied only between three and five eggs and the mean was  $3.93 \pm 0.54$ . Four-egg clutches were the mode, making up 80.4% of the total. This also closely approximates clutch sizes in *Z. l. pugetensis* (Blanchard 1941), and the nominate race, *Z. l. leucophrys* (Clement in Bent 1968:1273). In *Z. l. gambelii*, however, the clutch size is larger (4.81, Williamson et al. 1966; 4.66, Oakeson 1954). In them, five is the modal clutch size (Williamson et al. 1966).

In many studies it has been seen that clutch size increases in early spring and decreases as the nesting season progresses; renesting ap-

parently produces fewer eggs than initial nesting (Lack 1954; Davis 1955). It is generally assumed that this occurs because of worsened trophic conditions. We divided the three nesting seasons of *Z. l. oriantha* into quarters and then determined the mean clutch size for the various quarters. The means in succession from first quarter to last quarter were 3.92, 3.91, 4.00, and 3.97. The mean was 3.94 for initial clutches and 4.00 for renests. This suggests that food availability is constant throughout the nesting season (highly doubtful) or that it is not affecting clutch size seasonally in *Z. l. oriantha*.

#### ATTENTIVENESS DURING INCUBATION

We made many routine observations of behavior during incubation in *Z. l. oriantha*. So far as we know, all incubating was done by the female. In 1969 and 1970, we observed seven different females incubating complete clutches. They were watched from concealment at all times of the day for a total of 44.6 hr. During these observations, the females were on the nest 61.4% of the time. Their activities were devoted almost exclusively to brooding or to foraging. Brooding bouts averaged  $23.4 \pm 12.6$  min (range, 2–60 min). Foraging bouts averaged  $18.3 \pm 18.4$  min (range, 3–53 min).

The beginning of incubation was difficult to determine. We noticed that females sometimes sat tightly on freshly completed nests without eggs. This may have been a first manifestation of broodiness or simply their attempts to shape the nest cup. When we flushed females from an empty nest, they had a tendency to abandon it and build another. Once the first egg was laid the females began sitting for several hours each day. Our impression is that this behavior was nonrhythmic and occurred mostly in the morning hours. Females were not observed to sit at night until the last or next-to-last egg had been laid. True incubation may have actually begun with the onset of nighttime sitting because from then on attentiveness during the day seemed to be regular and consistent in pattern. Incubation has been frequently observed to begin with the laying of the penultimate egg (Davis 1955; Jehl 1968).

In a beautifully documented study of incubation in Tree Sparrows (*Spizella arborea*), Weeden (1966) has shown that the activity pattern of incubation was established gradually during egg-laying. In contrast to our admittedly meager data on *Z. l. oriantha*, she found that the first attentive interval of *S. arborea* females occurred at night. Some day-

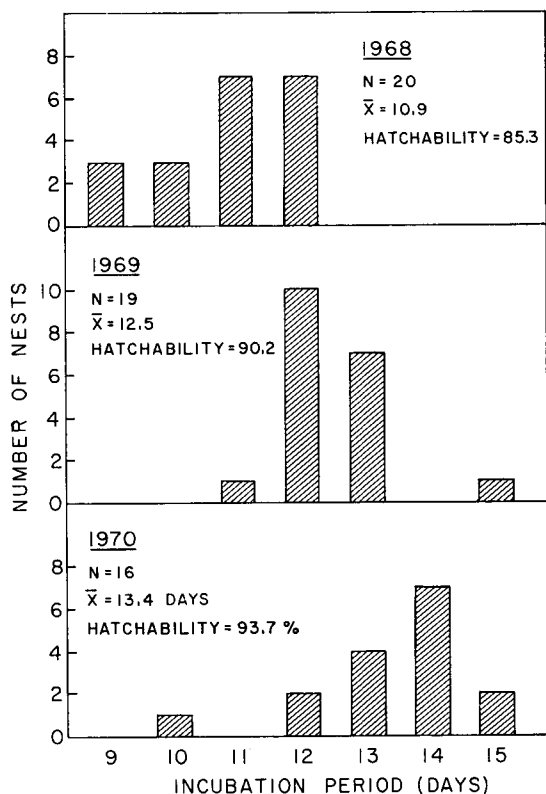


FIGURE 4. Distribution of incubation periods of *Zonotrichia leucophrys oriantha* in the central Sierra Nevada.

time attentiveness began with the penultimate egg and a complete pattern of daytime attentiveness began on the day of clutch completion.

#### INCUBATION PERIOD

The incubation period was measured as the interval between the day the last egg was laid and the day the last chick hatched. It varied considerably among individuals and from year

to year for the population (fig. 4). The mean incubation period was shortest in 1968 (10.9 days) and longest in 1970 (13.4 days). In 1969 and 1970, it was significantly longer ( $P < 0.01$ ) than in 1968. An increased hatchability accompanied the increase in incubation period. It seems probable that the longer incubation periods in 1969 and 1970 were related to the more severe weather conditions in those years. However, a comparison of mean daily air temperatures (as taken at Tioga Pass by the U.S. Park Service) during incubation to incubation period does not reveal a statistically significant relationship between them. As shown by Kendeigh (1940, 1963), the relationship of ambient temperature to incubation period is complex, with the rate and magnitude of temperature change both having important effects. Probably it is necessary to measure egg temperatures throughout incubation to determine the effect of ambient conditions on incubation. At the very least, a record of air temperature in the microenvironment of the nest is needed.

#### MORTALITY

We have examined mortality according to nest location (on vs. above ground) and its causes in terms of three major categories: predation, weather, and human interference (table 4). Probably the main predators were long-tailed weasels (*Mustela frenata*), coyotes (*Canis latrans*), and Belding ground squirrels (*Spermophilus beldingi*). Other potential predators in the area that may have had some effect were badgers (*Taxidea taxus*) and Clark's Nutcrackers (*Nucifraga columbiana*). We have seen weasels in pursuit of *Z. l. oriantha* and once found a fresh coyote scat beside a newly robbed nest. We feel, however, that ground squirrels were the most important predator. They were abundant in the study area, and we

TABLE 4. Causes of mortality in *Zonotrichia leucophrys oriantha*.

Nest Site	Year	Predation		Weather		Human Interference		Total Viable Individuals	(% Total Mortality)
		Eggs	Nestlings	Eggs	Nestlings	Eggs	Nestlings		
On ground:									
	1968	24	5	0	0	11	4	78	56.4
	1969	10	4	7	3	3	1	34	82.4
	1970	38	8	15	0	5	6	138	52.2
	Total	72	17	22	3	19	11	250	57.6
Above ground:									
	1968	12	3	0	4	7	3	50	58.0
	1969	19	15	0	9	7	6	121	46.3
	1970	12	19	13	0	3	0	80	58.8
	Total	43	37	13	13	17	9	251	52.6



TABLE 5. Time of predation of eggs and nestlings in *Zonotrichia leucophrys oriantha*.

	Day												
	0	1	2	3	4	5	6	7	8	9	10	11	
Eggs taken during laying		11		4	3								
Eggs taken after clutch was completed			4	4	7	3	4	14	13	11	11	3	4
Nestlings taken			3	5	9	8	3						

have seen them devour eggs on two occasions and nestlings on one occasion. In each of these cases, the nest cup remained in good condition following the squirrel's visit. This was what we usually found when a nest had been robbed. Occasionally the nest was torn apart by a predator and twice we found feathers at the site, indicating that the incubating female had been killed and eaten along with the eggs. This was undoubtedly not the work of ground squirrels. Verbeek (1970) described similar destruction of nests among Water Pipits (*Anthus spinoletta*) and attributed it to long-tailed weasels.

When we examine more closely the time in the nesting cycle when predation occurred, we see that eggs were most likely to be taken during laying on the first day (table 5) and during incubation on days 6 through 9. There was no known predation of nestlings beyond their sixth day. Holcomb (1969) also saw a pattern in American Goldfinches (*Spinus tristis*) wherein nestlings were more likely to be taken during the middle portion of nest life. As he suggests, this is probably due to their increase in size, noise, and activity. *Z. l. oriantha* that are 7 days of age or older have the motor and thermoregulatory abilities to survive out of the nest (Morton and Carey 1971). These older nestlings may be avoiding predation by hiding in nearby vegetation when a predator approaches.

Human interference occurred mostly because of our work, especially on thermoregulation studies of nestlings. Tourists and fishermen were also responsible for some of the mortality. In several cases, eggs were abandoned for reasons actually unknown to us, but we felt human interference was likely and these have been included in that category.

Consulting table 4, we can see that predation of eggs was the greatest cause of mortality in nests both on and above the ground. The relative numbers are greater for those on the ground. This may be because nests on the ground are more likely to be found by pred-

ators, especially ground squirrels. In nests built above ground, there was nearly as much total predation of nestlings as there was of eggs. Most of this occurred in 1969 and 1970. We think this happened because, in 1969 and 1970, the growth of vegetation was greatly retarded and nests were much more visible to predators. If weasels were mainly responsible for predation in above-ground nests, the effects of sparse vegetation was probably multiplied because there were greater numbers of weasels on the study area in 1969 and 1970 than in 1968. We have no good quantification of their numbers but a rough index is provided by our field notes. In them we find that weasels were seen 4 times in 1968, 16 times in 1969, and 15 times in 1970.

The net effects of weather on nesting success varied greatly from season to season. In 1968, the only loss was due to a hailstorm that battered apart a nest above ground containing four day-5 nestlings. The nestlings were dumped on the ground and did not survive. There was no mortality observed due to weather in nests on the ground.

In 1969, the situation was reversed because 29.4% (10 of 34) of the viable individuals (fertile eggs + nestlings) in nests on the ground were killed because rain on top of a heavy snowpack caused creeks to rise and flood nests on the ground. Relatively few nests were built on the ground in 1969 (fig. 2), and the high mortality in them due to weather suggests that they were placed in suboptimal sites. In contrast, only 7.4% (9 of 121) of those in nests above ground were lost because of weather effects.

In 1970, no nestlings died from weather effects. A considerable number of eggs were lost, however, mainly in the week-long snowstorm in June. Apparently the females could not keep the nests free of snow and forage adequately at the same time.

In some ways, such as in the large seasonal cycle in trophic conditions and in the occurrence of summer storms, high altitude is the ecological equivalent of high latitude. There is an indication that adverse weather may at times be the most important factor limiting productivity of bird populations at high latitude (Jehl and Hessel 1966; Jehl 1968) although severe storms may also be survived without apparent detriment (Oakeson 1954). In contrast to our study, Verbeek (1967, 1970) reported no mortality due to weather in Horned Larks and Water Pipits nesting at high altitude. Obviously, mortality due to weather in both of these environments can vary enormously from year to year, depending upon the severity and

duration of storms and when they occur in relation to the nestling cycle. For example, we noticed that rain and hail tended to cause mortality in nestling *Z. l. oriantha* when they were about 5 or 6 days of age. At that time, the nests had undergone considerable wear and were more likely to be damaged. Furthermore, the nestlings were not old enough to survive outside the nest if it did come apart.

Most of the loss of eggs due to human interference occurred because the females abandoned when they were flushed from the nest. If a female abandoned, she usually did so the first time she was flushed or not at all. Nestlings were lost from a variety of handling misadventures, mostly during deep-body temperature measurements. Usually only eggs were abandoned, but once a female abandoned day-1 nestlings when a blind was erected 2 m from the nest.

#### RENESTING

In our experience, *Z. l. oriantha* nearly always renested if they lost their eggs or nestlings. If a second effort failed, they tried again and again. We observed one female in 1970 that built at least four nests, laid four complete clutches, and had all of them robbed by predators.

In 26 cases we were able to determine the interval between the loss of a nest and the laying of the first egg in a new nest. The mean interval was  $6.8 \pm 3.9$  days (range, 2–16 days). This compares to an interval of 7 days noted by Oakeson (1954) for one case in *Z. l. gambelii*, and a mean of 6.75 days noted by Berger and Radabaugh (1968) for 12 cases in the Kirtland's Warbler (*Dendroica kirtlandii*).

The case wherein we observed a 2-day interval was unusual. The first nest was built on the ground near the shore of Tioga Lake in a 240 m<sup>2</sup> marshy area covered with thick, dry grass about 25 cm high. The nest was little more than a lined cup made totally of dry grass. At 11:20 on 28 June 1970, the female was incubating four eggs. At 11:20 the next day, the eggs were gone and the female was seen carrying grass. At about 05:30 on 30 June, she laid an egg in a new nest located only 8 m south of the previous one and constructed in the same simple fashion. Assuming the first nest was robbed as soon as we left it, the maximum time between predation and the laying of the first egg in the new clutch was 43 hr. The bottom of the new nest was thin and wet from the wet ground beneath it. One more egg was laid on 1 July and then the nest was abandoned. This female did not renest again to our knowledge.

TABLE 6. Productivity of *Zonotrichia leucophrys oriantha* nesting at Tioga Pass meadow, Mono County, California.

	1968	1969	1970
Total no. pairs	28	23	25
Mean clutch size	3.7	3.9	4.0
Hatchability (%)	86.2	89.8	93.2
Mortality (%)	57.0	54.2	54.5
Second broods	0	3	2
Young fledged/pair	1.4	1.8	2.0
Total no. young fledged	39	41	50

When a nest was lost, the new nest was built within the pair's territory, a mean distance of  $35.6 \pm 30.8$  m (range, 5–150 m) from the previous nest. We noted one case, however, wherein a new site was not selected. At 08:45, 18 July 1969, a female was flushed from a nest containing one egg. When the nest was checked again 4 hours later, the egg was gone and the cup lining had been pulled completely out. At 06:30, 19 July, the female was flushed from the same nest, now repaired. One egg was present. When the nest was checked at 06:45, 20 July, the cup was again torn apart and the egg was gone. The female may have built another nest subsequently but we did not find it.

#### PRODUCTIVITY

We obtained accurate information on productivity at Tioga Pass meadow during all 3 years. Our figures provide some insight on the effect of late winters on reproductive success (table 6).

The total number of pairs using the meadow was greatest in 1968 when the maximum amount of habitat was available at nesting time and least in 1969 when much of the area was still covered with snow. However, the number of pairs present in a given year was not a good indicator of productivity (total young fledged) for the meadow. Productivity was lowest in 1968 and highest in 1970. Clutch size, hatchability, and mortality all favored greater productivity in 1969 and 1970 as compared to 1968. Probably of greatest importance was the prolonged wet period provided by melting snow in the latter 2 years. This caused conditions favorable for raising young to persist until quite late in the summer so that more renesting efforts were possible including even some second broods.

#### SUMMARY

The chronology of events in the reproductive cycle and the nesting success of *Zonotrichia*

*leucophrys oriantha* were studied for 3 summers (1968–1970) in the central Sierra Nevada.

The birds migrated into the breeding area in late May and early June, with males tending to arrive ahead of females. Gonadal development continued in both sexes for about 2 weeks following arrival. Maximum gonadal size was maintained for about 2 weeks in the female population and for 6 weeks in the males. The size of the cloacal protuberance closely paralleled testicular size.

Males, especially adults, showed a greater propensity to be recaptured than females. Adults returning to the meadow occupied the same area that they did in the previous year.

Environmental conditions greatly affected the timing and length of the reproductive cycle and reproductive success. Clutch starts occurred over a period of 35 days in 1968, 44 days in 1969, and 50 days in 1970. The mean date for clutch starts was 16 June 1968, 28 June 1969, and 24 June 1970. These variations could be attributed directly to storms and snowpack. In 1968, there was a light snowpack and it melted off early. The breeding meadows became dry and unsuitable for nesting by early July. In 1969 and 1970, the snowpack was heavier and the meadows remained wet and green through mid-summer and nesting continued until late July.

The net effect on productivity of the prolonged seasons in 1969 and 1970 was to increase the number of young fledged per pair and per unit area of breeding habitat over that of 1968. Involved in the increase in productivity were larger clutches, increased hatchability, decreased mortality, and the occurrence of some second broods.

Nest location was also affected by the presence of snow during the nest building period, especially in 1969, when many nests were placed in willows and scrub pine.

The first egg was laid an average of 2.5 days after the nest was completed. Eggs were laid one per day in the early morning. The mean clutch size for 143 nests was 3.93 (mode = 4). Clutch size did not vary with season or between initial clutches and renests.

Females began the incubation process while still laying eggs. They sat on the nest for several hours each day from the first egg onward. Full-time incubation was signaled by the occurrence of nighttime sitting at the time the clutch was completed or when the penultimate egg was laid. When incubating, females sat on the nest an average of 61.4% of the time during daylight and continuously at night. The incubation period ranged from 9 to 15

days and was significantly longer in 1969 and 1970 than in 1968.

Mortality in the 3 summers was 55.1% (276 of 501 fertile eggs and nestlings). In nests built on the ground, mortality was 57.6% (144 of 250) and in nests built above ground, it was 52.6% (132 of 251).

There were three major courses for mortality: predation, weather, and human interference. Of these, predation was the most important. The Belding ground squirrel was probably the most important predator. It was observed eating eggs and nestlings and was abundant in the study area. Long-tailed weasels may also have been an important predator, especially in 1969 and 1970 when they seemed to be more numerous than in 1968.

Despite the slightly greater susceptibility of nests on the ground to predation, *Z. l. oriantha* seem to prefer to build them there. An offsetting factor is that nests above ground are more likely to be damaged by storms, particularly if they have been worn by the activity of nestlings. Nests in either location may be abandoned during a prolonged snowstorm, and nests on the ground are more likely to be flooded.

Following the loss of a clutch or brood, re-nesting nearly always occurred. Several attempts were made if necessary. The mean interval between loss of a nest and laying of the first egg in a new nest was 6.8 days. The new nest was located within the same territory, a mean distance of 35.6 m from the previous nest.

#### ACKNOWLEDGMENTS

We wish to acknowledge financial support from the Frank M. Chapman Memorial Fund, the American Philosophical Society, The Research Corporation, and from a College Science Improvement Program Grant (GY 4754) to Occidental College from the National Science Foundation. The following people have our gratitude for assisting in many ways with this project: Ronald Baldrige, Susan Budd, Lawrence De Boer, Cynthia Carey, John Gallup, Jorge Orejuela, and Hsing-chu Tung. Barbara B. DeWolfe made many helpful suggestions on the manuscript.

#### LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1957. Checklist of North American birds. Fifth ed. AOU, Baltimore.
- BANKS, R. C. 1964. Geographic variation in the White-crowned Sparrow, *Zonotrichia leucophrys*. Univ. California Publ. Zool. 70:1–123.
- BERGER, A. J., AND B. E. RADABAUGH. 1968. Returns of Kirtland's Warblers to the breeding grounds. Bird-Banding 39:161–186.

- BLANCHARD, B. D. 1941. The White-crowned Sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. Univ. California Publ. Zool. 46:1-178.
- CLEMENT, R. C. 1968. Eastern White-crowned Sparrow. In A. C. Bent [ed.] Life histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and allies. U.S. Nat. Mus. Bull. 237.
- DAVIS, D. E. 1955. Breeding biology in birds. p. 264-308. In A. Wolfson [ed.] Recent studies in avian biology. Univ. Illinois Press, Urbana.
- DEWOLFE, B. B., AND R. H. DEWOLFE. 1962. Mountain White-crowned Sparrows in California. Condor 64:378-389.
- HILTON, F. K. 1968. Endocrine control of seminal-glomus growth and function in starlings of different ages. Physiol. Zool. 41:364-370.
- HOLCOMB, L. C. 1969. Age-specific mortality of American Goldfinch nestlings. Auk 86:760-761.
- JEHL, J. R., JR. 1968. The breeding biology of Smith's Longspur. Wilson Bull. 80:123-149.
- JEHL, J. R., JR., AND D. J. T. HUSSELL. 1966. Effects of weather on reproductive success of birds at Churchill, Manitoba. Arctic 19:185-191.
- KENDEIGH, S. C. 1940. Factors affecting length of incubation. Auk 57:499-513.
- KENDEIGH, S. C. 1963. Thermodynamics of incubation in the house wren, *Troglodytes aedon*. Proc. XIII Int. Ornithol. Congr., Ithaca, p. 884-904.
- KING, J. R., D. S. FARNER, AND L. R. MEWALDT. 1965. Seasonal sex and age ratios in populations of the White-crowned Sparrows of the race *gambelii*. Condor 67:489-504.
- KING, J. R., D. S. FARNER, AND M. L. MORTON. 1965. The lipid reserves of White-crowned Sparrows on the breeding ground in central Alaska. Auk 82:236-252.
- KING, J. R., B. K. FOLLETT, D. S. FARNER, AND M. L. MORTON. 1966. Annual gonadal cycles and pituitary gonadotropins in *Zonotrichia leucophrys gambelii*. Condor 68:476-487.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, New York.
- MORTON, M. L., AND C. CAREY. 1971. Growth and development of endothermy in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*). Physiol. Zool. 44:177-189.
- NICE, M. M. 1937. Studies in the life history of the Song Sparrow. I. A population study of the Song Sparrow. Trans. Linnaean Soc., N.Y. 4: 1-247.
- OAKESON, B. B. 1954. The Gambel's sparrow at Mountain Village, Alaska. Auk 71:351-365.
- VERBEEK, N. A. M. 1967. Breeding biology and ecology of the Horned Lark in alpine tundra. Wilson Bull. 79:208-218.
- VERBEEK, N. A. M. 1970. Breeding ecology of the Water Pipit. Auk 87:425-451.
- WALKINSHAW, L. H. 1939. Nesting of the Field Sparrow and survival of the young. Bird-Banding 10:107-114.
- WALKINSHAW, L. H. 1944. The eastern Chipping Sparrow in Michigan. Wilson Bull. 56:193-205.
- WEEDEN, J. S. 1966. Diurnal rhythm of attentiveness of incubating female Tree Sparrows (*Spizella arborea*) at a northern latitude. Auk 83:368-388.
- WILLIAMSON, F. S. L., M. C. THOMPSON, AND J. Q. HINES. 1966. Avifauna investigations. p. 437-480. In N. J. Wilimovsky and J. N. Wolff [eds.] Environment of the Cape Thompson Region Alaska. U.S. Atomic Energy Comm.
- WOLFSON, A. 1954a. Sperm storage at lower-than-body temperature outside the body cavity in some passerine birds. Science 120:68-71.
- WOLFSON, A. 1954b. Notes on the cloacal protuberance, seminal vesicles, and a possible copulatory organ in male passerine birds. Bull. Chicago Acad. Sci. 10:1-23.

Accepted for publication 8 June 1971.