

NEST PREDATION IN THE MOUNTAIN WHITE-CROWNED SPARROW¹

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Abstract. Predation was the largest cause of failure in 1,132 *Zonotrichia leucophrys oriantha* nests, followed by desertion and inclement weather. Mean annual predation rate was 29.9% and did not vary significantly over the 19 years of the study. This was attributed to the presence of a large, stable population of Belding's ground squirrels, a known predator on *Z. l. oriantha* nests. Predation rate was highest during the nestling period, next highest during laying, and lowest during incubation. Mean daily predation rate for the whole nesting cycle was 2.0% per day. Investigator activities at nests frequently caused desertion during laying but seldom thereafter. These activities may have attracted predators on occasion but no convincing, pervasive effect could be demonstrated. Antipredator behaviors included several distraction displays and seasonal shifts in nest locations from above-ground to ground and from pines to willows. Predators at the nest were vigorously attacked but usually to no avail. Nest predation rates did not vary with parental age nor with clutch size.

Key words: Nest predation; desertion; weather; *Zonotrichia leucophrys*; high altitude; montane; reproductive biology; nesting success; age effects.

INTRODUCTION

Predation is usually the primary cause of nesting failure in land birds (Ricklefs 1969, Best and Stauffer 1980, Perrins and Birkhead 1983, Martin 1988a), but investigators may still be underestimating its effects on such important traits as ecological diversification (Martin 1988a, 1988b; Ricklefs 1989), clutch size (Skutch 1949, Lima 1987, Martin 1988c, Kulesza 1990), and the evolution of reproductive strategies (Martin 1992). Studies of nest predation over a long term on the same population would seem particularly useful to our understanding of how such a potent agent of natural selection might influence the nesting habits, including antipredator behaviors, and ultimately the reproductive success of avian species. Herein we present 19 years of data on nest predation and other causes of nest failure in an open nesting migratory bird, the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*). This is an intracontinental migrant that winters primarily in Mexico and summers and breeds in montane settings of the western United States (Morton and Allan 1990). The study area was a series of subalpine meadows in the upper portions of Lee Vining Canyon near Tioga Pass, Mono County, California. This location is in the

Sierra Nevada Mountains at 37.5°N latitude at an elevation of about 3,000 m.

METHODS

Nests were found by thoroughly searching the habitat and by watching mated birds, especially females, for cues. Once a nest was located the spot was marked with a 2-cm diameter identification tag that was hung 3-5 m away on a tree or shrub, along with a 10-cm piece of red yarn.

The number of visits made to a nest subsequent to discovery and the time spent there at each visit varied greatly over the years depending upon the current focus of the study. Our activities at a nest ranged from simple walk-by checks at irregular intervals to see if it was still active, to more prolonged visits wherein data were collected. The latter included numbering eggs to get laying order and measuring them with calipers, measuring plumage of nestlings, determining their thermoregulatory abilities, weighing them, affixing bands, and performing laparotomies for sex identifications. We also performed a variety of measurements or techniques on nesting adults including body weight, fat class, bill length, molt status, blood sampling, and cloacal lavage.

A nest was assumed to be depredated when it was found empty after having previously been known to contain eggs or nestlings, except when we thought fledging had occurred. Cases wherein only part of a clutch or brood disappeared were

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TABLE 1. Known or suspected predators of *Z. l. oriantha* eggs and nestlings at Tioga Pass.

| Avian | Mammalian |
|---|--|
| California Gull <i>Larus californicus</i> | Marten <i>Martes americana</i> |
| *Clark's Nutcracker <i>Nucifraga columbiana</i> | Badger <i>Taxidea taxus</i> |
| Common Raven <i>Corvus corax</i> | Long-tailed weasel <i>Mustela frenata</i> |
| **Cassin's Finch <i>Carpodacus cassinii</i> | Coyote <i>Canis latrans</i> |
| | Yellow-bellied marmot <i>Marmota flaviventris</i> |
| | ***Belding's ground squirrel <i>Spermophilus beldingi</i> |
| | Golden-mantled ground squirrel <i>Spermophilus lateralis</i> |
| | Yellow-pine chipmunk <i>Tamias amoenus</i> |
| | Lodgepole chipmunk <i>Tamias speciosus</i> |
| | **Douglas' squirrel <i>Tamiasciurus douglasii</i> |
| | Montane vole <i>Microtus montanus</i> |

* Observed removing eggs.

** Observed eating eggs.

*** Observed eating both eggs and nestlings.

not counted except when it eventually resulted in a total loss. For example, there were a few occasions when an egg a day would disappear from a nest until all were gone. We suspected that the predator in these instances was a small rodent, but egg removal by a conspecific could not be ruled out.

We noted in our data base that the predator was "avian" if the nest itself, including the cup, appeared undisturbed or "mammalian" if the nest was knocked down or had its lining strongly indented or torn out. Equivocal cases were noted as unknown. We realize that this terminology cannot be relied on to describe predator type in every case. It is quite possible, for example, that coyotes sometimes removed eggs or nestlings without discernible effects on the nest.

Predation rates per day were calculated according to Mayfield's (1961) technique wherein only the number of days that nests were under observation were taken into account so that nests found at some point after the onset of laying had occurred could also be included in the analysis. Clutch size was assigned once the number of eggs in the nest remained unchanged for two consecutive days.

The data presented in this study were obtained in 1968 to 1970, 1973, 1976, and 1978 to 1991. During these 19 years we collected information on 1,132 *oriantha* nests (mean = 59.6, SD = 19.5, range = 24-92 per year). Due to lapses in investigator efforts, uncontrollable circumstance, or to ongoing field experiments following the initial discovery, there were sometimes insufficient data on a nest to warrant its inclusion in every analysis presented herein.

RESULTS

PREDATOR TYPES

A variety of known and potential predators were observed on the study area at one time or another (Table 1, note: reptiles were absent from the area). Among the birds, California Gulls were present almost daily but they seemed mostly occupied with obtaining fish from streams and lakes or garbage from campers, or simply with traveling. Clark's Nutcrackers live in large numbers among pines that border the study area and frequently venture into meadows occupied by *oriantha*. We observed them robbing an *oriantha* nest only once, however. In that case, the nutcracker flew away with intact eggs one at a time, as though caching, until all had been removed. The same behavior was noted in a Clark's Nutcracker depredating the eggs of a Hermit Thrush (*Catharus guttatus*). In another case, however, we observed a nutcracker while it ate all four nestlings of a Yellow-rumped Warbler (*Dendroica coronata*) while perched on the nest rim. Common Ravens were rarely seen in the early years of the study but have become more numerous in recent years. Other corvids which live within the watershed but which we have not seen in contact with *oriantha* are Steller's Jays (*Cyanocitta stelleri*) and Pinyon Jays (*Gymnorhinus cyanocephalus*). On one occasion we came upon three Cassin's Finches devouring broken eggs that were lying on the ground just outside an *oriantha* nest. These finches were numerous on the area but we do not think that they are usually predaceous on *oriantha*.

Among mammals, Belding's ground squirrels were probably the most important predator.

TABLE 2. Probable causes of nest desertion in *Z. l. oriantha* other than weather.

| Causes | n |
|--|----------|
| Naturally occurring | 21 total |
| Partial loss of clutch | 14 |
| Infanticide | 4 |
| Vole | 2 |
| Cowbird tossed eggs | 1 |
| Investigator induced | 64 total |
| Marking and measuring eggs | 21 |
| Female flushed from nest | 11 |
| Egg implanted with thermocouple | 8 |
| Female held too long in trap | 6 |
| Blind placed too close to nest | 5 |
| Female implanted with hormone | 5 |
| Excessive blood taken from female | 2 |
| Nestlings collared for food collection | 1 |
| Other types of manipulations | 5 |

Many hundreds live on the study area and we observed them consuming *oriantha* eggs on two occasions and nestlings on another, all from nests built on the ground. They also took eggs of other species including those of the Dark-eyed Junco (*Junco hyemalis*), Spotted Sandpiper (*Actitis macularia*) and Mallard (*Anas platyrhynchos*). Additionally, we observed a Douglas' squirrel eating the eggs from an *oriantha* nest located in a pine tree. These were our only direct observations of mammalian predation although there were other episodes that made us feel that coyotes, in particular, might sometimes have had substantial impact (see below). The deer mouse *Peromyscus maniculatus* is present on the study area and has been identified as an egg robber on alpine ground nesters (Verbeek 1970). It was not listed in Table 1 because we never observed evidence of mouse predation, that is the presence of egg fragments in a nest or eggs punctured as though by mouse incisors (Maxson and Oring 1978).

CAUSES OF NEST FAILURE

The focus of this report will be upon predation, the greatest cause of egg and nestling mortality, and to a lesser extent upon desertions and weather effects. Desertion was the cause of mortality in 11.8% of the nests; 75% of the cases of desertion ($n = 85$) in which we were able to assign probable causes were due to investigator impact (Table 2). Although Brown-headed Cowbirds (*Molothrus ater*) seemed in recent years to be more noticeable on the study area, we knew of only one case in which an egg was laid in an

oriantha nest (desertion did not occur although the clutch was later depredated). In a second instance the physical evidence indicated that a bird had stabbed two *oriantha* eggs with its mandibles and dropped them 1 m from the nest leaving the two other eggs of the clutch undisturbed. This pattern of egg removal resembled the behavior of Brown-headed Cowbirds known to parasitize Dusky Flycatcher (*Empidonax oberholseri*) nests at Tioga Pass (M. E. Pereyra, pers. comm.). Since the female at this nest deserted, we attributed it to cowbird activity (Table 2).

Other naturally occurring cases of desertion were attributable to infanticide and to partial loss of a clutch. In three cases of the former, recently hatched nestlings were pecked on the head and neck and left dead in the nest or just outside it. Desertion then occurred even if one or more of the nestlings was still alive. In another case a student, H. L. Tung, was observing a nest from a blind at the time eggs were hatching. An adult *oriantha* of undetermined sex appeared at the nest, quickly killed two of the hatchlings, then flew away with them.

Partial loss of a clutch sometimes occurred such that eggs disappeared from the nest at the rate of one or two per day until two or fewer remained. The female then stopped incubating. These partial clutch reductions were tallied as desertion rather than predation although they may have been the handiwork of small rodents. However, because we sometimes found one or more of the seemingly unscathed eggs nearby, we suspect that not all of these egg removals were by predators and that some could have been by con-

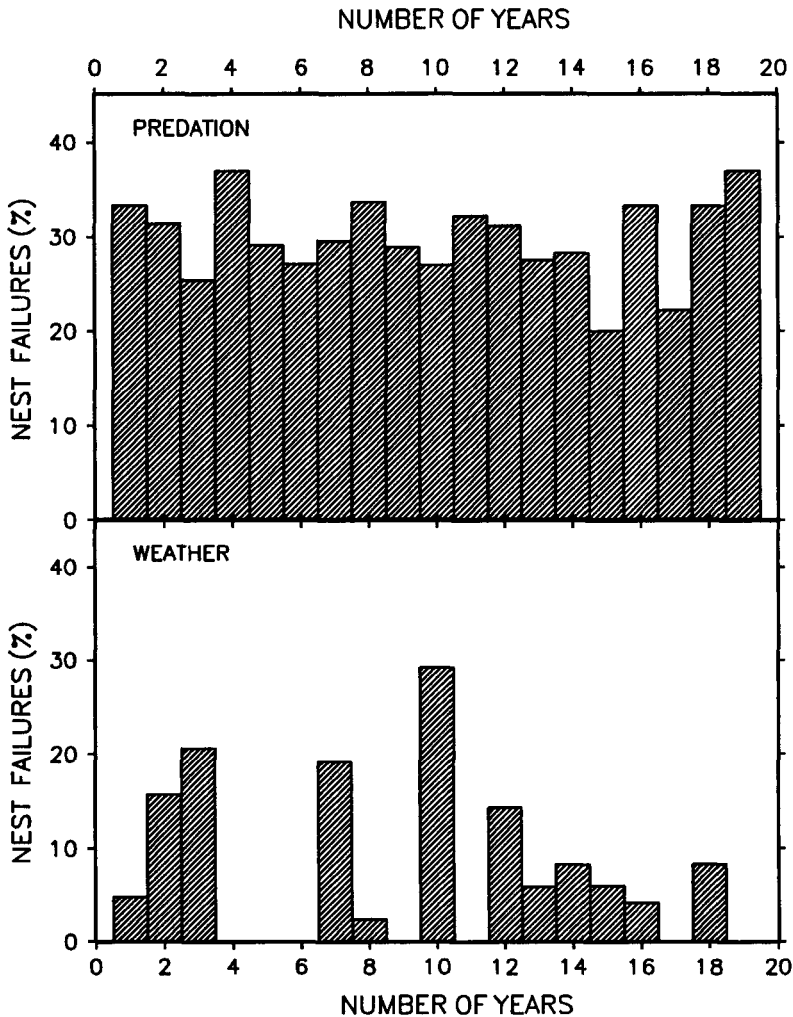


FIGURE 1. Annual rates of nest failure in *Z. l. oriantha* at Tioga Pass due to predation (upper panel) and to weather conditions (lower panel). Data arranged chronologically for 19 years. Total number of nests was 1,132.

specifics. The majority of the nest desertions in this study were associated with various research activities that stressed the attending female to the point where she would no longer return to the nest (Table 2).

ANNUAL PREDATION RATES

The average annual rate of nest predation was 29.9% (SD = 4.5%, $n = 19$), and ranged from 20.0% in 1987 to 37.0% in both 1973 and 1991 (Fig. 1, upper). There was no significant inter-annual variation in the predation rate ($\chi^2 = 9.2$, $P > 0.9$). In contrast, nest mortality due to weather effects (storms) over the same time pe-

riod averaged 7.3% (SD = 8.6%) and were much more stochastic, ranging from 0% in seven different years to 29.2% in 1982 (Fig. 1, lower), an inter-annual variation that was highly significant ($\chi^2 = 125.5$, $P < 0.001$).

DAILY PREDATION RATES

There were 11,416 nest days in this study useful for calculating daily predation rates according to the Mayfield (1961) method. These were divided among periods of laying (1,432 nest days), incubation (6,074 nest days), and with nestlings (3,910 nest days). Predation rates per day were 2.1% during laying, 1.6% during incubation, and

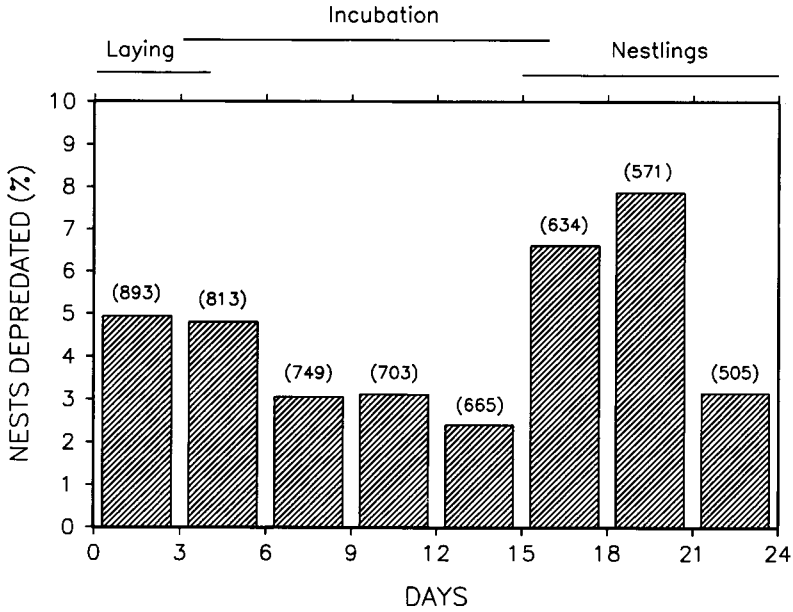


FIGURE 2. Nest predation frequencies in *Z. l. oriantha* at various stages of the nesting cycle. Numerals above bars indicate number of nests involved in each three-day interval. Incubation overlaps with laying and presence of nestlings because onset of full time incubation and of hatching are asynchronous.

2.6% during the nestling period. For the whole nesting cycle combined, the rate was 2.0% per day. Although these rates were not quite significantly different ($\chi^2 = 5.17, P > 0.05$), they suggest that nest predation might not occur uniformly across time. A plot of predation percentage

as a function of stage of the nesting cycle shows this to be the case (Fig. 2). During incubation, predation was highest in the first three-day interval (4.8%) and lowest in the last (2.4%). Females first began a regular pattern of nest attentiveness in the first interval, and this was also

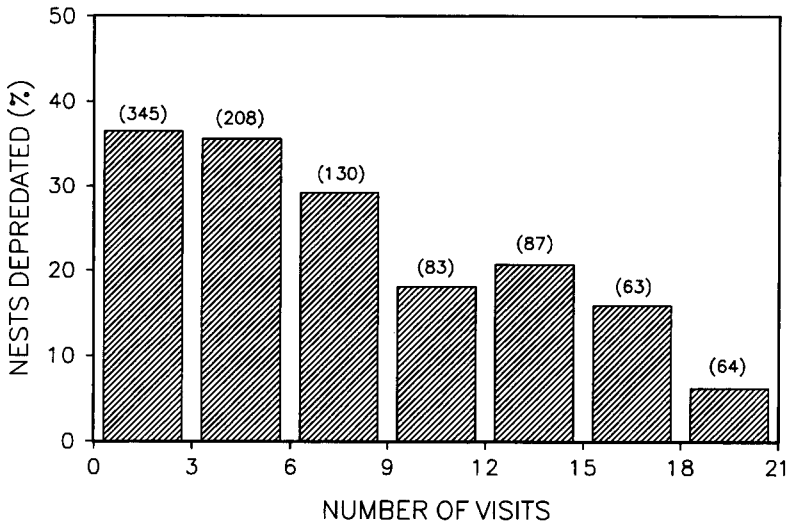


FIGURE 3. Nest predation frequencies in *Z. l. oriantha* in relation to total number of visits by investigators to the nest. Numerals above bars indicate number of nests in each class interval.

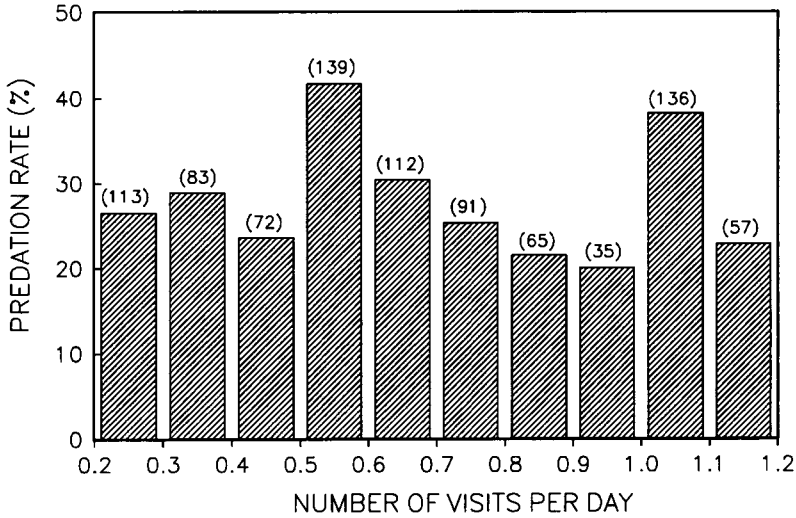


FIGURE 4. Nest predation frequencies in *Z. l. oriantha* in relation to average number of investigator visits per day made to the nest. Numerals above bars indicate number of nests in each class interval.

when we usually measured egg dimensions. In the first three days after hatching predation escalated to 6.6% then to 7.9% in the next interval. Because the number of nests involved in this analysis decreased through time as nests were lost, the total number of nests robbed in a given three-day interval was not as variable as one might expect from Figure 2. For example, 19.1% of all nest losses occurred during days 0–3 (laying) of the cycle and 18.2% during days 15–18 (first appearance of nestlings).

INVESTIGATOR EFFECTS

The degree to which investigator activities affect reproductive success is a matter of considerable concern in studies of nesting birds (Major 1990). In the present study, a female sometimes deserted immediately following our visit to her nest, particularly if the visit occurred during the laying period or early in incubation and when it included on-site activities such as measuring eggs. Were our activities also attracting predators to the nest site? One way to answer this is to examine nest predation rates as a function of total number of investigator visits. This shows that predation frequency decreased as total number of visits increased (Fig. 3). Although this might seem counterintuitive, it probably means that the harder it was for a predator to locate a nest, the longer the nest survived and the more visits we could make to it. When the visitation rate was considered, rather than total number of vis-

its, predation frequency was found to vary significantly ($\chi^2 = 21.8$, $P < 0.01$) but it did not do so in any regular pattern (Fig. 4).

These data do not support the hypothesis that predators cue on nests because of investigator activity. However, over the years we felt considerable apprehension about this mainly because of nest losses that were known to occur within a few hours of a visit, especially when we were weighing nestlings (Mead and Morton 1985). There also is other evidence. For example, in late summer and fall we often utilized a 24-station trapline in order to perform band-and-release studies. On several occasions, tracks left in fresh snow indicated that a coyote had followed us around the trapline. Obviously, the same behavior could have occurred earlier in the season when we were checking nests.

Also, one year during a 10-day period in June when all nests contained only eggs, we experienced an unusually high degree of predation on a portion of the study area. On the east side of a meadow, within an area of about 4 ha, 10 of 13 *oriantha* nests were depredated. In contrast, in an area of about the same size, on the west side of the meadow, roughly 100 to 200 m distant, only 4 of 16 nests were taken during the same time period. These rates were different ($\chi^2 = 7.74$, $P < 0.01$). We were concerned that a coyote that we observed nearly every morning hunting on the east side or a Clark's Nutcracker that could have been observing us from trees that

TABLE 3. Predation rates on nests of *Z. l. oriantha* of known age. *n* = number of nests.

| Age, years | Females | | Males | |
|------------|----------|--------------|----------|--------------|
| | <i>n</i> | % Depredated | <i>n</i> | % Depredated |
| 1 | 342 | 26.0 | 235 | 21.3 |
| 2 | 155 | 20.6 | 156 | 26.9 |
| 3 | 103 | 22.3 | 80 | 22.5 |
| 4 | 31 | 19.4 | 40 | 27.5 |
| 5+ | 22 | 40.9 | 28 | 10.7 |

edged the east side was using our nest visiting activities to find nests. We did not actually observe either animal at a nest, however, and have no proof that a predator was trailing us or associating our presence with that of active nests. It is also possible, of course, that predators were sometimes frightened away from an area or nest, rather than being attracted to it, by the presence of an investigator.

AGE

Is there evidence that *oriantha* might through experience be more effective at hiding or defending their nests from predators? We often knew the specific identity and age of tending adults so it was possible to find out if predation frequencies varied with parental age and presumably experience. At 653 nests we knew the female's age

TABLE 4. Annual variation in nest locations of *Z. l. oriantha* and in snow depths¹ on the Tioga Pass study area.

| Year | Nests | | Snowpack (cm) ¹ |
|------|-------------|----------|----------------------------|
| | % on Ground | <i>n</i> | |
| 1968 | 60.0 | 35 | 114 |
| 1969 | 27.7 | 47 | 342 |
| 1970 | 65.1 | 63 | 176 |
| 1973 | 40.7 | 27 | 204 |
| 1976 | 89.1 | 55 | 79 |
| 1978 | 49.2 | 59 | 263 |
| 1979 | 56.4 | 78 | 227 |
| 1980 | 47.6 | 82 | 263 |
| 1981 | 74.7 | 75 | 173 |
| 1982 | 56.2 | 89 | 294 |
| 1983 | 67.9 | 56 | 376 |
| 1984 | 55.4 | 74 | 205 |
| 1985 | 74.5 | 47 | 146 |
| 1986 | 43.1 | 58 | 243 |
| 1987 | 81.4 | 43 | 113 |
| 1988 | 88.9 | 18 | 121 |
| 1989 | 60.6 | 33 | 158 |
| 1990 | 70.0 | 60 | 91 |
| 1991 | 53.3 | 92 | 167 |

¹ Measured by State of California snow survey crews ca. 1 April.

TABLE 5. Comparisons of nests of *Z. l. oriantha* at Tioga Pass built on the ground or in vegetation above the ground.

| | On ground (%) | Above ground (%) | <i>P</i> |
|--------------------|---------------|------------------|----------|
| Number of nests | 667 (61.1) | 424 (38.9) | <0.001 |
| Fledging success | 317 (47.5) | 204 (48.1) | >0.5 |
| Depredated | 207 (31.0) | 112 (26.4) | >0.1 |
| Avian predator | 117 (56.5) | 75 (67.0) | >0.05 |
| Mammalian predator | 90 (43.5) | 37 (33.0) | >0.05 |

(range = 1–8 years) and at 539 nests we knew the male's age (range = 1–8 years). Predation rates did not vary in a consistent manner with age for either sex (females: $\chi^2 = 5.6$, $P > 0.1$; males: $\chi^2 = 4.6$, $P > 0.1$), and older birds fared no better than yearlings (Table 3).

NEST DEFENSE

We have never known *oriantha* to drive off a predator once it had located a nest. This is not to say that they were ineffective in distracting or harassing potential predators prior to discovery, thereby decreasing predation rates. In the few cases wherein we saw the actual act of predation on eggs, the adults only gave alarm calls or fluttered near the attacker. They were much more aggressive toward a Belding's ground squirrel observed eating nestlings, actually buffeting it with their wings, but the squirrel was undeterred.

NEST PLACEMENT

Nests were often built on the ground in marshy areas that were sometimes so wet that the bottom of a nest, including the interior cup, would be soaked. To us this appeared to be predator-avoidance behavior because ground squirrels, in particular, tended to travel around such areas rather than through them. The overall percentage of nests built on the ground in marshy areas or other locations varied greatly from year to year and was related to snow conditions. In drought years such as 1976 when snowpack was light, *oriantha* built nearly 90% of their nests on the ground, a proportion that decreased considerably in other years when snowpack was greater (Table 4). Regression of the percentage of nests built on the ground on snowpack was significant (data in Table 4; $r^2 = 41.3\%$, $P = 0.003$).

For all years combined 61.1% of the nests were located on the ground and 38.9% were above it in willows or pines, a significant asymmetry in distribution (Table 5). Young were fledged from 47.5% of the ground nests and 48.1% of the above-ground nests, an insignificant difference. Predation rates were 31.0% in ground nests and 26.4% in above-ground nests, again not different (Table 5). Avian predators took a greater number of nests than mammalian predators in both nest types, with the percentage being greatest in above-ground nests (67.0%). Predator type did not quite vary significantly for the two categories of nest placement, however ($\chi^2 = 3.31, P > 0.05$).

SEASON

To detect seasonal variations in predation rates and in nest placements, we combined data from all 19 years of the study. Common calendar dates were not useful because of the large interannual variation in snowpack at Tioga Pass. Snowpack strongly affects vegetation phenology and nesting schedule (Morton 1978, Morton and Allan 1990). Nesting schedule is affected because snows must melt for proper nest sites to become available. Since we recorded snow cover every year, the date of total snow disappearance was used as a common seasonal reference point. The data show that predation was higher in the first group of nests each season (interval 1) than any of the other groups ($\chi^2 = 6.18, P < 0.025$, Table 6) and

TABLE 6. Seasonal changes in nest predation in *Z. l. oriantha*. Data are for dates of clutch initiations combined from 19 years into six intervals. Intervals are defined by number of days prior to date of 0% snow cover, the date when all snow had melted off a large meadow on the study area. Successful nests were those that fledged at least one young.

| Intervals | Number of clutch initiations | Percent depredated | Percent successful | Percent built on ground |
|----------------------|------------------------------|--------------------|--------------------|-------------------------|
| 1. (46 days or more) | 84 | 37.9 | 30.3 | 55.4 |
| 2. (45-36 days) | 201 | 22.7 | 47.2 | 55.8 |
| 3. (35-26 days) | 264 | 31.0 | 50.0 | 60.0 |
| 4. (25-16 days) | 156 | 22.4 | 60.8 | 57.9 |
| 5. (15-6 days) | 186 | 22.6 | 60.6 | 63.2 |
| 6. (6 days or less) | 200 | 26.7 | 57.6 | 63.9 |

that there was a tendency for more nests to be located on the ground as the season progressed ($\chi^2 = 11.8, P < 0.05$, Table 6). There was also a seasonal shift in the substrate utilized for above-ground nests (Fig. 5). Early on, at a time when willows were often unleafed and served poorly to camouflage nests, pines were preferred. Later, as the willows leafed out and developed dense crowns, *oriantha* started building in them and by the end of the season about 87% of all above-ground nests were constructed in willows. This is a significant seasonal change ($\chi^2 = 31.4, P < 0.001$).

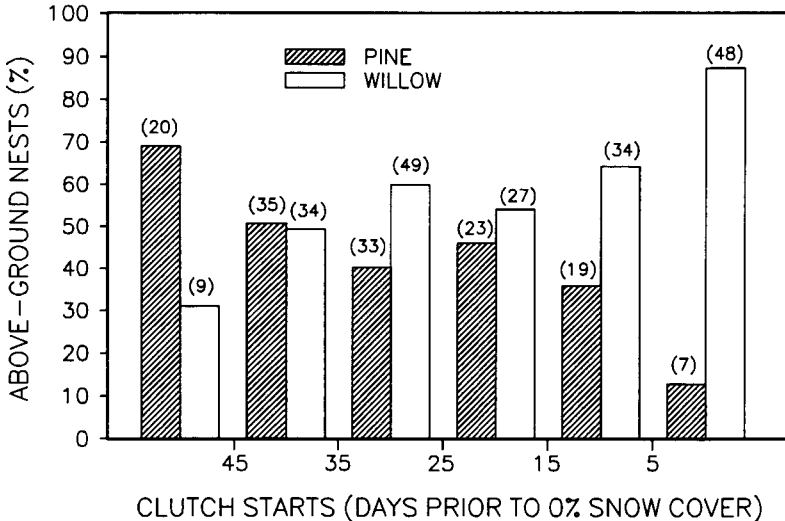


FIGURE 5. Seasonal changes in vegetation used for placement of above-ground nests by *Z. l. oriantha*. Numerals above bars give number of nests. Intervals on abscissa for clutch initiations indicate days prior to 0% snow cover (see Table 6).

CLUTCH SIZE

Females usually laid four eggs but there were enough three- and five-egg clutches for us to see if the dynamics of nest failure were related to clutch size. They were not. Neither success rate nor cause of failure varied significantly with clutch size.

DISCUSSION

The known and suspected nest predators of *oriantha* at Tioga pass include more than twice as many species of mammals as birds (Table 1). The act of predation itself was seldom observed directly but the physical evidence at nests, coupled with our many years of behavioral observations, suggests that the Belding's ground squirrel was the principal predator. This rodent was usually present on the study area at a density of about 5 individuals per ha, excluding juveniles (Sherman and Morton 1984) and this consistency in its population size is probably why there was no significant annual variation in nest predation rate. This contrasts markedly with the stochastic nature of weather effects on nest survival (Fig. 1). An important trait of ground squirrels as predators is that they will take both eggs and nestlings, quite unlike the behavior of snakes, which appeared to specialize on nestlings of sea-level populations of White-crowned Sparrows *Z. l. nuttalli* (Patterson et al. 1980).

Desertion was a large source of nest mortality in this study, mostly due to the presence of investigators at nests during or immediately after the laying period, a time when females were quite prone to desert if disturbed. Investigator activities that induced desertion the most were marking and measuring of eggs, flushing the female accidentally, and implanting eggs with thermocouples (Table 2). Females flushed from eggs or otherwise disturbed when in full incubation or with nestlings rarely deserted. Additional desertions, not included in the present analysis, also occurred when we inadvertently disturbed females at sites where they were building nests or sitting in ones that were fully constructed but still empty. Since most desertions occurred early in the nesting cycle when the female was unintentionally confronted at the nest, it seems reasonable to assume that our presence was the ecological equivalent of nest discovery by a predator. Perhaps the best strategy under these circumstances for producing maximum lifetime num-

bers of offspring is to desert and renest (see Coleman and Gross 1991). We know that *oriantha* readily produce replacement clutches, usually within five to seven days, and as frequently as four or five times in a season if necessary (Morton et al. 1972).

It is difficult to compare with confidence predation rates in this study to those found in other studies because of the investigator activity at our nests which obviously contributed to desertion and perhaps at times to predation frequencies. Nonetheless, the portion of all nest losses due to predation, 59.4%, and the 2.0% daily mortality rate are almost exactly the same as those reported by Ricklefs (1969) from a summary of 50 studies involving 29 species of Temperate Zone land birds with altricial young.

Nest predation rates did not vary with parental age (Table 3), so we assume that the ability to hide nests from predators or to prevent them from raiding the nest did not change with experience. This is not to say that choice of nest sites is unimportant in *oriantha*. Clearly the opposite is true. Microclimatic conditions such as solar radiation levels (Walsberg and King 1978) and direction of prevailing winds (Zerba and Morton 1983a) strongly affect their choice of nest sites. In the present study, it appears that nest sites also may be located so as to minimize predation frequency. There are no control data available and microclimatic factors may complicate analyses, but nests were often built on very wet ground, a practice that is known to deter mammalian predation (Schulze-Hagen 1984). In addition, when data were standardized according to the schedule of snow disappearance, predation rates were highest early in the season before grasses were grown and willows were leafed out (Table 6). As the season progressed females tended to place more of their nests on the ground (Table 6). There was also a substantial shift in the vegetation selected for above-ground nests, from mostly pines early in the season to mostly willows late in the season (Fig. 5). By then the willows were completely leafed out and probably provided a safer, more sheltered environment than previously. The pines, of course, did not show seasonal changes in foliage density. Nest visibility must be coming into play here because elevated nests of *oriantha* at Tioga Pass have more than twice the mass of ground nests (Kern 1984).

Active attacks of *oriantha* on predators that were robbing nests seemed to be an ineffective strategy although our data on this are meager. They exhibit other behaviors, however, that may have antipredator value. For example, females often slip off the nest very quietly and inconspicuously when approached. Those on above-ground nests do not fly, rather they hop into surrounding vegetation or drop straight to the ground before running. Those leaving ground nests when surprised often perform an apparent distraction display wherein they lift and slowly wag their tail while running away. This may mimic a running rodent and thus serve to divert predators such as coyotes from the nest (Miller 1951). Incubating females alternate bouts of incubation and foraging during the daylight hours that are approximately 20 min and 8 min duration, respectively (Zerba and Morton 1983b). They return from foraging by flying to the vicinity of the nest but almost always travel the last few meters discretely and on foot. They do likewise, and so does the male, when feeding nestlings. Neither parent will take food into the nest when a predator is nearby. In addition, when we handled older, protesting nestlings, the adults usually came in immediately to close range and performed distraction displays wherein they fluttered erratically, sometimes with fanned, lowered wings.

Did cues emanating from nests or investigator activities influence predation rates? The answers are probably yes to both questions. Certainly nest predation increased sharply after hatching (Fig. 2), presumably because of increased noise, odors, and activity levels associated with presence and rearing of nestlings. Investigator effects are not so easy to deduce. Based on total number of visits to nests or upon rate of visits, there was no influence detected (Figs. 3, 4). However, coyotes were known to follow an investigator at times and in one instance may have been responsible for a spate of nest losses. Such episodes, if rare, can easily become submerged in a large body of data and never be apparent statistically. Also, in an earlier analysis of predation rates on *oriantha*, we found that daily predation rates on nestlings nearly tripled during times when nests were visited frequently in order to weigh nestlings and obtain their growth rates (Mead and Morton 1985). In summary, our activities appeared to enhance nest predation in some situations. These

results are intermediate between those obtained in other studies which ranged from no differences in survival rates between visited and unvisited nests (Willis 1973, Nilsson et al. 1985, Martin and Roper 1988) to definitely lower survival rates in visited or disturbed nests (Westmoreland and Best 1985, Major 1990). Obviously no two studies are conducted identically and investigator influences must vary with the work schedule and methods employed. The potential for obtaining misleading or misinterpreted results is great because these variations in techniques could cause alterations of parental nest defense behaviors and subsequent predation rates (Knight and Temple 1986). In any event, correlational studies provide a relatively weak approach to questions regarding predator-investigator interactions and definitive answers are more likely to come from carefully controlled, experimental techniques (Göttmark 1992).

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