ABSTRACT

The reproductive biology of a migratory passerine, the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) was studied for 25 summers in the Sierra Nevada of California at Tioga Pass. Data were obtained on individuals of known age and sex from time of arrival at subalpine breeding meadows to departure for wintering areas in Mexico about four months later. During the summer season many aspects of the reproductive cycle were examined. These included the social system, nesting habits, seasonal and lifetime reproductive success, gonadal development and hormone secretion rate, energy balance as measured by fluctuations in body mass and fat and by doubly-labeled water, molt, and migration departure schedules. Developmental changes in nestlings, along with their survival and dispersal were also investigated. The cardiovascular and respiratory systems of birds pre-adapt them for living at high altitude but achieving reproductive success in montane settings requires adjustments to unusual environmental conditions such as increased solar heating, low nocturnal temperatures, sudden intense storms, and large interannual variations in residual snowpack. Emphasis was placed, therefore, not only on the key features of migration and reproductive biology probably found in all passerine migrants, but also on how these were affected or altered in response to environmental variation. Special attention was paid to underlying physiological mechanisms and this approach, along with the unusual location, helps to distinguish this long-term field study from others.

Both sexes tended to return to previously occupied areas although site fidelity was greater in males than in females and mate switching between years occurred in 34.1% of returning pairs. Modal number of mates per lifetime was one and the maximum was six. Pairing usually occurred soon after arrival on the study area but it could be delayed by several weeks in years of deep snowpack. Although females were guarded by their mates, at least one-third of the nestlings were the product of extra-pair fertilizations. Females were aggressive and female-female conflicts sometimes delayed settling by one-year-olds, which were then often shunted to less desirable territories. Polygyny occurred in 3.5% of males, and the number of fledglings produced from their nests increased from 3.1 to 5.5 per season. Fitness in females was unaffected by engagement in polygynous matings.

Median time of survival, once one year of age was attained, was 1.9 years for both sexes and survival rate of adults was about 50% per year. This was not different from survival rates found in a sedentary conspecific (*Z. l. nuttalli*) so migration itself does not appear to induce extra mortality in White-crowned Sparrows.

Males arrived at breeding areas with partially developed testes, which continued to enlarge for about one month, no matter the environmental conditions. Plasma testosterone levels were high throughout this period although testis size and testosterone concentrations were greater in older adult males (age 2+ years) than in one-year-olds. Females of all ages, on the other hand, arrived with only slightly enlarged ovaries, which remained in this condition until shortly before nesting began. This could be a month or more in heavy snow years when nesting sites were covered and unavailable. If nesting sites were provided to such delayed females by avalanche-deposited trees or by investigators, however, they built nests and ovulated within four days. Thus, availability of nesting sites was shown at times to exert proximate control over the reproductive schedule.

Body mass varied greatly in females during the nesting cycle. They gained quickly in the three days preceding their first ovulation then lost during laying and, slowly, during incubation. During the day or so that it took for a brood to hatch females lost about 8% of their body mass. It was hypothesized that this occurred because females were spending maximum time on the nest, even at the expense of self maintenance, in order to minimize hatching asynchrony.

Eggs were laid at dawn at 24-hour intervals and did not vary in size with clutch size or female age. No consistent pattern with laying order was discovered although last-laid eggs were most frequently the largest. Egg size seemed to be affected by prevailing ecological conditions and it varied interannually in individuals and in the population. Clutch size decreased steadily with calendar date despite large interannual variations in habitat conditions, including vegetation development. This response was likely due to a photo-

periodically controlled down-regulation in ovarian function as females progressed gradually toward the condition of complete photorefractoriness.

Hatching asynchrony was considered at length and was suggested to be the by-product of a mechanism that has evolved to turn off a physiological phase of reproduction (ovulation) while simultaneously turning on a behavioral one (full-time incubation). A model of this response, the "hormonal hypothesis," is presented.

Nestlings grew rapidly (with more feedings being provided by the female parent than the male), reached thermal independence by Day 7 of age, and fledged on Day 9. Logarithmic growth rate constants, obtained during the first four days after hatching, increased with hatching order and with brood size. The hatching order effect was attributed to brooding behavior by females; they tended to sit tightly until all eggs had hatched, and as a result first-hatched chicks were not maximally provisioned. Small broods (one or two chicks) tended to be produced at the end of the season when arthropod food supplies were probably dwindling and large broods (5 chicks) only when unusually favorable trophic conditions existed; in most cases (87%) brood size was three or four chicks.

More than half of the nests (53%) failed to fledge young. About 30% of nests were consistently lost to predators, the remainder to investigator impacts and to storms. Despite the stochasticity of storm occurrence and severity, and even in the face of multiple nesting failures, reproductive output was maintained because of vigorous renesting efforts.

Individuals were known to be engaged in reproduction at up to nine years of age and the number of fledglings produced per season did not vary with age (experience) or sex. Mean lifetime reproductive success was not different for the sexes, being 8.14 fledglings for males (range = 0–26) and 7.10 fledglings for females (range = 0–23). These lifetime numbers are relatively high for passerines and indicate that *Z. l. oriantha* is well suited for reproducing in montane environments.

Postnuptial or prebasic molt lasted for about seven weeks in individuals and began about five days earlier and lasted about three days longer in males than in females. Data from females showed clearly that molt did not begin until they had become photorefractory; they never laid eggs once molt was under way. Still, molting overlapped with the period of parental care in more than 70% of adults of both sexes.

Premigratory fattening required about nine days in both juveniles and adults and the shift in weight-regulation set point (induction of hyperphagia) was found to occur within the span of a single day. Fattening began as molt ended although the two events were not coupled physiologically. On average, juveniles left on migration three days earlier than adults.

In addition to providing a large data base on life history parameters and reproductive physiology, this study revealed a variety of responses that promoted survival and reproductive success in conditions encountered at high altitude. These conditions and the responses to them were: *(1) Deep snowpack.* In heavy snow years *oriantha* terminated migration at the appropriate latitude but tended to stage in foothill areas in Great Basin shrubsteppe rather than ascend to the breeding habitat. Because of this, arrival at the subalpine was sometime delayed by days or weeks. Once settled on the breeding area they exploited an array of foraging niches, including the snow surface itself, and they were euryphagic. If energy balance could not be maintained they flew back down to the staging areas, as shown by radio tracking, and remained there, usually for several days before ascending again. This sequence of movements was repeated several times if necessary. Females compensated somewhat for delays in nesting imposed by late-lying snow by altering their choice of nest sites. Rather than wait for completely thawed locations on the ground they built in the tops of short, shrubby pines and even in the branches of unleafed willows. During the wait for nest sites to appear (which could be as much as two months) testicular growth was completed. In contrast, and probably to save energy, ovaries remained small but on the brink of development during this time. *(2) Storms.* Early in the season, before clutches were started, *oriantha* often responded to storms by moving to lower altitudes. However, if snow cover had diminished and clutches were being produced, females tended not to move; rather, they remained and defended their nests. If a nest was lost to weather, or to any other factor, renesting was initiated at once and usually took only five days even though the complete sequence of courtship behaviors was repeated. Temporal efficiency

of this response was abetted by pair-bond and territory retention and as many as five nesting attempts per season were known to occur. *(3) Solar heating.* Females protected eggs and nestlings from solar radiation by shading them with their bodies. Uncovered nestlings, even on the day of hatching, were capable of panting and neonatal down may also have acted as a parasol. *(4) Cold nights and thermolytic winds.* Early in the season, before nesting had begun, *oriantha* roosted on the periphery of meadows in lodgepole pines and pairs were sometimes located in the same tree. Presumably trees provided more favorable microclimates than undeveloped meadow vegetation. Nests were often placed on the lee side of shrubbery and those built above the ground had thicker floors and more densely woven, wind-resistant walls than those built on the ground. Body temperature of incubating females, as shown by egg temperature, drifted down as air temperature decreased, especially in above-ground nests. At the coldest air temperatures this trend was reversed, presumably by shivering. *(5) Rapid onset of winter conditions.* In order to prolong breeding without risking exposure to seasonally deteriorating weather conditions while still allowing time for molting and premigratory fattening, *oriantha* adults saved time by molting while still engaged in parental care. And juveniles from late nests compensated by molting at a relatively early age.

Because many individuals were handled soon after their arrival on the study area, as well as just prior to departure some four months later, it was possible to discover characteristics of physiology and behavior associated with migration itself. These involved the following: *(1) Migration schedule.* Males tended to arrive before females and older birds before yearlings. Since a higher percentage of older males were known to breed, it was suggested that early male arrival is important to territory acquisition and retention. As a group, juveniles tended to leave on fall migration ahead of adults so their primary directional tendencies must be genetic rather than learned. Although White-crowned Sparrows gather into flocks on winter areas, the arrival and departure data from *oriantha* indicate that migration occurs independently or, at most, in small flocks. *(2) Hyperphagia.* Only the very earliest of arriving birds, adult males all, still had fat deposits. Furthermore, autumnal premigratory fattening occurred quickly and obese birds left immediately. This suggests that presence of large fat stores may activate migration behavior and that the altered metabolic states associated with fueling migration, namely hyperphagia and its energy storage correlates, are regulated to match rather precisely the period of migration. Hyperphagia was also exhibited by stopover migrants (*Z. l. gambelii*). *(3) Hematocrit.* Contrary to initial expectations, packed blood cell volume or hematocrit was high in newly arrived birds then decreased during the summer while they were in residence; it increased again in those preparing to depart in the fall. Increased hemopoietic activity appears to be another feature of migration physiology.

It appears that environmental adaptation in migratory passerines occurs mainly through flexibility in their behavior and physiology and that sometimes these responses can involve trade-offs in energy costs and in survival.

Key Words: clutch size, dispersal, hatching asynchrony, high altitude, migration, molt, reproductive success, snow conditions, White-crowned Sparrows, *Zonotrichia leucophrys.*