PREFACE

This monograph describes a long-term study of the reproductive biology of a migratory sparrow at one of its high altitude breeding areas in the Sierra Nevada Mountains of California. The study's inception is probably best marked by a June afternoon in 1968 when our field crew arrived at Tioga Pass for the first time. There were four of us in that initial group, three Occidental College undergraduates, Judy Horstmann, Janet Osborn, and David Welton, and myself, at that time a young Assistant Professor. Guided by Dick Banks' recently published doctoral dissertation on geographic variation in White-crowned Sparrows (*Zonotrichia leucophrys*), we had been searching the Sierra for a potential study site. We wanted a location that was accessible and that held a robust population of the subspecies designated as the Mountain White-crowned Sparrow (*Z. l. oriantha*). Being a careful scientist, Banks had scrupulously listed the collection sites for the museum specimens he had been studying. We reasoned that those areas that had yielded the most specimens would likely have the largest populations. But this strategy had not been working out. Kaiser Pass, on the western slope, for example, was well-represented in museums, but in an extensive search of the area, only one pair of white-crowns was located. I suspected that over-grazing by cattle had altered the habitat so much in the intervening years that it had become unsuitable for our birds, but the students had another hypothesis. They kept suggesting, sometimes rather slyly I thought, that the museum collectors had simply shot them all! Now, however, as we drew near Tioga Pass, excited murmurs rose from within the vehicle. Large expanses of subalpine meadows, just emerging from beneath the melting snowpack, were coming into view. Here was undisturbed habitat of the type we were looking for and lots of it. As soon as we pulled over and stepped out, White-crowned Sparrows, with their distinctive black-and-white striped heads, could be seen and heard all around us. We fanned out across a meadow, peering into and beneath the leafing-out willows. Almost immediately, Jan discovered a nest. By the end of the afternoon a total of 12 had been located, all of them either fully constructed and ready for laying or already with one or more eggs.

In the following days and weeks we continued to find nests and began to capture and band the breeding adults. The surrounding countryside was explored on foot as well as other areas within easy driving range such as Lundy Canyon, Virginia Lakes, and Sonora Pass. Gradually it became clear that the meadows near Tioga Lake and along upper Lee Vining Creek, when linked together, would make a fine study area. So, after obtaining permission from the U. S. Forest Service, we settled into a nearby campground and began to study the reproductive biology of Mountain White-crowned Sparrows in earnest.

There were many motivations behind this decision: the need to establish a research project that would generate the enthusiasm and participation of undergraduate students, getting my children out of Los Angeles for the summer, being able to live in a beautiful outdoor setting, but mostly this direction was chosen because I was sure it would be interesting and productive. As a research assistant for my Master's thesis adviser, L. R. Mewaldt, I had learned a great deal about conducting field studies and about the habitat preferences of White-crowned Sparrows and their allies. Later, again as a research assistant, this time for my doctoral dissertation adviser, D. S. Farner, I spent a summer in Alaska doing field work which included collecting, dissecting, and fixing sparrow brains for neurosecretion studies. Several publications came from that one summer of work, but the enduring message for me from the Alaskan experience was that very few good field studies had been done in North America on the reproductive biology of migrants, and practically nothing at all on their migration schedules, mating systems, molt, or premigratory fattening responses. The biology of juveniles, particularly after fledging, was also poorly understood. In fact, this whole area of avian biology, of passerine migrants on their summering grounds, especially in locations where large variations in environmental conditions occurred, seemed open to investigation and I was stimulated to pursue it. The initial plan was to spend three summers at Tioga Pass, but the area proved to be so interesting that this eventually was stretched to three decades, and came to include studies of Belding's ground squirrels (*Spermophilus beldingi*) and Yosemite toads (*Bufo canorus*), as well as White-crowned Sparrows.

Exceptional progress in our understanding of avian biology occurred during the second half of the 20th century. Among the numerous reasons for this was the development of new techniques, many of them adapted from molecular biology, new theory, and increased computational and statistical powers. This growth in knowledge was also aided by an increase in the number of scientists willing to devote themselves for prolonged periods to the investigation of a single population or species under natural conditions, in other words, to engage in long-term field studies. For practical reasons, including investigator interest and availability of study areas, these have often centered on the reproductive biology and behavior (social systems, especially) of passerines. Some prominent examples would be those conducted on Florida Scrub-jays (*Aphelocoma coerulescens*; Woolfenden and Fitzpatrick 1984), Pinyon Jays (*Gymnorhinus cyanocephalus*; Marzluff and Balda 1992), Black-capped Chickadees (*Poecile atricapillus*; Smith 1991), European tits (*Parus* spp; Perrins 1979), Northern Wheatears (*Oenanthe oenanthe*; Conder 1989), Dunnocks (*Prunella modularis*; Davies 1992), Meadow Pipits (*Anthus pratensis*; Hötker 1989), Prairie Warblers (*Dendroica discolor*; Nolan 1978), Indigo Buntings (*Passerina cyanea*; Payne 1989), Song Sparrows (*Melospiza melodia*; Nice 1937, Hochachka et al. 1989), and Red-winged Blackbirds (*Agelaius phoeniceus*; Orians 1980, Searcy and Yasukawa 1995).

Long-term studies have contributed new information to a broad spectrum of ideas and hypotheses, but most, by necessity, have been limited in scope. And often they have had a similar approach, one that has combined and applied principles of ecology, evolution, and behavior through multiple annual cycles or seasons. In so doing investigators, like those cited above, have advanced avian biology and they have also helped to form and stimulate the sub-discipline of behavioral ecology.

This study shares characteristics with theirs and many others in that it has involved the accumulation of natural history and life history data (age and size at maturity, longevity, number, size, and sex ratio of offspring, etc.; Stearns 1992). Its focus is different, however, in that it tends to emphasize physiology more than behavior or ecology.

Avian physiology has traditionally been studied mostly in the laboratory, often with domesticated species. A significant component, however, especially with regard to photoperiodic, metabolic, and endocrine responses, has involved wild birds, mainly passerines. And recent technological advances utilizing radioisotopes and miniaturization of transmitters, for example, have allowed expansion of this work on physiological principles in field situations.

A major strength of long-term field studies is that they invariably reveal a great deal about the natural histories of organisms, and through the aid of permanent markers, such as numbered leg bands, these histories can sometimes span the lifetimes of individuals. More than 400 years ago, dating at least to Francis Bacon, it was already understood that natural history was the base upon which other scientific disciplines were built. Not so quickly grasped, however, was just how difficult it can be to obtain reliable, interpretable data of this type. They may, for example, vary with time, with characteristics of individuals, such as sex and age, with weather, and with trophic conditions, and this multitude of variables can act individually or in concert. Thus, natural history data often seem imprecise, unreliable, and non-replicable. Yet they can instruct us about the realities of the organism's life (of great importance to understanding ecosystem function and to conservation efforts) and fulfill one of the necessities of good science—the development of the right questions (Evans 1985). Such questions and the investigations and theory they inspire, when addressed to naturally oscillating systems, can contribute heavily toward achievement of one of modern biology's primary goals—translation of the real world into mathematical models (Rand 1973, Schaffer 1974). Another strength of field studies is that they inevitably assess phenotypes, the physical manifestations of genetic systems interacting with the environment. Phenotypes are the targets of selection and they are crucial to understanding its focus and process (Dean 1998).

In the minds of some ecologists, long-term studies are rarely well planned from the outset and have inescapable problems because their interpretations and conclusions are often based on correlations (Dunnet 1991). Most recognize their value to population and community ecology, however (Krebs 1991), and the data sets have considerable intrinsic value when it comes to understanding the frequency, duration, and amplitude of natural variations in ecological systems (Dunnet 1991). This approach to science can be cast as being in conflict with the experimental or hypothetico-deductive method (Taylor 1989), but actually the two are complementary. Furthermore, experiments are an inevitable and valuable part of long-term studies. These can be ones designed to work under field conditions, but there are also natural experiments that occur because of large fluctuations in environmental conditions. The latter are individually unrepeatable, of course, but they can add significant new dimensions to the research. Choice of study site is important here because some locations are more naturally endowed than others with environmental gradients or variation. As one ascends to the tops of mountains or toward polar regions, for example, environmental variation increases. Thus, high altitude and high latitude locations are ideal for studies of environmental adaptation.