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CHAPTER 1: Introduction

THE *ZONOTRICHIA*

The genus *Zonotrichia* contains five species: *Z. capensis,* the Rufous-collared Sparrow; *Z. albicollis,* the White-throated Sparrow; *Z. querula,* the Harris's Sparrow; *Z. leucophrys,* the White-crowned Sparrow; and *Z. atricapilla,* the Golden-crowned Sparrow (American Ornithologists' Union 1998). Members of the genus can be found almost anywhere in the Americas, from the subarctic slopes of Canada and Alaska in the north to Cape Horn in the south. *Zonotrichia capensis,* which has multiple subspecies, occurs from the highlands of Middle America southward through much of South America and may well be the most widely distributed bird of that part of the world (Johnson 1967). The other four species live solely in North America and all five have at least some populations that are migratory. From data on allozymes, morphometrics, and mitochondrial DNA profiles, Zink (1982) and Zink et al. (1991) concluded that speciation within the *Zonotrichia* probably occurred in the Pleistocene, but before 140,000 yr ago. The oldest living member appears to be *Z. capensis,* and since it resides at low latitudes the genus may have originated in the Neotropics.

Information on the four North American species has now been compiled for *The Birds of North America* series and it is apparent that many features are shared by the group. For example, they prefer wintering habitat (most of which occurs in the U.S.) that includes elements of thick, shrubby cover mixed with open ground. Thus, they are likely to be found in weed patches, hedgerows, brushy ravines, and along the edges of forests and cultivated fields. Breeding takes place mostly in Canada and Alaska and, again, the preferred habitat often contains shrubby, patchily distributed vegetation. Forest openings, parklands, meadows, and tree clumps near tree line are used by *Z. albicollis* (Falls and Kopachena 1994); birch-willow shrublands and wet sedge meadows by *Z. querula* (Norment and Shackleton 1993); boreal forest, tundra, alpine meadows, and coastal scrub by *Z. leucophrys* (Chilton et al. 1995); and shrubby tundra at or above tree line by *Z. atricapilla* (Norment et al. 1998). All of these species tend to be omnivorous, eating seeds, fruits, buds, flowers, grass, and terrestrial arthropods, the latter being the major food source for dependent young.

The *Zonotrichia,* especially *Z. albicollis* and *Z. leucophrys,* have been widely used in both laboratory and field investigations of avian biology due, in part, to their abundance and ease of maintenance in captivity. Because the present study was based on a population of *Z. leucophrys,* an expanded discussion of their characteristics follows.

White-crowned Sparrows

Zonotrichia leucophrys are said to be sexually monomorphic although females are slightly smaller than males and as adults their head markings are usually not as bold. The plumage of adults has the same appearance year around and its most distinctive feature is a black- and white-striped head; a pair of black stripes in the crown is separated by a white median stripe and bordered by white eyebrow or superciliary stripes. In juveniles that have completed the postjuvenal (first prebasic) molt the head stripes are brown instead of black and buffy instead of white.

Like *Z. capensis,* this is a polytypic species with five generally recognized
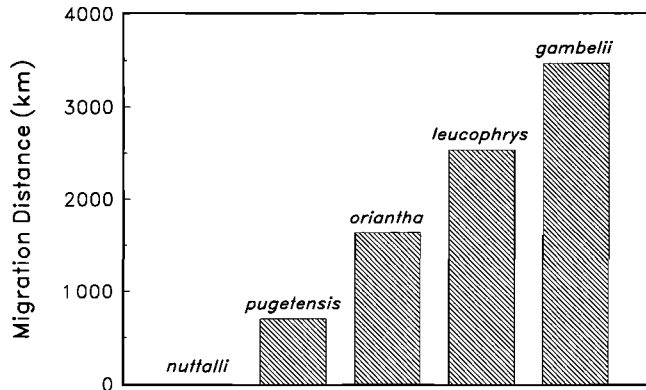
FIGURE 1.1. Approximate migration distances of subspecies of *Zonotrichia leucophrys*, as measured from the middle of summer and winter ranges (*Z. l. nuttalli* is nonmigratory).

subspecies that are fairly distinct in their distributions, including very little overlap of breeding areas. These are *Z. l. leucophrys, Z. l. oriantha, Z. l. gambelii, Z. l. pugetensis,* and *Z. l. nuttalli.* Only *nuttalli* is sedentary; the others are migratory with *pugetensis* being the weakest and *gambelii* the strongest migrant (Fig. 1.1). Both summer and winter ranges of all five subspecies are confined to the North American continent and their distributions have been carefully mapped (Chilton et al. 1995, Dunn et al. 1995). Dunn et al. (1995) have also described in detail the nuances of morphology that distinguish the subspecies and have included high-quality photographs and drawings of both adults and juveniles.

The subspecies can be separated using morphological traits such as length of tarsus, bill, wing and tail; color of the back, rump and bend of the wing; and extent of the white superciliary stripe. This stripe extends to the bill, including the lores, in *nuttalli, pugetensis,* and *gambelii,* but is interrupted by black lores at the anterior corner of the eye in *leucophrys* and *oriantha.* In areas where white- and black-lored forms are sympatric, intermediates are common (Banks 1964, Lein and Corbin 1990). Banks (1964) felt that the two black-lored forms should be merged into one subspecies but Godfrey (1965) did not agree. He described differences in coloration of ventral parts (breast, flanks, and undertail coverts) in the two that seemed to warrant their continued separation. For the purposes of this treatise, *oriantha* will be considered distinct from the nominate form.

Although *leucophrys* and *oriantha,* the two red-backed, black-lored subspecies, can be difficult to distinguish in the museum tray, their breeding ranges are separated by more than 1,500 km of unsuitable habitat (Cortopassi and Mewaldt 1965). It is possible, however, that the two may mingle on wintering areas in northeastern Mexico (Friedmann et al. 1950).

Rand (1948) speculated that subspeciation occurred in White-crowned Sparrows when their range was invaded by glaciers during the Pleistocene. He suggested that four populations survived in refugia, one in the southeast (*leucophrys*), one in the Yukon-Bering Sea area (*gambelii*), one in the Rocky Mountains (*oriantha*), and another along the Pacific Coast (*nuttalli-pugetensis*). Post-Pleistocene range expansion from these refugia then led to secondary contact between *oriantha* and *gambelii* in southwestern Alberta, an area where considerable genetic

introgression, detectable in both song and plumage phenotypes, has occurred (Lein and Corbin 1990). Recent data on rates of evolution in mitochondrial DNA in 35 species of North American passerines has thrown into doubt many of these old ideas about fragmentation of ancestral species into refugia by glacial advances (Klicka and Zink 1997). If the molecular clock used by these investigators is correct, then a great many of these species originated much earlier than the late Pleistocene.

The Pacific coastal complex of White-crowned Sparrows consists of a linear series of populations, often residing no more than a few hundred meters from the beach, that extends on its south-north axis some 1900 km from California to British Columbia. The southern-most breeding populations are *nuttalli* and these intergrade to the north with those of *pugetensis,* the latter being largely migratory (Grinnell 1928; Blanchard 1941, 1942; Mewaldt et al. 1968, Mewaldt and King 1978, DeWolfe and Baptista 1995). *Gambelii,* the most widely distributed of the subspecies, breeds from the Cascade Mountains near the northern border of Washington to above the Arctic Circle in Canada and Alaska (Farner 1958a, Banks 1964). *Leucophrys* breeds in eastern subarctic Canada, primarily in Manitoba, Ontario, and Quebec (Dunn et al. 1995). The various subspecies tend to winter between 20° and 45° N latitude with *leucophrys* being restricted mostly to the eastern half of the U.S. and the other groups to the western half as well as Mexico. Wintering *gambelii* occur in many of the western states of the U.S. as well as several of those in northern Mexico, including Baja California. About 0.3% of the individuals in wintering *gambelii* flocks sampled in Kern County, California were actually *oriantha* (Hardy et al. 1965).

The Mountain White-crowned Sparrow

The specific population investigated by us belongs to that subspecies designated as *Z. l. oriantha,* the Mountain White-crowned Sparrow. It breeds in montane regions of the western U.S., primarily along two major axes, one being formed by the Rocky Mountains to the east and the other by the Sierra Nevada and southern Cascades to the west. The Great Basin lies between these cordilleras and within it there are small, isolated mountain ranges that also harbor breeding *oriantha.* The northern limits of their distribution in the Rocky Mountains extends slightly into southern British Columbia, Alberta, and Saskatchewan, and the most northerly of the Sierra Nevadan populations is succeeded by populations still further to the north in the Cascades of Oregon.

Subalpine meadows at elevations of 2,500 to 3,500 m are selected most often as nesting habitat in both the Sierra Nevada (Morton et al. 1972a) and Rocky Mountains (Hubbard 1978). Sometimes alpine tundra is utilized, such as at Independence Pass in Colorado (3,680 m) and Beartooth Pass in Montana (3,350 m). Hubbard (1978) has shown that tree islands (krummholz) supply important protection for *oriantha* that nest in the alpine. They are known to nest at considerably lower elevations than this, however, especially at the highest latitudes of their summer range: for example, 1,500 m in northern Montana (King and Mewaldt 1987), and even down to 800 m in southern Saskatchewan (Banks 1964). Breeding populations are often disjunct and can be separated at times by hundreds of kilometers, as in the northern Great Plains of Montana where they are a component of insular montane avifaunas (Thompson 1978, Lein 1979). Inter-popu-

lational gene flow has not been studied in *oriantha,* but it seems possible that they function as a metapopulation over at least some of their range.

In an 800-km transect of habitat occupied by territorial or breeding *oriantha* in the Sierra Nevada and Cascade ranges, DeWolfe and DeWolfe (1962) concluded that five habitat components were common to all areas containing nesting birds: grassland, bare ground, shrubbery, fresh water, and tall conifers. Although lush subalpine meadows are often preferred sites for reproduction, a population of more than 40 pairs did occur at one time at 1,830 to 1,890 m on Hart Mountain in southeastern Oregon near a small riparian area in a generally arid landscape dominated by aspen (*Populus tremuloides*) and big sagebrush (*Artemesia tridentata*; King et al. 1976, King and Mewaldt 1987). Summering *oriantha* are also abundant in sagebrush flats of the Warner Mountains of northeastern California (T. Hahn, pers. comm.). Based on personal travels to many montane settings containing reproductively-active *oriantha,* I would add to the description of DeWolfe and DeWolfe (1962) that although water is always present at breeding areas, its forms can vary from thin sheets of snowmelt to permanent bodies such as streams and lakes, alone or in combination. Furthermore, tall conifers are sometimes absent, but it seems highly important for shrubbery to be present and that at least some elements of it be dense and low to the ground. Tall willows, for example, can sometimes be sufficient, but not when their lower branches have been heavily browsed by ungulates.

During their survey, DeWolfe and DeWolfe (1962) found that meadows suitable for *oriantha* were usually patchily distributed and sometimes so small that they contained only one to a few breeding pairs. We found the same thing a decade later while doing a 500-km transect confined to the Sierra Nevada and undertaken for the purpose of recording *oriantha* songs. Eight or fewer males were found at nine of the 14 sites sampled (Orejuela and Morton 1975). In the high country near Tioga Pass there are many small, wet meadows scattered near tree line, often in association with cirques or tarns, that hold breeding pairs, but not in every year. This intermittent use of small pieces of habitat may represent a microcosm of what can happen on a much larger scale, even at the massif or mountain range level. For example, King and Mewaldt (1987) documented the demise of the population at Hart Mountain whereas Balda et al. (1970) discovered the establishment of another in the San Francisco Mountains of Arizona. Local extinctions and colonizations would seem to be a normal part of *oriantha* biology, a trait that is typical of insular populations in general (King and Mewaldt 1987).

Friedmann et al. (1950) considered the primary wintertime distribution of *oriantha* to be from southern areas of California, Arizona, New Mexico, and southwestern Texas, throughout Baja California, and down to latitude 20° N in mainland Mexico (Fig. 1.2). Much of their information on wintering birds was probably obtained from collections made by Chester C. Lamb in the 1930s and 1940s. Twenty-seven of Lamb's specimens are deposited in the Moore Laboratory of Zoology at Occidental College. Five individuals were taken at or near sea level in Sinaloa, and the other 22 (from eight additional states) at elevations between 1,000 and 2,000 m. In December 1993 Maria E. Pereyra and I attempted to revisit many of Lamb's original collecting sites in mainland Mexico, but saw no *oriantha,* nor even very much of what could be considered suitable habitat. Nearly everything had been overgrazed by domestic livestock or placed under tillage.
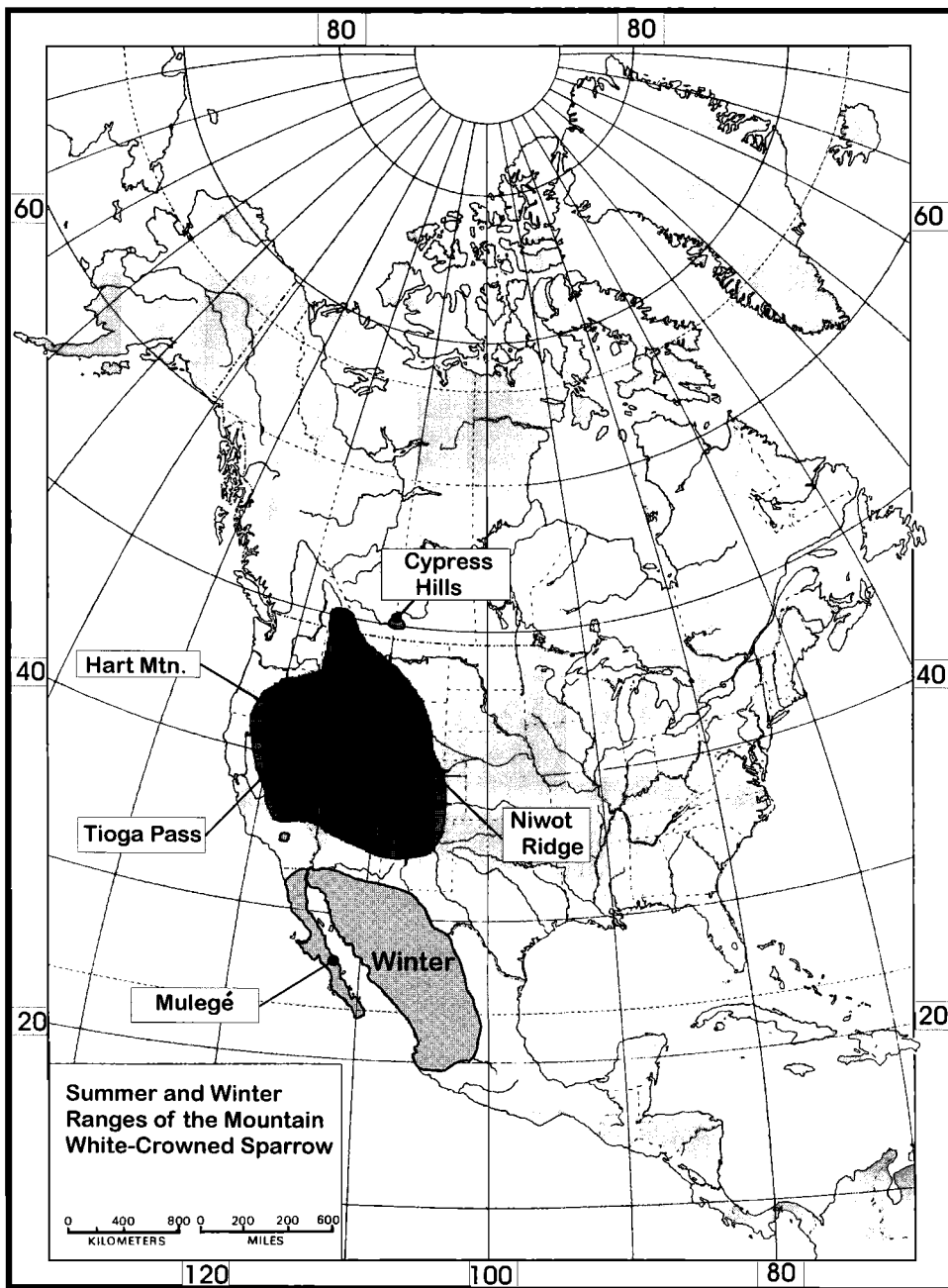
FIGURE 1.2.   Summer and winter ranges of *oriantha*. Locations marked on the summer range are where studies have been conducted: Tioga Pass, California (the present study); Hart Mountain, Oregon; Cypress Hills, Alberta and Saskatchewan; Niwot Ridge, Colorado. Range outlines taken from Banks (1964) and L. R. Mewaldt (pers. comm.). The winter range location, Mulegé, Baja California, is where a wintering *oriantha* from Tioga Pass was recovered in 1997 (see text).

Recently, however, new information was obtained on where the study population might be overwintering. On 7 March 1997 one of our banded birds, a four-year-old male, was captured and released near Mulegé, Baja California, Mexico by Robert C. Whitmore of West Virginia University (see Fig. 1.2). This same bird (band no. 138117256) was subsequently captured on our study area, some 2,100 km to the north, on 5 May 1997. White-crowned Sparrows appear to be abundant on agricultural lands in the Mulegé area during the winter months (Whitmore and Whitmore 1997).

Features of Montane Environments

The large seasonal changes in environmental conditions, capricious weather, low oxygen tensions, and relatively simple habitat structure of the alpine and subalpine regions of the North Temperate Zone renders them inhospitable for year-around occupancy to all but a few species of vertebrates. Among birds, winter residents mainly include a few parids and corvids that are caching specialists, but diversity increases in summer when migrants from a wide array of taxa arrive for their reproductive seasons. A key problem for these migrants, of course, is to synchronize their arrival time and subsequent reproductive effort with the availability of food. The solution to this problem of temporal phasing can be expected to be the product of intensive natural selection on migration schedules and on mechanisms that initiate and terminate reproduction—an ideal natural system for investigating proximate or ecological factors (Chapter 5).

Three primary climatic variables change substantially in association with changes in altitude: temperature, moisture, and wind (Krebs 1972). Air temperature (T_a) decreases and wind velocity increases as one goes up a mountain. In accordance with the universal gas law and the adiabatic lapse rate, air rising in an elevational gradient will tend to accumulate water vapor until it is saturated; condensation then occurs leading to cloud formation and to precipitation (Rosenberg 1974). Large diurnal fluctuations in T_a occur, but its biotic impact appears to have reduced significance at high elevations because differences between microclimates tend to be already exaggerated (Swan 1952). The high winds, decreased availability of soil moisture due to freezing, and variable snowpack greatly influence the phenology and distribution of plants (Griggs 1938, Weaver 1974, Owen 1976, Weaver and Collins 1977). And climatic factors can combine to cause powerful summer storms, with precipitation in the form of rain, hail, or snow, that are potent selective events on annual productivity. Small mammals that have emerged from hibernation can suffer high mortality (Morton and Sherman 1978) and there may even be localized extinctions of some insect species (Ehrlich et al. 1972). Such storms can be non-density dependent disasters to breeding birds and cause high mortality in eggs, young, and even in adults (Morton et al. 1972a, Eckhardt 1977, Gessaman and Worthen 1982).

Seasonality of environmental factors also comes strongly into play at high altitude. For example, the residue of winter precipitation, the snowpack, as well as other factors such as soil temperature, T_a, and daylength can strongly affect plant phenophases such as seed germination; seedling, leaf and shoot growth; and flowering and fruiting. In addition, late-lying snow shortens the growing season (Weaver 1974, Weaver and Collins 1977, Ostler et al. 1982). The earlier phenophases, leaf and shoot growth for example, tend to be the ones most affected; for

every 10% increase in snowpack above the long-term average, they are delayed up to eight days (Owen 1976). Certain plants can "catch-up" somewhat, but the condensation or telescoping of their development can lead to substantial decreases in annual productivity (Billings and Bliss 1959, Scott and Billings 1964, Weaver 1974, Owen 1976, Weaver and Collins 1977). One might safely assume, therefore, that snowpack could influence avian reproduction by modifying the availability of vegetation used for nesting sites, and/or by affecting the abundance of plant and insect food. It, and other seasonally variable events such as the swing in T_a, must have been key components in the evolution of migration and reproduction schedules in birds that are seasonal breeders in montane settings.

Birds are generally well suited for coping with the low partial pressures of oxygen encountered at high elevation. Their lung/air-sac system is efficient for gas exchange, myoglobin concentrations increase with physical conditioning, their hemoglobin has a very high affinity for oxygen (Faraci 1991), and many species have mixed types of hemoglobin, which gives them flexibility in the range over which oxygen can be bound and released, a decided advantage for making large altitudinal movements (Stevens 1996). They also have enhanced cardiovascular conditioning; their hearts (and stroke volumes) are large compared to mammals of similar size, and, unlike mammals, their cerebral circulation is maintained even during hypoxia-induced hypocapnia. They are alert and behave normally at 6,100 m, an altitude that renders mice comatose (Faraci 1991). Additional adaptation has occurred within the passerines because heart and lungs are larger in highland-dwellers than in lowland ones, and seasonal altitudinal migrants, such as those in the present study, closely resemble highland birds in their morphological and physiological characters (Norris and Williamson 1955, Carey and Morton 1976).

Despite the potential hazards of montane habitats, they can be favorable locations for reproduction. Even though summer is relatively brief, possessed of uncertain temporal boundaries, and can often include violent storms with high winds and sub-freezing temperatures, it is also a time when there is a rich pulse of plant and insect food that can be used to rear offspring.

The events that transpire during the few months that a migrant is on its breeding ground encompass the defining moments of the bird's life, the time when it does or does not pass its genes to a new generation. A manifestation of this is that the timing and duration of breeding seasons vary substantially, both among and within species, and even among members of the same population. Because of environmentally-related differences in selection pressures, the control systems that regulate gonadal function vary in sensitivity to the cues that affect them (Wingfield et al. 1992). Therefore, if the variation expressed in avian breeding systems is to be grasped, and the outcome of environment-reproduction schedule interactions predicted, it is necessary to understand not only the underlying biological systems, but also how they operate within a context of environmental variability. These problems can be pursued productively through the medium of the long-term study at locations such as high altitude.

THE STUDY AREA

The study contributing to this monograph was conducted during 25 yr, the last 20 being consecutive: 1968–1970, 1974, 1976, 1978–1997. The study area was located on the upper slopes of Lee Vining Canyon in the Sierra Nevada Mountains
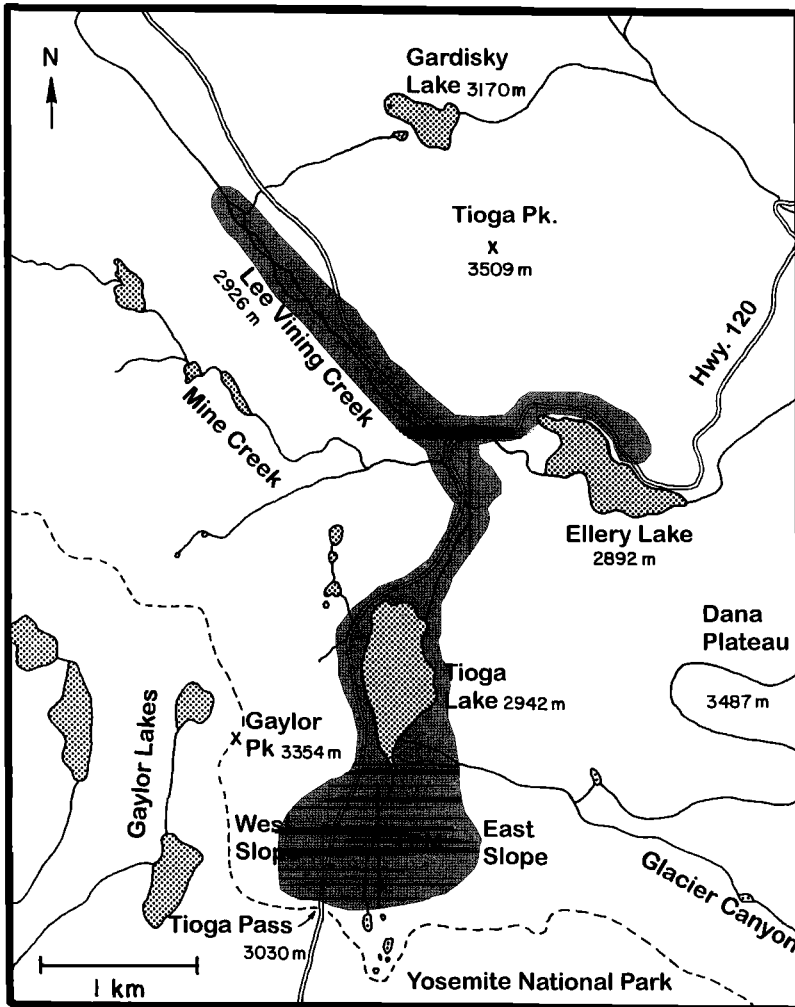
FIGURE 1.3. The Tioga Pass study area (shaded area). Nesting studies of *oriantha* were conducted primarily along Lee Vining Creek, toward the north end of the study area, and on Tioga Pass Meadow (TPM), which lies between Tioga Lake and the boundary of Yosemite National Park at the south end of the study area.

near Tioga Pass, Mono County, California, at about 37.8° N latitude and 119.2° W longitude. Throughout its length Lee Vining Canyon, like many canyons of the eastern Sierra Nevada, has been carved and shaped by uplift, fluvial down-cutting, and repeated glaciations. Its upper branches often begin as cirques and its lower terminus is marked by a broad alluvial fan that extends into Mono Lake. California State Highway 120 follows the canyon bottom, or along the northern wall, from its junction with Highway 395 near the canyon's mouth, up to Tioga Pass then downward into Yosemite National Park.

Once the final vestiges of glacial ice disappear (about 13,000 yr ago in upper Lee Vining Canyon) it still takes considerable time for mature vegetation to become established on the ice-scoured rock and glacial till that is left behind (Pielou

TABLE 1.1.   MEAN MONTHLY AIR TEMPERATURE AND PRECIPITATION OBTAINED AT ELLERY LAKE, CA, 1931–1987

	Temperature (C)			Precipitation (cm)
Month	Daily	Maximum	Minimum	
January	−4.93	1.91	−11.78	10.51
February	−5.08	1.91	−11.97	9.50
March	−2.89	4.17	−10.13	7.56
April	−0.19	6.86	−7.19	4.42
May	3.52	10.19	−3.21	2.47
June	7.97	14.69	1.09	1.64
July	12.75	19.86	5.67	1.90
August	12.29	19.36	5.17	1.78
September	8.76	15.79	1.69	2.05
October	3.97	10.19	−2.34	3.43
November	−0.39	5.62	−6.59	7.09
December	−3.75	2.43	−9.93	10.36

Source: National Oceanic and Atmospheric Administration, Carson City, Nevada.

1991). Stabilization of the climate in its present form occurred about 4,000 to 4,500 yr ago, in the late Holocene (Grayson 1993), so modern community patterns have emerged only within the last few thousand years (Graham et al. 1996). This means that *oriantha* have probably been at Tioga Pass for only that period of time, or less.

In present times subalpine meadows in the upper portions of Lee Vining Canyon are kept green in summer by the melting snowpack, and a series of these were incorporated into our study. They are bounded by mature stands of lodgepole pine (*Pinus contorta*) and contain sedges, grasses, several species of willow (*Salix*), and a fair number of young, scrubby lodgepoles, a vegetational assemblage that is common in the Sierra Nevada at this elevation zone (Chabot and Billings 1972). The study area is irregularly shaped, tending to follow the streams that flow in the canyon bottom for about 7 km between elevations of 2,900 m at Ellery Lake to 3,000 m at Tioga Pass. The total area involved is about 280 ha, although most of the birds and most of our efforts were confined to a series of
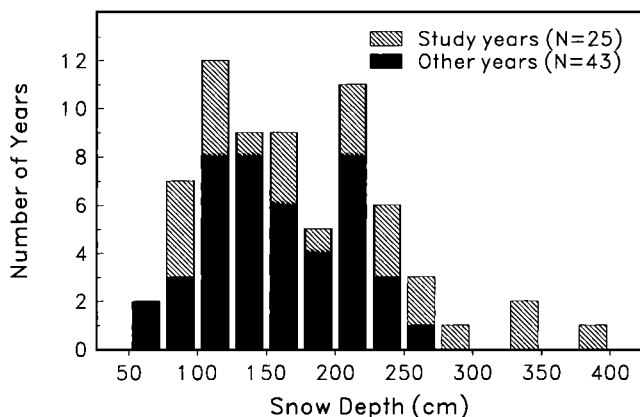

FIGURE 1.4.   Frequency distribution of snow depths measured 1 April on TPM by State of California Snow Survey crews (1927–1994); 65 yr of data, from State of California Bulletin 120, Water Conditions in California.

TABLE 1.2. Snow Conditions on Tioga Pass Meadow Measured On or About 1 April During the Years of the Study

Year	Snow depth (cm)	Water content (cm)	Snow density (%)
1968	113.5	41.7	36.7
1969	342.1	143.8	42.0
1970	176.3	71.1	40.3
1973	204.2	70.6	34.6
1976	79.0	28.7	36.3
1978	263.4	116.3	44.2
1979	227.1	86.4	38.0
1980	262.6	114.0	43.4
1981	173.0	56.4	32.6
1982	294.4	119.6	40.6
1983	375.7	159.3	42.4
1984	205.0	93.7	45.7
1985	145.8	53.3	36.6
1986	243.3	116.3	47.8
1987	113.3	33.5	29.6
1988	121.2	46.7	38.6
1989	158.0	67.1	42.4
1990	90.9	33.5	36.9
1991	167.4	51.3	30.7
1992	108.2	38.9	35.9
1993	227.1	88.9	39.1
1994	94.0	32.0	34.1
1995	327.7	130.6	39.8
1996	230.1	96.8	42.1
1997	210.3	83.1	39.5

Notes. Water content is determined from snow mass. Snow density is water content ÷ snow depth × 100.

stream-side meadows on the upper, northerly end of Lee Vining Creek, and especially on a single subalpine meadow bounded by Yosemite National Park on the south and Tioga Lake on the north (Fig. 1.3). This was called Tioga Pass Meadow, or TPM, and, more than any other location, it was the focal area of the study.

There is considerable annual variation in T_a and precipitation at high altitude and, fortunately, many years of data for these parameters were available from a site at the northeast end of the study area (Ellery Lake). They show that May through October were the warmest and driest months (Table 1.1). These were, in fact, the only months when mean T_a was above freezing, and the same months of the year when *oriantha* were likely to be present at Tioga Pass. Precipitation from 39 storms was recorded by us with rain gauges on TPM during the study.

Data on snowpack depth and snow density were also available. These were gathered on a regular schedule each winter from a transect set up on TPM by State of California employees for the purpose of predicting water runoff from the Lee Vining Canyon watershed. Measurements taken on or about 1 April can be used as an indicator of the winter's maximum snow depth or snowpack because melting usually exceeds accumulation beyond that date. The 1 April data show that maximum snowpack varied interannually about five-fold at Tioga Pass during the 68 years that snow depth was measured (Fig. 1.4). Mean depth was 172.1 cm

(SD = 66.4 cm). Note that the four years of deepest snowpack: 1969, 1982, 1983, and 1995 (Table 1.2), all occurred during the time of our study.

The subalpine meadows making up the study area were in good condition. They are part of the Inyo National Forest and were not grazed by domestic livestock nor traversed by off-road vehicles during the study period.