

# THE SUMMER BIOLOGY OF AN UNSTABLE INSULAR POPULATION OF WHITE-CROWNED SPARROWS IN OREGON<sup>1</sup>

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**Abstract.** We analyzed nest productivity, population size, and temporal aspects of nesting, molting, and premigratory fat deposition in an isolated population of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) on the eastern slope of Hart Mountain, Oregon, from 1972 to 1986. This population, nesting from 1,800 to 2,300 m, is near the lower altitudinal limit of *oriantha*'s geographic distribution at the latitude of southern Oregon. Hart Mountain is an isolated massif separated by unsuitable habitat from nearby populations of this bird in the Steens Mountains (80 km) and the Warner Mountains (65 km). The sex ratio of adults was probably 1:1. The number of pairs in a defined sample area diminished from 41 in 1974 to 16 in 1979, and to a smaller but unmeasured number by 1982 to 1986. Losses of eggs and nestlings to predators and to snowstorms were comparatively very large, and productivity (0.99 to 1.72 fledged young per pair per year) was inadequate to replace losses of adults. The year-to-year return ratio ("minimum survivorship") of adults was likewise comparatively low, 0.37 in males, 0.31 in females, indicating that mortality was unusually large or that breeding-area fidelity was poor. Analysis of return ratios in relation to population size showed that new *oriantha* were recruited to the study population from other localities, but not in sufficient numbers to maintain stability. Summer time budgets of *oriantha* on Hart Mountain were very similar to time budgets of two other populations of these birds in the subalpine zone, suggesting that the Hart Mountain population was not stressed by shortages of time. The postnuptial and postjuvinal molts, in fact, were longer than those of *oriantha* in a subalpine population. We suggest that we witnessed in 1972 to 1986 the declining phase of repeated cycling of numbers, or of extinction and refounding, that may characterize insular populations or populations at their limits of distribution. On Hart Mountain, heavy losses of progeny to predators and weather were not being compensated by recruitment of adults from nearby sources.

**Key words:** Nest mortality; adult mortality; breeding-area fidelity; recruitment; island biogeography; molt; annual cycle; White-crowned Sparrow.

## INTRODUCTION

In their survey of the summer distribution of the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada of California and the southern Cascade Mountains of Oregon, DeWolfe and DeWolfe (1962, see also DeWolfe 1968) described breeding populations of this bird as typically small and often widely separated from one another by unsuitable habitat. Such insular grouping is imposed not only by discontinuous subalpine habitat in the Sierra Nevada and the Cascade Range, but also by discrete altitudinal islands comprising the isolated ranges of the Great Basin (see Banks 1964, Johnson 1975). Such small, disjunct populations may

be especially susceptible to cycles of extinction and refounding (MacArthur 1972). Records of such events are scant or equivocal in birds that inhabit montane islands. In the case of *Z. l. oriantha*, however, it is reasonably certain that new breeding populations have been founded at the southern extremity of its summer range in California (Baptista and King 1980) and Arizona (Balda et al. 1970). It is plausible but less well documented that breeding populations have also become extinct near the northwestern limit of the summer range in the Cascade Mountains of central Oregon (DeWolfe and Dewolfe 1962). Through about a decade we documented the steady decrease and then apparent stabilization of an insular population of this bird on Hart Mountain, southeastern Oregon, near the lower altitudinal limits of its range at this latitude. In this report we analyze several features of the pop-

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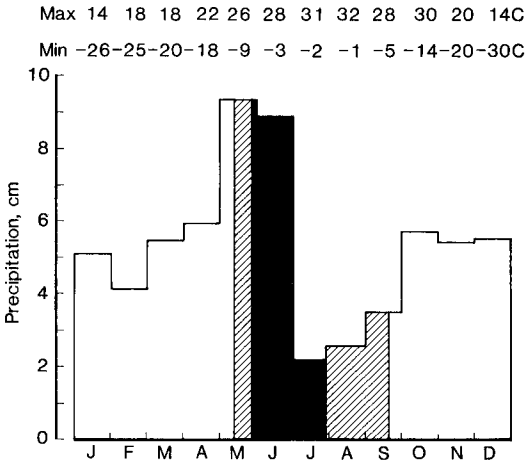


FIGURE 1. Mean monthly precipitation (1940 to 1979) and absolute minimum and maximum monthly temperatures (1971 to 1980) at the Camp Creek study site. Hatched plus blackened part of the histogram represents period when resident female White-crowned Sparrows are present. Blackened area represents nesting period from completion of earliest clutch to departure of latest nestling from the nest.

ulation's nest productivity, adult return rate to the breeding area, seasonal time budget, and physical environment that may account for its recent decline.

The Mountain White-crowned Sparrow is a medium-distance intracontinental migrant that winters in Mexico and the extreme southwestern United States and breeds in the Sierra Nevada, the Rocky Mountains, and the desert ranges of the Great Basin. This bird is commonly regarded as a summer resident of subalpine meadows, although it occurs as a breeder also in or near riparian vegetation at altitudes as low as 1,500 m in northern Montana (L. R. Mewaldt, unpubl. observ.), and even 800 m in the Cypress Hills of Saskatchewan (Banks 1964). Long-term investigations of subalpine breeding populations have been conducted by Morton and associates in the Sierra Nevada (e.g., Morton and Welton 1973, Morton 1978, Zerba and Morton 1983) and by Hubbard (1978) in the Front Range of Colorado.

MATERIALS AND METHODS

THE STUDY AREA

The study area at large comprised about 136 ha along two unnamed creeks bracketing the site of Old Camp Warner at an elevation of 1,830 to 1,890 m on the eastern slope of Hart Mountain

National Antelope Refuge, Lake County, Oregon (42°26'N, 119°43'W). For convenience, we dubbed the northernmost of these streams "Blue Sky Creek," and the southernmost (the location of our research camp) "Camp Creek" (see figs. 1 and 3 in Mewaldt and King 1985). Both creeks are spring-fed and flow steadily throughout the year. Hart Mountain is an isolated massif that forms the eastern wall of the Warner Valley. The plant community occupied by breeding *Z. l. oriantha* is predominantly an *Artemisia tridentata*/*Festuca idahoensis* association, but is dissected by small watercourses and a riparian association featuring *Pinus ponderosa*, *Populus tremuloides*, *Alnus tenuifolia*, and *Salix* sp. Locally, *Purshia tridentata* is a subdominant with *Artemisia*, and *Juniperus occidentalis* is characteristic of the open slopes. Small meadows below springs or along creeks are dominated by *Carex* sp. and *Veratrum californicum*, and superficially resemble the subalpine meadows popularly regarded as the typical breeding habitat of *Z. l. oriantha*.

The climate of Hart Mountain and vicinity is cold and dry in the winter, and warm to hot and dry in the summer. April, May, and June are the wettest months, when 38% of the annual precipitation falls, on the average. Our data (Fig. 1) are based on correlations with the 40-year record from Refuge Headquarters, 15 km NE of our study site on Camp Creek, and 180 m lower in altitude. We corrected the Headquarters data to Camp Creek conditions by means of correlations in 19 periods through 6 years in which we had simultaneous data from the two sites. Headquarters is on an open plateau about 1 km east of the crest of the mountains, while the study site at Camp Creek is on a SE-facing slope close beneath the crest. Air temperatures at Camp Creek are only 1 to 2°C less than at Headquarters, but precipitation averages 2.28 × greater at Camp Creek because of the convective cooling of moist air from the west as it rises over the mountain crest a few hundred meters from the study area.

OBSERVATIONS

Our observations at Camp Creek spanned 14 years. We began fieldwork in 1972 (8 days), increased this to 31 days in 1973, and thereafter from 1974 through 1979 systematically netted the entire sample area (50 to 142 days per year, appropriately distributed through the season and sample grid). We did not visit Camp Creek during the nesting seasons of 1980 or 1983 to 1985.

In 1981 and 1982 we conducted extensive observations and sporadic netting (40 and 46 days) but we did not systematically sample the entire Camp Creek area. In 1986 we concluded our program at Camp Creek by a 2-day census of singing males.

We caught White-crowned Sparrows in mist nets, occasionally supplemented by traps, along both branches of Camp Creek from their origins to the confluence of the joined branches with Guano Creek. This is a beeline distance of about 1,300 m. We refer to this as the "Camp Creek study area." In connection with a general survey of the local avifauna, we typically opened 8 to 10 12-m  $\times$  2-m nets for about 7 hr (dawn until 11:00) each netting day. These nets were rotated systematically among 61 established netting sites so as to sample the entire study area. A typical season consisted of about 3,600 net hr of effort. We obtained basic information about reproductive status, body mass, and molt from examination of captured and recaptured birds bearing USFWS bands. Beginning in 1975 we also color-banded all *oriantha* that we caught. At the time of each capture or recapture we recorded the date, time, net-site, wing-chord (at first capture, and after the end of molt), cloacal protuberance and brood-patch scores, and status of molt. We supplemented the foregoing information with (1) observations of nests, leading by extrapolation to the dates on which clutches were completed and, by the method of Mayfield (1975), to estimates of nest productivity; and (2) records of the status of molt at 4-day intervals in 12 adults and seven juveniles captured on 2 to 10 July from breeding populations several kilometers from Camp Creek and kept outdoors in individual cages (22  $\times$  40  $\times$  27 cm) where fresh water and chick-starter mash were freely available.

## RESULTS AND DISCUSSION

### ARRIVAL ON THE BREEDING GROUNDS

We have exact records of the dates of *oriantha*'s spring arrival at Camp Creek only for 1976, when we began field work on 15 April. We heard one *oriantha* sing on 30 April, and captured the first returning male (a former resident from 1975) on 1 May. We captured five additional resident males on 3 to 7 May, and the earliest resident female on 7 May. The subsequent pattern of capture indicated that the summer-resident *oriantha* had all arrived by 12 to 15 May. The earliest clutches

were completed on 27 May in that year, or 20 days after the arrival of the earliest females, and 26 days after the earliest males.

The schedule of spring arrival by summer-resident *oriantha* at Tioga Pass (ca. 3,000 m) in the Sierra Nevada of California does not differ by much from that at Camp Creek. The bulk of the breeding *oriantha* arrived at Tioga Pass during 10 to 15 May, the males tending to precede females (Morton 1976). Exceptionally, a few males arrived as early as 2 May (Morton 1978). The earliest clutches were completed during 28 May to 9 June, or 2 to 3 weeks after the arrival of the majority of the summer residents.

At Niwot Ridge (ca. 3,500 m) in the Front Range of the Colorado Rockies, the earliest male *oriantha* were recorded (3 years) on 10 to 19 May, and females arrived about a week later. Hubbard (1978) found that the interval between arrival of the earliest males and the completion of the earliest clutches was 30, 36, and 38 days in 3 years of observation. In both the Front Range and the Sierra Nevada, *oriantha* evidently arrive earlier in the adjacent lowlands and loiter there until the snow in the breeding areas has melted sufficiently to uncover feeding sites. On the breeding grounds the birds form pairs, but otherwise do not engage intensely in sexual activity (chasing, persistent singing) until nesting habitat is free of snow. On Hart Mountain, winter snow cover has usually dissipated by early May, and does not typically influence the time of the first nesting cycle.

### ADULT SEX RATIO

The apparent adult sex ratio and the capture ratio of *oriantha* at Camp Creek and in two other montane populations are shown in Table 1. Males consistently outnumbered females among sampling years (not shown) as well as among localities. The capture ratio (percentage of males captured including repeats) showed, however, that males were easier to catch than females. This raises the possibility that the sex ratio was actually 1:1 but was distorted by sampling methods that favored the capture of males. Morton et al. (1972a), who used mainly traps, concluded that sampling bias was negligible because it was found that the sex ratio of immature *oriantha* at Tioga Pass was 55.4% males (capture ratio 58.0% males, probability of no difference = 0.392). They could not envisage a bias favoring the capture of one sex or the other in immatures. Because the sex

TABLE 1. Sex ratios and capture ratios of White-crowned Sparrows at three localities during the summer.

Locality	Years in sample	Sex ratio			Capture ratio		
		No.	% Male	$P^a$	No.	% Male	$P^b$
Camp Creek	6	250	59.6	0.0024	532	64.8	0.156
Tioga Pass <sup>c</sup>	3	245	56.3	0.048	779	66.9	0.032
Niwot Ridge <sup>d</sup>	3	163	58.9	0.023	373	67.3	0.061

<sup>a</sup> Probability that the sex ratio is 1:1.

<sup>b</sup> Probability that the capture ratio and sex ratio do not differ.

<sup>c</sup> Data from Morton et al. (1972a).

<sup>d</sup> Data from Hubbard (1978).

ratios of adults and immatures were alike (56.3 vs. 55.9% males), Morton and colleagues suggested that more males than females were hatched, and that this imbalance continued through later years. This conclusion may be correct, but we are also impressed by how the temporal scope of sampling in a nesting population can affect the results of sex-ratio analysis. For instance, the apparent adult sex ratio of Cassin's Finches (*Carpodacus cassinii*) at Camp Creek was 66.0% males during the period when most females were incubating or brooding, 49.1% males when both sexes were free-ranging, and 57.6% males as the grand seasonal mean (Mewaldt and King 1985). The grand mean is close to the grand means in populations of *oriantha* at Camp Creek, Tioga Pass, and Niwot Ridge (Table 1), and hence raises the possibility that all are biased by inclusion of a span of time during which females are less likely than males to be netted or trapped. The data for *oriantha* at Camp Creek are not sufficient to support an analysis like that applied to Cassin's Finches. We are therefore unable to conclude unequivocally that the adult sex ratio in *oriantha* there is other than 1:1.

#### DISTRIBUTION OF NESTING WHITE-CROWNED SPARROWS ON HART MOUNTAIN AND VICINITY

We did not find *oriantha* nesting or exhibiting territorial behavior below an altitude of about 1,800 m (5,900 ft) on Hart Mountain or adjacent localities to the east and west. Records of nesting *oriantha* at Adel (1,380 m) at the south end of the Warner Valley (DeWolfe 1968, but see Banks 1964) and at Spanish Lake (1,790 m, 7 km SE of Camp Creek; Banks 1964) are general geographic descriptors for specimens collected at higher altitudes nearby. The nearest known breeding populations of *oriantha* are in the Warner Mountains (Barley Camp, 1,890 m) and the Steens Mountains (Fish Lake, 2,225 m) about 65

km SW and about 80 km NE, respectively, from Camp Creek. The low-lying plains and valleys that separate these populations offer no suitable nesting habitat, and probably also impede late-summer dispersal by juveniles.

Wherever they are found on Hart Mountain, *oriantha* tend strongly to nest near watercourses, as DeWolfe and DeWolfe (1962) also found in the Sierra Nevada. Of 77 *oriantha* nests found at or near Camp Creek, 60% were 10 m or less from running water, and 77% were within 30 m or less. The most distant nest was 175 m away from a stream. As the number of nesting *oriantha* at Camp Creek dwindled (see beyond) the distance between nests and running water also diminished. For instance, by 1979 the population was no more than a third of its size in 1975, and all 12 nests found in that year were 20 m or less from a creek, and 10 were within 10 m or less. This was not an artifact of variable sampling, as we searched for nests and territorial males over the same routes that we had used in previous years. We surmise that the clumping of nesting territories nearer to streams in 1979 resulted from a relaxation of competition for preferred habitat as population size diminished. By 1982 the breeding population had decreased still more (see beyond) and singing males were found only along the two branches of Camp Creek above an elevation of 1,860 m. All but one of the 11 or 12 males detected in 1986 were also confined to this same part of the study area, although the population had increased from its level of 1982. The upper branches of Camp Creek are characterized by small meadows and terraces edged by corn lily (*Veratrum californicum*), which we surmise constitutes the habitat that *oriantha* strongly prefers.

#### BREEDING-SITE FIDELITY

White-crowned Sparrows that returned to Camp Creek to breed usually settled in or near their

territory of the previous year. On a large-scale map we plotted the summer ranging centers of individuals, as defined by capture and recapture (for details, see Mewaldt and King 1985), and then analyzed the year-to-year differences among ranging centers as a measure of breeding-site fidelity. The Camp Creek study plot is about 1,300 m long. Ranging centers for males in 71 pairs of years from 1–2 to 1–5 averaged ( $\pm$ SE)  $113 \pm 12.5$  m apart. Females averaged  $160 \pm 22.7$  m apart in 16 pairs of years from 1–2 to 1–4. By Mann-Whitney *U*-test,  $0.05 < P < 0.10$  that the means are the same in the sexes, which is consistent with the finding that breeding dispersal tends to be greater in male than in female birds (Greenwood 1980). We cannot, however, completely exclude the possibility that the sexual difference is an artifact of sampling. The year-to-year return ratio (see beyond) is smaller in females than males, and hence there are fewer females than males in the older age cohorts in which site-fidelity might be more exact. In any case, the data show clearly that returning *oriantha* strongly tend to nest in the same tenth of Camp Creek's riparian strip that they occupied during the previous summer.

#### REPRODUCTIVE CYCLE

We quantified the reproductive condition of males by examination of the cloacal protuberance (CP index on a scale of 0 to 3). CP 2 and 3 reflect enlarged and turgid protuberances (which contain the seminal vesicles), which we take to indicate the presence of sperm. We used the development of the brood patch to estimate the reproductive condition of females (BP index on a scale of 0 to 4). BP 0 refers to a feathered and inactive venter; BP 1 corresponds to a defeathered and visibly vascularized patch; BP 2 extends this to moderate edema; BP 3 indicates maximum development (heavily edematous and usually wrinkled); and BP 4 indicates a regressing patch (dry, defeathered, and commonly scaly). BP 1 to 2 occur during egg laying, BP 2 to 3 during incubation, and BP 4 begins in about the middle of the nestling stage.

Figure 2 depicts a 7-year (1973 to 1979) composite of the seasonal variation of reproductive status in the population of *oriantha* at Camp Creek. A composite sample such as this does not reveal exactly the course of events in a given year unless the cycles are temporally coincident among the years of the sample. If they are not, the initial

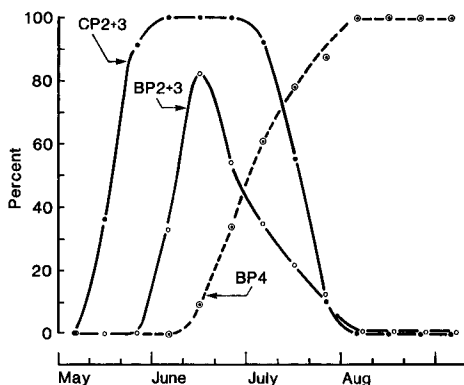


FIGURE 2. Percentages of White-crowned Sparrows at Camp Creek with functional cloacal protuberances (CP 2+3), functional brood patches (BP 2+3), or regressed brood patches (BP 4), 1973 to 1979. See Tables 2 and 3 for sample sizes.

and final dates of cyclic events will be determined only by the data from the earliest and latest seasons. Our samples of CP and BP indexes within years are too small to support a rigorous analysis of year-to-year variants. We therefore rely for this on 3 years of records on the dates of clutch completions (Fig. 3).

Males arrived on the breeding grounds with CP indexes of 0 or 1, but the mean index increased rapidly in the ensuing 2 weeks (Fig. 2) so that nearly all males were at stage CP 2+3 by late May (Table 2). This probably paralleled the final growth of the testes to their maximum size (cf. fig. 1 in Morton et al. 1972a). The males remained at CP 2+3 until late June or early July in the composite picture, but it is likely that the regression of the cloacal protuberance occurred earlier than this in some years in which reneating was slight (e.g., 1976, Fig. 3). By late July or early August all males had become sexually quiescent (CP index less than 2, Table 2). The regression of the cloacal protuberance probably paralleled the involution of the testes, as it did at Tioga Pass (Morton et al. 1972a).

We can correlate the variation of the BP index with independent records on the dates of clutch completions (cf. Fig. 2, Fig. 3). The beginning of the nesting season as judged by clutch completions was nearly invariant (26 to 30 May) in the 3 years for which we have data, even though weather and vegetative growth differed markedly among these seasons (e.g., vegetative growth was early and luxuriant in 1975, later and sparse in 1976). The winter snow pack at Camp Creek

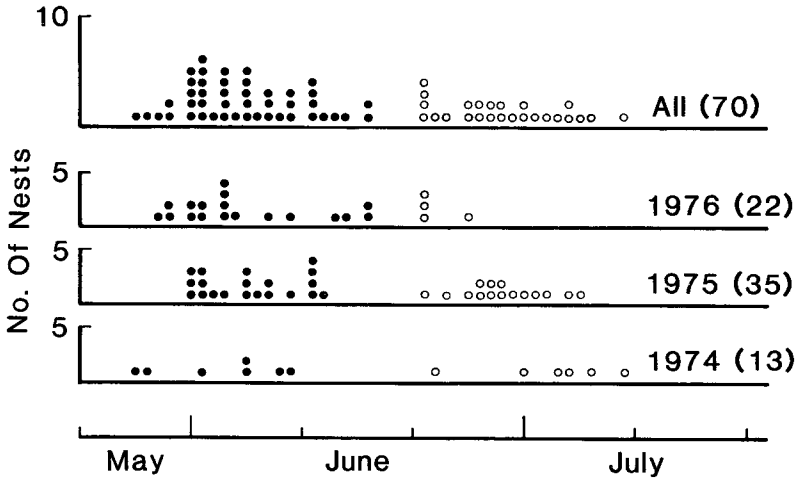


FIGURE 3. Temporal distribution of clutch completions in White-crowned Sparrows at Camp Creek. Filled circles designate first nests, and unfilled circles designate re-nests. Subtract 4 days to estimate the beginning of egg laying.

disappears in April or early May, and so the birds nesting there are not initially constrained by snow cover. In contrast, at higher altitudes where snow-melt is later or more variable among years, the date on which the nesting cycle begins is much more variable and is correlated with snow cover (Hubbard 1978, Morton 1978).

The increase of the BP index to a functional level was closely correlated with our records of egg laying and the onset of incubation (cf. Fig. 2, Fig. 3, Table 3), which provides assurance that our analysis of the BP data is correct. At the peak of the nesting season in mid-June, about 80% of the females were laying eggs, incubating, or in the first few days of the nestling period (BP 2+3). Accordingly, about 20% (the earliest breeders) had reached BP 4 (Fig. 2). Beyond this peak, the curves of BP 2+3 and BP 4 were approximately inverse, as would be expected if we have sampled the population accurately. The rate at which the mean BP index diminished in the population slowed in late June in correlation with re-nesting by females whose first nest(s) failed. Re-nesting was especially prominent in 1975, when a heavy snowfall on 17 to 18 June destroyed all but one of 22 nests in our sample. In more favorable years with fewer re-nesting attempts (e.g., 1976, Fig. 3) we surmise that the regression of the brood patch in the population is more rapid and that 100% BP 4 is reached earlier than in our composite analysis. It is nevertheless evident (Fig. 2) that all but a few females conclude incubation by late July.

NEST SITES

Eighty-four percent of *oriantha* nests on Hart Mountain were on the ground in low grass or beneath sage bushes (*Artemisia tridentata*). Nests above ground were mainly in sage bushes or tufts of rye-grass (*Elymus* sp.) (Table 4). At other localities and higher altitudes, *oriantha*'s predilection for building nests on the ground is affected by the depth of snow and the extent of run-off at the time of nest-building. At Tioga Pass, Morton et al. (1972a) found that 60% of *oriantha* nests were on the ground in two relatively snow-free years, but only about 20% were on the ground in another year in which snow was deeper and run-off greater. On Niwot Ridge, Hubbard (1978)

TABLE 2. Frequency distribution of cloacal protuberance indexes in male White-crowned Sparrows at Camp Creek, 1973 to 1979.

Interval	n	% in CP index				Mean CP index
		0	1	2	3	
1-10 May	5	0	100	0	0	1.0
11-20 May	22	5	59	32	4	1.4
21-31 May	41	0	10	17	73	2.6
1-10 June	48	0	0	2	98	3.0
11-20 June	42	0	0	7	93	2.9
21-30 June	86	0	0	10	90	2.9
1-10 July	70	0	7	26	67	2.6
11-20 July	57	0	44	33	23	1.8
21-31 July	10	20	70	10	0	0.9
1-10 Aug	7	70	30	0	0	0.3
11-20 Aug	6	67	33	0	0	0.3
21-31 Aug	19	100	0	0	0	0.0

TABLE 3. Frequency distribution of brood-patch indexes in female White-crowned Sparrows at Camp Creek, 1973 to 1979.

Interval	n	% in BP index					Mean BP index <sup>a</sup>
		0	1	2	3	4	
1-10 May	1	100	0	0	0	0	0.0
11-20 May	7	100	0	0	0	0	0.0
21-31 May	21	90	10	0	0	0	0.1
1-10 June	31	42	26	10	22	0	1.3
11-20 June	29	0	10	28	52	10	2.2
21-30 June	53	2	9	25	30	34	1.5
1-10 July	24	0	4	17	17	62	0.9
11-20 July	45	0	0	0	20	80	0.6
21-31 July	10	0	0	0	10	90	0.3
1-10 Aug	1	0	0	0	0	100	0.0
11-20 Aug	4	0	0	0	0	100	0.0
21-31 Aug	7	0	0	0	0	100	0.0

<sup>a</sup> BP 4 taken as BP 0 in computing means.

found that only 11% of *oriantha* nests were built on the ground, the majority being 21 to 80 cm above ground mainly in clumps of spruce krummholz. In wet meadows about 180 m below Hubbard's study area on Niwot Ridge 11 of 23 *oriantha* nests (48%) were built on the ground, mainly at the base of willow bushes (80%). Nests above the ground were mainly in spruce trees (75%) at the lower edges of the meadows, where run-off pools prevented nesting on the ground. Nests above ground level ( $n = 12$ ) ranged from 8 to 200 cm, averaging 127 cm (J. R. King, unpubl. observ.).

#### POSTNUPTIAL AND POSTJUVENAL MOLT IN CAPTIVES

The replacement of flight feathers during postnuptial molt in captives at Hart Mountain did not differ in detail from the pattern in captives at Tioga Pass (Morton and Welton 1973: fig. 3) but was slower. As at Tioga Pass, the onset of the molt was signaled by the shedding of the innermost primary (P1), and its end by the disappearance of pins and brushes in the body tracts. The captive males at Hart Mountain (Table 5) began postnuptial molt about 5 days earlier than females ( $P < 0.001$ , by  $t$ -test) and molted about 8 days longer ( $P < 0.001$ ). Captive males and females at Tioga Pass did not differ from each other in these characteristics. The molt of captives at Hart Mountain began 15 to 20 days earlier than at Tioga Pass and lasted 5 to 11 days longer ( $P < 0.01$  for differences in the duration of molt in both males and females). We and Morton and his associates used similar criteria and measurements developed during earlier collab-

TABLE 4. Nest sites of White-crowned Sparrows on Hart Mountain.

Main supporting or concealing plant	No. of nests			% in substrate
	On ground	Above ground <sup>a</sup>	Both	
<i>Artemisia tridentata</i>	23	7	30	39
Low grass or sedge	20	0	20	26
<i>Veratrum californicum</i>	9	1	10	13
Duff of pine woods	7	0	7	9
<i>Chrysothamnus</i> sp.	4	0	4	5
Tufts of <i>Elymus</i> sp.	1	3	4	5
<i>Symphoricarpos</i> sp.	1	1	2	3
Sum	65	12	77	100
Percent	84	16	—	—

<sup>a</sup> Mean height = 33 cm, range = 20-61.

oration (e.g., Morton et al. 1969) and it is unlikely that differences in our results reflect differences of methods.

Postjuvenile molt began in five of the seven captives about 13, 9, 7, 6, and 6 days before the date of capture, as judged from the pattern of molt in the two birds that began to molt after that date. On average, the postjuvenile molt in captives began on 2 July  $\pm$  4.2 days and lasted 58 days (Table 5). At Tioga Pass this molt began in captives on about 30 July (Morton et al. 1972b: fig. 5) and lasted 32 days (Table 5). Some or all of this relative abbreviation of the molt at Tioga Pass may result from its later beginning, as in the Common Chaffinch, *Fringilla coelebs* (Vinogradova 1982). Differences in the date on which the postjuvenile molt began in captives have no biological significance, since onset is linked to chronological age (see beyond), which is not like-

TABLE 5. Calendar of postnuptial and postjuvenile molts in captive White-crowned Sparrows caged outdoors (mean  $\pm$  SD,  $n$  in parentheses).

	Camp Creek	Tioga Pass <sup>a</sup>
Postnuptial molt		
Duration, days		
Males	60.7 $\pm$ 2.7 (6)	49.6 $\pm$ 6.2 (16)
Females	52.8 $\pm$ 3.3 (6)	48.0 $\pm$ 4.0 (14)
Beginning date (July)		
Males	10.0 $\pm$ 3.0 (6)	30 Jul-1 Aug <sup>b</sup>
Females	15.2 $\pm$ 3.3 (6)	28 Jul-2 Aug <sup>b</sup>
Postjuvenile molt		
Duration, days	58.0 $\pm$ 3.4 (7)	32.4 $\pm$ 4.6 (7)

<sup>a</sup> From Morton et al. (1972b), Morton and Welton (1973), for birds captured in early July.

<sup>b</sup> Range of means for two seasons of study. Sample sizes = 9 and 10 males, 10 and 11 females.

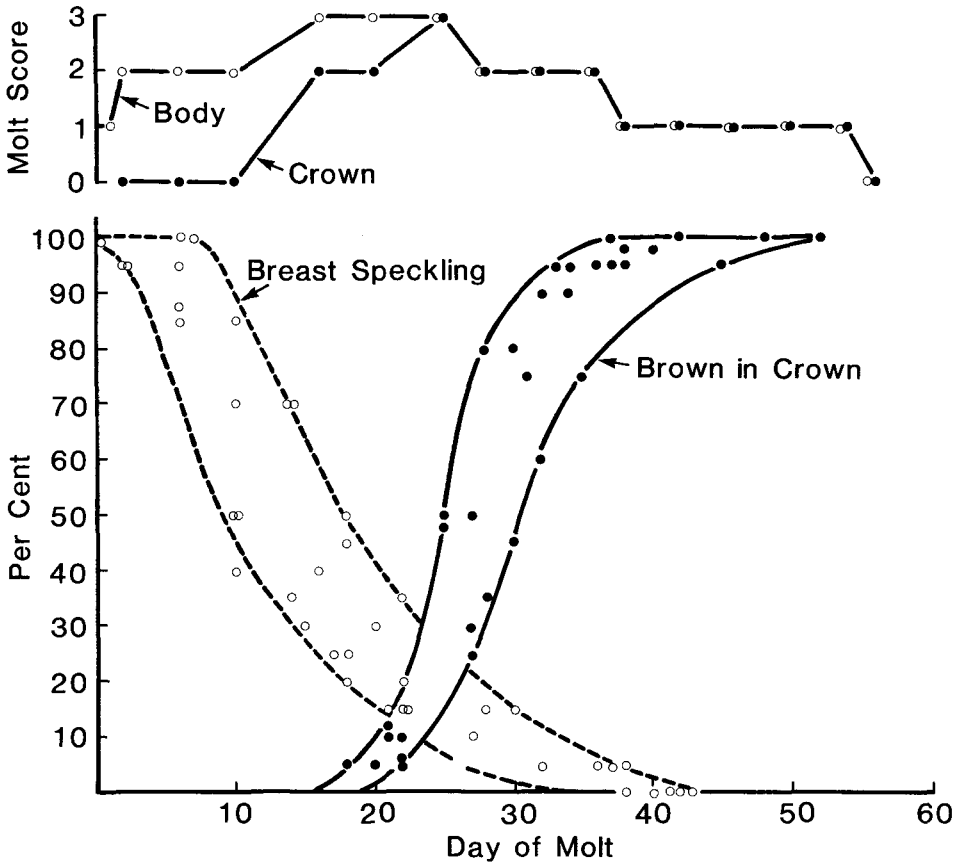


FIGURE 4. A profile of postjuvenile molt in captive White-crowned Sparrows caged outdoors at Camp Creek, 1976. Molt scores for body and crown, at the top, correspond to no molt (0) and to "light" (1), "medium" (2), and "heavy" (3) molt. "Breast speckling" refers to the change from the streaked or speckled juvenile breast plumage to the pure gray first-year plumage. "Brown in crown" refers to acquisition of tan lateral crown stripes, which replace the cryptic pattern of the juvenile plumage. The curves were fitted by eye to emphasize the limits of variability.

ly to average the same in small samples ( $n = 7$  in both cases). In both localities, the postjuvenile molt in free-living birds began before the post-natal growth of the flight feathers (especially the rectrices) was complete—a relationship known in at least 11 other species of finches (Sutton 1935, 1941). Morton et al. (1972b) found that postjuvenile molt began on the average ( $\pm$ SD) at  $34 \pm 5.2$  days after hatching in seven captive juveniles at Tioga Pass.

#### MOLT IN FREE-LIVING BIRDS

Morton et al. (1969) showed in *Z. l. gambelii* that the schedules of postnuptial and postjuvenile molt were essentially alike in captive and free-living birds. We assumed that this was true also in *Z. l. oriantha*, and therefore used criteria obtained from the captives to estimate the onset

and stage of molt in birds captured and recaptured from the free-living population. For adults, we prepared a phase diagram similar to figure 3 in Morton and Welton (1973), supplemented by measurements of feather length in relation to the day of molt. This enabled us to estimate the day of molt in free-living birds with a maximum error of about  $\pm 2$  days. For juveniles, we used a profile consisting of the percentage of "speckling" in the breast (which changes progressively toward clear gray from the speckled pattern of the juvenile plumage), the percentage of brown in the crown (which changes from cryptic streaks to the broad tan and brown stripes of the first winter plumage), and the molt scores of crown and body (Fig. 4). This enabled us to estimate the day of postjuvenile molt with an error of about  $\pm 4$  days.

The estimated mean date ( $\pm$ SD) on which



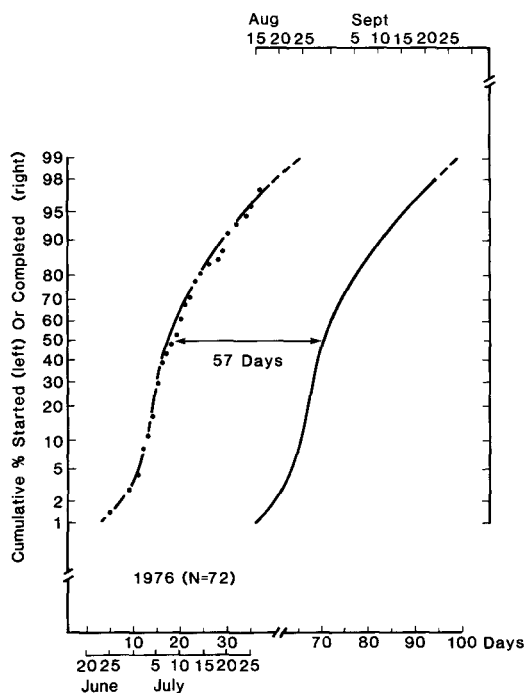


FIGURE 5. The temporal course of the postnuptial molt in free-living White-crowned Sparrows at Camp Creek, 1976, males and females combined ( $n = 72$ ). The curve at the left (dates at bottom left) shows the cumulative percentage of birds that had started the molt, and the curve at the right (dates at upper right) shows the cumulative percentage that had completed the molt (see text).

postnuptial molt began in free-living birds on Hart Mountain in 1976 (the only year for which we have a sample spanning the entire molting season) was 15 July  $\pm$  7.8 days in 21 females, and 8 July  $\pm$  5.3 days in 51 males. In females this is exactly the same date as in the captives, and in the males is only 2 days earlier than in the captives (Table 5). Thus, the onset of molt was about a week later ( $P < 0.001$ ) in females than in males at Hart Mountain, which is the same relationship found in several coastal populations of *Z. l. nuttalli* and *Z. l. pugetensis* (Mewaldt and King 1978a). At Tioga Pass, Morton and Welton (1973) showed in nine pairs of *Z. l. oriantha* that males began the postnuptial molt, on the average, 19.5 days after the eggs had hatched, and females 27.6 days after this event—a difference that is correlated with the longer period in which the females attend the fledglings.

The mean dates of molt onset cited above help to verify that the captives were an accurate analog of free-living birds, but tell us nothing about

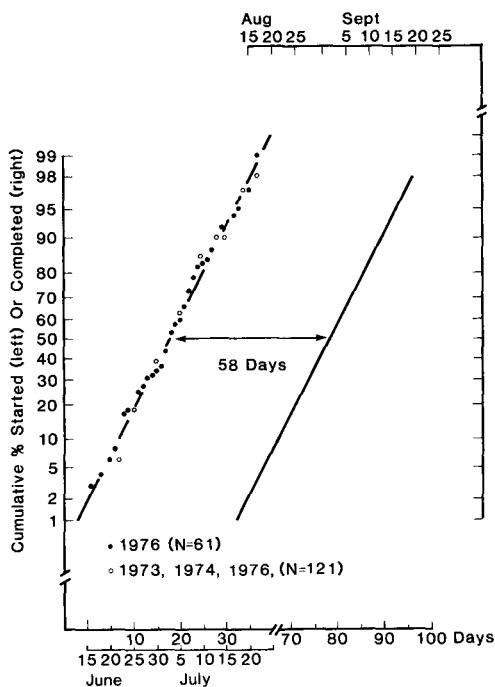


FIGURE 6. The temporal course of postjuvinal molt in free-living White-crowned Sparrows at Camp Creek, 1976. See Figure 5.

the temporal course of molt in the population. This is shown as a probability plot (Fig. 5) for Hart Mountain in 1976. We combined males and females, which produced a bimodal or platykurtic distribution because molt in males and females was not exactly simultaneous. We assumed that the end of molt had the same frequency distribution as its start (the points and curve at the left in Fig. 5) but occurred about 57 days later (the median duration of postnuptial molt in captive males and females). We also assumed that the duration of molt was the same in early- and late-molting individuals, which is reasonable since we caught birds in the terminal stages of remigial molt as late as 9 September. The earliest birds (all males) began the postnuptial molt on about 22 June (the 1% point in Fig. 5). The earliest breeders known to us should have fledged their young on 18 June 1976 (28 May + 21 days), and we thus estimate that molt began in adults, on the average, 25 days after the young had hatched. This is consistent with the averages reported by Morton and Welton (1973) for *oriantha* with known nesting histories (19.5 days in males, 27.6 days in females).

A comparison of Figures 2 and 5 shows that

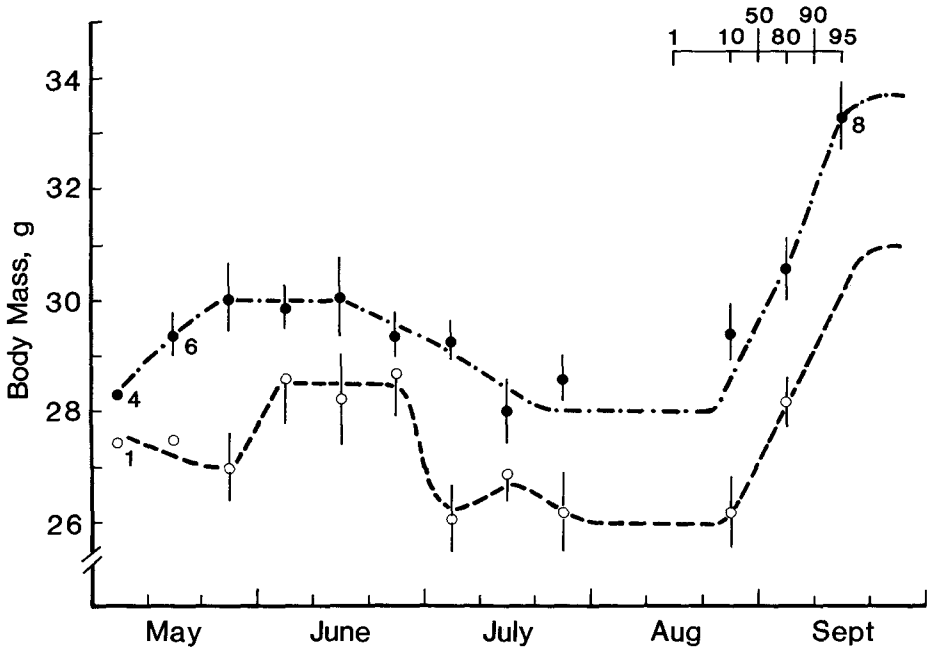


FIGURE 7. Mean body weights (09:00 to 15:00) and 95% confidence intervals of free-living adult White-crowned Sparrows (filled circles = males, unfilled circles = females) at Camp Creek. Sample size = 10 unless otherwise shown. Scale at upper right shows percentage completion of postnuptial molt in the population (from Fig. 5).

postnuptial molt and reproductive activity are in general mutually exclusive, as in *Z. l. oriantha* at Tioga Pass (Morton and Welton 1973), *Z. l. gambelii* in central Alaska (Morton et al. 1969), and *Z. l. nuttalli* in coastal California (Mewaldt and King 1978b). Apparently there have been no selection pressures on the seasonal time budgets of these populations that have caused the telescoping of molt and reproduction, such as occurs occasionally in other species of birds (e.g., Payne 1972).

We estimated the onset and progress of postjuvinal molt in the free-living *oriantha* at Camp Creek (Fig. 6) from criteria obtained from captives (Fig. 4). The onset of postjuvinal molt in the population spanned about 40 days, beginning on about 13 June (the 1% point in Fig. 6). If the duration of postjuvinal molt is 58 days (Table 5) and is temporally invariant, then the line at the right in Figure 6 shows that the molt was completed by 99% of the population by 24 September. Adding samples from 1973 and 1974 (unfilled circles) does not change the relationship, which suggests that the year-to-year timing of postjuvinal molt does not vary by much. The end of the postjuvinal molt coincides with the

end of the postnuptial molt (Fig. 5) and with the departure of the last resident *oriantha*.

#### VARIATIONS OF BODY WEIGHT

We confined our analysis of the summer cycle of body weight (=“mass”) in adults to birds captured between 09:00 and 15:00 in order to minimize variation resulting from the daily weight cycle. This reduced sample sizes below our goal of 10 in some cases and produced a 20-day gap in the record in August (Fig. 7). We were able to compensate for this, in part, by resorting to data obtained from captives (Fig. 8).

In general, variation of body weight in adults resembled that found in *oriantha* at Tioga Pass by Morton and Welton (1973). Body weight in both males and females reached a peak in mid-June and then decreased significantly late in the nesting season or early in molt. Weights then increased slowly during molt (Fig. 8), dropped slightly at the end of molt, and then increased sharply as a result of premigratory fattening. The cyclic change of weight during molt may reflect in part the changes of fat-free body mass and water content that accompany the regeneration of the plumage (Chilgren 1977), but the molt-

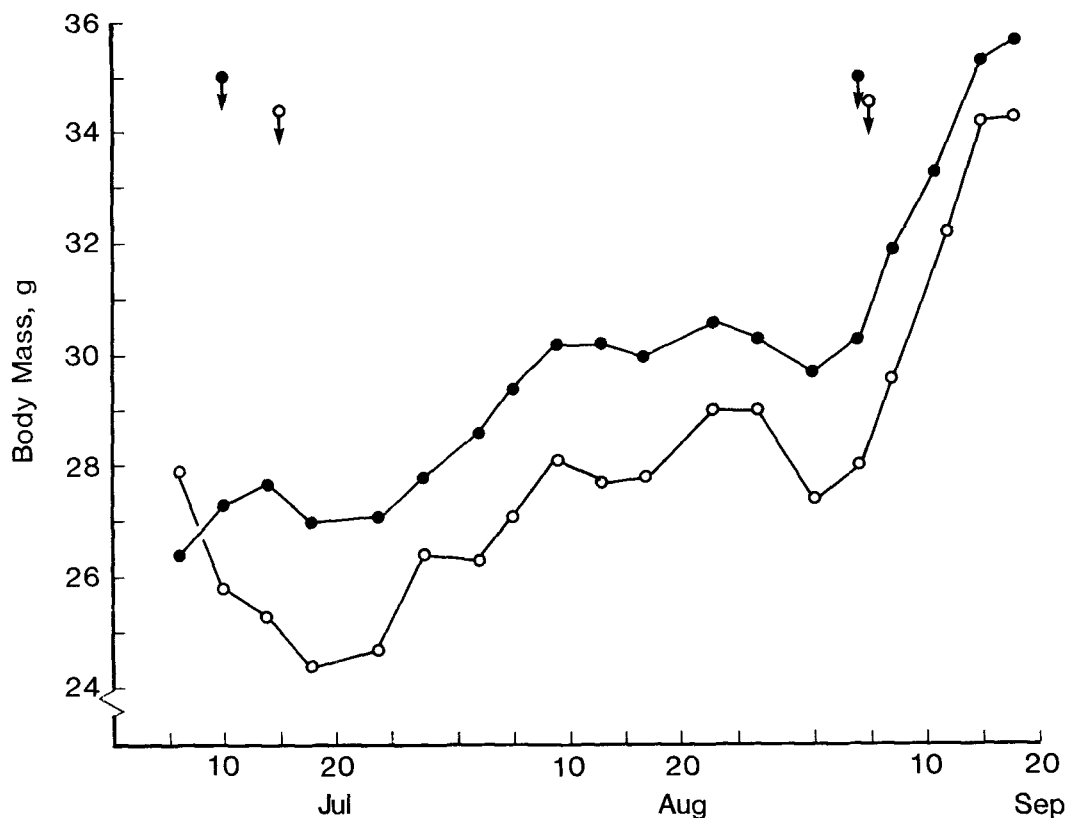


FIGURE 8. Mean body weights of White-crowned Sparrows caged at Camp Creek, 1976. Filled circles indicate adult males ( $n = 6$ ), unfilled circles indicate adult females ( $n = 6$ ). Weights of immature (HY,  $n = 7$ ) birds fall midway between adult males and females, but data have been omitted to minimize clutter. Arrows pointing downward indicate beginning and end of postnuptial molt.

related increase of weight is too large to result from this alone and must reflect an accumulation of fat. From a carcass analysis of *oriantha* at Tioga Pass, Morton (1976) in fact showed that the fat content of the body increased by about 40% (males) or 80% (females) between its mid-summer low (coinciding with the nestling-fledgling period) and the postnuptial molt period.

The premigratory increase of body weight in both the captive and the free-living birds (juveniles as well as adults) began at Camp Creek during the first week of September (Figs. 7, 8). The increases above the postmolt minima were 21% in captive males, 20% in females, and 16% in juveniles. The onset of premigratory fattening at Hart Mountain coincided closely with that at Tioga Pass (Morton 1976), in both localities beginning immediately after the end of the postnuptial or postjuvenile molt. The exodus of summer-resident *oriantha* from Hart Mountain

coincided with the increase of body mass in the population and occurred in a brief period between the end of August and mid-September. Our latest record of a summer resident at Camp Creek is 19 September.

#### POPULATION DECLINE AND ITS CORRELATES

We estimated the numbers of resident *oriantha* on the Camp Creek sample plot by the Schnabel method (Schnabel 1938, Brower and Zar 1977, Nichols et al. 1981). We have previously reviewed the suitability of this method for use at Camp Creek (Mewaldt and King 1985). The numbers of *oriantha* diminished by more than half during 1974 to 1979 (Table 6). Our netting schedules after 1979 were not adequate to support estimates by the Schnabel method, but it was obvious from other criteria that the numbers of *oriantha* continued to diminish until at least

TABLE 6. Estimates of numbers of White-crowned Sparrows present in the Camp Creek sample area during the summer.

Year	$n \pm SE$
1974	82 $\pm$ 10
1975	65 $\pm$ 5
1976	57 $\pm$ 1
1977	41 $\pm$ 6
1978	33 $\pm$ 4
1979	33 $\pm$ 4

1982. For instance, from 1975 onward we had counted the numbers of singing males along standard routes that included Blue Sky Creek and adjacent Guano Creek as well as Camp Creek. On 16 to 18 June 1982 we detected only three or four singing males (all on Camp Creek above an elevation of 1,860 m) during three censuses along a route that regularly included 17 to 21 singers in 1975 to 1976. This decrease of *oriantha* was widespread on Hart Mountain. Singing males were common along upper Guano Creek and Deer Creek in 1975 to 1976, for instance, but had become scarce by 1982. We have no additional records until 19 to 20 June 1986, when we found 10 (perhaps 11) singing male *oriantha* during two surveys along the standard routes. All males but one occupied territories on the two branches of Camp Creek above an elevation of 1,860 m. We found one mated male on Blue Sky Creek at about this same elevation. We believe that the population of *oriantha* at Camp Creek increased between 1982 and 1986, but not to the level of 1979.

A thorough explanation of the causes of the decline of *oriantha*'s numbers documented by Table 6 and subsequent observations would require a full demographic analysis, which is beyond our reach. We can, however, identify some of the parts of the puzzle.

*Nest productivity.* Because of snowstorms and heavy predation the survival of eggs and nestlings to the stage of nest-departure is low at Camp Creek. Snowstorms on 17 to 19 and 24 to 25 June in 1975 caused incubating *oriantha* to abandon all but one of 22 nests. The birds promptly initiated a replacement cycle in which the mean number of young fledged per pair, as estimated by the Mayfield method (Mayfield 1975, Johnson 1979), in a sample of 20 nests was 0.99. Mean clutch size was 3.50 eggs and mean hatchability was 1.00. Predators destroyed 72% of viable eggs

and nestlings. In 1979, six of seven nests were deserted by the attending adults during a snowstorm on 16 to 17 June, but we found no evidence of renesting. In 1976, the breeding season was free of snowstorms, and the mean number of fledgings per pair per nesting cycle was 1.10 in a sample of 25 nests (mean clutch size 3.70, hatchability 0.889). Because of renesting by some pairs, the mean number of nesting cycles per pair in 1976 was 1.56, or a mean of 1.72 fledged young per pair. Predators destroyed 66% of viable eggs and nestlings.

Losses to predators such as those observed in 1975 and 1979 (72 and 66%) are very large compared with losses in other populations of *oriantha* and other ground-nesting passerines in the north temperate zone. We estimated from data in Morton et al. (1972a) that only 33 to 41% of viable eggs and nestlings in ground-level nests were depredated during a 3-year study of *oriantha* at Tioga Pass, California. Analogous data from Niwot Ridge, Colorado, yielded estimates of 36 to 52% depredation during a 4-year study (Hubbard 1978). The data from Tioga Pass and Niwot Ridge bracket the mean loss—38%—of viable eggs and nestlings to predators that we computed for six species of passerines from data summarized by Ricklefs (1969: table 1). The loss of *oriantha* eggs and young to predators at Camp Creek in 1975 to 1976 was clearly exceptionally heavy. The reasons for this are not obvious. Unlike Tioga Pass and Niwot Ridge, however, Camp Creek is within the altitudinal range of snakes (at least *Pituophis melanoleucus*) and the Brown-headed Cowbird (*Molothrus ater*). Brown-headed Cowbirds (six to 12 females) were present at Camp Creek every year, and parasitized six of 42 *oriantha* nests in 1975. Three of these parasitized nests were destroyed by a snowstorm, and the other three produced no sparrows (King et al. 1976).

Such heavy pressure from nest predators and brood parasites is amplified by a weather pattern that features heavy snowstorms during the egg/nestling season about every fifth year on the average. A conservative estimate based on observations of the effects of mild, medium, and heavy snowstorms at Camp Creek is that 15 cm of wet snow will cause virtually all incubating *oriantha* to desert their nests, and we suspect that the threshold may be as little as half this depth if the snow lasts for more than a day. Forty years of weather data from Hart Mountain are available

in the monthly *Climatological Data* reports of the National Oceanic and Atmospheric Administration (NOAA), but these summaries yield few data about snow depth. Records and notes in the Refuge Headquarters diary, however, supplement the NOAA data and permit reasonably reliable estimates of storm frequency and snow depth in 20 of 26 years between 1953 and 1979. Snowfall accumulating to 15 cm or more in one day occurred within the limits of the nesting season in 8 years, and 12 cm accumulated in each of 3 additional years. In 7 of these 11 years the storms occurred during 13 to 31 May, and hence may have merely delayed the onset of nesting or destroyed only the earliest eggs (cf. Fig. 3). In the remaining 4 years of the 20-year record the storms coincided with the peak of the nesting cycle, and probably caused severe losses of eggs and nestlings, as in 1975 and 1979.

We have only scant comparative data from other localities. Near Gothic, Colorado, *oriantha* renested following total destruction of eggs by snowfall (Ehrlich et al. 1972). On Niwot Ridge, Colorado, *oriantha* did not begin to nest until after the last spring snowstorm during a 4-year study, and documented losses of eggs or nestlings to bad weather were insignificant (Hubbard 1978; J. R. King, unpubl. observ.). At Tioga Pass, California, a snowstorm during 1 year of a 3-year study destroyed 13% of viable eggs and nestlings, and rainfall on a heavy snowpack in another year caused flooding that drowned 29% in ground-level nests (Morton et al. 1972a). Eggs and nestlings in elevated nests escaped, however, and loss in all nests combined was 12%. Thus, in eight nesting seasons of data from various montane localities distant from Hart Mountain the loss of *oriantha* nests to snowstorms or flooding was total in one year and no more than 13% in two other years. In comparison, the effects of snowstorms at Camp Creek seem more frequent and severe. A fully persuasive analysis of local differences in the effects of snowstorms on nest productivity would require long runs of data—say 50 years—at each locality. Until such data become available, we conclude tentatively that Hart Mountain's weather as well as its nest predators take a comparatively heavy toll of the reproductive output of the population. If storms occur early enough in the nesting season *oriantha* may renest and compensate for earlier loss, as at Camp Creek in 1975. This delay probably entails disadvantages, such as crowding the time available

for the postnuptial and postjuvenile molts, and offsetting the rearing of nestlings to the hottest part of the summer. In 1975, the latest nests in the replacement cycle contained nestlings through the second half of July and into the first week of August. July at Camp Creek is warm to hot during the day and relatively dry. On the average, rain falls on fewer than 2 days. The maximum daily air temperature may reach 31°C on several days in July, and the operative temperature at the nest may be greater than this (Webb and King 1983a, 1983b), imposing a potential heat stress on eggs, nestlings, and brooding parents. We do not know of any nests that were abandoned by the parents during the renesting cycle in 1975, but we observed two nests in late July in which 5- to 7-day-old nestlings were "listless and seemed dehydrated" at midday. This suggests that nestlings may be exposed to heat stress in late nests, and illustrates that the unusual weather regime at Hart Mountain may occasionally pose a double hazard to reproduction—snow early, heat late.

*Adult return ratios.* Capture-recapture methods for estimating survival of adults between nesting seasons yield reliable results only if breeding-site fidelity is perfect and all returning banded birds are recaptured, or known from recapture later to have been alive in a previous year. Even though it may be possible by saturation trapping, as at Camp Creek, to capture essentially all returning survivors from a previous year, it is never possible to know if all survivors have returned. For this reason we prefer to use the term "adult return ratio" rather than the more usual "minimal adult survival." So that our estimates would not be biased by transient birds that did not nest at Camp Creek, we included only birds that were known to have resided there in a previous summer. The return ratios of *oriantha* were 0.37 for males and 0.31 for females (Tables 7, 8). These are at the low end of the annual return rates for small-bodied passerines in general (e.g., Farner 1955, Payevsky 1974), and also less than in most of the passerines for which we have similar data from Camp Creek (Table 8). Return ratios for all other species except Yellow Warblers and McGillivray's Warblers substantially exceed those of White-crowned Sparrows, and indicate typical survival and breeding-site fidelity. Recruitment is apparently adequate to maintain the population of warblers in spite of their low return ratios, as we have no evidence that they diminished in numbers during

TABLE 7. Returns of White-crowned Sparrows 1 year old and older banded at Camp Creek.

Year	First capture	Number returned in year					
		2	3	4	5	6	7
<b>Males</b>							
1973	3	—	—	—	—	—	—
1974	24	1	—	—	—	—	—
1975	27	10	0	—	—	—	—
1976	15	13	5	0	—	—	—
1977	7	3	4	1	0	—	—
1978	8	2	3	2	0	0	—
1979	17	1	0	1	1	0	0
Totals	101	30	12	4	1	0	0
<b>Females</b>							
1973	1	—	—	—	—	—	—
1974	17	0	—	—	—	—	—
1975	18	4	0	—	—	—	—
1976	19	4	0	0	—	—	—
1977	12	2	1	0	0	—	—
1978	4	1	0	1	0	0	—
1979	15	0	0	1	0	0	0
Totals	68	11	1	2	0	0	0

the course of our investigation. Recruitment into the *oriantha* population, however, was inadequate to maintain stable numbers (Table 6). If we assume that the sex ratio in the *oriantha* population was 1:1 and that return ratios did not vary with age, year, or cohort of recruits, then we can estimate the numbers of new recruits each year (examples in Table 9). To maintain a hypothetical stable population of 41 female *orian-*

*antha* (the number present in 1974) would require 28 new female recruits each year. If (a) the sex ratio of hatchlings were 1:1, (b) the production of fledglings were 1.72 (or 0.86 females, as in a year free of snowstorms), and (c) the return ratio of progeny were 0.31 (equal to that of adult females), then a population of 41 females would produce about 11 of these recruits each year. This is a liberal estimate, since nest productivity is reduced by snowstorms in about one year in five, and the return ratios of juvenile passerines are thought to be less than those of adults (Ricklefs 1972). At a minimum, however, 17 (28 minus 11) female recruits dispersing from other breeding localities would be needed each year to maintain the Camp Creek population of *oriantha* at 41 pairs. Because the population was declining rather than stable, the actual number of recruits estimated as described above decreased from 19 to 10 to 11 from 1975 through 1978 to 1979, and the estimated number of recruits dispersing from other localities decreased from 8 to 5–7 (Table 9). It is conceivable that these recruits originated as natal dispersers (in the terminology of Greenwood and Harvey 1982) from other breeding groups of *oriantha* on Hart Mountain. Unless these groups had much higher adult return ratios and nest productivities than in *oriantha* at Camp Creek, however, they had no surplus progeny that could serve as a source of dispersers without accelerating the decrease of their own numbers. Through the mid- to late 1970s we caught fewer *oriantha* and heard fewer singing

TABLE 8. Mean year-to-year return ratios of selected species at Camp Creek, 1973 to 1979.

Species	Sex	Return ratio <sup>a</sup>	n <sup>b</sup>
Dusky Flycatcher	Males	0.62 ± 0.07	40
( <i>Empidonax oberholseri</i> )	Females	0.51 ± 0.08	27
American Robin	Males	0.70 ± 0.03	80
( <i>Turdus migratorius</i> )	Females	0.83 ± 0.02	72
Yellow Warbler	Males	0.39 ± 0.08	29
( <i>Dendroica petechia</i> )	Females	0.27 ± 0.18	9
MacGillivray's Warbler	Males	0.59 ± 0.07	33
( <i>Oporornis tolmei</i> )	Females	0.24 ± 0.10	13
Green-tailed Towhee	Males	0.56 ± 0.14	13
( <i>Pipilo chlorurus</i> )	Females	— <sup>c</sup>	4
Song Sparrow	Males	0.63 ± 0.07	24
( <i>Melospiza melodia</i> )	Females	— <sup>c</sup>	4
White-crowned Sparrow	Males	0.37 ± 0.06	53
( <i>Z. l. oriantha</i> )	Females	0.31 ± 0.11	16
Cassin's Finch	Males	0.64 ± 0.02	264
( <i>Carpodacus cassinii</i> )	Females	0.60 ± 0.03	157

<sup>a</sup>  $\bar{x} \pm SE$ , according to method of Roberts (1971) as modified by Mewaldt and King (1985).

<sup>b</sup> Bird years known to be lived by individuals present two or more years.

<sup>c</sup> Insufficient number of recaptures for analysis.

TABLE 9. Estimates of females recruited into the Camp Creek sample population.<sup>a</sup>

Cohort of recruits	Years					
	1974	1975	1976	1977	1978	1979
<b>A. Hypothetical stable population</b>						
1974	41	13	4	1	0	0
1975	—	<b>28</b>	9	3	1	0
1976	—	—	<b>28</b>	9	3	1
1977	—	—	—	<b>28</b>	9	3
1978	—	—	—	—	<b>28</b>	9
1979	—	—	—	—	—	<b>28</b>
Population size	41	41	41	41	41	41
Alien recruits	—	17	17	17	17	17
<b>B. Decreasing population (Table 6)</b>						
1974	41	13	4	1	0	0
1975	—	<b>19</b>	6	2	1	0
1976	—	—	<b>18</b>	6	2	1
1977	—	—	—	<b>11</b>	3	1
1978	—	—	—	—	<b>10</b>	3
1979	—	—	—	—	—	<b>11</b>
Population size	41	32	28	20	16	16
Alien recruits	—	8	9	4	5	7

<sup>a</sup> Annual return ratio in each cohort assumed to be 0.31. Annual nest productivity per female per year assumed to be 0.86 (=1.72/2) female fledglings, of which 0.31 return to Camp Creek. Total recruits (diagonal ranks of **boldface** numerals) = recruited progeny plus alien recruits.

in all of our regular netting sites, in parallel with their decrease at Camp Creek, and we conclude that the decrease of their numbers was widespread on Hart Mountain.

The balance point between gain and loss in *oriantha*'s population at Camp Creek was dominated by an annual adult return ratio so low that it could not be compensated by recruitment of progeny at any plausible level of nesting success and hatching-year survival. Apparent recruitment of dispersers from other localities was not sufficient to prevent a decrease of population size. Because other breeding groups, also decreasing in size, on the mountain were not likely to be a net source of natal dispersers, we hypothesize that the new recruits into the Camp Creek population each year were dispersers from localities outside Hart Mountain for which postnatal site-fixation was weak. According to this postulate, additions to the breeding group were recruited from among spring migrants. If so, it is evident that migrating *oriantha* are not likely to encounter Hart Mountain in large numbers every year, and (or) that habitat cues there are near a threshold that triggers a preference response in only a few migrating individuals. This might be expected of a locality near an animal's distributional limits, and is potentially another of the

TABLE 10. Summer time budgets of female Mountain White-crowned Sparrows at three localities.

Period (days):	Locality <sup>a</sup>		
	Camp Creek (3/60)	Tioga Pass (4/201)	Niwot Ridge (4/55)
♀♀ on breeding grounds <sup>b</sup>	130	133	142
Prereproductive <sup>c</sup>	13	15	26
Reproductive <sup>d</sup>	70	73	61
Postreproductive <sup>e</sup>	47	45	55
Molting, individuals <sup>f</sup>	53	48	?
Molting, population <sup>g</sup>	76	65	59

<sup>a</sup> Camp Creek: this investigation; Tioga Pass: elevation 3,020 m, central Sierra Nevada, California; Niwot Ridge, elevation 3,125 to 3,475 m, Front Range, Colorado; numerals in parentheses = number of years of study/number of nests used to define nesting schedule.

<sup>b</sup> Error = About 2 days for arrival, 4 days for departure.

<sup>c</sup> From arrival of first female to completion of first nest.

<sup>d</sup> From first egg of earliest clutch to day 8 postfledging from latest nest (young semi-independent but still attended by one parent). Postnatal molt may begin at the end of this period.

<sup>e</sup> From the end of the reproductive period to departure on migration.

<sup>f</sup> Data from Table 5. Note that the difference between Camp Creek and Tioga Pass is greater in males and juveniles than in females.

<sup>g</sup> From first initiation to last completion of molt in the population.

local factors that affect the stability of the population. It should not be overlooked, however, that the adult return ratio apparently plays a large role in the dynamics of population balance, and may be related more to events on the wintering grounds or during migration than to the characteristics of the nesting grounds.

*Summer time budget.* The duration of the season favorable for nesting, molting, and ancillary events decreases as altitude or latitude increases, and birds at high altitudes and latitudes must abbreviate their behavioral and physiological cycles accordingly (Morton 1976). On the basis of the hypothesis that some peculiarity or constraint of the summer time budget of *oriantha* at Camp Creek might help account for their decreasing numbers we compared their summer time budget with time budgets of populations at Tioga Pass (3,020 m; Morton and colleagues, many publications) and Niwot Ridge (3,475 m; Hubbard 1978; J. R. King, unpubl. observ.). Only the general results of this analysis are germane to the present context, and so we refrained from details and attempted to compress a statement of criteria and assumptions into footnotes in Table 10. The summer time budgets at the three localities are similar, and the budgets from Camp Creek and Tioga Pass differ mainly in the longer period of molt in individuals and in the population at Camp Creek (cf. Table 5). Population size at Tioga Pass has been relatively stable since at least 1968 (M. L. Morton, pers. comm.). The

*oriantha* at Niwot Ridge stay on the breeding grounds about 10 days longer than at the other localities, mainly because they linger after the postnuptial molt has ended. They also loiter for about twice as long during the prereproductive period, feeding on a rich source of aeolian insects carried to Niwot Ridge by prevailing winds from the east and deposited on the snow. This enables them to commence nesting as soon as melting of the unpredictable snowpack uncovers suitable nesting substrates. They compensate partly for this delay by spending about 10 days less in reproductive activity than at the other localities, in part because of better initial synchrony among pairs and in part because loss to predation and weather is relatively low and renesting cycles are fewer than at Tioga Pass and Camp Creek.

In sum, we have not detected any shortages of time in the summer schedule of essential activities by *oriantha* at Camp Creek. Indeed, they seem not to have exploited the plasticity of their behavioral and physiological cycles to the extent possible by overlapping nesting with molting (e.g., Payne 1972), by abbreviating the molts to the spans typical of Tioga Pass (cf. Table 5), or both. Such adjustments could substantially lengthen the period available for renesting, and hence help to compensate for the unusually heavy losses of nests to predation and weather at Camp Creek. We can only speculate that such adjustments have not occurred because either (a) hot, dry weather after mid- to late July is unfavorable for reproduction (see above), and a relaxation of the reproductive time budget would be of no avail, or (b) populations of *oriantha* at Camp Creek have been too unstable to be subjected over several generations to selection for adaptation to local conditions.

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