cannot be dismissed but is unlikely because both House Wrens and Rufous-and-White Wrens breed over a larger portion of the year than the portion during which interspecific infanticide was evident or apparent (pers. observ., Morton and Farabaugh 1979). The hypothesis of competition for food, however, is supported by the temporal distribution of infanticidal events.

The association between food shortage and infanticidal behavior admits the possibility that the interspecific infanticide was related to competition for food. The association is also consistent with Wien's (1977) assertion that competitive processes may only be expressed during extreme conditions in variable environments. The House Wrens, renesting in the same boxes, did not begin to feed new nestlings for approximately one month after the nesting failure. Rufous-and-White Wrens in the area would therefore have reduced the food demands of House Wrens for that time, possibly making the food available to themselves. Both species were observed to search for insects and spiders on the ground in similar locations, suggesting the potential for competition, but more information on the diversity of prey items and foraging substrates utilized by each species is needed. While this is the first case of interspecific infanticide associated with a food shortage, additional and more detailed observations of interactions between these two species of wrens during another food shortage may establish more firmly the conditional nature and the selective basis of the infanticide.

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SEASONAL CHANGES IN BILL LENGTH IN SUMMERING MOUNTAIN WHITE-CROWNED SPARROWS[1]

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Key words: Bill length; seasonal changes; Zonotrichia leucophrys; *White-crowned Sparrow; montane biology.*

Bill dimensions have served as a primary source of information in a wide range of avian biology studies. Bill length, in particular, has been of value because it is an easily measured, highly heritable, morphological character that is directly correlated with feeding ecology and thus especially responsive to natural selection (Van Valen 1965, Willson 1969, Rothstein 1973, Boag and Grant 1978, Smith and Zach 1979).

It has been known for several decades that bill lengths vary seasonally, being longer in summer by as much as 10%. This effect seems greatest and most predictable in species that exhibit a winter-summer switch in diet from seeds to insects (Clancey 1948; Steinbacher 1952; Davis 1954, 1961; Selander 1958; Selander and Johnston 1967; Johnson 1977).

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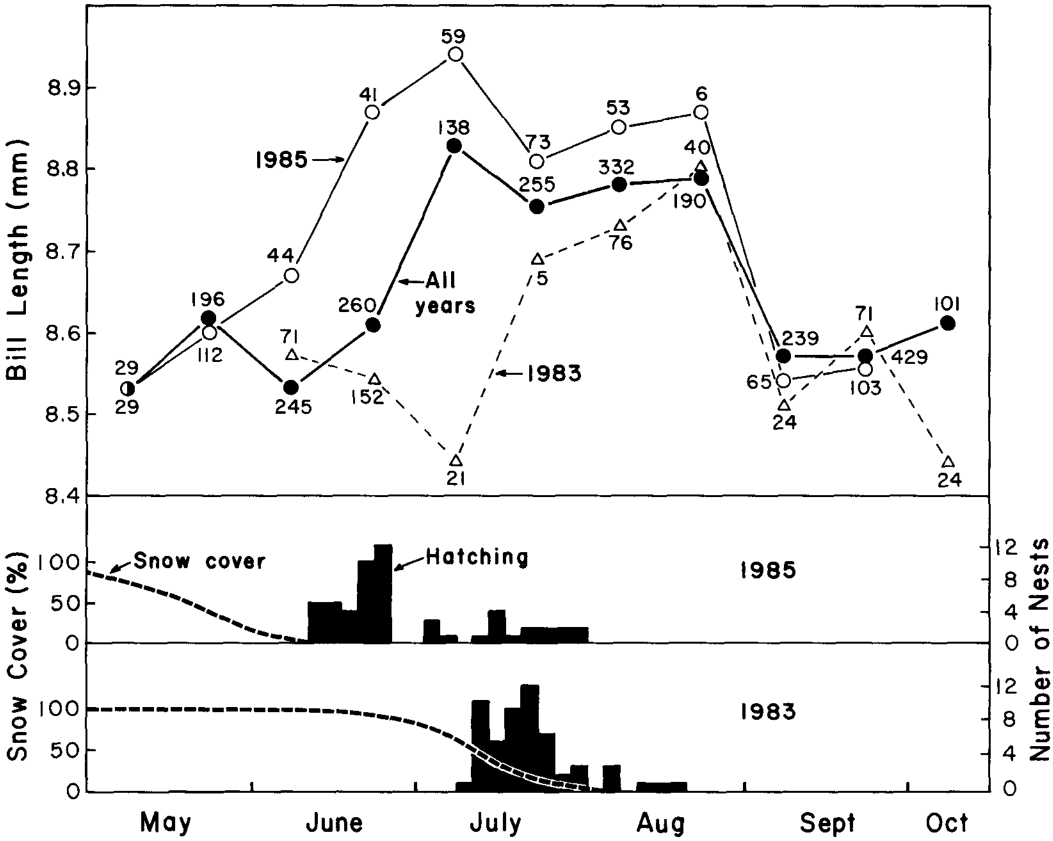

FIGURE 1. Seasonal changes in mean bill length and hatching schedule in *Zonotrichia leucophrys oriantha* and of snow cover on the study area. Numerals give sample sizes.

Most of the studies incorporating bill lengths have relied upon museum specimens, thus the magnitude and timing of changes in populations, let alone individuals, usually have been unknown. Herein we report bill lengths obtained during four summers (1982 to 1985) on adult members of a banded, migratory population of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) from the time of their arrival on the breeding grounds in May or June until their departure in September or October.

METHODS

The study area was a group of subalpine meadows in the Sierra Nevada near Tioga Pass, Mono County, California that contained about 70 pairs of adults each summer. We conducted routine live-trapping operations in the morning hours on this population throughout the season. All birds were banded and data files were compiled on every individual. At the time of trapping we recorded body weight, fat class, bill length, wing length, and molt status. Bill length was measured to the nearest 0.01 mm with vernier calipers from the anterior edge of the nostril to the bill tip. All measurements were made by the senior author.

RESULTS

There was a clear-cut seasonal change in bill lengths of adult *Z. l. oriantha* when data for all years were combined (Fig. 1). Bills became significantly longer as the summer progressed (compare May and June versus July and August, Table 1A). They then decreased significantly and rather quickly to a length indistinugishable statistically from that of early summer (Table 1A). Data used in Figure 1 were not separated for the sexes because their mean bill lengths were very similar (Table 1B), and because plots of the data did not reveal consistent sexual differences in the seasonal pattern.

During the four years of our study there was considerable interannual variation in the cycle of bill lengths, with elongation occurring earliest in 1985 and latest in 1983 (Fig. 1). Disappearance of snow from the study area and appearance of nestlings also had quite different schedules in these two years (Fig. 1). The timing of bill-length decrease did not, however. Mean bill length, as a result, was significantly shorter in 1983 than in 1985 (Table 1C).

To determine the magnitude of seasonal bill-length change in individuals, we selected minimum and max-

TABLE 1. Bill length measurements of adult *Zonotrichia leucophrys oriantha*. *P* values determined by *t*-tests.

	Mean	SD	*n*	*P*
A. Months (all years)				
May, June	8.58	0.34	730	<0.001
July, August	8.78	0.31	915	<0.001
September, October	8.58	0.31	769	
B. Sex (all birds)				
Males	8.66	0.40	1,412	>0.05
Females	8.64	0.32	1,002	
C. Year				
1983	8.59	0.34	484	<0.001
1985	8.68	0.33	586	
D. Sex (selected birds)				
Males, minimum	8.55	0.23	10	<0.001
Males, maximum	9.18	0.20	10	
Females, minimum	8.40	0.26	10	<0.001
Females, maximum	9.03	0.25	10	

imum bill lengths measured for 10 males and 10 females that had been trapped repeatedly in a given season (mean number of captures was 18.6 for males and 16.1 for females). For each sex the total change in bill length was highly significant (Table 1D). The relative magnitude of the change for each sex was identical, 7.4%.

DISCUSSION

Our data appear to be the first ever reported for seasonal changes in bill length in the same individuals. The results agree with those obtained on populations in several other studies in that bills of adults invariably increased in length during the summer. The surprise was that they then also decreased rather quickly and were short again before the birds left on fall migration. Hints of this type of cycle can be found in the data of others. Banks (1964), for example, found that bills were shorter in early and late summer than in midsummer in some of his *Z. l. oriantha* samples. And three of seven taxa of *Leucosticte* measured by Johnson (1977) seemed to follow a similar pattern.

Davis (1954, 1961) has discussed most thoroughly the bill length-increase phenomenon. He rejected Clancey's (1948) hypothesis that the response was selected for because the birds would have a longer bill, better suited for insect catching, at a time when insects were most available. He also felt it unlikely that increased protein intake, in the form of insects, was responsible for an acceleration of bill growth. Davis reasoned that seasonal variation in bill length occurred because of some variable environmental factor. An increased abundance of insects in summer was most likely to be that factor because it prompts dietary changes, from granivory to insectivory, that affect the degree of mechanical wear on the constantly growing bill tip. Insect capturing and eating is not likely to be as abrasive as pecking in the ground for seeds, then hulling them. This hypothesis, by extension, would explain the late summer decrease in bill length observed in our study as being caused by a return to granivory.

Data from two years with greatly different phenologies help to resolve these questions. In 1983 the snowpack at Tioga Pass was unusually heavy and clearing of the meadows by meltoff was delayed as was the reproductive schedule of *Z. l. oriantha*. Bill lengths did not increase until late July. In 1985, the pack was light, meltoff and reproduction occurred relatively early and the increase in bill length was already evident in May and June. Miller (1941) noticed an analogous effect in *Junco hyemalis*. Bill lengths were significantly shorter in a Nevada population prevented by deep snows from reaching their breeding area than in a Utah population that had already begun the breeding cycle because of more favorable conditions. For early season changes, Miller's data and ours are in accord with Davis's hypothesis that bill length is linked to food availability. Late season changes are another matter, however. In all four years of our study, even such disparate ones as 1983 and 1985, the rapid decrease in bill length occurred during early September. It seems unlikely that levels of insect abundance each year follow similar calendar schedules. We know, in fact, that they do not. In 1984 and 1985 we assayed insect abundance with pan traps and plots of the data show that the peaks in abundance occurred a full month apart, being earliest in 1985. The difference between 1983 and 1985 would be expected to be even greater.

The common physiological event observed by us to occur during the period when bills shorten is the postnuptial molt. This molt usually starts in late August or early September and lasts for seven weeks in individuals (Morton and Welton 1973). Growth of new feathers requires a considerable deposition of protein for that purpose (see Murphy and King 1984). It seems possible that the growth rate of the bill could be slowed during this time because of protein reallocation. Protein intake may also decrease simultaneously. We make this suggestion because insect biomass at Tioga Pass is at or near a seasonal low in September. Also, our observations of birds in heavy molt indicate that they exhibit lessened mobility, no longer engaging in flycatching behavior, for example. They become quite secretive, tending to stay within thick cover and restricting their feeding choices accordingly. Thus three factors, lessened availability of high protein food, protein reallocation, and, probably of greatest importance, changes in foraging behavior could all be contributing to the autumnal decrease in bill length observed in *Z. l. oriantha.* A final point, obvious but worth stating, is that changes of the magnitude we describe and their temporal characteristics must be taken into consideration by those who wish to attach significance to intra- and interspecific variations in bill length.

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