North American Bird Bander

Volume 3 | Issue 4 Article 2

1978

Latitudinal Variation in Prenuptial Molt in Wintering Gambel's White-crowned Sparrows

L. Richard Mewaldt

James R. King

Latitudinal variation in prenuptial molt in wintering Gambel's White-crowned Sparrows

L. Richard Mewaldt and James R. King

Wintering Gambel's White-crowned Sparrows, *Zonotrichia leucophrys gambelii*, complete an extensive prenuptial molt and accumulate substantial fat deposits prior to leaving on northward spring migration. To study these relationships and other facets of the biology of White-crowned Sparrows, the Western Bird Banding Association, with the encouragement of Professors Charles T. Collins and Arthur E. Staebler, and then President Michael San Miguel, sponsored the "White-crowned Sparrow Project" from 1974 to 1977 (Staebler 1974a, 1974b, 1974c; Mewaldt 1975, 1976). Some aspects of the prenuptial molt including its timing in relation to latitude and ambient temperature are the concern of this report.

Thirty-seven WBBA members, all permittees in the United States or Canadian North American Bird Banding programs, provided data. More than 20,000 bird-lines of data were submitted in 1975, 1976, and 1977. Cooperating station operators extend from San Diego, California to Juneau, Alaska, and from the Pacific Coast to Oklahoma and Texas. Some of these records have been used in this report and most will be used in reports in preparation. Cooperators who contributed are named in the Appendix.

Methods

Most cooperators were advantageously located in appropriate habitat to capture, band, and recapture White-crowned Sparrows on their wintering grounds. A few cooperators were located on migratory routes and a few on the breeding grounds of one of the races. Ground traps baited with grain, or mist nets were used to capture birds. To encourage uniformity and to facilitate analysis, cooperators submitted their findings on project schedules, SJSU ABL 71-1 (see North American Bird Banding Manual, 1977, Vol. II, page 5-7 for schedule format). Additional data, especially some used in this report, were supplied in a prescribed format under notes. These included certain feather measurements and notes on the prenuptial molt. Feathers were measured to the nearest whole millimeter from emergence from the skin to the tip.

Prenuptial molt

The extent, pterylographic sequence, and duration of the prenuptial molt in *gambelii* have been described by Law (1929), with refinements by Michener and Michener (1943). The careful observations of the Micheners may be consulted for details of the involvement of each of the feather tracts. In general, most body feathers, some but not all of the wing coverts, and all head feathers are usually replaced. Not replaced are the nine primaries, secondaries 1 to 6, the alula, and rectrices 2-2 to 6-6. Usually, but not always, replaced are secondaries 7 to 9, and the decks (rectrices 1-1). Law (1929) suggested that because secondaries 7 to 9 and the decks molt independently of the other remiges and rectrices, they are really modified coverts. Because of their general accessibility for observation and measurement, we selected the decks and secondaries 7 to 9 for more detailed study.

Feather growth rates

The length of time required to replace each feather in molt has an important bearing on the duration of the molting process. Sufficient numbers of measurements of the decks of the same individual birds at intervals of 3 to 14 or so days were made by five cooperators (Table 1). As will be shown later (Fig. 1) the growth rate of the decks becomes less through time, but the mean rate of growth from emergence to completion is 2.75 ± 0.40 mm (standard deviation) per day. Rate of growth was not significantly different ($P<0.001$) between any two stations even though the extreme distances between them approximate 1000 km and 6

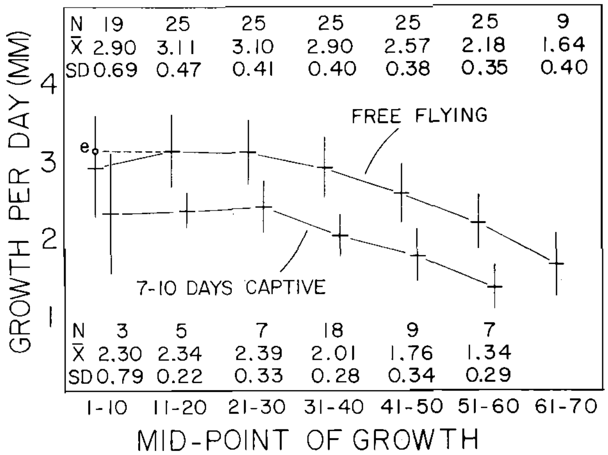


Figure 1. Deck (rectrices 1-1) growth per day in relation to mid-points between members of pairs of deck measurements in Gambel's White-crowned Sparrow. Lower curve represents growth during the first 7 to 10 days in captivity. The symbol e is an estimate of true growth in the first 10-day period (see text).

degrees of latitude. Chapel (1977) making an independent analysis of his own data reports an average growth rate of 2.7 mm per day. It thus takes 25.5 days to regrow a 70 mm deck from emergence, or about 27 days from normal shedding. As the new feather develops, the old feather remains rather weakly attached and drops when some activity of the bird dislodges it. In the case of the decks, our casual observations suggest this is usually one or two days prior to emergence of the feather bud from the skin.

Growth rate is about 3.12 mm per day for the first ten days from emergence (Figure 1) and drops to considerably less than 1.00 mm per day in the final 2 or 3 days. The measured rate of 2.90 mm per day in the 1-10 mm growth range (Figure 1) is distorted downward because some measurements were taken as zero when the decks had not yet emerged from the papilla.

There are but few comparative data on the growth of the flight feathers in crowned sparrows. In caged *gambelii* exposed to natural weather and photoperiod at Fairbanks, Alaska (captured 15-20 days before the onset of molt), the total growth rate to full length in primaries 1, 5, and 9 averaged 2.76, 3.04, and 2.32 mm per day (Chilgren 1978). He, too, found the rate of growth to be initially higher than the overall average and that the rate later diminished, as in the growth of the feathers already described in this report.

We measured deck growth rate for the first 7 to 10 days in captivity for 49 *gambelii* at San Jose (Figure 1 and Table 1). Overall growth rate was 1.97 mm per day, or 0.78 mm less per day than the overall rate in five populations of free flying birds. This depression in rate of feather growth in the first days in captivity apparently disappears when the birds have become adjusted to cage life. This suggests, however, that investigators should excercize caution in the interpretation of feather growth rate data of birds during at least the first ten days of their captivity.

We took similar paired measurements several days apart of secondaries 7 and 8 from free flying *gambelii* in the San Jose winter population in 1977. Growth rates from emergence of about 2.25 mm per day (Table 1) are about 0.50 mm less per day than the rate for the decks in the same group of birds.

The pattern of prenuptial molt

Information on the sequence and intensity of molt in various components of the plumage is available only for the populations of *gambelii* at San Jose

Table 1. Growth rates of decks (rectrices 1—1) at several locations in California and Arizona and of secondaries 7 and 8 at San Jose, California, in Gambel's White-crowned Sparrow. Each observation consists of two measurements of the same feather upon capture of the same bird several days apart.

Location	Observations	Feather days of growth	Growth (mm)	Growth per day (mm)
Rectrices 1—1 in free living birds				
Grizzly Is., CA (1975 & 1976)	62	709	1911	2.70
San Jose, CA (1976 & 1977)	111	895	2487	2.78
Fresno, CA (1976)	34	325	897	2.76
Cave Creek, AZ (1975 & 1976)	35	305	850	2.79
Fallbrook, CA (1977)	34	272	743	2.73
Rectrices 1—1 in birds free living to captive[1]				
San Jose, CA (1975)	49	438	864	1.97
Secondary 7 in free living birds				
San Jose, CA (1977)	13	89	203	2.28
Secondary 8 in free living birds				
San Jose, CA (1977)	30	166	371	2.23

[1]First measurement upon capture and second after 7 to 10 days in captivity.

Table 2. Sequence of molt of selected plumage components in Gambel's White-crowned Sparrows in 1977 at San Jose, California.

Date	5 Feb	12 Feb	16 Feb	20 Feb	23 Feb	28 Feb	5 Mar	12 Mar	19 Mar	26 Mar	2 Apr	6 Apr	10 Apr	17 Apr	23 Apr
Number of birds	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35
Body molt															
none	33	21	19	12	2	1						5	15	23	27
light	2	14	12	21	27	17	8	1			9	18	14	10	6
medium			4	2	5	17	23	20	4	8	16	7	5	2	2
heavy					1		4	14	31	27	10	5	1		
Rectrices 1 — 1															
old	33	31	28	30	22	12	11	7	5	1	3	2	2	1	2
grow	2	4	7	5	13	23	24	27	25	11	3	2	1	1	1
new								1	5	23	29	31	32	33	32
Secondary 7															
old	35	35	33	35	34	24	15	9	5	2	2	1	5	7	
grow			2		1	11	18	26	14	15	5	2		1	
new							2		16	18	28	32	30	27	—
Secondary 8															
old	34	25	18	16	9	6	3	1							
grow	1	10	17	19	26	22	23	15	2	1	1	2			
new						7	9	19	33	34	34	33	35	35	—
Secondary 9															
old	34	29	30	30	29	28	18	11	4	1	1				
grow	1	6	5	5	6	6	11	19	12	11	4	2			
new						1	6	5	19	23	30	33	35	35	—
Crown molt															
Number of birds[1]	24	26	22	21	20	21	26	22	19	14	13	16	11	16	22
% each renewed															
0%	24	26	22	20	15	16	16	11	1						
1 to 49%				1	5	5	10	10	12	6	1				
50 to 99%								1	5	6	4	1	2		
100%									1	2	8	15	9	16	22

[1]Only second year birds were judged for completeness of crown molt.

and the Snake River Canyon of southeastern Washington. We have greater detail from San Jose (Table 2), which shows that growth in the body tracts, decks, and in secondaries 8 and 9 begins essentially simultaneously, followed by the onset (if any) of growth in secondary 7 about 15 days later and the onset of crown molt about 20 days later. The growth of the decks in individual birds is complete about ten days later than secondary 8; about the same time as secondaries 7 and 9; and 10-15 days before the end of body molt. The renewal of the crown plumage is completed several days before the completion of growth in the body plumage. From an examination of the last three samples (Table 2) in each plumage category we find that about 5 percent of the birds failed to renew their decks (cf. Chapel 1977, who reports the same proportion at Fresno, California), about 14 percent did not renew secondary 7, all replaced secondaries 8 and 9, and all second-year birds completely replaced their crown plumage, thus acquiring the black-and-white pattern of the adult plumage.

Several elements of the prenuptial molt in *gambelii* contrast with those of the *Z. l. nuttalli-pugetensis* complex of the Pacific Coast (Mewaldt et al., 1968). For example, of *nuttalli* from southerly latitudes (35°-40° N) held captive at San Jose, none renewed their decks or secondaries. Many to most *pugetensis* from intermediate latitudes (41°-49° N) renewed decks (60-80%) and at least secondaries 8 and 9 (85%). Nearly all free-flying *gambelii* (this study), probably from a wide range of northerly latitudes (50°-68° N), wintering at San Jose renewed decks (95%), secondaries 8 and 9 (nearly 100%) and secondary 7 (86%). We have additional data confirming the intermediate position of *pugetensis*. A sampling of birds wintering at San Jose (Table 3) shows that of 40 April-caught birds, less than 60% renewed their decks; and from half (secondary 7) to nearly all (secondary 8) renewed secondaries 7, 8, and 9. Blanchard (1941) reported that no *nuttalli* molted decks, and that of 57 late spring *pugetensis*, 22 definitely molted their decks, 12 definitely did not, and the remaining 23 were in doubtful status.

Thus in accordance with their nativity, these three races of White-crowned Sparrows (*nuttalli*, *pugetensis*, and *gambelii*) exhibit a stepped cline, from south to north, in population involvement in the prenuptial molt. Coincident with this cline in flight feather molt, crown molt is absent to partial in *nuttalli*, nearly always complete in *pugetensis* (e.g. Blanchard, 1941), and complete in *gambelii*. The thoroughness of the crown replacement in second year *gambelii* is confirmed by all project cooperators sampling them on the race's extensive winter range.

Geographical variation of prenuptial molt

Sufficiently detailed and temporally distributed data are available from eight locations extending through 13 degrees of latitiude from San Diego, California north to the Snake River Canyon of southeastern Washington. We have analyzed these data by plotting on a probability scale (e.g. Figure 2) the cumulative percentages of *gambelii* through the molting season at each locality that had the deck rectrices in growth or fully grown. A probability scale (the vertical axis in Figure 2) converts a normal (or "S-shaped") cumulative distribution of data to a straight line and greatly simplifies the analysis. All eight probability plots are essentially linear, as in Figure 2, and demonstrate that the onset and completion of molt are normally distributed in time at these sample sites. We can therefore very easily compare geographical variants in the calendar of molt by comparing a selected reference point on the probability scale (e.g. 50%) and its corresponding dates. The duration of molt in the decks (or the body) can also be estimated as the elapsed days between the regression lines on the basis of the assumption that the first birds to begin the molt are also the first ones to finish it, and so on through the population.

Several significant points emerge from this analysis (Table 4). First, the graphic estimate of the duration of molt in the decks varies from 24 to 27 days, averaging 25.6 days. This agrees well with the average (25.5) determined by direct observation of individuals (Table 1 and accompanying text) and verifies the sensitivity of the graphic analyses. Note that there is no significant or consistent geographic variation in the time it takes a deck remige to grow to its full length. This is an unexpected result that we shall return to later.

Second, the duration of the body molt in individuals, as estimated graphically, exceeds that of deck molt at both San Jose and in the Snake River

Table 3. Percent incidence of deck and secondary replacement in the prenuptial molt of Puget Sound White-crowned Sparrows wintering at San Jose, California 1976 and 1977

				Secondaries					
		Decks		Seven		Eight		Nine	
Month	Number	Old (%)	Grow[1] (%)	Old (%)	Grow[1] (%)	Old (%)	Grow[1] (%)	Old (%)	Grow[1] (%)
Feb	80	85	15	99	1	72	28	99	1
Mar	79	62	38	69	31	15	85	57	43
Apr	40	42	58	50	50	2	98	12	88

[1]Includes decks or secondaries newly grown.

Canyon (the only sites for which we have adequate data on this aspect of body molt), being 15 days shorter at the northern site, and beginning about 23 days later (Table 5). This resembles the progressive northward abbreviation of postnuptial molt in *Z. l. nuttalli* and *Z. l. pugetensis* (Mewaldt and King, 1978) and amounts to the same proportional reduction (28%) in the two molts between equivalent latitudes. The calendar reduction, however, is 15 days for prenuptial molt (this paper) compared with 22 days for postnuptial molt (Mewaldt and King, 1978).

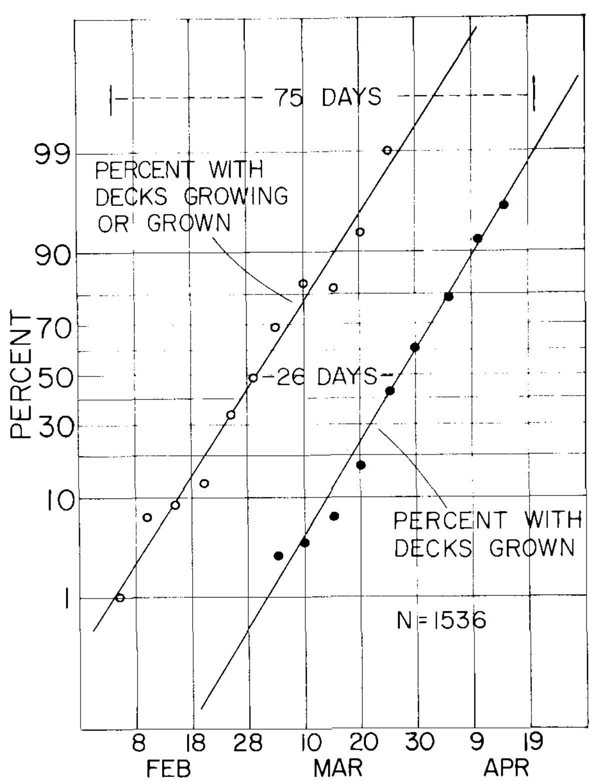


Figure 2. Progress and duration of deck (rectrices 1-1) molt in Gambel's White-crowned Sparrow at San Jose, California. Data for 1975, 1976, and 1977 are combined. Ninety-eight percent of the population completed deck molt in the 75 days between 4 February and 20 April.

Table 4. Temporal aspects of the growth of decks (rectrices 1—1) in Gambel's White-crowned Sparrow during the prenuptial molt in relation to latitude and January temperature.

Locality (Cooperator years)	Lat. (°N)	Jan. mean temp. (°C[1])	Date on which 50% of population have decks: Growing	Complete	Mean duration of deck molt in days	Duration of deck molt in 98% of population in days	Synchrony ratio[2]	Number of obs.
Portal, AZ (Spofford, 76)	32	7	10 Mar	—	—	—	—	111
San Diego, CA (Johnson, 76-77)	33	13	02 Mar	27 Mar	25	77	3.1	101
Fallbrook, CA (Ferris, 77)	33	13	27 Feb	25 Mar	26	82	3.2	309
Cave Creek, AZ (Radke, 75-76)	34	11	24 Feb	22 Mar	26	80	3.1	274
Fresno, CA (Chapel, 75-76)	37	7	09 Mar	03 Apr	25	62	2.5	980
San Jose, CA (Mewaldt, 75-77)	37	9	01 Mar	27 Mar	26	75	2.9	1536
Pleasanton, CA (Jacobson, 75-76)	38	8	08 Mar	03 Apr	26	70	2.7	119
Benicia, CA (Stoner, 75-76)	38	8	13 Mar	—	—	—	—	458
Grizzly Is., CA (Gill, 75-76)	38	8	07 Mar	03 Apr	27	61	2.3	709
Snake River, WA (King, 55-66)	46	1	30 Mar	23 Apr	24	49	2.0	687

[1]USDA, 1941

[2]Duration in population (98%)/duration in an individual.

Third, the synchrony of molt among individuals in a population increases northward (Table 4), as indicated by the 77 to 82 days for deck molt in the population (98% as determined graphically) in southern California and Arizona, 61 to 75 days in central California, to 49 days in southeastern Washington. This is also reflected in the ratios of the duration of deck molt in an individual to the duration of deck molt in the population which ranges from 3.2 in the south (San Diego) to 2.0 in the north (Snake River Canyon). Although the sample size is marginal ($N = 8$) for analysis by the z* transformation of the product-moment procedure (Skokal and Rohlf, 1969), the correlation between latitude and duration of deck molt in the populations is significant ($r = -0.909$, $P < 0.05$). This implies that latitude, or more properly some correlate of latitude such as temperature or photoperiod, accounts for 83 percent ($r^2 = 0.826$) of the variability in the sample.

When we make the test with temperature as the related variable, we find the correlation between temperature and the duration of deck molt in the populations is even more significant ($r = 0.934$, $P < 0.05$). We can point out that the sign (+ or —) of the derived value of r is not relevant. Together with the correlated finding that temperature accounts for 87 percent ($r^2 = 0.872$) of the variability, these tests suggest that the role of decreasing late winter temperature, more than some other consequences of increased latitude, influences the timing of the prenuptial molt to be later in the spring season.

The increased coordination of events with increasing latitude (or altitude) is a common finding in our investigations of the White-crowned Sparrow. It is expressed in the extreme, for instance, as a population/individual ratio of 1.2 for the postnuptial molt of *gambelii* at 65°N in central Alaska (King, unpublished data). This ratio (1.2) may be compared with the synchrony ratios in prenuptial molt in Table 4.

Fourth, the progressive northward delay in the onset of prenuptial molt (Table 4) averages 3.4 days per degree (by linear regression), closely conforming with the "bioclimatic rule" (Hopkins 1920) that phenological development is delayed by 3 to 4 days for each degree of latitude northward. The onset of postnuptial molt in the Pacific coastal *Z. l. nuttalli-pugetensis* complex does not follow this

"rule" but is instead correlated with the end of the breeding season (Mewaldt and King, 1978). We further note that rates of phenological change and geographical differences in biological responses, related to increasing day length, are much more prominent, and thus predictable, in these middle and higher latitudes in late winter and spring than in mid-summer.

Finally, we return to the apparent paradox presented by a geographically invariant period of growth in the deck remiges coupled with a northward decrease in the duration of the total prenuptial molt. *A priori*, we had expected to find an increase of growth rate of the decks with increasing latitude, but this clearly is not true (Tables 4 and 5). Although the basis for the abbreviation of head and body molt relative to deck molt is not clear from our own data, we note that Chilgren (1978) found in captive *gambelii* that the shedding interval between feathers in a tract was progressively shorter by about 21% between temperatures of 25 and 5° C and that the intervals between the onset of molt in various tracts likewise were generally shorter at colder temperatures. In effect, the sequence of molt was compressed without necessarily involving a reduced rate of growth in individual feathers. We believe that this is a plausible explanation for our results, but recommend continued investigation to examine its credibility for free-living birds.

Summary

The results of this cooperative investigation provide a reliable calendar for the onset of prenuptial molt in Gambel's White-crowned Sparrow and show that it is progressively delayed northward. The rate and duration of growth of the deck rectrices in individual birds are geographically invariant, as is probable also for all the feathers. The northward reduction in the duration of the total molt probably results from a temperature-dependent reduction of the shedding interval between feathers within a tract and from a compression of the time interval between the onset of molt in various tracts. This, however, requires additional investigation before acceptance as a reliable generalization. The synchrony of prenuptial molt among individuals in a population progressively improves northward. The net result of the aforementioned geographic differences and other adjustments is an environmentally induced reduction of the time devoted to prenuptial molt in both individuals and populations in the north. This is presumably a result of co-evolution of time requirements of molt and other events of the birds' annual cycle in relation to environmental seasonality.

Table 5. Comparative timing and duration of body molt and deck molt in wintering Gambel's White-crowned Sparrows in Washington and California.

	Body molt			Deck molt		
	Start	Finish	Duration	Start	Finish	Duration
Snake River Canyon Washington	15 Mar	23 Apr	39 days	30 Mar	23 Apr	24 days
San Jose California	20 Feb	15 Apr	54 days	1 Mar	27 Mar	26 days

The WBBA Cooperative White-crowned Sparrow Project has provided in a relatively short time a data base that would have required decades to produce by isolated investigators. As exemplified by this report, the cooperative work has illuminated biological patterns on a large regional scale. Like all sound research, it has also identified significant questions for further investigation.

Literature cited

Blanchard, B.D. 1941. The White-crowned Sparrows *(Zonotrichia leucophrys)* of the Pacific seaboard: environment and annual cycle. Univ. Calif. Publ. Zool. 46:1-178.

Chapel, M. 1977. The biology of a wintering population of Gambel's White-crowned Sparrows near Fresno, California. M.A. Thesis, California State University, Fresno. 83pp.

Chilgren, J.D. 1978. Effects of photoperiod and temperature on postnuptial molt in captive White-crowned Sparrows. *Condor* 80:222-229.

Hopkins, A.D. 1920. The bioclimatic law. *Journal Wash. Acad. Sci.* 10:34-40.

Law, J.E. 1929. The spring molt in Zonotrichia. *Condor* 31:208-212.

Mewaldt, L.R. 1975. White-crowned Sparrow Project 1974-75. *Western Bird Bander* 50:50-51.

Mewaldt, L.R. 1976. White-crowned Sparrow Cooperative Project, present and future. *North American Bird Bander* 1:87.

Mewaldt, L.R. and J.R. King. 1978. Latitudinal variation in postnuptial molt in Pacific Coast White-crowned Sparrows. *Auk* 95:168-179.

Mewaldt, L.R., S.S. Kibby, and M.L. Morton. 1968. Comparative biology of Pacific Coastal White-crowned Sparrows. *Condor* 70:14-30.

Michener, H. and J.R. Michener. 1943. The spring molt in the Gambel Sparrow. *Condor* 45:112-116.

Sokal, R.R., and F.J. Rohlf. 1969. Biometry. W.H. Freeman & Co., San Francisco. 776pp.

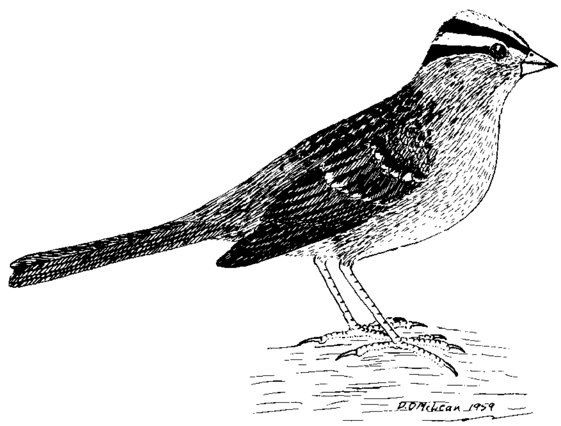
Staebler, A.E. 1974a. New W.B.B.A. venture: cooperative banding projects. *Western Bird Bander* 49:6.

Staebler. A.E. 1974b. W.B.B.A. cooperative banding project: White-crowned Sparrow. *Western Bird Bander* 49:22.

Staebler, A.E. 1974c. Progress report of the W.B.B.A. cooperative White-crowned Sparrow banding project. *Western Bird Bander* 49:66.

U.S. Department of Agriculture. 1941. Climate and Man. Yearbook of Agriculture. 1248pp.

Avian Biology Laboratory, San Jose State University, San Jose, California 95192 and Department of Zoology, Washington State University, Pullman, Washington 99164.



Appendix

Ernest R. Abeles	Woodland Hills, California
Keith A. Arnold	College Station, Texas
Carl Barrentine	Ellensburg. Washington
Kathryn B. Burk	Tucson, Arizona
Michael Chapel	Fresno, California
Charles T. Collins	Morongo Valley, California (Long Beach California)
Charles E. Corchran	Tucson, Arizona
Lloyda T. Cowley	Corvallis, Oregon
Bruce E. Deuel	Gridley, California
Richard L. Doutt	Santa Barbara, California
Donald S. Farner	Camano Island, Washington (Seattle, Washington)
Reed W. Ferris	Fallbrook, California
R.H. Gerstenberg	Reedley, California
Robert E. Gill, Jr.	Grizzly Island, California (Anchorage, Alaska)
Herman H. Gray	Chester, California
Dennis G. Hicks	Ellensburg, Washington
Elgin B. Hurlbert	Pacific Grove, California
Patricia Jacobson	Pleasanton, California
Virginia P. Johnson	San Diego, California
Edgar T. Jones	Oldman River, Alberta (Edmonton, Alberta)
James R. King	Snake River Canyon, Wash (Pullman, Washington)
Andrea Lajoie	Menlo Park, California
John MacDonald	Los Gatos, California
L. Richard Mewaldt	Hart Mountain NWR, Ore San Jose, California
Point Reyes Bird Observatory	Stinson Beach, California
Eleanor L. Radke	Cave Creek, Arizona
Shirley S. Spitler	Yuma, Arizona (Tucson, Arizona)
Sally F.H. Spofford	Portal, Arizona
Emerson A. Stoner	Benicia, California
Fern R. Tainter	San Luis Obispo, California
Don V. Tiller	Calipatria, California
James R. Travis	Los Alamos, New Mexico
Van A. Truan	Pueblo West, Colorado
Michael E. Ward	Arroyo Grande, California
John S. Weske	Norman, Oklahoma (Washington, D.C.)
Ralph B. Williams	Juneau, Alaska
Jerry Wooding	Carbondale, Colorado