

AGE- AND SEX-RELATED VARIATION IN SIZE AND CROWN PLUMAGE BRIGHTNESS IN WINTERING WHITE-CROWNED SPARROWS

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The White-crowned Sparrow (*Zonotrichia leucophrys*) is one of the most commonly studied and banded bird species in North America (King 1974; Mewaldt 1956, 1975, 1976). Despite this attention, sexing techniques that use external characteristics have not been established clearly (King and Mewaldt 1981, Sheppard and Klimkiewicz 1976). Males average larger and heavier than females (Banks 1964, Wood 1969), but the existence of substantial geographic variation has required that sexual limits be determined at the subspecific or even population level (Mewaldt 1977, Sheppard and Klimkiewicz 1976). This species' age dimorphism in winter crown plumage is well-known, but attention has not been previously directed to the variation in non-breeding crown appearance that exists within age groups. We report here a study of age- and sex-related variability in several characteristics of Gambel's White-crowned Sparrows (*Z. l. gambelii*) wintering around Santa Barbara, California, including wing length, weight, fat levels, tarsus length, bill length, and crown appearance. We show that individuals of this race can be sexed reliably on the basis of wing length. Also, as indicated by the work of others, we show that most other morphological characters average larger in males. We also demonstrate that crown plumage variation is sex-related in both immatures and adults.

METHODS

The sparrows in this study were live birds or museum specimens trapped or collected from the coastal plain within 25 km of the University of California at Santa Barbara (UCSB), Santa Barbara County. A subsample of 165 live birds was trapped from 0700 to 1400 between 22 January and 10 March 1978 and represents a random sample of White-crowned Sparrows from 4 sites. Sex was determined by laparotomy. We weighed each bird to the nearest 0.1 g and estimated its fat reserve by scoring fat in the furcular depression on a 7-point scale (0-6) modified after Helms and Drury (1960). Wing length was measured to the nearest mm along the chord of the unflattened right wing. A second subsample of 1039 live birds caught at various locations around UCSB over 3 years (1978-1981) was measured for wing length only and was not laparotomized. Following Mewaldt (1977), we categorized birds with tan and brown crowns as immatures (HY or SY according to the nomenclature of the Bird Banding Laboratory) and those with black and white or gray crowns as adults (AHY or ASY).

The 120 *gambelii* study skins we used are housed in the Vertebrate

Museum, UCSB. Collection dates are mid-September to late February 1943 to 1983. Age was determined by crown plumage differences and the sex noted on specimen labels was assumed correct. These birds were measured for wing, tarsus, and bill length and scored for crown plumage brightness. Wing length was measured as for live birds (above), but to the nearest 0.1 mm. Tarsus length was measured, to 0.1 mm, from the posterior edge of the right tarsometatarsus to the first undivided scute closest to and on top of a bird's foot. We believe that our techniques are accurate enough to justify measurements to 0.1 mm as a sample of 42 live adults measured twice in one season showed that the mean difference between each bird's first and second measurement was 0.4 mm for wing length and 0.2 mm for tarsus length. We measured bill length, to 0.1 mm, from the anterior edge of the right nostril to the bill tip.

Our criteria for quantifying crown appearance used study skins from the Vertebrate Museum, UCSB. We chose a series of 4 adults and 4 immatures (Fig. 1) that span the variation in crown appearance in these age categories. The bird with the most contrast between the dark lateral and the light medial crown stripes was assigned a score of 1, the dullest specimen a score of 4. Lateral stripes in adult sparrows are uniformly black, except in the dullest birds, which have some brown feathers, so our scoring for this age category concentrated on the central stripe, which ranges from bright white (1), to a dark gray (4). For immatures, all parts of the crown vary in color and brightness with plumages ranging from rich dark brown lateral stripes and a contrasting light tan central stripe (1), to a streaked medium brown plumage across the entire crown with almost no sign of separate stripes (4). The two intermediate specimens in each age category were chosen to create equal intervals between the extremes. For this study, the crown appearance of sparrows was recorded by matching each bird with the closest of the 4 specimens in the appropriate age series (1, 2, 3, or 4) or assigning it to one of the 3 intermediate categories (1.5, 2.5, or 3.5). All crown plumages were scored by GNF.

RESULTS

Wing length.—The sexes of the Gambel's White-crowned Sparrow are substantially different in wing length distributions (Fig. 2). In our sample of laparotomized birds, adult males averaged 78.2 mm ($N = 49$, $SD = 1.43$) and adult females 74.2 mm ($N = 34$, $SD = 1.43$), a highly significant difference ($t = 16.3$, $P < 0.001$). Immature males averaged 77.5 mm ($N = 43$, $SD = 1.59$) and immature females 72.8 mm ($N = 39$, $SD = 1.47$), also a significant difference ($t = 13.8$, $P < 0.001$). Our sample of museum specimens shows the same patterns, with adult males and females averaging 78.0 mm ($N = 44$, $SD = 1.67$) and 74.2 mm ($N = 29$, $SD = 1.77$), respectively ($t = 9.29$, $P < 0.001$), and immature males and females averaging 77.0 mm ($N = 27$, $SD = 1.11$) and 73.4 mm ($N = 20$, $SD = 1.14$), respectively ($t = 10.9$, $P < 0.001$). There were no significant differences ($P > 0.05$) between comparable series of live and museum specimens.



FIGURE 1. Photographs of our White-crowned Sparrow crown appearance series; adults (top) and immatures (bottom). Plumage varies in each age category from the brightest and most distinct crown (1) to the dullest crown (4). Birds in this study were matched with the closest specimen in these series (1, 2, 3, or 4) or judged as intermediate to 2 of the specimens (1.5, 2.5, or 3.5).

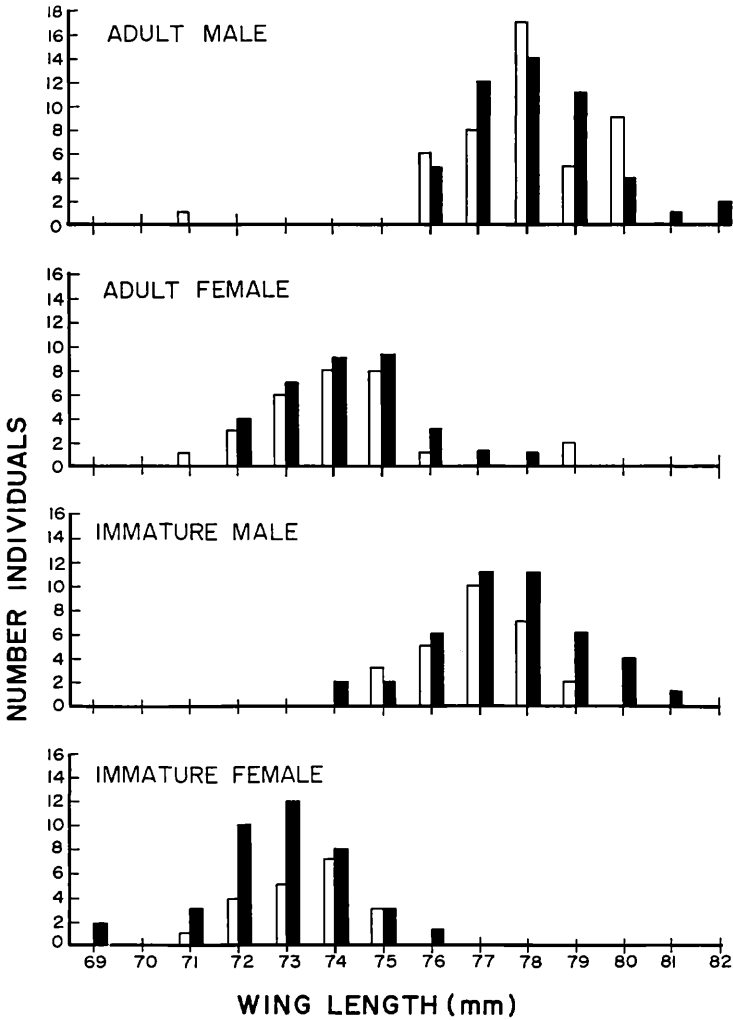


FIGURE 2. Wing length distributions for museum specimens (open bars) and live White-crowned Sparrows sexed by laparotomy (solid bars).

These data also show that adults are significantly larger in wing length than immatures of the same sex. For the laparotomized birds, adult males averaged 0.7 mm larger than immature males ($t = 2.22, P < 0.05$) and adult females averaged 1.4 mm larger than immature females ($t = 4.11, P < 0.001$). In the museum sample, adult males averaged 1.0 mm larger than immature males ($t = 2.76, P < 0.01$) and adult females 0.8 mm larger than immature females ($t = 1.78, P < 0.05$).

A striking feature of the wing length distributions from these data is

the small degree of overlap between sparrows of different sex within an age category (Fig. 2). In the combined data of live birds and museum specimens, 95.4% (83 of 87) of the adults with wing lengths ≥ 77 mm were male and 98.2% (55 of 56) with wing lengths ≤ 75 mm were female. It is also possible that two very large females (79 mm) and one unusually small male (71 mm) in the museum sample were mis-sexed, since they appear totally out of place in the data (Fig. 2). We conclude that these wing-length criteria are quite reliable for determining sex in White-crowned Sparrows of the Santa Barbara area. Only adult sparrows with wing lengths of 76 mm cannot be confidently sexed (11.1% of the males, 6.2% of the females). Among immatures in the combined sample, 98.4% (63 of 64) of the birds with wing lengths ≥ 76 mm, were male and 96.3% (52 of 54) with wing lengths ≤ 74 mm were female. Only immatures at 75 mm cannot be sexed (7.0% of the males, 10.9% of the females).

Wing length data for the 1039 sparrows that were not laparotomized present further evidence that bimodality exists in the distributions of both adult and immature birds (Fig. 3). Note that the intermediate regions of low frequency in Figure 3 correspond with the areas of separation between the sexes in Figure 2 (i.e., 76 mm in adults, 75 mm in immatures). Assuming our data are representative of other Gambel's Sparrow populations, this bimodality may prove useful for other researchers who plan to sex White-crowned Sparrows of this race. However, noticeably skewed sex ratios at the extremes of the Gambel's Sparrow's winter range (King et al. 1965) may mask the central region. Figure 3 also appears to confirm that adults have longer wings than immature birds. Assuming no difference in sex ratios between the age classes, adults average 1.4 mm larger (adult \bar{x} = 76.5 mm, N = 443; immature \bar{x} = 75.1 mm, N = 596; χ^2 = 23.1, P < 0.001, median test).

Weight and fat scores.—In our sample of live birds, males were significantly heavier than females of the same age (Fig. 4). Adult males averaged 27.8 g (N = 49, SD = 1.98), and adult females 25.7 g (N = 34, SD = 1.84), a difference of 2.1 g (t = 4.81, P < 0.001). Immature males averaged 27.6 g (N = 43, SD = 1.96), and immature females 25.0 g (N = 39, SD = 2.09) a 2.6 g separation (t = 5.84, P < 0.001). Adult birds did not average heavier than immatures of the same sex (males t = 0.53, NS; females t = 1.53, $0.10 > P > 0.05$) which suggests that the larger wings of adults do not reflect a larger body mass.

Visible fat scores did not differ between the sexes (adults χ^2 = 0.01, NS; immatures χ^2 = 0.76, NS; median tests) or between birds of different ages (males χ^2 = 0.33, NS; females χ^2 = 0.00, NS); thus, lipid reserves do not seem to be a factor in the analyses of body weight (above). The median fat score for all birds, our category 3, represents fat noticeably filling the furcular depression, but to a level less than half full. This category is intermediate to McCabe's (1943) "little fat" and "moderate fat" and is comparable to Helms and Drury's (1960) fat class of 2.

Since individual weight is known to increase through the nonbreeding season for the Gambel's Sparrow (King and Farner 1966, King and

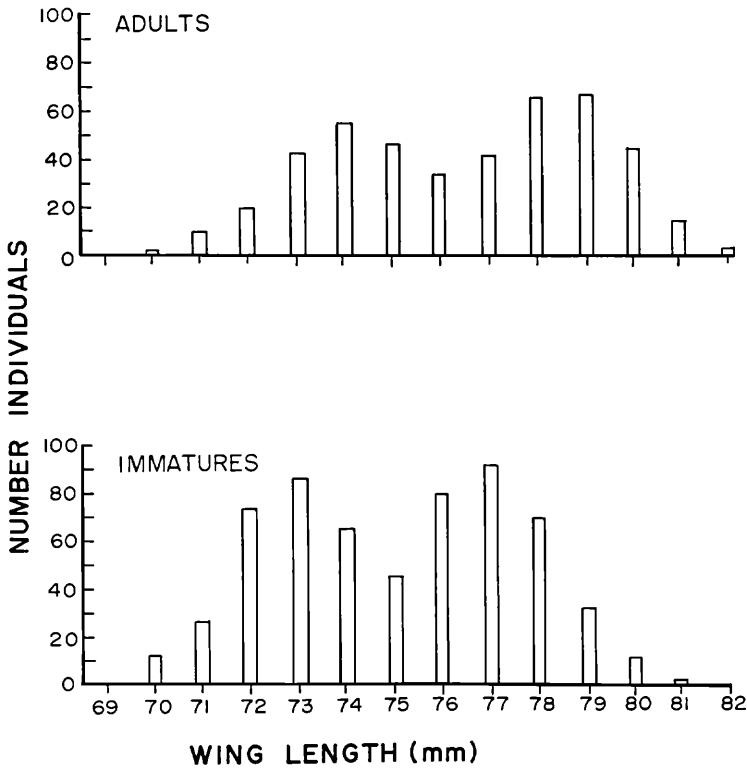


FIGURE 3. Wing length distributions for adult ($N = 443$) and immature ($N = 596$) White-crowned Sparrows captured in the Santa Barbara area in the 3 winters between 1978 and 1981.

Mewaldt 1981) and to vary diurnally in other emberizids (Helms and Drury 1960), it is possible that weight data collected over a more limited time period than in this study would demonstrate a more distinct separation between the sexes. However, it is clear that this temporal variability confounds the use of weight as a sexing criterion.

Tarsus length.—Tarsus length and the other parameters that follow were not measured in the sample of laparotomized birds, so the remaining results deal only with the museum specimens. Adult males averaged 21.6 mm ($N = 44$, $SD = 0.69$) in tarsus length and adult females 20.9 mm ($N = 29$, $SD = 0.80$), a difference of 0.7 mm ($t = 3.80$, $P < 0.001$). Tarsus length averaged 21.8 mm ($N = 26$, $SD = 0.43$) in immature males and 21.0 mm ($N = 20$, $SD = 0.57$) in immature females, a 0.8 mm separation ($t = 5.53$, $P < 0.001$). There is no difference between birds of different ages (males $t = 1.33$, $P \approx 0.10$; females $t = 0.29$, NS). Similarly, adults and immatures do not differ in the diameters of their tarsi (Rothstein 1979).

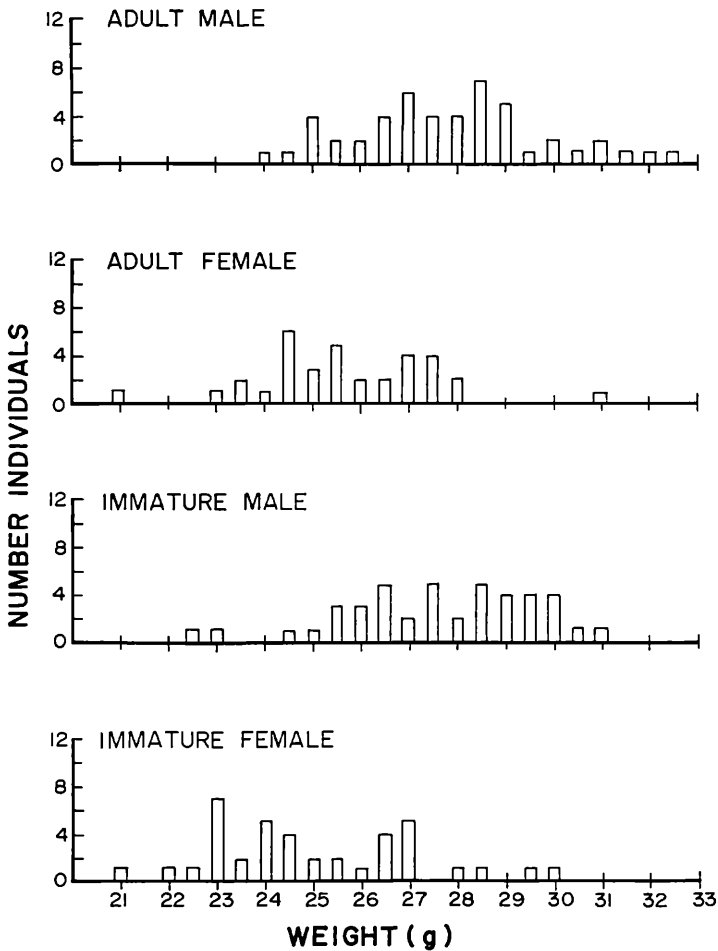


FIGURE 4. Weight distributions for live White-crowned Sparrows sexed by laparotomy. Individuals were weighed to 0.1 g, but are here grouped in 0.5 g categories.

Bill length.—Although adult males averaged slightly larger than adult females (7.66 mm, SD = 0.26, $N = 43$ vs. 7.60 mm, SD = 0.32, $N = 27$, respectively) and immature males averaged slightly larger than immature females (7.63 mm, SD = 0.23, $N = 27$ vs. 7.56 mm, SD = 0.28, $N = 20$, respectively), there were no significant sex-related differences in bill lengths (adult $t = 0.87$, NS; immature $t = 0.94$, NS). Also, the combined mean for adults (7.63 mm, SD = 0.28, $N = 70$) did not differ significantly from that for immatures (7.60 mm, SD = 0.25, $N = 47$) ($t = 0.59$, NS).

Bill length is known to change temporally (Davis 1954) and this may make it difficult to demonstrate significant sex- or age-related differences

in this character even if such differences exist. Further complicating this problem is the fact that bill parameters in passerines are generally more variable than other physical dimensions (Rothstein 1973).

Crown appearance.—Within both age classes, males average significantly brighter in crown plumage than females (adults: $z = 4.39$, $P < 0.001$; immatures: $z = 2.17$, $P = 0.02$; Mann-Whitney U tests with correction for ties; Table 1). Among adults, 47.7% (21 of 44) of the males and only 10.3% (3 of 29) of the females were ranked 1, 1.5, or 2, and conversely, only 11.4% (5 of 44) of the males and 58.6% (17 of 29) of the females fell in the brightness categories of 3.5 and 4. However, roughly a third of both sexes were ranked in the intermediate categories of 2.5 and 3. Among immatures, 72.0% (18 of 25) of the males and only 30% (6 of 20) of the females were scored at 1 or 1.5, while the remaining birds were ranked 2 or greater.

DISCUSSION

Wintering Gambel's White-crowned Sparrows show sex-related differences in nearly every character we examined. Within an age category, males average significantly larger than females in wing length, tarsus length, and weight and they possess noticeably brighter and more contrasting crown plumages. Adults do not differ from immature birds of the same sex in tarsus length or weight, but wing length increases for these sparrows between their first and subsequent winters. Bill length did not differ between birds of different sexes or ages.

It is not clear why immatures should have shorter wings than adults when the two age groups do not differ in weight or other measurements. Individuals measured as immatures and then as adults demonstrate definite increases in wing length (Rothstein and Fugle, unpublished data), so our results are not due to directional selection for sparrows with long wings. Since the wing feathers of immatures must serve them both on the breeding grounds when they are not full-grown and during their first winter after they are fully developed, it is possible that natural selection results in a compromise wing length that is shorter than what is optimal for adults. An increase in wing length between first-winter and adult Harris' Sparrows (*Z. querula*) is accompanied by an increase in weight after the first year (Rohwer et al. 1981). This suggests that White-crowned Sparrows reach a mature body mass more rapidly than congeneric Harris' Sparrows, but that in both species individuals may show smaller wings during the first winter as an adaptation to a lower body weight, compared to adults.

Gambel's Sparrows (*Z. l. gambelii*) around Santa Barbara, California, can be reliably sexed using wing length criteria. Adults ≥ 77 mm and immatures ≥ 76 mm are almost always ($>95\%$ of the time) males, while adults ≤ 75 mm and immatures ≤ 74 mm are almost always ($>96\%$ of the time) females. Adults at 76 mm and immatures at 75 mm must remain undetermined, but this represents less than 10% of all sparrows (Fig. 3).

TABLE 1. The distribution of crown appearance scores for museum specimens of White-crowned Sparrows. Low scores indicate bright and contrasting plumage.

	Score							N
	1	1.5	2	2.5	3	3.5	4	
	Adult crown							
Male	5	10	6	11	7	3	2	44
Female		1	2	6	3	8	9	29
	Immature crown							
Male	5	13	4	3				25
Female	4	2	7	4	2	1		20

We cautiously suggest that these sexing criteria are applicable through most of the winter range of the *gambelii* subspecies. Banks (1964) found little variation among mean wing lengths for breeding populations of this race throughout Alaska and western Canada, suggesting considerable subspecific uniformity. His data for *gambelii* show a range in wing lengths comparable to this study (although absolute values are slightly smaller) and appear to indicate restricted sexual overlap as we have reported here for wintering birds. Our delineation between the sexes is greater than one would expect from viewing Banks' data, because Banks' breeding samples lump immature and adult wing lengths. All summer birds display adult crowns acquired in a prenuptial molt, but first-year birds do not replace their immature remiges until their first postnuptial molt. Although sexing criteria similar to ours may be applicable throughout the range of *gambelii*, other workers should construct histograms of their own data for comparison with the distributions in Figures 2 and 3 because techniques for measuring wing length vary among researchers and because there may be slight geographic variation in size.

Banks' (1964:105) figure summarizing wing length data for geographic groupings throughout the breeding range of the White-crowned Sparrow suggests that all subspecies can be sexed by wing length with some accuracy (although Pacific Coast races appear to show greater overlap between the sexes than other races). Wood (1969) gives wing lengths for sexing White-crowned Sparrows (male ≥ 80 mm, female ≤ 75 mm, unknown 76–79 mm), but these differ from those presented here and are undoubtedly applicable only to *Z. l. leucophrys* of middle and eastern North America (see Mewaldt 1977, for maps of this species' races). Sexing criteria for *Z. l. leucophrys* might be improved by considering adult and immature wing lengths separately, as we have done here for *Z. l. gambelii*. Lumping of the two age categories may explain why Wood's (1969) "unknown" size range is so much greater than ours. Sexing criteria for the remaining White-crowned Sparrow races must still be accurately defined.

Wing length measurements have been shown to be useful for sexing

individuals in several other North American sparrows (Fam. Emberizidae, Subfam. Emberizinae), including Harris' Sparrow (*Z. querula*, Rohwer et al. 1981), White-throated Sparrow (*Z. albicollis*, Atkinson and Ralph 1980), Dark-eyed Junco (*Junco hyemalis*, Grant and Quay 1970, Balph 1975), Clay-colored Sparrow (*Spizella pallida*, Knapton 1978), and American Tree Sparrow (*S. arborea*, Heydweiller 1936). Delineation between the sexes was markedly improved in those studies in which first-year and adult birds were considered separately (i.e., Harris' Sparrow, American Tree Sparrow). Unfortunately, age distinctions are not easily made in many sparrows.

Our findings with regard to crown variability complement recent studies of winter plumage characteristics in other *Zonotrichia* species. In Harris' Sparrows, adults almost always show brighter crown and throat plumages than first-year birds and, although there is substantial overlap, males average brighter than females within either age class (Rohwer et al. 1981). This pattern is almost identical to what we report here for White-crowned Sparrow. It is perhaps significant to point out that White-crowned Sparrows are widely considered to be age-dimorphic but with no plumage variation related to sex (e.g., Rohwer 1975, Watt 1982), while Harris' Sparrows are thought of as continuously variable (Rohwer 1975, Rohwer et al. 1981). The winter plumage patterns of these 2 species are actually more similar than is generally recognized, although this may not be true for all races of the White-crowned Sparrow as Watt (1982 and pers. comm.) failed to find sex-related plumage variation in wintering *Z. l. leucophrys*, unlike our findings for *Z. l. gambelii*. There is disagreement over the correlates of winter crown plumage variation in White-throated Sparrows. Vardy (1971) suggests there are overlying patterns of males averaging brighter than females and adults averaging brighter than first-winter birds, but Atkinson and Ralph (1980) found only that adult males average brightest while broad overlap in characteristics make the other age-sex categories indistinguishable by appearance. The variable winter crown plumage of the Golden-crowned Sparrow (*Z. atricapilla*), the only other North American *Zonotrichia*, has not been investigated thoroughly (Kelly 1968).

The relationship between plumage differences and sex in Gambel's Sparrows is theoretically perplexing. If crown appearance functions to signal the sex of an individual, it does so with only partial accuracy. Possibly, the correlation is only a by-product of sexual differences in hormones or some other physiological state that influences crown brightness and is not due to selective pressures favoring signals that indicate sex; but there may be selective pressures on crown plumage for signaling status within wintering flocks (Rohwer 1975). However, such pressures cannot completely explain the existing crown variability. We have demonstrated elsewhere that Gambel's Sparrows use crown brightness differences to assess relative dominance ability among flockmates, but only if the differences are large, such as exists between adults and immatures and between average adult males (bright) and females (dull) (Fugle et

al. 1984). Within single age and sex classes (i.e., adult male, adult female, immature male, immature female) crown differences do not correlate with and thus do not signal relative dominance ability (Fugle and Rothstein, unpubl. data). In addition, adult males almost always dominate in encounters with sparrows of the other age-sex categories (Fugle 1983) and yet, we have shown here that there is substantial overlap in crown plumage brightness between adult males and females.

This study further confounds our attempts to explain the evolutionary stability of the signaling system in this species (Fugle et al. 1984). We have previously asked why intrinsically subordinate sparrows such as adult females do not possess bright crowns and thereby "cheat," i.e., falsely signal that they are adult males. We now must also ask why so many dull adult males exist when their dominance abilities warrant a brighter crown from which they would seemingly benefit. It is clear that the proximate and ultimate determinants of crown appearance in the White-crowned Sparrow require further investigation.

SUMMARY

We investigated variability in size and winter crown appearance in the Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) by examining 165 laparotomized birds and 120 museum specimens. Our analyses show (1) males average significantly larger than females of the same age in wing length, weight and tarsus length, but not bill length; (2) adults average approximately 1 mm larger in wing length than immatures of the same sex, but do not differ from them in weight, tarsus length, or bill length; (3) about 90% of the *Z. l. gambelii* can be sexed reliably by wing length; and (4) variation in crown color is sex-related within adults and immatures, with males possessing plumages with more contrast between crown stripes. We compare our results to findings for other emberizid sparrows and we discuss the functional significance of sex-related crown variability in the context of status signaling.

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EDITORIAL

Having served as editor of the *Journal of Field Ornithology* for the past five volumes, there is a certain nostalgic feeling about passing the editorial pen on to my successor. I have enjoyed working with the officers of the Northeastern Bird Banding Association, authors, reviewers, associate editors, editorial assistants, and many wonderful people at Allen Press. I owe special debts of gratitude to the NEBBA Council for their constant support; to Review Editor Jed Burtt who has nurtured the continuing growth of our unique and highly valued review section; and to my wife, Bette, who has not only endured my absences due to editorial duties, but who has contributed immensely as an Associate Editor. My thanks to Allen Press, however, are given with the greatest feeling of respect. I have served in an editorial capacity for journals published by Allen Press for the past 20 years. No editor could ask for more from a publisher than the quality final product and friendly, personal service that Allen Press provides.

Where has the *Journal of Field Ornithology* been and where is it going? My predecessor, David Johnston, and the NEBBA Council, had the wisdom to change the *Journal's* name—because the *Journal* had changed. Indeed, ornithology has changed. Bird banding has gone from a backyard pastime and tool of a few ornithologists, to being an important tool of most field ornithologists. However, it is not the only tool. Indeed, it is not the only important way of marking birds for study. Various wing tags, dyes, radio-transmitters, and now radio-isotopes and fluorescent chemicals are used. Thus, the name Bird-Banding had become a restrictive misnomer. Fortunately editorial policies did not restrict subject matter to that implied by the title. As the *Journal of Field Ornithology*, our publication has grown in stature and is perhaps becoming more of an international journal than other North American journals. The past five volumes of the *Journal* have included authors from at least 45 states, 8 Canadian provinces and 17 countries. As might be expected, the *Journal* has also grown in size: to an average of 467 pages per volume since 1981, from an average of 408 pages per volume in the preceding five years. We can all be proud of the increased role that our journal is playing in world ornithology. Recently our president, John Kricher, suggested that NEBBA change its name to the "Association of Field Ornithologists"—a name which he argues would better indicate our broadened focus and perspectives. I strongly endorse his suggestion.

Finally, I feel that the *Journal* is in good hands with our new editor, Jed Burtt, who has been intimately involved with the *Journal* under the past two editors.—Jerome A. Jackson.