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SEASONAL PLUMAGE DIMORPHISM IN THE SWAMP SPARROW

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Abstract.—Swamp Sparrows (*Melospiza georgiana*) show considerable variation in crown color. Males have brighter, more rusty crowns than females. This is particularly evident in the breeding season, when virtually all males have completely rusty crowns, and most females have brown striped crowns. Seasonally acquired sexually dimorphic plumage is not found in the closest relatives of the Swamp Sparrow and may relate to this species' highly variable territory size associated with marsh breeding.

DIMORFISMO ESTACIONAL DEL PLUMAJE DE *MELOSPIZA GEORGIANA*

Resumen.—El gorrion *Melospiza georgiana* muestra variaciones en la coloración de su corona. Los machos tienen la corona mas acanelada y brillante que las hembras. Esto es más notable durante la época reproductiva donde la coloración de la corona de los machos contrasta con la coloración parda de esta en las hembras. Este dimorfismo sexual no se encuentra ni si quiera en géneros evolutivamente cercanos tales como *Passerela, Zonotrichia* o *Junco*. Este fenómeno es asociado a lo variable del tamaño del territorio de estas aves, lo cual esta relacionado con la utilización de hábitats anegados.

Since Rowher's (1975) paper on Harris' Sparrows (*Zonotrichia querula*), a considerable amount of research has focused on the functional significance of variation in head markings of sparrows (Watt 1986a). An important step in understanding the adaptive value of plumage patterns is to determine how these patterns vary with sex, age, and season. Swamp Sparrows (*Melospiza georgiana*) have crowns that range from dull brown to bright rust. Although most descriptions state correctly that Swamp Sparrows in the non-breeding season generally have duller crowns than in the breeding season, within seasons the variation in crown color has been almost universally ascribed to differences in age (Dwight 1900, Godfrey 1986, Ridgeway 1901, Roberts 1955, Witherbee 1968). Field identification guides have often attributed most variation in crown color to age (Peterson 1980, Robbins et al. 1983). I present data showing sexual dimorphism in crown color that is expressed particularly strongly during the breeding season.

METHODS

My data come from two sources: birds that I captured in mist nets and color-banded in Crawford County, Pennsylvania during the breeding season (20 males and 17 females) and specimens in the collection of the National Museum of Natural History (111 males and 85 females, both *M. g. georgiana* and *M. g. eurycrypta*). Sex of the mist-netted birds was determined by presence of a cloacal protuberance or singing for males and presence of a brood patch, brooding, or incubation in females. Age and sex of museum specimens were determined from information on the

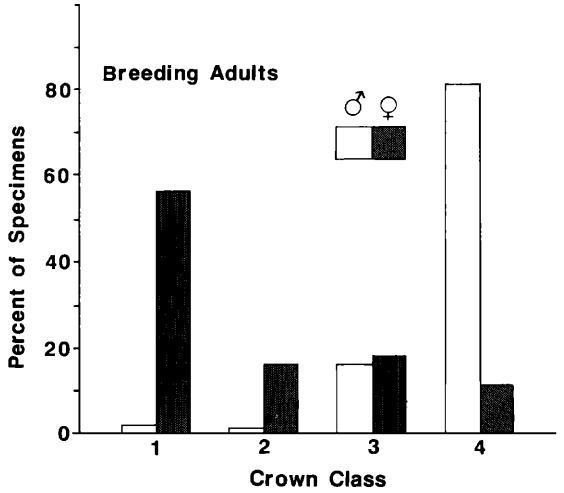


FIGURE 1. Percentage of breeding season adult male and female Swamp Sparrows in different crown classes (1 = dullest, 4 = brightest, see text). n = 131 males and 92 females.

collection tag. Specimens collected between 15 Apr. and 15 Aug. were considered to be breeding and between 15 Nov. and 15 Mar. non-breeding.

Birds were classified into one of four categories based on crown brightness: 1 = mostly brown and black feathers with a gray or yellowish median stripe and no more than 5% rusty-tipped feathers; 2 = black or brown with some rust (5–50%) and often a median stripe; 3 = similar to 2 but with over 50% rusty-tipped feathers; and 4 = solid rusty patch edged with black, often with brownish on nape and black on forehead. Museum specimens were classified into one of the four categories by an observer unfamiliar with the specimen designation.

The hypotheses that males are brighter than females, adults are brighter than immatures, and breeding season birds are brighter than non-breeding birds were tested with a one-tailed Smirnov test (Conover 1980). To estimate the degree to which the sexes differ in crown color I calculated an overlap index derived from one developed by Schoener (1968). The index is calculated by taking the sum of the lesser of the two values of the percent of individuals of each sex represented in a crown class. This sum is divided by two so that the index varies from 0 to 50% and corresponds to the percentage mistakes one would make if one assigned the sex of a specimen based entirely on crown class.

Ridgeway (1901) suggested that the presence of dull-crowned birds in the breeding season indicated that the rusty cap was acquired in the second pre-nuptial molt. I recorded the crown change in nine immature Swamp Sparrows kept at the National Zoological Park through their first pre-nuptial molt in April.

RESULTS

Breeding season specimens show strong dimorphism (Fig. 1): 85% of males and only 10% of the females had completely rusty crowns (crown class 4). The crown class distribution of live birds was statistically indistinguishable from the museum specimen sample and the two samples have been pooled for presentation and analysis. The difference between the sexes was statistically significant ($P < 0.001$) and the overlap index was 15%. Birds in crown class 4 were brighter rust on the back and wing coverts as well.

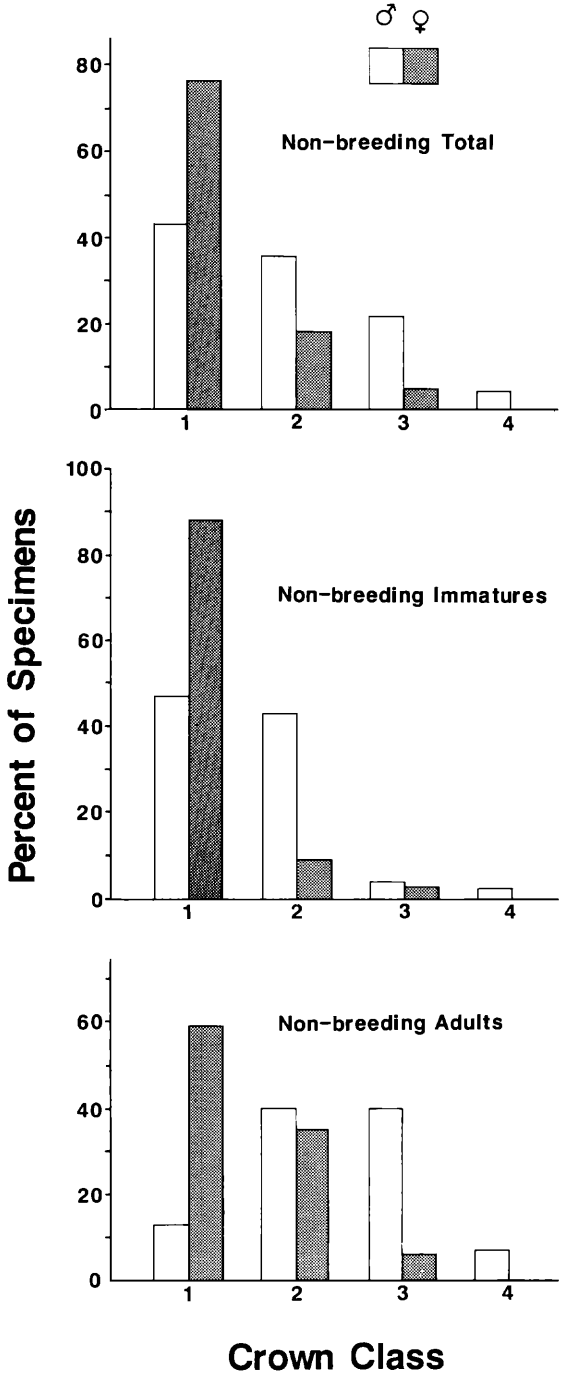
Non-breeding specimens were duller, most birds fell in categories 1–3. Males were significantly brighter than females (Fig. 2a, $P < 0.001$), but the overlap was large (35%). Both sexes were significantly duller in the non-breeding season than in the breeding season ($P < 0.01$, Fig. 2b, c), and within age classes males were brighter than females ($P < 0.05$).

There was no indication that the complete red cap of breeding males was acquired in the second prenuptial molt. Five immature males kept in captivity acquired class 4 crowns and one male had a class 3 crown, whereas three females molted into class 1–2 crowns.

DISCUSSION

Swamp Sparrows show significant dimorphism in crown color in all plumages, but only in the breeding season is the overlap in the distribution of the two sexes sufficiently small to be helpful in determining the sex of an individual. This dimorphism results primarily from males acquiring complete rusty caps. The fact that winter adult males rarely have complete rusty caps suggests that the dimorphic plumage is not just a function of age, but is seasonally acquired. Seasonal sexual dimorphism is found in some migratory species such as warblers and tanagers (Hamilton and Barth 1962), but is relatively rare in sparrows and is not found in other *Melospiza* or closely related genera (*Passerella, Zonotrichia, Junco*). The distribution of crown brightness changes from normal to bimodal between winter and summer in the White-throated Sparrow (*Zonotrichia albicollis*) and this is due partly to the increasing brightness of males in the breeding season (Watt 1986b). However, the variation is not explained by sexual dimorphism to the degree that it is in Swamp Sparrows.

The bright head markings of Swamp Sparrows are restricted to breeding season males, to a degree not found in *Zonotrichia* (Watt 1986a), suggesting that their primary function is either in mate attraction or territorial defense. Because seasonally acquired plumage dimorphism is not found in closely related species, its function might be associated with some unusual aspect of the breeding behavior of Swamp Sparrows. For example, the extreme density and small territory size that often characterizes portions of Swamp Sparrow populations might select for a bright plumage badge. On my study site, as many as 10 territories were located in a 0.6 ha area. However, over most of my 10 ha study site, Swamp Sparrow territory size was comparable to Song Sparrows. In areas of high Swamp Sparrow densities, I captured many males in May and June


♂ ♀
Non-breeding Total
Non-breeding Immatures
Non-breeding Adults
Percent of Specimens
Crown Class
0
20
40
60
80
100
1
2
3
4

that were not local territorial residents. These were primarily birds with adjacent or nearby territories.

Adjacent Song Sparrow territories showed no such pattern of extreme clumping, nor did I catch many "intruding" males during the breeding season. In the areas of high Swamp Sparrow density, chasing and aggressive "growl" notes are very common throughout the summer. Such high variability in territory size might be expected in a marsh breeding species (Verner and Willson 1966). Although Swamp Sparrows are not commonly polygynous (Witherbee 1968), as are many other marsh dwelling species, the great variation in spacing and the clumping of many small territories may present the opportunity for a great deal of male-male competition. This in turn may select for a bright plumage badge even in an apparently monogamous species (e.g., Studd and Robertson 1985). Whatever the specific selective forces on crown color in Swamp Sparrows, the pattern of acquisition suggests that social interaction during the breeding season in this, and perhaps other, species (such as White-throated Sparrow) may overshadow dominance relationships during the nonbreeding season.

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FIGURE 2. Percentage of non-breeding male and female Swamp Sparrows in different crown classes: (a) pooled (n = 55 males and 49 females); (b) adults (n = 15 males and 17 females); (c) immatures (n = 40 males and 32 females).

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