CROWN COLOR AND DOMINANCE IN THE WHITE-CROWNED SPARROW

JOHN PARSONS AND LUIS F. BAPTISTA[1]
Moore Laboratory of Zoology, Occidental College, Los Angeles, California 90041 USA

ABSTRACT.—Wintering flocks of Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) consist of black-and-white crowned adults and brown-crowned hatching year birds. White-crowned birds are dominant to brown-crowned birds in free-living unmanipulated flocks. Premature development of the adult crown was effected in juveniles by plucking the crown feathers. Juveniles with induced black-and-white crowns gained high rank when introduced to a strange flock of juveniles and a strange flock consisting of both age classes, indicating that crown color and not age *per se* communicates social status. Disguised (plucked) juveniles reintroduced to their former flock, consisting of all brown-crowned juveniles, did not rise in the peck order. Thus, White-crowned Sparrows may use other cues (besides crown color) to recognize individuals. Previous experience takes precedence over crown color in determining hierarchies. The two-signal system of Gambel's Sparrow is compared with two-signal systems in other avian species, and the adaptive significance of hierarchies in Gambel's Sparrow is discussed. *Received 6 June 1979, accepted 15 April 1980.*

MANY migratory species of birds stay in flocks during migration and on their wintering grounds. Flocking individuals must compete with each other for available resources. The benefits of flock living must outweigh the costs of intraspecific competition, however, or flocking behavior would not be maintained. For example, flocks may: (1) provide many more eyes to detect predators, (2) provide members to deter predation by mobbing behavior, (3) confuse predators by the predator swamping effect, and/or (4) provide members with information about food sources (Bertram 1978).

Intraspecific competition by flock members may result in fighting, which may lead to injury and/or death. Natural selection may reduce actual fighting by the establishment of dominance hierarchies. The latter requires that dominants and subordinates recognize each other. This may be accomplished by morphological characteristics, subtle behavior patterns or postures, or recognizing stereotyped positions and feeding stations of flock members (Shields 1977, Pearson 1979). The correlation of certain plumage characteristics and dominance has been shown in a number of species, such as Chaffinches (*Fringilla coelebs*, Marler 1955a); Evening Grosbeaks (*Hesperiphona vespertina,* Balph et al. 1979); White-throated Sparrows (*Zonotrichia albicollis*, Harrington 1973, Hailman 1975, Ficken et al. 1978); Dark-eyed Juncos (*Junco hyemalis*, Balph et al. 1979, Ketterson 1979a); Harris' Sparrows (*Z. querula*, Rohwer 1975, 1977); and Red-winged Blackbirds (*Agelaius phoeniceus*, Rohwer 1978).

Rohwer (1975: 607) called attention to two forms of plumage variability in winter-flocking species, polymorphic (e.g. Harris' Sparrows or juncos) and dichromatic (e.g. Chaffinches or White-throated Sparrows). Different races of the White-crowned Sparrow (*Zonotrichia leucophrys*) may fall into one or the other category. The sedentary subspecies *Z. l. nuttalli* is polymorphic for crown color circumannually, because yearlings often breed in various stages of incompletely molted crowns (Blanchard 1941, Banks 1964, Ralph and Pearson 1971). Winter flocks of the migratory

[1] Present address: Department of Ornithology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118 USA. Send reprint requests to LFB.

TABLE 1. Correlation of age class (determined by crown color) and success in aggressive encounters in free-living White-crowned Sparrow flocks. Numbers in the table are actual counts of encounters observed.

Location	Age class[a]			
	A > A	A > J	J > A	J > J
UNBAITED FLOCKS				
Los Angeles (Arcadia) Arboretum	4	22	0	8
Occidental College (1976)	14	31	0	31
Palos Verdes	7	22	0	1
Totals	25	75	0	40
BAITED FLOCKS				
Eagle Rock	2	15	8[b]	29
Occidental College (1978)	49	62	2	6
Occidental College (1979)	36	10	0	4
Totals	87	87	10	39

[a] A = adult; J = juvenile; > indicates outcome of encounters with the winner to left of the symbol and loser to the right.
[b] Probably one juvenile attacking the same adult repeatedly.

subspecies *Z. l. gambelii* (= Gambel's Sparrows), the subjects of this paper, are dichromatic for crown color. Adults have black-and-white crowns and hatching year birds have brown crowns.

Balph et al. (1979) have stressed the need for information on the behavior of a variety of winter flocking birds before a generalized model of status signalling can be generated. We studied winter flocks of Gambel's Sparrows in the field and in captivity to answer the following questions: (1) How does status signalling apply to Gambel's Sparrows exhibiting dichromatism of plumage? Are white-crowns dominant over brown-crowns? (2) Is a white-crowned bird dominant over a brown-crowned bird because the white-crown confers dominance to an individual, or is it dominant simply because it is older and more experienced?

METHODS

Gambel's Sparrows winter in large flocks in southern California, arriving about mid-September or early October (Blanchard and Erickson 1949). These flocks consist of individuals of two distinct crown colors. We studied social behavior in free-living *Z. l. gambelii,* looking for a correlation between crown color and dominance. Captives were sexed by laparotomy, color-banded for individual recognition, and housed in outdoor aviaries (2 × 2 × 3 m). Birds were starved for 3–5 h, and peck orders were then determined by counting the number of times each individual displaced other members of a group at a small feeder. Only active displacements involving obvious supplants, aggressive displays, or combat were considered.

Plucking the crowns of juvenile White-crowned Sparrows induces the development of adult-colored crowns several months before the normal onset of prenuptial molt (Emlen 1938, Morton 1962). We plucked the crowns of some juveniles, held them in isolation until adult crowns grew in (6 weeks), and then introduced them to captive groups of other conspecifics familiar or unfamiliar to them. This enabled us to test the respective roles of crown color, age *per se,* and previous experience in determining positions in the dominance hierarchy.

RESULTS

FIELD OBSERVATIONS

Adults invariably dominated juveniles in naturally foraging winter flocks of Gambel's Sparrows (all of 75 encounters recorded at three locations) (Table 1). Juveniles occasionally won encounters with adults when flocks were attracted to baited areas

TABLE 2. Peck order among captive *Zonotrichia leucophrys gambelii* as determined by aggressive encounters.[a]

	Loser							
Winner	A1 M	A2 M	A3 M	J1 M	J2 M	J3 F	A4 F	J4 F
A1	—	23	10	16	15	13	6	9
A2	1	—	15	20	36	13	2	12
A3	3	4	—	19	19	9	17	4
J1		1	1	—	29	19	17	15
J2		1	4	1	—	15	5	6
J3		1	1			—	14	11
A4	1	24			1	1	—	5
J4								—
A1	—	18	18	20	72	31	9	12
A2		—	33	15	64	33		14
A3			—	24	38	10	12	12
J1				—	109	46	47	20
J2					—	30	23	17
J3						—	15	14
A4		38					—	18
J4								—

[a] A = adult; J = juvenile; M = male, F = female. Birds are listed vertically and horizontally in order of dominance rank. Top ranking bird located at the top and left, lowest ranking bird at the bottom and right. Numbers in table are actual counts of wins. Gaps in the table indicate no encounters observed. Each aggressive encounter is tallied to the right of the winner (found in the vertical "winners" column) and below the loser (found in the horizontal "losers" column). The term "stabilization" refers to a sequence of observations when dominance reversals (numbers below the diagonal) are rare or have ceased, usually 2–4 weeks following introduction of unfamiliar birds. Upper part of the table shows the hierarchy before stablization (data from 12 to 24 February are pooled). Lower part of the table shows the stablized peck order (26 February–17 March). Note the dominance triangle involving A2 and A4, i.e. A4 scored 38 wins over A2 but lost to all other birds.

(10 of 87 encounters), but most instances appeared due to one juvenile that repeatedly chased the same adult. Data were collected from six flocks residing at three different localities, indicating a general tendency for adults to dominate juveniles in free-living flocks.

As Gambel's Sparrows are sexually monomorphic, we had no indication of the role of sex within age classes in dominance hierarchies, hence the laboratory studies that follow.

LABORATORY STUDIES

Sex versus age.—In some fringillids males are dominant to females in wintering flocks (Knapton and Krebs 1976, Balph 1977), whereas in others females are dominant over males (Hinde 1955–1956, Thompson 1960, Coutlee 1967). There is some anecdotal evidence that an adult female *Z. l. nuttalli* dominated adult males, which in turn usually dominated other females and juveniles (Stewart and Darling 1972). The dominant female was observed singing repeatedly. In the related Rufous-collared Sparrow (*Z. capensis*), females are dominant to males in the nonbreeding season (Smith 1978). It was desirable, then, to examine the role of sex in dominance hierarchies of *Z. l. gambelii* under controlled laboratory conditions.

Two groups (only one is illustrated) composed of adults and juveniles were sexed by laparotomy and put in aviaries (Table 2). Upon initial introduction of birds into an aviary, instances of combat and dominance reversals were frequent. When these became very infrequent or ceased to occur, the peck order was considered stabilized (Table 2). Hierarchies were for the most part linear. Adults tended to dominate juveniles, supporting field observations, and males tended to dominate females. A peck-triangle between adult female A4 and adult male A2 is evident in Table 2.

TABLE 3. Peck order among six juvenile males.[a]

	Loser					
Winner	*P1	*P2	*P3	C1	C2	C3
*P1	—	3	18	12	18	15
*P2		—	10		4	5
*P3			—	19	16	6
C1		3		—	23	6
C2				2	—	18
C3						—

[a] * = plucked, full black-and-white crown; C1 = 40% black-and-white, 60% brown crown; C2 = 50% black-and-white, 50% brown crown; C3 = all brown crown. Data were taken from 17 March to 2 April.

Peck-triangles have been described for a number of fringillid species (Wessell and Leigh 1941, Tordoff 1954, Marler 1955b, Sabine 1959).

Crown color versus age: plucking experiments.—Are adults dominant over juveniles by virtue of their age and experience alone, independent of crown color, or may the white crown act independently of age as a dominance-conferring signal? To answer this question we set up a group of six juvenile males. Because birds of one sex were involved, the potentially confounding variable of intersexual dominance was avoided. Before introduction into the experimental aviary, these were housed as two separate groups of three each. One group was plucked and developed full adult crowns (P1, P2, P3 in Table 3). Two members of the unmanipulated group (C1, C2) grew some black-and-white crown feathers due to adventitious or prenuptial molting. When placed in an experimental aviary the birds formed a stable hierarchy, with black-and-white crowned birds on top (Table 3). Crown color and high dominance status occurred independently of age class.

A second group was set up consisting of three adult males, one adult female, two juvenile males, and two juvenile females. These birds formed a stable, almost linear hierarchy in which the three adult males ranked highest (Table 2). One adult male (A2) formed a dominance triangle with the adult female (A4). The same female was subordinate to three juveniles. We then induced premature coronal ecdysis in three additional juvenile males and a female by plucking their crowns and isolating them until their adult crowns grew in. These four juveniles with adult crowns and a fourth brown-crowned juvenile (a control) were introduced to the established group described above.

A dominance advantage due to previous residence in a cage has been reported for a number of avian species (Tompkins 1933, Schjelderup-Ebbe 1935, Collias 1944, Guhl and Ortmann 1953, Brown 1975), yet plucked juvenile males P1 and P2 obtained the alpha and third-rank positions upon introduction to an aviary-acclimated flock (Table 4). Plucked female P3 dominated all normal-crowned juveniles but was subordinate to all other adult-crowned birds. Brown-crowned juvenile C1, held earlier with the plucked group as a control, molted after introduction to the flock and developed a full adult crown by May. With the onset of molt, C1 sang and displayed with higher frequency and rose in status to the beta position. This was the only instance of crown-molt occurring during the experiment.

Crown color versus familiarity.—We have established that adult crown color is associated with high dominance status when strange individuals meet an established flock. Are brown-crowned flock members conditioned to accept adult-crowned birds

TABLE 4. Peck order after introduction of plucked juveniles.[a]

	Loser										
Winner	*P1 M	*C1 M	*P2 M	A1 M	A2 M	A3 M	*P3 F	J1 M	J2 M	J3 F	A4 F
*P1	—	6	11	2	7	17	5	4	9	8	2
*C1		—		3	5	1	5	9	2	3	2
*P2			—	4	2	5	5		1	3	2
A1				—	7	8	5	3	1	3	1
A2					—	9	6	1	3	4	1
A3						—	12	8	6	2	1
*P3						1	—	3	3	1	
J1								—	9	3	1
J2									—	1	3
J3										—	2
A4			1		8		2				—

[a] *P = plucked; C = molted. Three plucked juveniles (P1, P2, and P3) with full black-and-white crowns and one unmanipulated juvenile (C1), who later molted and developed the adult crown, were introduced from their aviary into the aviary of the established group in Table 2. The peck order before stabilization (19 March–12 April) is not illustrated. Data after stabilization are presented (18 April–7 May). Bird J4, who appears in Table 2, died on 16 April.

as dominant due to previous attacks from adults, or does the adult crown *per se* confer dominance status on an individual? To answer this question we set up a group of 10 juveniles (five males, five females). For reasons unclear to us, the peck order in this group failed to stabilize completely. Several dominance triangles were evident and reversals were many (Table 5A). We removed what we considered the four lowest ranking individuals, plucked their crowns, and isolated them until adult crowns grew in. These birds were then reintroduced to their former group. One plucked and one unplucked female died. The resultant peck order assumed more order than previously (Table 5B). The triangle between M4 and F4 disappeared. The triangle between F3 and M1 remained. One and two reversals were scored for M5 over M1 and M2, respectively. None of the plucked birds (M5, F3, F4), however, rose appreciably in the flock hierarchy. The advantage gained by previous domination of an individual appears to take precedence over any advantage gained by having a black-and-white crown *per se*.

DISCUSSION

Our field observations of Gambel's Sparrow flocks indicate that black-and-white crowned birds (adults) dominate brown-crowned birds (juveniles). Our laboratory studies reveal that in undisguised flocks males are generally dominant over females within each age class (e.g. Tables 2, 5A). These data are similar to those for other finches (Marler 1955a, Knapton and Krebs 1976, Balph et al. 1979).

Intraspecific competition in wintering Gambel's Sparrow flocks appears to be reduced in a number of ways. (1) Each wintering flock occupies an exclusive home range (Mewaldt 1964). (2) Sex ratios vary geographically (King et al. 1965). Because males tend to dominate females, intersexual competition may be reduced, as the sexes need not occur together in a locality where resources may be in short supply (Ketterson 1979b). (3) Dominance hierarchies are formed, with adults dominating juveniles: because our field observations of unmanipulated flocks at several localities reveal that juveniles do not usually dominate adults (Table 1), Gambel's Sparrow hierarchies must be classified as despotic.

TABLE 5. Fourth group—dominance hierarchy, A. 27 October–25 November. All juvenile (brown) crowns. B. After reintroduction of low-ranking plucked birds, 30 December–12 January.[a]

A.	M1	M2	M3	M4	F1	F2	M5	F3	F4	F5
M1		33	12	16	11	31	16	11	17	5
M2			26	11	8	4	8	11	14	3
M3				14	11	29	13	8	9	6
M4	13		2		15	4	1	9		14
F1	1	4	8			3	4	7	13	4
F2		24	2	16	10		22	10	16	5
M5				16	3			11	15	2
F3	8									
F4				8		1		3		2
F5						1				

B.	M1	M2	M3	M4	F1	*M5	*F3	*F4
M1		26	29		14	13		6
M2			19	17	15	8	13	6
M3				18	10	8	10	2
M4					6	10	12	19
F1						17	21	14
*M5	1	2					12	5
*F3	15							5
*F4								

[a] * = plucked. F2 and F5 died.

Some reversals of juveniles over adults were seen in our baited and captive flocks. Perhaps by our setting out bait, birds that normally avoid each other come together, allowing the observer to record otherwise rarely occurring reversals. Attracting birds to a common food source also increases the chances of temporary reversals due to "mistakes," as suggested by Dilger (1960). Among captives, hunger may be at least partly responsible for temporary reversals, as subordinates may challenge dominants more readily in time of need (Wiley and Hartnett 1979). Some juveniles may be dominant over some adults, such as the adult female being subordinate to the juveniles (Table 2) and what was apparently one juvenile consistently attacking the same adult in one free-living baited flock (Table 1).

Our plucking experiments have demonstrated that crown color enables individuals to achieve high dominance status. Prior experience appears to take precedence over crown color, however, as plucked birds reintroduced to their former flock mates did not move up in the hierarchy. Clearly, birds must recognize individuals by more than one cue. Cues may be behavioral, postural, or simply the positions of individuals relative to each other (Shields 1977, Pearson 1979). Possibly subordinate disguised individuals reintroduced to their former flock mates assume subtle "submissive" postures and are thus recognized by their former dominant flock mates. Alternately, flock mates may recognize each other as individuals, possibly by subtle plumage characteristics (Shields 1977).

The highly conspicuous visual cue, the white crown of the adult sparrow, may serve as a conditioned reinforcer. Perhaps fledglings are attacked by adults about the time of self-sufficiency, forcing them to disperse or join flocks of juveniles that form before migration. These juveniles are conditioned to perceive black-and-white crowned (adult) individuals as aggressive and dominant, avoiding the latter or assuming submissive postures. They are thus accorded low rank in the flock as a result of their learned (conditioned) behavior. Juveniles may thus react to disguised

strangers with subtle submissive signals, encouraging the strangers to attack and achieve dominance status.

The fact that disguised juveniles were dominant to adults (Table 4) is surprising. Rohwer and Rohwer (1978) noted that subordinate Harris' Sparrows dyed to look like dominants did not ascend in rank but were socially persecuted. On the other hand, dyed birds injected with testosterone increased in social status. Our plucking experiments involving two age classes were conducted in mid-April to early May and may not be comparable to data collected earlier in the year. It is conceivable that our plucked birds were also receiving increasing testosterone titres from their gonads due to longer natural photoperiods. They were, in fact, behaving like Rohwer and Rohwer's (1978) disguised and testosterone-injected birds.

Dominance hierarchies in Gambel's Sparrows are maintained by a two-signal system that differs in a number of ways from other two-signal systems studied to date. In the related White-throated Sparrows, bright-crowned birds are also dominant to brown-crowned birds (Harrington 1973, Ficken et al. 1978). Crown dichromatism in Gambel's Sparrows disappears after juveniles molt into adult plumage; however, dichromatism in White-throated Sparrows is permanent and genetically determined (Thornycroft 1975, Ficken et al. 1978). Crown dichromatism serves in maintaining order in winter flocks of Gambel's Sparrows (this study), whereas that in White-throated Sparrows also serves in recognition of morphs in a disassortative mating system (Lowther 1961).

In Gambel's Sparrows dichromatism is age related, whereas in Chaffinches and Evening Grosbeaks it is sex-related. In Gambel's Sparrows dichromatism reduces aggression between age classes, whereas in Chaffinches and Evening Grosbeaks it reduces intersexual aggression (Marler 1955b, Balph et al. 1979). Marler's (1955a) disguised subordinate female Chaffinches in established flocks rose in social status. Disguised low-ranking Gambel's Sparrows in established flocks did not rise in the hierarchy (Table 5B). Marler's data also differ from Rohwer's (1977), whose disguised Harris' Sparrows not only did not rise in status but were socially persecuted.

Studies of other avian species have demonstrated or suggested that high dominance rank provides an increased chance of survival (Murton et al. 1966; Fretwell 1968, 1969; Smith 1976). Rohwer and Rohwer (1978) found that dominant Harris' Sparrows occupied richer winter habitats than subordinates. In intraspecific competiton for food and survival within winter flocks of Gambel's Sparrows, selective pressure would favor the black-and-white crowned birds. Why, then, does natural selection maintain the juvenile brown crown? The benefits of living in a flock must far outweigh the cost of being relegated to a subordinate position. In species in which juveniles pass through a period of surbordinate status during development, low status would better ensure an individual's chance of survival if it were allowed to stay with the group rather than if it wintered by itself. Because subordinates do not challenge the social order, the flock functions with little fighting, and constructive activities are allowed to proceed (Brown 1975).

Adult Gambel's Sparrows are veterans of one or more migratory journeys and return to winter in the same area annually (Mewaldt 1964). Hatching year birds appear to learn the characteristics of their wintering area in their first winter (Ralph and Mewaldt 1975). It has been suggested that the more cryptic brown color may help camouflage inexperienced juvenile White-crowned Sparrows from predators (Ralph and Pearson 1971).

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