SIGNALS OF STATUS IN WINTERING WHITE-CROWNED SPARROWS, ZONOTRICHIA LEUCOPHRYS GAMBELII

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Abstract. The possibility of plumage status signalling within the social systems of wintering birds has been a controversial issue. Our results are the first to demonstrate conclusively the reality of such signalling. Data from eight groups of captive white-crowned sparrows (*Zonotrichia leucophrys gambelii*), each with 8 to 11 different individuals, show that immature and adult females with crowns painted to resemble more brightly coloured, dominant adult males consistently win encounters with control birds of their own age and sex. These experiments demonstrate that signals that correlate with age (adult versus immature) and sex (adult male versus adult female) are used by the birds as reliable indicators of relative dominance position. Our demonstration of status signalling draws attention to the need to explain how such a system can be evolutionarily stable and we discuss some suitable models.

Animal behaviourists have long been intrigued by the possibility that birds use the size or intensity of external markers to signal relative dominance status within social groups. Many researchers have shown a correlation between differences in an external marker and social rank (Collias 1943; Guhl & Ortman 1953; Harrington 1973; Rohwer 1975; Gjesdal 1977; Ficken et al. 1978; Balph et al. 1979; Ketterson 1979; Searcy 1979), but in these studies the significance of the marker is obscured by other factors that also correlate with the presumed signal, such as age, sex and size. The best means to determine whether a putative signal really functions in communication is to alter experimentally the signal in question while holding constant, or randomizing all other possible determinants of status. In one such experimental study, Marler (1955) worked with the sexually dimorphic chaffinch (*Fringilla coelebs*) and painted the breasts of females to simulate the red coloration of males. He found that these females improved in relative dominance position in winter social groups. Since this red marking is contained on feathers that are maintained through an entire year (Witherby 1920, page 93), it seems likely that the male marker evolved under breeding selective pressures (e.g. for reproductive isolation or to signal a sexual role) and has secondarily been used as an indicator of status, as males are usually dominant over females in winter.

Recently, considerable attention has been concentrated on the possibility of status sig-

nalling within winter flocks of certain species that show variation in plumage related to age as well as sex (Rohwer 1975, 1977; Shields 1977; Baker & Fox 1978; Balph et al. 1979; Ketterson 1979; Parsons & Baptista 1980). These studies have also been concerned with the subtle variation in plumage within age and sex classes. In contrast with the case of the chaffinch, alternative functional explanations for the plumage variation in some of these recently studied species are not so evident, especially if the moult sequence of a species frees its non-breeding appearance from restraints that breeding requirements might impose. Although the existence of status signalling in species with such variable winter plumages has been accepted by some (Barash 1982, page 207; Krebs & Dawkins 1981, page 108; Rohwer 1982), previous attempts to demonstrate it (Rohwer 1977; Parsons & Baptista 1980) have had small sample sizes, inadequate controls and/or unclear results (see Discussion below). Our experiments reported here involved the non-breeding crown plumage of the Gambel's white-crowned sparrow (*Zonotrichia leucophrys gambelii*), and are the first to conclusively demonstrate the effectiveness of winter plumage signals as determinants of the relative social rank of individuals.

In the 'Gambel's' sparrow in winter, adult birds (> 1 year old) have crowns striped black and white, whereas immature birds (< 1 year old) possess more cryptic crowns, striped brown and tan (see Fig. 1). Within either age group, the crowns of males generally show brighter coloration and/or more contrast between stripes than those of females (Fugle & Rothstein, in preparation). Adults are usually dominant over im-

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matures and males dominate females within either age category (Fugle & Rothstein, in preparation). Thus a clear correlation exists between crown brightness and relative social rank. We chose to examine whether the differences in crown plumage between the age categories and between adult males and females serve as signals of status in this species. Importantly, the pre-nuptial, post-nuptial and post-juvenile moults of the Gambel's race involve the complete replacement of crown feathers (Michener & Michener 1943), suggesting that the variation in winter plumage is functionally related only to conditions during the non-breeding season.

Methods

Our experiments were of two types. In both we controlled for individual differences in age and sex by using birds from a single age and sex category. Experiment 1 involved only immature females. Using thinned black and white enamel paint ('Testors', Rockfield, IL), we altered the crowns of some of these sparrows—experimentals—to closely resemble adult crowns (Fig. 1d, Plate I). A complementary group of birds —controls—were left with brown and tan crowns, but we controlled for the experimental manipulation by painting these birds with either similarly thinned clear enamel paint (Fig. 1f, cages 1–4) or brown and tan paint (cage 5). Experiment 2 (cages 6–8) used only adult females as subjects. Some of these sparrows — experimentals — were painted with black and white enamel paint to resemble the bright crown typical of adult males (Fig. 1d), while others — controls — were painted to duplicate the duller black and grey crown of adult females (Fig. 1e). No signs of ill-effects from the painting were encountered.

We set up eight separate groups of birds, each composed of 8–11 different individuals; there were five replicates of experiment 1 (cages 1–5) and three of experiment 2 (cages 6–8). All the birds within each group were captured on the same day from large flocks in Goleta, Santa Barbara County, California during 1980 or 1981. Birds were measured, colour-banded for individual recognition, painted, and then released into observation cages on the day of capture. The simultaneous introduction of birds controlled for the influence of prior residence on dominance relationships (Guhl & Allee 1944; Thompson 1960; Balph 1977; Searcy 1979). Sex was initially determined by wing length (Fugle

& Rothstein, in preparation) and was later confirmed by gonadal inspection after the completion of each experiment. Among 76 subjects, two males were discovered and deleted from the following analyses. Our cages, measuring $2.4 \times 1.2 \times 1.8$ m, were housed in indoor rooms with temperature and light period controls adjusted to simulate conditions occurring naturally at the start of the experiments. Food consisted of commercial wild bird seed and high-protein game bird feed.

Aggressive interactions were observed from a blind, starting 1–2 days after a group was released into its cage. The frequency of interactions was increased by the temporary removal of food for up to 2 h before viewing. Food was returned just before viewing and we then recorded the winner and loser of active encounters, i.e. when a bird moved toward another individual who then gave way. Observations continued until all or most intra-group dominance relationships were known. The cage groups were housed for the following periods: 1 : 16 Jan.–2 Feb. 1980; 2 : 21 Jan.–11 Feb. 1980; 3 : 3 Feb.–4 Mar. 1980; 4 : 12–29 Feb. 1980; 5 : 29 Nov.–7 Dec. 1980; 6 : 29 Nov.–11 Dec. 1980; 7 : 12–23 Dec. 1980; 8 : 19–30 Jan. 1981.

We determined dominance relationships within the eight separate cages on the basis of observed intra-group aggressive interactions (Table I). An overall winner and loser were designated for each bird pair within a group by noting which of the two sparrows had the most and least wins, respectively, out of the total number of encounters between them. For example, bird Rx dominated Px 37 times (cage 1, Table I), but Px never dominated Rx. Thus, the Rx–Px pairing gives Rx one overall win and Px one overall loss. Most pairings were clearly one-sided, with one bird dominating in all encounters. Out of a total of 310 bird pairings, it was impossible to distinguish an overall winner and loser in only two cases (both in cage 3). Once two sparrows each won half the total interactions between them, and once we failed to observe any encounters between two birds. These individuals were credited with ties. Overall records were computed by totalling each sparrow's win, loss and tie designations for its intra-group pairings. Linear dominance hierarchies were constructed for each experimental cage using these overall records (Table I). In those cases where two sparrows tied in overall records, the bird that dominated in that particular pairing was given the higher rank.

PLATE I
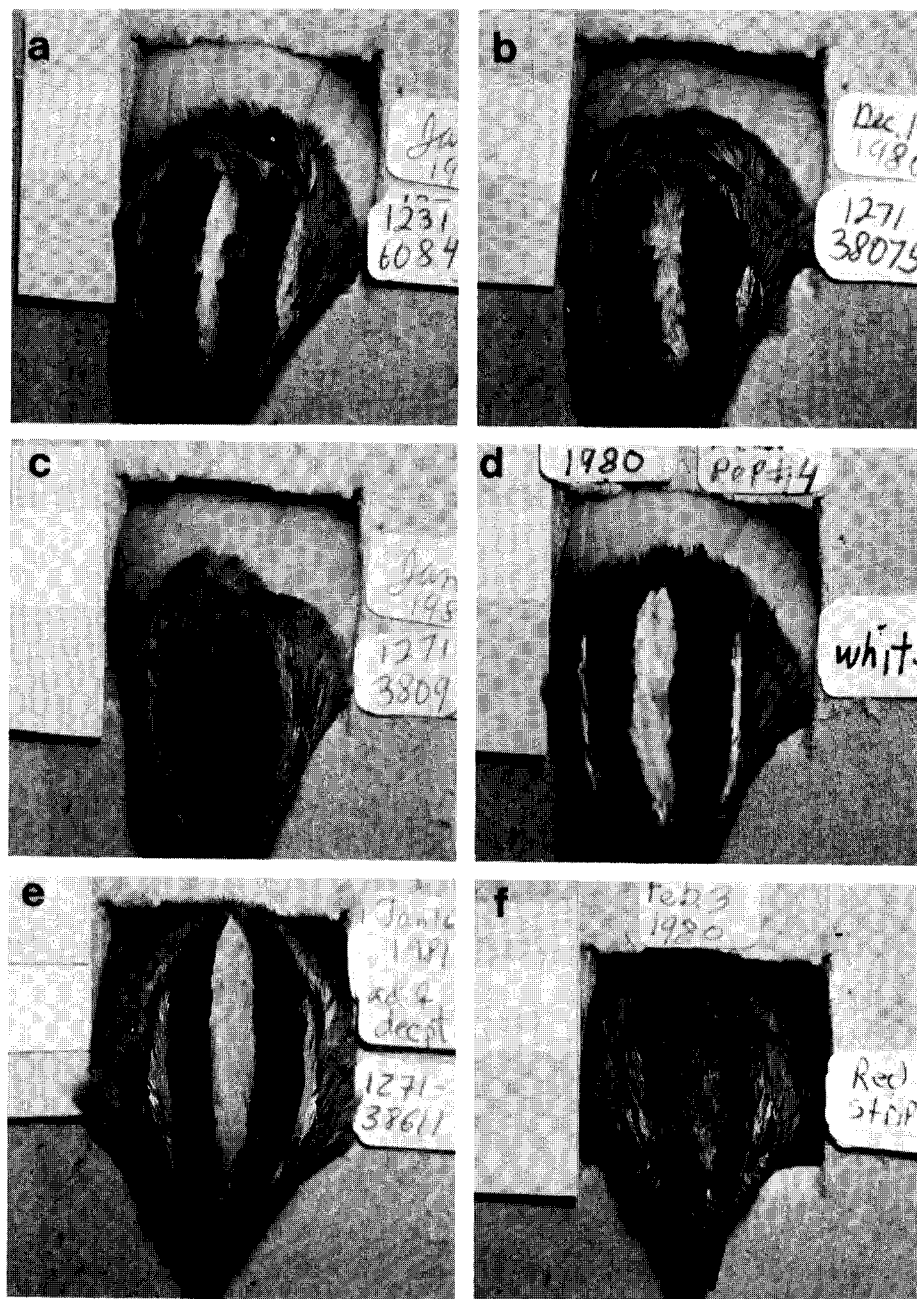
Fig. 1. Photographs of white-crowned sparrow crowns: (a) typical adult male, (b) typical adult female, (c) immature, (d) bird painted as an 'adult male' ('experimental' of experiments 1 and 2 — the individual shown here is an immature female used in experiment 1), (e) bird painted as an 'adult female' (control of experiment 2), (f) bird painted as an immature (control of experiment 1, clear paint).

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Table I. Dominance Hierarchies for the Eight Different Cages of White-crowned Sparrows

Cage 1

	Rx	Px	Wx	Rc	Wc	Bc	Kc	Pc	W-L
Rx	—	37	23	27	25	16	25	19	7-0
Px		—	12	5	7	4	5	7	6-1
Wx		1	—	17	13	2	9	17	5-2
Rc				—	29	27	26	3	3-4
Wc			1		—	10	7	11	3-4
Bc					1	—	3	7	2-5
Kc		2	1				—	18	1-6
Pc			1	27	1	1	1	—	1-6

Cage 2

	Bx	Kx	Wx	Rx	Px	Rc	Kc	Bc	W-L
Bx	—	14	17	22	9	38	20	5	7-0
Kx		—	7	8	8	12	5	1	5-2
Wx		2	—	12	5	24	13	5	5-2
Rx		1	4	—	10	35	13	6	4-3
Px					—	41	17	1	3-4
Rc						—	33	8	1-6
Kc			1				—	8	1-6
Bc	11						2	—	1-6

Cage 3

	Nx	Rc	Zx	Px	Gx	Bx	Kc	Yc	W-L-T
Nx	—	9	5	6	7	1		1	6-0-1
Rc		—	11	8	6	8	2	7	6-1-0
Zx		1	—	5	6	4	2	3	5-2-0
Px				—	10		4	8	3-4-0
Gx				7	—	7	4	8	3-4-0
Bx						—	2	8	2-4-1
Kc						2	—	5	1-4-2
Yc								—	0-7-0

Cage 4

	Zx	Gc	Rx	Kx	Wx	Bx	Pc	Sc	Yc	W-L
Zx	—	21	23	18	15	26	10	9	14	8-0
Gc		—	20	23	5	13	14	6	8	7-1
Rx			—	29	23	27	32	21	10	6-2
Kx				—	7	17	27	11	6	5-3
Wx			1	1	—	7	9	10	3	4-4
Bx		1	1		1	—	34	21	8	3-5
Pc							—	4	8	2-6
Sc							1	—	3	1-7
Yc									—	0-8

Cage 5

	Rx	Lx	Ox	Bx	Sx	Yx	Ec	Pc	Dc	Kc	W-L
Rx	—	6	10	10	5	8	8	15	9	11	9-0
Lx		—	8	7	8	17	7	10	10	5	8-1
Ox			—	16	9	21	9	8	3	10	7-2
Bx				—	14	15	6	6	4	4	5-4
Sx				2	—	13	7	17	5	11	5-4
Yx						—	14	19	15	14	4-5
Ec							—	9	7	7	3-6
Pc							1	—	10	5	3-6
Dc				8			1		—	7	1-8
Kc										—	0-9

Cage 6

	Px	Ix	Kx	Dx	Ec	Lc	Rc	Wc	Sx	Yc	W-L
Px	—	4	5	10	7	5	6	6	6	7	9-0
Ix		—	11	8	10	5	20	6	5	10	8-1
Kx			—	10	18	5	17	8	4	11	7-2
Dx				—	14	10	21	2	6	7	5-4
Ec			9		—	8	20	9	9	17	5-4
Lc				1	1	—	10	7		10	4-5
Rc					1	1	—	12	8	17	3-6
Wc							1	—	5		3-6
Sx						10		4	—	10	1-8
Yc										—	0-9

Table I continued

Cage 7	Px	Kx	Rx	Bx	Wc	Dc	Ec	Yc	Ix	Lc	W-L
Px	—	12	10	5	5	6	11	16	4	5	9-0
Kx		—	10	13	15	16	21	12	7	10	8-1
Rx			—	5	7	6	8	10	11	8	7-2
Bx				—	15	12	25	13	3	8	6-3
Wc					—	16	30	15	4	9	5-4
Dc						—	21	22	13	12	4-5
Ec							—	13	10	5	3-6
Yc								—	8	12	2-7
Ix									—	15	1-8
Lc										—	0-9

Cage 8	Bx	Wx	Kx	Yx	Px	Lc	Rc	Ec	Oc	Dc	Ic	W-L
Bx	—	6	20	9	19	1	2	6	2	9	5	10-0
Wx		—	4	4	9	2	8	2	7	3	5	9-1
Kx			—	15	23	6	7	7	17	21	7	8-2
Yx				—	15	2	4	2	7	4	4	7-3
Px					—	10	12	11	23	24	9	6-4
Lc						—	7	3	14	12	6	5-5
Rc							—	7	11	5	7	4-6
Ec								—	5	6	7	3-7
Oc									—	9	8	2-8
Dc										—	12	1-9
Ic											—	0-10

Birds are listed vertically and horizontally in order of dominance rank with the alpha bird at the top left and the omega bird at the bottom and extreme right. Aggressive encounters are scored to the right of the winner and below the loser. W-L-(T) columns give each bird's overall win-loss-(tie) record versus each of the other birds in its cage. Cages 1–5 contained immature female subjects with the crowns of experimental birds (x) painted to simulate an adult male appearance and control birds (c) painted to match an immature crown coloration (experiment 1). Cages 6–8 contained adult female subjects with experimental birds (x) painted to a bright 'adult male' crown and control birds (c) painted to a duller 'adult female' crown (experiment 2).

If plumage brightness signals relative dominance status in white-crowned sparrows, the experimental birds should have dominated the control birds within each cage. We employed two methods to test the null hypothesis that plumage coloration had no effect in determining the outcome of dominance interactions. First, we calculated Mann–Whitney U values for each cage to examine whether intra-group dominance hierarchies represented random orderings with respect to the experimental and control subsamples. To combine the information from different replicates of the same experiment, we converted the U values for each cage into a z statistic (Siegel 1956), summed the z values for all the cages of an experiment and then divided the sum by $\sqrt{k}$ to restore unit variance

$$(z_c = \sum_{i=1}^{k} z_i / \sqrt{k}).$$ The individual cage z values

are derived from sample sizes that are too small for them to be used in estimating probabilities from a normal distribution table, but when the independent tests are combined, the resulting z_c statistic is much closer to normal and a normal table can be used (P. Chesson, personal communication). We present probabilities based on individual cage U values and on the z_c values for each experiment type.

Our second approach to assess the dominance relationships between experimental and control sparrows did not rely on our dominance rankings. Instead, we used sign tests to investigate whether experimental birds had more overall wins (+) or losses (−) against the control birds of their group. For example, in a cage with five control sparrows, each experimental bird could have an overall win–loss record against controls ranging from 5–0 (all wins) to 0–5 (all losses). Thus, experimentals with records of 3–2 or better would be noted as having more overall wins (+), whereas those with records of 2–3 or worse would fall in the more-losses category (−).

Results

In all cages, with very few exceptions, bright experimental (x) birds were dominant over dull control (c) sparrows (Table I). Mann–Whitney U tests show that experimental birds occupied the upper ranks of the intra-group dominance hierarchies. Individual cage U values are significant for each replicate ($P < 0.05$) except cages 3 and 4 ($P = 0.196$ and $P = 0.095$, respectively). The combined probabilities for each experiment

type are highly significant (experiment 1: $z_c = 4.27$, $P < 0.001$; experiment 2: $z_c = 3.63$, $P < 0.001$). Overall records show that experimental birds had winning records against the control birds of their cages in almost all cases. In experiment 1, 23 of 24 experimentals had winning records against controls, as did 13 of 15 in experiment 2 ($P < 0.001$ and $P = 0.004$, sign tests).

We have found that differences in size and weight are not reliable predictors of dominance relationships among sparrows from the same age and sex category (Fugle & Rothstein, in preparation), so these factors should not be expected to account for the results in this work. However, to test for possible confounding factors, we conducted correlation tests of social rank against rankings for wing length, tarsus length, bill length and weight at capture (Spearman rank correlation tests; Siegel 1956). Analysing these four variables in each of the eight cages gave a total of 32 tests. We found only two significant correlation coefficients. Social rank was negatively correlated with bill length in cage 1 ($r_s = -0.714$, $P < 0.05$) and positively correlated with tarsus length in cage 8 ($r_s = 0.626$, $P < 0.05$). Since only two of 32 tests were significant and these showed opposite trends, we conclude that the effects of the crown manipulations alone were responsible for the domination of control birds by experimentals.

Discussion

Our experiments clearly demonstrate that crown brightness in the Gambel's white-crowned sparrow is more than a mere correlate of dominance. This winter plumage marker can itself influence the acquisition of social rank and is a true signal of status between adult and immature birds (at least immature females) and between adult males and adult females. We are unable to say whether the association between the crown signal and dominance is learned through repeated encounters with individuals of different plumage types or whether it is genetically controlled. Clearly, in this work, it was the initial behaviour of control individuals towards the artificially brightened experimentals that determined the dominance relationships, since the latter could not have been aware of their heightened signal.

We have found (Fugle & Rothstein, in preparation) that within isolated age and sex groups (i.e. adult males, adult females, immature males, immature females), natural varia-

bility in crown brightness does not correlate with dominance rank. This suggests that status signalling within age and sex categories is minimal or non-existent. We are left with the interpretation that differences in crown brightness are respected as signals in the white-crowned sparrow only when they are extreme, i.e. the large differences between adults and immatures and large, generally sex-related differences in adults and, possibly, in immatures. A comparable signalling system has been proposed for the dark-eyed junco, *Junco hyemalis* (Balph et al. 1979). In reviving the status signalling question, Rohwer (1975, 1977) created a controversy partly because he suggested that signalling might occur along a subtle continuum that crosses age, sex and size categories (Shields 1977; Baker & Fox 1978; Balph et al. 1979). We have no evidence that this is the case for the white-crowned sparrow.

Rohwer (1977) attempted experimentally to demonstrate status signalling in the Harris sparrow (*Zonotrichia querula*) through the alteration of individual plumage signals with dyes and bleach. Unfortunately, these experiments have small sample sizes and contain no controls for the effect of the manipulations (i.e. handling, anaesthetizing, and dyeing or bleaching). Most important, the experiments cannot safely evaluate whether experimental birds were treated as strangers to the flock, familiar birds with changed plumage or, as Rohwer believed, birds showing incongruence between signal and behaviour. Any one of these, in conjunction with an experimental bird's response to the changed behaviour of its flockmates, might explain the results observed. Balph et al. (1979) and Ketterson (1979) offer similar critiques of Rohwer's study.

Parsons & Baptista (1980), also working with the Gambel's white-crowned sparrow, plucked the crown feathers from several immature birds, causing the premature development of adult appearance. Relative to unaltered birds, these individuals did unusually well in dominance interactions within small cage groups. Although the results from this ingenious approach suggest status signalling, and are consistent with what we have demonstrated here, it is difficult to determine specifically what caused the success of the plucked birds. There were few controls for the variable treatment of subjects, particularly with respect to the plucking manipulation. The latter may affect birds in ways in addition to inducing premature development of adult

feathers, e.g. it might alter the levels of hormones that are linked to changes in aggression. The latter is especially critical since plucked immatures were inexplicably dominant over true adult males, a rare event in nature (Parsons & Baptista 1980; Fugle & Rothstein, in preparation).

As has been noted by other authors, the existence of status-signalling would pose an evolutionary dilemma. This dilemma now assumes increased importance with the conclusive demonstration of status signalling presented here. Given the obvious advantage of dominance in individual conflicts, why has selection failed to result in all birds having the most dominant plumage signal? In the white-crowned sparrow, for example, why do adult females and all immatures have duller plumage than adult males? We must explain how birds of low intrinsic dominance ability have greater fitness by displaying a subordinate signal rather than a more dominant plumage type.

Much discussion has centred around individual selection hypotheses which attempt to explain how the spread of birds with signals that do not match their underlying abilities ('cheaters') is controlled through social interactions (Rohwer 1977; Dawkins & Krebs 1978; Rohwer & Rohwer 1978; Balph et al. 1979; Ketterson 1979; Rohwer & Ewald 1981). We recognize two critical but largely untested assumptions in these hypotheses. First, 'cheaters' are the recipients of intense probings or escalated contests (Maynard Smith & Parker 1976) from intrinsically superior birds that would not challenge them if they showed a reliable signal. This could result if birds are most frequently challenged by individuals that share a similar plumage signal (Rohwer & Rohwer 1978; Balph et al. 1979; Ketterson 1979; Rohwer & Ewald 1981). Secondly, cheaters suffer greater costs in their contests with intrinsically superior birds (first assumption) than they would as non-cheaters in contests against individuals of their own true dominance category, and overall, the challenges cheaters receive result in costs that outweigh the benefits of cheating. Regardless of the costs and benefits occurring in interactions with intrinsically superior birds, our results suggest that cheaters could benefit by dominating individuals of their own true age and sex category. However, whether cheaters could still dominate their true equals in the presence of intrinsically more dominant birds still requires investigation, as does the question of whether

cheaters might even dominate at least some individuals of intrinsically superior age and sex classes.

Additional hypotheses that consider maladaptive aspects of wearing a signal that does not match underlying abilities have been suggested (Balph et al. 1979). A generally overlooked alternative (but see Dawkins & Krebs 1978) is that some 'cheating' does indeed occur, but is held in check by frequency-dependent selection. One possible model assumes that bright coloration allows cheaters to dominate non-cheaters of their own age and sex category, but also incurs a heightened risk of predation. When brightly coloured cheaters are rare, the risk is outweighed by the benefits of dominating a large number of non-cheaters of equal dominance ability. However, when cheaters are common and there are fewer non-cheaters to dominate, the total benefits will be small and possibly outweighed by the predation risk. Perhaps there are white-crowned sparrows that display an adult non-breeding crown coloration, but are in actuality immatures. As far as we know, the nature of moult patterns in juvenile *Z. l. gambelii* has not been investigated extensively enough to exclude this possibility. A critical test of this frequency-dependent model would be to age birds by some means other than plumage, such as skull ossification, and to determine whether any birds show discrepancies between their true age and the age suggested by their plumage signal.

Lastly, it is important to distinguish between proximate and ultimate determinants of dominance. Our experiments show that crown brightness is used as a signal of relative dominance ability and therefore is a proximate determinant of status. However, we should not lose sight of the ultimate determinants themselves, which are likely to be factors such as differences among individuals in experience and size.

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