EXPERIMENTS ON THE CONTROL OF DECEPTIVE SIGNALS OF STATUS IN WHITE-CROWNED SPARROWS

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ABSTRACT.—We showed previously that crown plumage brightness signals relative dominance ability in White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). We now test the social-control hypothesis for the evolutionary stability of status signaling against invasion by individuals with brighter crowns than justified by their intrinsic dominance ability. "Cheating" immature females, with crowns painted to resemble bright adult males, and "control" immature females, with crowns painted a typical immature appearance or left unpainted, were released into two separate wild sparrow flocks and into two different captive groups that contained birds of all age and sex classes. In the field experiments, cheaters were more successful than controls in dominance interactions with other immatures; both groups were equally unsuccessful against adults. In the captivity experiments, cheaters generally dominated controls and were more successful than they in interactions with immature males and adult females but not with adult males. Cheaters did not receive more aggression from dominant individuals than did controls in any experiment, and in two experiments they received significantly less aggression. Thus, we found no socially mediated costs for sparrows with deceptive signals. Instead, we showed that immature females that cheat can benefit. The stability of the White-crowned Sparrow signaling system remains unexplained. We discuss the potential influence of predators on individual plumage differences and offer additional hypotheses for the control of deceptive signals. *Received 6 May 1986, accepted 1 October 1986.*

THE status-signaling hypothesis provides an explanation for the extensive variation that occurs in the winter plumage of some bird species (Rohwer 1975, 1982). The hypothesis proposes that individual appearance has evolved to indicate relative fighting ability, with dominants displaying the brightest plumage. A status-signaling system could benefit each individual because it would allow a bird to assess rapidly a competitor's fighting ability. Thus, disputes over resources could be settled without the time, energy, and risks of actual fighting. It is not readily apparent, however, how such a system can be stable evolutionarily (Rohwer 1975, Maynard Smith 1976, Zahavi 1977). Assuming that dominance is advantageous, selection should favor birds with plumages indicative of a higher status than their intrinsic abilities warrant (i.e. "cheaters"). Considerable discussion has focused on how a status-signaling system might be stable against the invasion of unreliable signals (Rohwer 1975, 1977, 1982;

Shields 1977; Dawkins and Krebs 1978; Maynard Smith 1978, 1982; Rohwer and Rohwer 1978; Balph et al. 1979; Barnard and Burk 1979; Ketterson 1979a; Rohwer and Ewald 1981; Fugle et al. 1984). All hypotheses attempt to explain how a deceptive signal is more costly (or less beneficial) than a reliable signal. Costs have been visualized as being mediated through social interactions, predation pressures, or plumage requirements during the breeding season.

Status signaling in winter bird flocks has been demonstrated conclusively only recently (Fugle et al. 1984, Jarvi and Bakken 1984, Rohwer 1985), although other observations are consistent with status signaling (Rohwer 1975; Balph et al. 1979; Ketterson 1979a; Parsons and Baptista 1980; Watt 1986a, b). We showed that wintering White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) utilize crown plumage brightness to assess the relative dominance ability of flock mates (Fugle et al. 1984). Immature female sparrows, whose tan-and-brown crowns were painted to resemble the black-and-white crown of adults, dominated control individuals of the same age and sex. Also, adult females painted with the brighter black-and-white crown typical of adult males (Fugle and Roth-

stein 1985) dominated control adult females. We found no correspondence between natural crown plumage brightness and dominance rank within isolated age-sex groups (Fugle 1983), so signaling appears limited to large age- and sex-related plumage differences.

We performed experiments designed to determine whether socially mediated costs for cheating can explain the stability of the White-crowned Sparrow status-signaling system. Observations on other species (Balph et al. 1979; Ketterson 1979a, b; Rohwer and Ewald 1981) indicated one possible form of social control of cheating by showing that aggression was most frequent between individuals with similar plumages, especially those with dominant plumage types. If such like-vs.-like aggression occurs, cheaters should receive more attacks than noncheaters from birds of intrinsically superior dominance ability. These challenges could involve costs (e.g. personal injury, poor location within a foraging group) that exceed the benefits of cheating (e.g. access to resources over individuals that would not otherwise be dominated). Like-vs.-like aggression may occur because the aggression reflects test fights or escalations (Maynard Smith and Parker 1976, Dawkins and Krebs 1978, Barnard and Burk 1979) between birds unable to discern quickly their relative dominance positions because they wear comparable status signals. Alternatively, birds may follow different social strategies, the result being that like-vs.-like competition is greater than like-vs.-nonlike competition because birds attempt to limit the presence of similar strategists within foraging flocks (Rohwer and Ewald 1981, Rohwer 1982).

To assess the importance of social control of cheating in White-crowned Sparrows, we created "cheaters" by painting immature female sparrows with adultlike crowns. Cheaters and control immature females were released into wild sparrow flocks and captive sparrow groups that contained typically dominant individuals of all sex and age classes (i.e. adult males, adult females, and immature males). We focused on two predictions: (1) *Dominance relationships.* Although our earlier aviary experiments (Fugle et al. 1984) showed that cheaters can dominate control sparrows, they involved only single age and sex groups to remove potential confounding variables. These experiments did not demonstrate that cheating is possible in the presence of more dominant age and sex classes. For

the experiments reported here, we predicted that some influence from sparrows of more dominant age and sex categories would prevent cheating immature females from dominating controls if social control of cheating was important. We determined win-loss records in dominance interactions in all experiments. (2) *Aggression frequencies.* If like-vs.-like aggression occurs, sparrows with deceptively bright crown plumages should experience higher aggression rates from intrinsically superior individuals relative to those experienced by noncheaters. We compared the relative amounts of aggression directed at cheater and control birds by individuals of dominant age and sex classes.

METHODS

SIGNAL MANIPULATIONS

Experiments included three types of immature females: (1) "Painted as Adult" (PA), "cheaters" whose crowns were painted black and bright white to resemble adult males; (2) "Painted as Immature" (PI), controls whose crowns were painted brown and tan to resemble immatures; and (3) "Unmanipulated" (U), controls that were handled, but whose crowns were not painted (field investigations only). Painting techniques were described by Fugle et al. (1984).

FIELD EXPERIMENTS

We "created" PA, PI, and U birds at two sites, "West Campus" and "Tamarisk Row," 1.5 km apart near the University of California, Santa Barbara Co., California. Sparrows were captured with Potter traps, aged by crown plumage, and sexed by wing length (Fugle and Rothstein 1985). All birds were color-banded. At each trapping interval (1–1.5 h), immature females were assigned to categories in a ratio of 2 PA:2 PI:1 U. Care was taken to distribute the largest and smallest birds evenly among the PA, PI, and U groups, even though we have found no correlation between dominance and size differences within age-sex categories (Fugle and Rothstein in prep.; see also Arcese and Smith 1985). We processed and released 23 immature females (9 PA, 9 PI, 5 U) and 53 sparrows of other age-sex classes at West Campus on 5 November 1980. We banded 27 immature females (11 PA, 11 PI, 5 U) and 46 other sparrows at Tamarisk Row on 3 February 1981. Numerous sparrows were unbanded at both sites. After banding, we observed birds near the capture site at a 1-m circular plot baited with commercial bird seed. We recorded the winner and loser of active dominance interactions in which one bird, the dominant, moved toward another, the subordinate, which then gave way. We did not record passive wins, i.e. when a subordinate individual

moved from the path of a dominant before the latter made any gesture. Observations occurred at various times of day during 30–90-min sessions. West Campus observations totaled 9 h on 7 days between 7 and 21 November 1980. Tamarisk Row observations totaled 10 h on 10 days between 4 and 18 February 1981. Observations ceased after 15–16 days because the artificial signals of the PA and PI birds became worn.

Dominance relationships.—No PA or PI individual was seen in greater than 25% of its category's encounters. Given these relatively even distributions, we combined win-loss records for each category at each site. In addition, interactions were primarily against unbanded and hence unsexed opponents (85.8% at West Campus, 82.8% at Tamarisk Row), because of the large numbers of birds using these sites. Therefore, we reduced the data to overall records for the PA, PI, and U categories vs. adult or immature sparrows (Table 1). Results for PIs and Us were statistically indistinguishable and were combined in all statistical analyses.

Aggression frequencies.—We contrasted the observed numbers of supplants PAs and PIs + Us received with the expected numbers based on a null hypothesis of randomly directed aggression. Expected numbers were calculated by determining the proportion each category (PAs or PIs + Us) made up of the total number of PAs, PIs, and Us seen after being banded and by multiplying this proportion by the total number of observed supplants of the three groups (Table 2). Because initiators of encounters never lost in either the field or captivity experiments, a bird's losses equaled the number of attacks directly against it.

CAPTIVITY EXPERIMENTS

For each of two experimental replicates, we used an outdoor aviary (5.3 × 1.0 × 2.9 m) containing 3 adult males, 2 or 3 adult females, 3 immature males, 5 PAs, and 4 or 5 PIs. Each replicate contained birds captured on the same day within 5 km of the University of California and released simultaneously into the cage. Observations ran from 10 to 23 December 1980 for replicate 1 and from 13 to 27 January 1981 for replicate 2. Sex was determined initially by wing length and was confirmed by laparotomy after our observations. All birds were color-banded. We noted the winner and loser of active dominance encounters. Nearly all aggressive interactions occurred in feeding groups on the ground, and these were increased by removing the 2 or 3 feeding dishes for up to 2 h before viewing.

Dominance relationships.—We constructed a dominance matrix (Table 3) for each replicate as done previously (Fugle et al. 1984). An overall winner and loser was designated for each bird dyad within each cage according to which sparrow had the most wins against the other. If the birds of a dyad had equal intrapair wins or had not been observed in interac-

tions, both were given a tie. The individual win-loss records were then used to rank the birds according to percentage wins (with ties deleted from consideration). The manipulated immature females (PAs and PIs) were ordered on the basis of their overall win-loss records against one another.

Aggression frequencies.—We tested the prediction that PAs would experience significantly more attacks from adults by summing the losses received by PAs plus PIs from each of the typically dominant age-sex categories (Table 4). Because replicate 1 contained 5 PAs but only 4 PIs, our null hypothesis was that PAs would have ⅝ of the summed losses to each dominance category in this cage. An assumption in our measure of aggression frequencies was that PAs and PIs had equivalent exposure to possible aggression from dominants. To test this assumption, we examined intraflock associations in the second captivity experiment by recording, every 20 s, the sparrows in the 1.0 × 0.8 m focal area in which they fed. For each observation during which one or more adult males was noted, the number of PA and PI birds was counted and these totals were tallied (Table 5). We followed the same procedures to assess association tendencies with adult females and immature males and used Chi-square tests to test for differences between PA and PI birds.

RESULTS

FIELD EXPERIMENTS

Site visitation.—All of the banded immature females were seen again except for 2 PIs at West Campus and 1 PI at Tamarisk Row. Individuals were seen during an average of 3.2 observation sessions (of 7) at West Campus and 6.2 (of 10) at Tamarisk Row. There were no differences among values for the PAs, PIs, and Us (*t*-tests).

Dominance relationships.—In the only direct interactions between immature females of different categories, PAs won 3 of 4 encounters with PIs. Immature females of all three categories lost every encounter with adults (Table 1), as in studies of unmanipulated White-crowned Sparrows (Parsons and Baptista 1980, Fugle 1983). However, PAs had better overall records against immatures than did PI or U birds. Comparing the PA record at each site with a combined PI and U record (Table 1) showed a suggestive probability for West Campus ($P = 0.11$) and a highly significant difference for Tamarisk Row ($P < 0.01$). The PA and PI + U records were also significantly different when the data from both sites were combined ($\chi^2 = 8.34$, $P = 0.004$). Because PIs and Us lost

TABLE 1. Win-loss records in dominance interactions for the three classes of immature females vs. immature and adult opponents in the field experiments (PA = painted with an adultlike crown signal, PI = painted with an immaturelike crown signal, U = handled, crown unpainted). Records against adults were not significantly different among the immature female groups (Fisher exact tests). Probabilities for the differences in records against immatures for PAs vs. PIs + Us are given in the table (Fisher exact tests or χ^2 tests).

| | | Opponents | | | | |
| | | Adults | | Immatures | | |
Site	Immature female group	Wins	Losses	Wins	Losses	P
West Campus	PA	0	2	4	4	=0.11
	PI + U	0	6	4	16	
Tamarisk Row	PA	0	10	7	16	<0.01
	PI + U	0	14	0	32	
Combined	PA	0	12	11	20	=0.004
	PI + U	0	20	4	48	

nearly all of their interactions (48 of 52) with other immatures, these interactions probably were mostly with males. This interpretation is supported by our findings that unmanipulated immature females rarely initiate interactions with any birds, whereas immature males have high initiation rates (unpubl. data).

Aggression frequencies.—The intensity of aggression in interactions involving PA birds appeared no different than that involving unmanipulated birds in nonexperimental flocks, as we noted no increase in especially aggressive interactions such as chases or "face-offs." The numbers of observed and expected encounters that adults initiated against PAs and PIs + Us were similar, with the fit being almost perfect when both sites were combined (Table 2). By contrast, there was a poor fit between the observed and expected aggression from immatures. PAs received significantly less aggression than expected at West Campus and in the

data for both sites combined (Table 2). Thus, the adult plumage of the PAs did not elicit heightened aggression from adults and actually reduced aggression from immatures. The reduced aggression from immatures probably was due to lessened attacks from immature males, because, as stated above, immature females rarely initiate interactions. Our methods did not take into account the possible effects of differences in associations, but none of our data suggested this possibility.

CAPTIVITY EXPERIMENTS

Dominance relationships.—PAs in replicate 1 showed a weak but nonsignificant tendency to occupy dominance ranks above PIs ($U = 8$, $P = 0.37$, Mann-Whitney U-tests; Table 3). Therefore, we have no evidence that the artificially bright signal benefited PAs in interactions with birds of their own age and sex in this sample.

TABLE 2. Observed and expected numbers of interactions initiated against the three classes of immature females in the field experiments. Values for χ^2 and P are based on interactions initiated by immatures. Interactions initiated by adults conformed almost perfectly to the expected values.

| | | | Initiated by | | | | |
| | | No. and | Adults | | Immatures | | |
Site	Immature female group	percentage present	Obs.	Exp.	Obs.	Exp.	
West Campus	PA	9, 40.9%	2	3.3	4	8.2	$\chi^2 = 3.65$
	PI + U	15, 59.1%	6	4.7	16	11.8	$P = 0.028$
Tamarisk Row	PA	9, 39.1%	10	9.4	16	18.8	$\chi^2 = 0.69$
	PI + U	14, 60.9%	14	14.6	32	29.2	$P = 0.41$
Combined	PA	18, 40.0%	12	12.8	20	27.2	$\chi^2 = 3.18$
	PI + U	27, 60.0%	20	19.2	48	40.8	$P = 0.038$

TABLE 3. Dominance matrices for the captivity experiments. Observed dominance interactions are scored to the right of the winner and below the loser. PA and PI immature females are ordered by their overall win-loss-tie (W-L-T) records against each other. Data for adult males and females and for immature males are not presented because they are not relevant to relative rankings of PAs and PIs.

Replicate 1, 10–23 December 1980

	LB	SR	Y	BK	DB	W	P	R	RB	W-L-T records
LB (PA)	—	2	2		1		6	2	3	6-0-2[a]
SR (PI)		—	18	4	6	5	6	10	10	7-1-0
Y (PI)			—	13	9	5	8	4	14	6-2-0
BK (PA)		1		—	7	5	6	10	12	5-2-1
DB (PA)					—	2	4	9	8	4-4-0
W (PA)						—	2	9	7	3-4-1
P (PA)		1	1		1	1	—	3	7	2-6-0
R (PI)								—	4	1-7-0
RB (PI)									—	0-8-0

Replicate 2, 13–27 January 1981

	P	Y	BP	R	LB	W	DB	SR	BK	RB	W-L-T records
P (PA)	—	3	3	2	1	7		1	2	2	8-0-1
Y (PA)		—	1			8	2	4	5	3	6-1-2
BP (PA)			—		2	10	1	6	2	7	6-2-1
R (PA)				—		1	1			2	3-1-5
LB (PA)					—				1	1	2-2-5
W (PI)						—	1	6		2	3-4-2
DB (PI)							—	1		1	2-4-3
SR (PI)					1			—		1	1-4-4
BK (PI)									—	1	1-4-4
RB (PI)										—	0-9-0

[a] LB died 19 December 1980.

However, 3 of 5 PAs (BK, DB, P) dominated one of the adult females, while none of the 4 PIs dominated an adult, a significant difference ($P < 0.05$, Fisher test). All PAs in replicate 2 ranked above all PIs ($U = 0$, $P = 0.004$; Table 3). PAs dominated in all 19 PA-PI dyads in which an overall winner could be determined. In addition, a PA was dominant in 10 of 11 discernable dyads between PAs and immature males, but there were no overall PI winners in 15 dyads between PIs and immature males ($P < 0.001$, Fisher test). Overall, these replicates indicate that even in the presence of intrinsically dominant birds, cheaters can benefit from their deceptive plumage in dominance interactions. Compared with noncheaters, they are more likely to dominate members of their own sex and age class (replicate 2) and even some members of normally dominant classes (adult females, replicate 1; immature males, replicate 2).

Aggression frequencies.—Contrary to predictions of social-control hypotheses, PAs in replicate 1 (Table 4) received significantly less aggression from adult males and females than did PIs. Thus, their bright signal seems to have reduced their likelihood of being supplanted. The only significant difference in the aggression received by PAs and PIs in replicate 2 was with regard to immature males, and, again, PAs received less. We can offer no conclusive explanation why significant differences occurred for adult males and females in replicate 1 but only for immature males in replicate 2 (Table 4). In both replicates, however, all significant deviations from randomness showed that PAs received less aggression than PIs.

PAs in replicate 2 were significantly more common on the aviary floor than PI birds whenever adult males, adult females, or immature males were also present, as indicated by mean values and overall distributions (P's < 0.02, Table 5). These results imply that the artificial crown of PA sparrows allowed them to remain closer to the true adults and immature males than could PIs. If anything, this should have increased the likelihood of encounters between PAs and other sparrows, and thus we have increased confidence in the results of Ta-

TABLE 4. The number of aggressive supplants directed at PA and PI immature females by sparrows of typically dominant age-sex categories in the captivity experiments.

Replicate	Immature female group	n	Supplants received from:		
			3 adult males	2 adult females	3 immature males
1	PA	5	81	37	100
	PI	4	92	62	81
			$\chi^2 = 5.27$	$\chi^2 = 13.2$	$\chi^2 = 0.02$
			$P < 0.05$	$P < 0.001$	NS
2	PA	5	67	48	1
	PI	5	58	39	56
			$\chi^2 = 0.65$	$\chi^2 = 0.93$	$\chi^2 = 53.1$
			NS	NS	$P < 0.001$

ble 4 and in our conclusion that the bright crown of PAs did not result in increased aggression.

Because PIs were less common than PAs when dominant birds were feeding (Table 5), they should have been more numerous when no dominants were feeding because PIs and PAs had similar masses and fat scores (unpubl. data). One or more PAs fed on 18 of 31 occasions when no dominants were present, whereas PIs fed on 26 of the 31 occasions, a significant difference ($\chi^2 = 3.84$, $P = 0.05$). The tendency to feed in the absence of the three dominant sex and age classes probably means that PIs, and hence nonexperimental immature females, feed in smaller groups than would cheaters or in groups with fewer experienced adults.

DISCUSSION

We detected no socially mediated costs of cheating signals in the White-crowned Sparrow. Instead, we extended previous work (Fugle et al. 1984) by showing, with field (Table 1) and aviary (Table 3) experiments, that immature females that cheat can dominate birds of their own age and sex even in the presence of intrinsically dominant individuals (i.e. immature males and adults). Furthermore, there was evidence that cheaters may enjoy dominance advantages over some individuals of typically more dominant age-sex categories. One of our most critical findings is that cheaters received less aggression than noncheaters in both the field (Table 2) and aviary (Table 4)

TABLE 5. Foraging associations of PA and PI immature females with sparrows of the typically dominant age and sex categories in replicate 2 of the captivity experiment. The number of foraging sparrows of all categories were recorded at 20-s sample intervals. Observations were grouped into three overlapping subsets: (A) when one or more adult males were present, (B) when one or more adult females were present, and (C) when one or more immature males were present. The table shows the number of samples in each subset at which 0, 1, 2, 3, or 4–5 PA and PI sparrows were foraging. Chi-square tests on the distribution of samples among the PA and PI abundance categories show PAs were significantly more common than PIs as foraging associates of all three dominant sparrow types (columns 3 and 4–5 combined to remove cells with expected values of less than 5; df = 3).

Immature female group	Total no. of samples	No. of samples with n PA and PI birds					Probability
		0	1	2	3	4–5	
(A) One or more adult males present							
PA	107	27	38	17	23	2	$0.01 < P < 0.02$
PI	107	22	51	24	9	1	$\chi^2 = 10.0$
(B) One or more adult females present							
PA	108	27	35	23	20	3	$0.01 < P < 0.02$
PI	108	43	37	19	8	1	$\chi^2 = 10.2$
(C) One or more immature males present							
PA	84	21	30	11	18	4	$0.001 < P < 0.01$
PI	84	24	36	18	6	0	$\chi^2 = 11.5$

experiments, in direct contrast to predictions from hypotheses for the social control of cheating. Lastly, cheaters also may feed in larger groups with adults (Table 5). Thus, relative to normal immature females, cheaters might receive more benefits from sociality in the form of predator avoidance or increased foraging efficiency. Overall, our experiments show considerable consistency in that each demonstrated at least one benefit of cheating and none demonstrated any costs.

The experiments involved birds that may have had prior contact in the field, which could have affected the manner in which manipulated birds were perceived. It is unlikely that this produced any serious biases. First, as pointed out above, local feeding flocks are so large (often >100 individuals) that it is unlikely most individuals recognize one another. Also, new individuals appear at sites throughout the winter. Second, even if there was individual recognition between manipulated and unmanipulated birds, it should have decreased the likelihood of PAs receiving any benefits because of their altered plumage. Thus, the trends showing successful cheating and benefits enjoyed by PAs might have been even stronger had we been able to factor out individual recognition based on prior contact. Third, Watt (1986a) did not attribute much importance to individual recognition in wintering White-crowned Sparrows.

Although our field and aviary experiments showed that cheaters (PAs) had better win-loss records against immatures than did controls (PIs + Us), evidence that cheaters had increased dominance against adults was less consistent. Adults may have been "fooled" by the cheaters less often than were immatures because their greater experience allowed them to correctly identify the cheaters as subordinates based on subtle behavioral cues. Recent work has shown that experience plays a role in dominance interactions (Wilson and Rothstein in prep.).

Hypotheses of socially mediated control of deceptive signals suggest that the bright appearance of cheaters should elicit more aggression from intrinsically superior individuals than the dull signal of noncheaters. This prediction is especially appropriate for species in which aggression is most frequent between individuals with similar plumages (Balph et al. 1979;

Ketterson 1979a, b; Rohwer and Ewald 1981). But our cheaters (PAs) did not experience more aggression than noncheaters (PIs) from the adult sparrows they resembled. Our experiments agree with field observations that showed no consistent pattern of like-vs.-like aggression among unmanipulated White-crowned Sparrows (Keys and Rothstein in prep.). We suggest that the only possible role like-vs.-like aggression might have in controlling cheating in White-crowned Sparrows is in nonfeeding interactions. Although our observations concentrated on feeding birds, we recorded the infrequent interactions that occurred away from the feeding area in the captivity experiments. Studies of nonfeeding birds might be especially informative. In any event, studies of species that showed like-vs.-like aggression were based largely on observations at feeding sites as in our study, so the absence of heightened adult-PA aggression in our experiments is significant in a comparative sense.

We can offer four reasons to explain why the PAs, with their bright adultlike signal, did not receive heightened aggression from adults. First, White-crowned Sparrows may possess a form of social organization in which like-vs.-like fighting does not occur. Like-vs.-like aggression may be adaptive because it allows individuals to control potential competitors in their social group (Rohwer and Ewald 1981) or to test the abilities of birds of similar status (Dawkins and Krebs 1978). But neither strategy may be economical at high densities. White-crowns in our study area are more abundant than Harris' Sparrows (Z. querula) in the populations studied by Rohwer and Ewald (1981). The latter caught 61 Harris' Sparrows in an entire winter, whereas we caught 76 and 73 White-crowns in single days of trapping at each of our two field sites. Enough other birds remained untrapped that most interactions of PAs, PIs, and Us were with unbanded birds. Basic differences in social behavior are suggested by Rohwer's (1977) discovery that heightened aggression was experienced by subordinate Harris' Sparrows dyed to look like dominants but not given hormone implants that would have allowed them to behave like dominants. In direct contrast, comparable White-crowns, the PAs, experienced decreased aggression. Another difference is that the birds Rohwer and Ewald (1981) studied in Kansas

were probably food stressed, whereas the southern California birds experience a more benign winter and may rarely undergo food shortages. Thus, while Rohwer and Ewald's (1981) social-control hypothesis may be appropriate for Harris' Sparrows, it may not be so for White-crowned Sparrows. Differences in social systems are also suggested by Watt's (1986a, b) finding that plumage variation functions in individual recognition in Harris' Sparrows but not in White-crowned Sparrows (*Z. l. leucophrys*).

Second, cheaters may have escaped aggression from dominants, despite their bright signal, because they behaved subordinately. Rohwer and Rohwer (1978) suggested that both the behavior and the appearance of Harris' Sparrows are important in eliciting aggression. Different classes of sparrows may recognize one another, in part at least, by their behavior, e.g. whether a bird moves rapidly or has upright posture (Rohwer 1977, Shields 1977). Presumably, our experimental cheaters (PAs) exhibited subordinate behaviors and thus were almost always dominated by adults. PAs probably learned to dominate other immature females and even some typically dominant sparrows because of the latter's avoidance responses to their "adult" signal. Thus, cheaters that behave like subordinates when confronted by intrinsically superior birds may be the reason cheaters did not experience heightened aggression from dominants in our study and a reason natural cheaters in the wild may not be controlled even in species in which like-vs.-like aggression has been demonstrated. Demonstrating like-vs.-like fighting in a nonexperimental context, as based on observations of unmanipulated birds, may not mean that a cheater that looks like a dominant bird but behaves more like a subordinate will suffer increased aggression. Such a cheater could still benefit from its dominance of birds in its own age-sex class.

Third, like-vs.-like aggression may be a consequence of subordinate sparrows avoiding brighter-plumaged dominants rather than individuals actively choosing interactions with birds of similar appearance. Subordinate individuals often move from the path of a dominant before an aggressive displacement occurs (pers. obs.). If this aversion is most pronounced when the dominant is dissimilar in appearance (i.e. when it is expected to be clearly domi-

nant), then the aggressive displacements that occur will be most frequent between birds of like plumage. This explanation is somewhat similar to the second in that it rests upon cheaters behaving like subordinates. It differs in that the heightened aggression is avoided by the direct action of the cheater, not by the cheater's subordinate behavior failing to elicit heightened aggression from true dominants, as in the second explanation. Social interactions cannot account for the maintenance of status signals if cheaters can avoid heightened costs of their deceptive appearance by avoiding true dominants while still reaping some benefits by dominating birds with abilities similar to their own. This view of intraflock interactions provides a simple ultimate reason for like-vs.-like fighting (i.e. subordinates avoid known dominants), whereas other explanations are more complex. While this interpretation of like-vs.-like fighting may apply to White-crowned Sparrows, it probably does not hold for Harris' Sparrows, as Rohwer and Ewald (1981) found such aggression in the latter species even when they controlled for encounter rates.

Last, although our experiments demonstrated no differences between cheaters and non-cheaters in the relative number of interactions with different types of true dominants, cheating might still be controlled if cheaters provoke relatively intense and hence more costly aggression from intrinsically superior birds (Rohwer 1977, 1982; Shields 1977; Dawkins and Krebs 1978; Rohwer and Rohwer 1978; Balph et al. 1979; Ketterson 1979a; Rohwer and Ewald 1981). We have no evidence that PAs experienced more intense interactions, even though we made a special effort to look for such interactions and would have noted them had they occurred in the confined conditions of the captivity experiments. Furthermore, if cheaters can avoid aggression of increased intensity simply by not resisting challenges or otherwise acting subordinately, then social interactions cannot control deceptive signals. Thus, if aggression of increased intensity (but not increased frequency) is to control cheating, it must be assumed that cheaters cannot avoid receiving intense challenges. This assumption may be correct for Rohwer and Ewald's (1981) Harris' Sparrows because dominants might not allow similarly plumaged birds to avoid intense fights

under the conditions of food scarcity that this species probably experiences.

Cheating would not present a theoretical problem if subordinate, dull-colored individuals have the same fitness as dominant, bright-colored ones. Such an equality might arise as an evolutionarily stable strategy (ESS; Maynard Smith 1982) if dominants incur extra costs because of their heightened aggression and if subordinates and dominants have equal potentials to be dominant but pursue different strategies, that is, if social rank and plumage brightness were not related to age-sex classes. Such an ESS explanation for the maintenance of status signaling has been indicated in studies of breeding Yellow Warblers (*Dendroica petechia*; Studd and Robertson 1985). Studd and Robertson (1985) suggested that their model also applies to birds that winter in social groups. This explanation, however, cannot apply to wintering White-crowned Sparrows. Birds with different plumage brightnesses do not have equal potentials to be dominant because social rank, body size, age, sex, and plumage brightness are intercorrelated. Adults dominate immatures (Parsons and Baptista 1980, Fugle 1983, this study) and are brighter in crown color (black and white or gray vs. tan). Within age classes, males dominate females (Fugle 1983) and are larger and more brightly colored (Fugle and Rothstein 1985). Furthermore, the ESS explanation is unlikely to apply to other wintering sparrows that have been the focus of much recent research because all of the species involved show similar relationships among social rank, plumage brightness, and age or sex classes (Balph et al. 1979; Ketterson 1979a, b; Rohwer et al. 1981; Watt 1986b).

Dominance in winter social groups need not involve escalated costs, unlike the apparently increased involvement in territorial defense incurred by breeding male Yellow Warblers that pursue a dominant strategy (Studd and Robertson 1985). Dominance interactions in wintering sparrows nearly always last less than a second because subordinates typically withdraw immediately (as in this study). While adult male White-crowned Sparrows initiate interactions more often than subordinate age-sex classes, their time spent on aggression is probably less than 1–2% of the total time spent at feeding sites (Keys and Rothstein in prep.).

Our results do not suggest that cheating signals are controlled through social interactions, so we focused on other hypotheses. Deceptive signals that are advantageous in winter could interfere with breeding-season behavior (Balph et al. 1979, Rohwer et al. 1980). However, the White-crowned Sparrow replaces signal-containing crown feathers before and after each breeding season (Michener and Michener 1943), so it would appear that this species' winter appearance is free from summer selection pressures. Crown brightness may be linked intimately with hormone levels and adaptive hormone decreases in winter may restrict the potential for deceptive signals, but this seems unlikely.

Cheating signals could be controlled by the influence of predators. Immature birds may be more prone to predation than adults because of their limited experience. This may explain the cryptic coloration of immatures in White-crowns and other species (Ralph and Pearson 1971). Young birds simply may be unable to afford a brighter appearance, even though it would benefit them in social interactions. Another factor that could cause individuals to vary in their need for cryptic plumage is the likelihood of being at the periphery vs. the interior of feeding flocks (Balph et al. 1979, Goldman 1980). In addition, we have explained how cheaters might exist successfully, but be held in check by frequency-dependent selection, as determined by risks of predation on the one hand and advantages in social interactions on the other (Fugle et al. 1984).

We are left with an intriguing predicament with regard to the maintenance of status signaling in the White-crowned Sparrow. Our experiments (Fugle et al. 1984, this study) suggest that deceptively bright status signals benefit individuals. Unless we propose that there are unknown physiological constraints on signals, which seems unlikely, we still must demonstrate how cheating signals are selected against in the White-crowned Sparrow.

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