

## IMPORTANCE OF DOMINANCE STATUS AND DISTANCE FROM COVER TO FORAGING WHITE-CROWNED SPARROWS: AN EXPERIMENTAL ANALYSIS

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**ABSTRACT.**—We address the importance of a nearby source of cover to foraging White-crowned Sparrows (*Zonotrichia leucophrys*) belonging to different classes of social status and plumage. An artificial source of cover was provided, in the form of a constructed bush, which allowed manipulation of the degree and position of cover. In various manipulations, the birds were offered no cover, the position of the cover was switched, and a simple perch was offered as an alternative to the bush. White-crowned Sparrows usually perched first in a nearby source of cover before they fed, and strongly preferred to feed close to the artificial bush. Experiments demonstrated that the bush was used as a source of cover and not merely as a perch. The bright-colored dominant adult birds fed closer to cover than did the more subordinate, dull-colored, and relatively cryptic immatures. Adults apparently displaced the latter from sites close to cover as immatures fed closer when no adults were present. These results may explain why dull-colored subordinate birds do not cheat by displaying the brighter plumage of dominant sex/age classes. Cheaters might be more prone to predation than noncheating subordinates because both classes might be forced to feed away from cover by inherently dominant birds (i.e. actual adults), but cheaters would be more conspicuous than noncheaters due to their brighter plumage. Thus, the potential benefits of cheating may not outweigh the increased cost of heightened susceptibility to selection by a predator. Received 4 November 1992, accepted 7 January 1993.

OVER THE WINTER, survival to the breeding season is the critical measure of fitness for migratory bird species. Therefore, individuals attempt to acquire enough food and, simultaneously, to avoid being eaten. By foraging in flocks, birds often reduce both the likelihood of starvation (Thompson et al. 1974, Baker et al. 1981) and the risk of predation (Hamilton 1971, Powell 1974). Concentration of individuals into flocks results in intraspecific competition, with increased fighting and possibly concomitant injury or death. Under such conditions, natural selection may favor individuals that recognize their relative likelihood of winning an encounter, thereby avoiding repeated escalated conflicts. A consequence of such a system is likely to be the establishment of dominance hierarchies (Gauthreaux 1978, Wagner and Gauthreaux 1990).

Winter foraging Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) have dominance hierarchies with adults dominant over immatures and, within each age class, males

dominant over females (Parsons and Baptista 1980, Fugle et al. 1984, Keys and Rothstein 1991). The birds recognize differences in plumage brightness among the four age-sex classes as status signals (Fugle et al. 1984), with males having brighter, more contrasting plumage than females (Fugle and Rothstein 1985). The "badge" of status for adults is a black-and-white striped crown, while immatures molt into a similarly patterned dark brown-and-tan crown before the winter season (Fugle and Rothstein 1985). Immatures could as easily molt into the adult crown of black and white feathers as in the congeneric White-throated Sparrow (*Z. albicollis*; Bent 1968, Atkinson and Ralph 1980). Why then do immature White-crowned Sparrows not realize a higher status by cheating? Previous studies on White-crowned Sparrows have demonstrated that cheating is a feasible strategy (i.e. a manipulated change in plumage coloration alone, with no correlated hormonal or other physiological changes, allows a bird to achieve a higher social status; Fugle et al. 1984, Fugle and Rothstein 1987). However, although subordinate birds manipulated to appear as dominants usually dominated control subordinates, they were still dominated by most inherently dom-

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inant individuals, especially adult males (Fugle and Rothstein 1987). This sort of question was first posed for a congener, the Harris' Sparrow (*Zonotrichia querula*; Rohwer 1975).

In this study we attempt to identify one major proximate consequence of social behavior by analyzing the relative feeding locations of different social classes of White-crowned Sparrows. Understanding the processes responsible for the evolutionary stability of status signaling is likely to be enhanced by a more complete understanding of the consequences of social status. Several studies have demonstrated that birds prefer to forage near a source of cover (Caraco et al. 1980, Grubb and Greenwald 1982, Schneider 1984, Lima 1990). Here we attempt to determine how birds perceive cover while feeding and whether the importance of cover may relate to the evolutionary control of cheating (e.g. cheaters might be more susceptible to predation than noncheating subordinates). In addition, no study has addressed the question of whether cover is important for protection from predation, as opposed to other possible uses (e.g. a place to perch before initiating a feeding session). We used an artificial source of cover, in the form of a constructed bush, which we placed in an open area. The importance of cover per se was tested by manipulating the presence and absence of the bush, by moving the bush, and by allowing the birds use of both the bush and a simple perch. Our results demonstrate that White-crowned Sparrows have a strong preference to forage near a source of cover. We show that one of the proximate advantages of being adult (dominant) is lower escape times afforded by feeding closer to cover, and we discuss the implications of this result to the question of dishonest signalling.

#### METHODS

Our study was conducted during the winter of 1989-1990 on the West Campus (Devereaux) of the University of California at Santa Barbara, Santa Barbara County. We performed observations of birds feeding on a 2 m × 6 m concrete slab in a mowed field. The slab was about 20 m south of an established feeding site, where food was provided in the winter of 1988-1989, as well as during 1989-1990. The established feeding site was at the base of a row of dense bushes and trees, and there was a parallel row at the south end of the field, about 70 m from the slab.

For a manipulable source of cover, we constructed an artificial bush (2.5 m high × 1.2 m × 1.2 m) from

cut conifer branches, which we were able to move easily to perform various manipulations (see below). We provided three feeding stations, consisting of transparent hard-plastic bowls (diameter 30 cm, depth 5 cm). Bowls were placed 0.3, 0.8, and 1.3 m from the outer branches of the bush. We placed abundant seed (millet) into each bowl at the beginning of every observation period, and replenished the seed if it was depleted (seldom). Therefore, the amount of food available was held constant. We prebaited bowls on the day before each observation period.

We collected data during 28 observation periods between 12 December 1989 and 11 February 1990. Observations were made in the mornings (0730 to 0930 PST) and in the late afternoon (1500 to 1700) from a motor vehicle parked parallel to, and 4 m south of, the bowls. Individuals were captured and color banded at the established feeding site in a concurrent study (Mullen 1990), and that site always had a small amount of seed present.

In treatment 1 (12-31 December 1989), we placed the artificial bush on the west side of the concrete slab (see Fig. 1 for diagrammatic representation of experimental set-up and manipulations). For treatment 2 (31 December 1989 to 3 January 1990), we switched the bush to the opposite (east) side of the bowls to control for any position effects. In treatment 3 (12-20 January 1990), we removed the bush and tested whether the birds would use the bowls without it. After treatment 3, we removed grass stems and small weeds (about 20 cm high) that grew between the west bowl (bowl 1 in treatment 1, bowl 3 in treatment 2) and the established feeding site, as we noticed birds using this vegetation for cover (i.e. running low to the ground through the grass) as they approached the feeding area. In treatment 4 (26 January to 4 February 1990), we placed the bush on the west. In treatment 5 (4 to 11 February 1990), we placed the bush on the west and a "perch pole" on the east. This tested whether the birds were using the bush for cover or merely as a perch before landing on the bowls (i.e. did the birds feed in the bowl closest to the bush simply because it was closest to their perch?). The perch was a single pole 2.5 m high (2.5 cm diameter) with five 30-cm-long cross perches 30 cm apart, starting at the top. We stacked three broken concrete blocks at the base of the pole for support. This afforded the birds a slight amount of cover at the base, but no cover elsewhere.

We noted the number of adults (black-and-white crowns) and immatures (light-and-dark brown crowns) at each bowl every minute (one count) while birds were foraging. We included all birds on the concrete slab, with birds not in the bowls counted as being at the bowl nearest to them. Birds halfway between two bowls were counted as at the bowl they faced. The timing of the first count of a feeding period was random, initiated according to a preset electronic minute metronome. We did not include counts with more

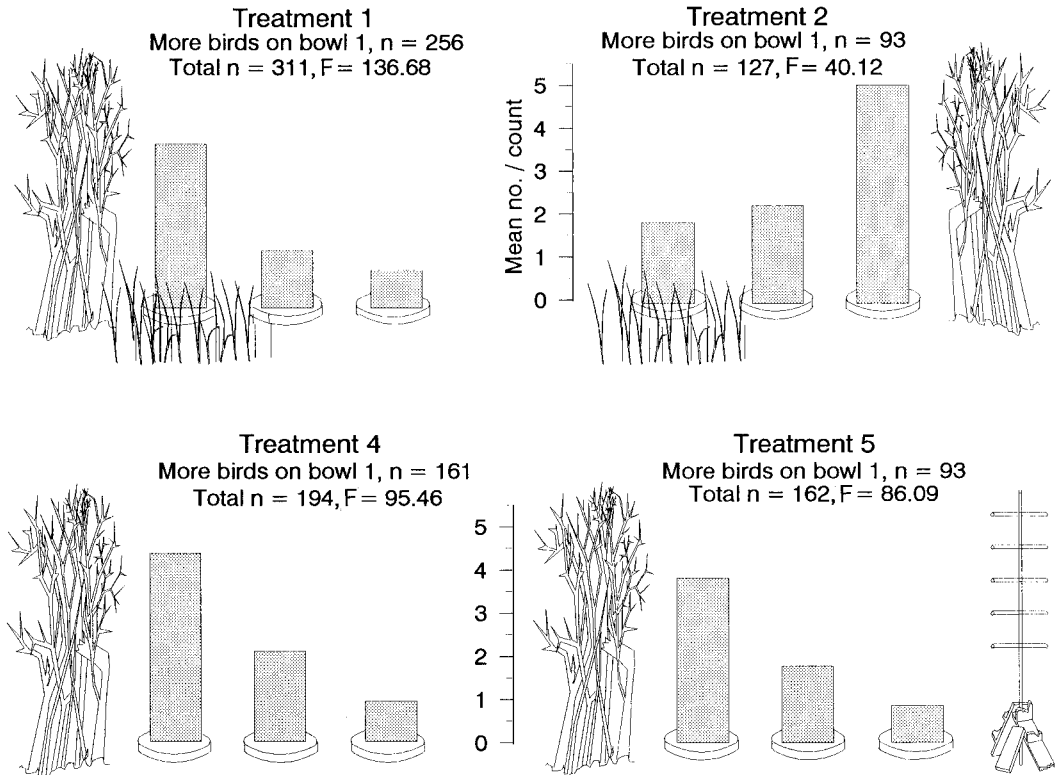


Fig. 1. Influence of distance from cover (artificial bush) on distribution of White-crowned Sparrows on feeding site. Diagrams of bush, grass, and perch (treatment 5 only) represent their respective locations for different treatments. Number of observations in which more birds were on bowl 1 than on either of other two bowls represented by  $n$ . Total  $n$  (number of observations) and  $F$ -values in each graph are for ANOVA ( $P < 0.001$  in all treatments). Mean for each bowl was different ( $t$ -tests,  $P < 0.05$ ) from those of other bowls in all comparisons in all treatments except for treatment 2, wherein means for bowls 2 and 3 were not different.

than 25 birds because we could no longer identify all the individual ages rapidly enough.

This type of design could suffer from the problem of repeated sampling of the same individual or pseudoreplication (Hurlbert 1984). Repeated sampling is an especially severe problem when many data are derived from a few individuals that may bias the data in one direction. However, when there are hundreds of individuals involved, as in our study (see below), there is no reason to expect results to be slanted in one direction or the other just due to the repeated sampling. Furthermore, we believe that each sample (count) is independent because:

(1) The average length of an individual's feeding bout was less than 1 min. We measured the length of individual feeding bouts using video of treatment 4. We randomly selected an individual whose color-band combination had been read onto the tape, and timed the duration of its feeding bout. The feeding-bout duration for 20 individuals averaged  $45.3 \pm \text{SE of } 6.6$  s (range 5–111 s). Only four birds fed for longer than

60 s (69, 102, 103, and 111 s) and, thus, were the only ones that could have been included in two consecutive counts. However, counts were random with respect to the initiation of a bird's feeding bout. So, for example, the individual feeding for 102 s would have had to initiate its bout 42 s or less before a count to be recorded in both that and the subsequent count. Note that the social composition of the other birds feeding would have changed dramatically between any two counts.

(2) A large amount of movement took place within our 1-min observation intervals. We measured the amount of movement on the feeding site using video of all treatments. We recorded data from seven sets of observations with each set consisting of 10 consecutive minutes of data recording. Each of the seven sets of data was from a different observation session on different days, and they were spread over all treatments. The start of a set was initiated randomly, and we then counted the number of birds coming onto and leaving the feeding site in a minute for 10 min.

The mean ( $n = 7$  sets of 10 min) number of birds arriving on bowl 1 was  $8.0 \pm 1.3$ , on bowl 2 was  $5.8 \pm 0.7$ , and on bowl 3 was  $2.3 \pm 0.6$ . The mean ( $n = 7$ ) numbers departing were: bowl 1,  $5.1 \pm 0.9$ ; bowl 2,  $3.9 \pm 0.4$ ; and bowl 3,  $1.2 \pm 0.2$ . As these numbers of arriving and departing birds per minute exceed the average numbers present on the bowls (see below), it is clear that there generally was a complete turnover of individuals after 1 min. The number leaving did not match the number arriving as we did not count birds leaving when all individuals flushed together. On average, all birds flushed together from the bowls once every 2.2 min, during these seven sets of data. Given that data were recorded every 1 min, this frequent flushing of entire flocks also reduces the likelihood of pseudoreplication because the system tended to "reset" itself after only two observations.

(3) A large number of different individuals used the feeding site. In total, 442 different color-banded individuals were captured at the site during the 1989–1990 winter season. Lincoln-index estimates of the number of birds using the feeding site (Blower et al. 1981) during two-day intervals over the study period were:  $350 \pm 109$  on 3–4 December;  $209 \pm 52$  on 10–11 December;  $179 \pm 33$  on 4–5 January;  $144 \pm 34$  on 28–29 January;  $240 \pm 66$  on 3–5 February; and  $227 \pm 56$  on 13–14 February. No individuals monopolized the feeding site.

We quantified proximity to cover with an index score in which a bird on bowl 1 (closest to cover) received a score of 1, on bowl 2 a score of 2, and on bowl 3 a score of 3. Our basic parameter for most statistical tests was the mean index score for all birds, or for adults and immatures separately, for each count. The closer to cover birds fed the lower the index score.

During treatment 5, we recorded the sequence of arrival of birds onto the bowls and also recorded where they flew when they left. We noted on a tape recorder a bird's origin, time elapsed since the previous bird had arrived, age, bowl, time of day, and when possible, individual band colors. We assumed birds that flushed as a group were responding to a perceived threat (a possible attack by a predator) even if in reality they were scared off by sudden movements of flock members. Precise data on the destination of birds leaving the patch were difficult to obtain because of large numbers of birds flushing at once. We simply recorded whether all, most, or some went to four possible destinations: the artificial bush, the perch, the natural bushes near the established feeding site, or some other destination (the latter being placed in a single category).

We analyzed the importance of cover in different treatments by ANOVA. The independent variable was bowl (levels 1, 2, and 3;  $df = 2$ ), and the dependent variable the number of individuals on each bowl. We performed  $t$ -tests between the mean number of birds on each bowl within each treatment. All of the remaining analyses were of index scores and, therefore,

we used nonparametric statistics. Unless stated otherwise, sample sizes in all cases were number of counts.

Several other species fed with the White-crowned Sparrows. These were present in much lower numbers and primarily included House Finches (*Carpodacus mexicanus*), Mourning Doves (*Zenaida macroura*), and Golden-crowned Sparrows (*Zonotrichia atricapilla*). These species were excluded from all analyses other than sequence of arrival.

## RESULTS

*Distance from cover.*—The data we present are for comparative purposes among bowls and, as such, we include only observations when there was at least one bird present on the experimental site. Too few White-crowned Sparrows utilized the site during treatment 3, when no cover was available, to allow for statistical analyses. In treatment 3, we made observations during three 2-h sessions. At the first session, 65 birds (not necessarily all different individuals) were noted during 19 counts, while the remaining 101 counts had no birds. During the second session no birds ever used the experimental site ( $n = 120$  counts) and, over the third session, 18 birds were noted during 15 counts ( $n = 120$  counts). Thus, the average number of birds present on the site when any were present (during first and third sessions) was

$$(65 + 18)/(19 + 15) = 2.4. \quad (1)$$

In contrast, during the other four treatments the average number of birds on the site when any were present was always at least five (Fig. 1), and there were never prolonged periods when no birds were present as in treatment 3.

The White-crowned Sparrows showed significant tendencies to feed close to cover (bowl 1) in each of treatments 1, 2, 4, and 5 (ANOVAs in Fig. 1). More birds were on bowl 1 than on either bowl 2 or bowl 3 in 73 to 83% of the observations (Fig. 1), whereas the null hypothesis would be 33% on each bowl. The remaining 17 to 27% of the counts included tied observations. When the position of the bush was switched from west to east (treatment 2), the birds reversed their feeding pattern, thus showing the importance of artificial cover. In treatment 4, the bush was switched back to the west, and the ground vegetation cleared. The birds once again switched their pattern so that significantly more fed on bowl 1. The addition of a perch opposite the bush (treatment 5) did not

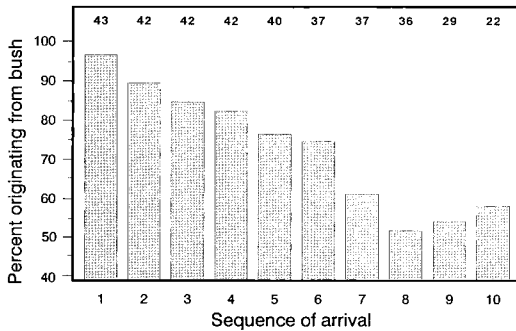


Fig. 2. Origin of birds moving onto feeding patch according to their sequence of arrival. Numbers above bars indicate sample size (number of flock visits), which decreased from 43 to 22 because some flocks did not have 10 birds arriving or birds began leaving before 10 birds had arrived.

change the distribution pattern, and as in treatments 1, 2, and 4 the number feeding decreased significantly from bowl 1 through bowl 3 (Fig. 1). This indicated that the birds perceived the bush as a source of cover and not merely as a convenient perch to use before landing on the feeding bowls (see below).

*Was the artificial bush perceived as a source of cover?*—Relevant data were collected only during treatment 5. The bush was the preferred point of origin for birds moving onto one of the feeding bowls ( $n = 493$  arrivals), as opposed to the perch ( $n = 7$ ) or the established feeding site ( $n = 173$ ). Examining only the first 10 birds arriving in a flock, birds early in the sequence of arrival moved onto the experimental patch from the bush, while as the sequence progressed, significantly more birds originated elsewhere (Fig. 2). For example, in 98% of 43 cases the first bird to arrive as a feeding group built up on the site went initially to the bush, and then to the food. The seventh through tenth bird did so in only 53 to 59% of the cases. The overall trend (Fig. 2) was significant ( $r_s = -0.952$ ,  $n = 10$ ,  $P < 0.01$ ) and indicated that the first birds exposing themselves were especially cautious in that they were most likely to go first to the protective cover afforded by the artificial bush. Overall, considering only the first 10 birds arriving, 281 birds arrived from the bush, 81 from the feeding site, 4 from the artificial perch, and 4 from an unidentified origin.

We assessed the destination of birds in 38 flocks that flushed naturally. All the birds flushed to the artificial bush in 11 flocks and

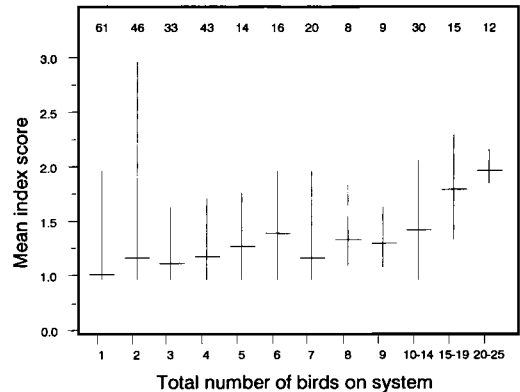


Fig. 3. Relationship between total number of White-crowned Sparrows foraging and mean index scores for treatment 1. Numbers indicate sample sizes (i.e. number of counts with each specified total). Vertical bars show range and horizontal bars indicate average of mean index score for all birds present at each count. Mean index scores shown to facilitate graphical presentation, but statistical tests performed using each count as individual data point. This treatment showed a significant positive correlation between index score and total number of birds, as did treatments 2, 4, and 5 (see text).

most did so in 20 flocks. There were only seven flocks in which most birds flushed to the bushes above the established feeding site. Only 10 birds ever flushed to the perch (5 occasions), and 4 to 10 times more individuals flushed to the artificial bush on each such occasion.

These data indicate that the birds perceived the artificial bush as a source of cover (from predation) and used it as: (a) a point of origin before exposing themselves (although, as the number of birds on the patch increased, more birds entered directly onto the patch); and (b) a source of cover when flushed under a potential threat.

*Relationship between feeding position and flock size.*—If there was competition for food or for feeding position, relatively more birds should have fed farther from cover when many were present because there might not have been room for all of them on the preferred bowl (closest to cover). Figure 3 is a plot of mean index scores for all birds present during counts against the total number of birds on the experimental patch in treatment 1. Graphs for the other treatments were similar and Spearman correlation tests showed that overall mean index scores increased significantly with numbers of birds in

TABLE 1. Number ( $\bar{x} \pm SE$ , with number of counts in parentheses) of White-crowned Sparrows using the feeding site during morning and afternoon sessions.

Treatment	Morning	Afternoon	$t^a$	df	$P$
1	4.19 $\pm$ 0.23 (189)	7.65 $\pm$ 0.68 (142)	-5.393	329	0.0001
2	7.48 $\pm$ 0.90 (73)	10.15 $\pm$ 1.04 (62)	-1.944	133	0.054
4	7.79 $\pm$ 0.80 (71)	6.94 $\pm$ 0.51 (126)	0.936	195	0.35
5	4.89 $\pm$ 0.30 (136)	11.55 $\pm$ 1.17 (33)	-7.959	167	0.0001

<sup>a</sup>  $t$ -test (two-tailed) of mean number of birds observed in morning and afternoon.

all treatments with sufficient data (treatment 1,  $r_s = 0.648$ ,  $n = 307$ ,  $P < 0.01$ ; treatment 2,  $r_s = 0.437$ ,  $n = 119$ ,  $P < 0.01$ ; treatment 4,  $r_s = 0.595$ ,  $n = 192$ ,  $P < 0.01$ ; treatment 5,  $r_s = 0.604$ ,  $n = 162$ ,  $P < 0.01$ ), indicating that all or most birds preferred to feed closest to cover unless precluded from doing so.

*Time of day.*—More birds fed on the site in the afternoon than in the morning in treatments 1, 2, and 5 (Table 1). As a probable consequence of this temporal difference, index scores were significantly higher in the afternoon (Table 2). However, the morning-afternoon contrast was not responsible for the significant correlations between index score and total number of birds (previous paragraph, Fig. 3). These correlations were still significant ( $P < 0.01$ ) in seven of eight tests when morning and afternoon data for treatments 1, 2, 4, and 5 were analyzed separately. To assess whether time of day provided a consistent bias in terms of age classes, we compared, for morning and afternoon counts, the proportion of the total number of birds present that were immatures. This proportion was significantly higher in the morning of treatment 1 (Mann-Whitney  $U$ -test,  $Z = 2.335$ ,  $P = 0.02$  (two-tailed),  $n_{\text{morning}} = 176$ ,  $n_{\text{afternoon}} = 135$ ), not significantly different for treatments 2 and 4, and almost significantly lower in the morning for treatment 5 ( $Z = 1.759$ ,  $P = 0.08$ ,  $n_{\text{morning}} = 129$ ,  $n_{\text{afternoon}} = 33$ ). Therefore, we concluded that time of day did not provide

a consistent bias as regards age class, and morning and afternoon data were combined for subsequent analyses.

*Spatial distribution of the age classes.*—We next determined whether the spatial distribution of adult birds was different from that of immatures. For each count we compared the index scores of adults with those of immatures (Table 3). Adult scores were significantly lower than immature scores (i.e. adults fed closer to cover) in treatments 1, 4, and 5, whereas the opposite was the case in treatment 2. We will discuss the divergent result from treatment 2 below.

We also compared the index scores of immatures feeding in the presence versus absence of adults (Table 4) to determine if immatures feeding with adults had higher scores (Table 3) because of the presence of adults, or because immatures simply chose inferior feeding sites. The significantly higher scores for immatures when feeding in the presence of adults in all treatments (Table 4) indicate that adults may displace immatures from positions closest to cover. However, the total number of birds per count also may influence these results, as more birds were present when immatures fed with adults than when they fed with no adults. To address this problem, we calculated a Kendall partial signed rank correlation (Siegel and Castellan 1988) for each treatment, holding the number of birds constant ( $z$ ), and correlating immature index score ( $y$ ) against the proportion

TABLE 2. Index scores ( $\bar{x} \pm SE$ , with number of counts in parentheses) of White-crowned Sparrows feeding in morning and afternoon. Low index score indicates that birds fed close to cover.

Treatment	Morning	Afternoon	$z^a$	$P^b$
1	1.25 $\pm$ 0.03 (176)	1.33 $\pm$ 0.03 (135)	1.56	0.06
2	1.48 $\pm$ 0.05 (70)	1.51 $\pm$ 0.06 (57)	0.48	0.32
4	1.33 $\pm$ 0.04 (69)	1.41 $\pm$ 0.03 (125)	1.54	0.06
5	1.39 $\pm$ 0.03 (129)	1.49 $\pm$ 0.05 (33)	1.94	0.03

<sup>a</sup> Mann-Whitney  $U$ -tests using one-tailed probabilities given that we predicted a higher score in afternoon when more birds fed.

<sup>b</sup> Individual  $P$ -values for each row. Combined  $P < 0.01$  for four rows together (Sokal and Rohlf 1981:780).

TABLE 3. Comparison of index scores of adult and immature White-crowned Sparrows when both were present during a count. Low score indicates that birds fed close to cover.

Treatment	Mean index score		Higher score <sup>a</sup>		<i>n</i> <sup>b</sup>	<i>z</i>	<i>P</i> <sup>c</sup>
	Adult	Immature	Adult	Immature			
1	1.37	1.50	38	80	182	-3.37	0.0007
2	1.88	1.58	50	22	79	4.80	0.0001
4	1.37	1.57	32	71	116	-4.08	0.0001
5	1.34	1.60	22	61	98	-4.48	0.0001

<sup>a</sup> Number of counts in which adults and immatures had higher mean score, with ties excluded.

<sup>b</sup> Total number of counts, which exceeds sum of preceding two columns given that it includes ties.

<sup>c</sup> Two-tailed probabilities of Wilcoxon paired signed ranks tests on adult versus immature indices.

of adults of the total number of birds on the system ( $x$ ; Table 5). The proportion of adults correlated significantly with immatures feeding at positions further from cover in two of the four treatments. While these analyses suggested that the presence of adults caused immatures to feed further from cover than they prefer, we cannot dismiss the possibility that immatures also choose worse feeding positions even in the absence of the demonstrated proximate influences from adults.

We attribute the results for treatment 2 (higher scores for adults; Table 3) to nonsocial factors. During treatment 2, birds (mainly adults) scuttled through low vegetation onto bowl 3 (recall that a *t*-test for mean numbers of birds on bowls 2 and 3 was not significantly different for treatment 2 only). Adults probably learned this route onto the system during treatment 1, when it led them directly to the preferred bowl (Fig. 1), and still used it even though the major source of cover (i.e. the bush) had been moved. If this interpretation is correct, adults in treatment 2 gradually should have learned to approach the system on a path that took them to the bowl that was then closest to cover (i.e. scores should have improved [become lower] with time). To test this expectation, we calculated a Spearman correlation of adult index score against session number (where session number was 1, 2, 3, or

4, corresponding to the four consecutive days over which observations were made) and found an  $r_s$  of  $-0.222$  ( $n = 90$ ,  $P < 0.05$ ). The slowness of adults to change their feeding behavior in response to the shifted cover is not surprising because the location of cover does not change from day to day under natural conditions. Immatures may have adjusted to the circumstances of treatment 2 more quickly than adults, because immatures may have been less conditioned into the approach route that brought birds to what was the preferred bowl in treatment 1. Treatments 4 and 5 were not affected by the low vegetation, as it was removed prior to treatment 4.

In treatment 2, the immatures had significantly higher scores when feeding in the presence of adults than when feeding alone (Table 4) indicating that, even though the adults had a higher mean index score (Table 3), they may have still displaced immatures. We checked this seemingly illogical result by examining the frequency distributions of mean adult and immature index scores for each count for each treatment. The frequency distribution of adult index scores for treatment 2 was bimodal in nature, with the two highest frequencies at scores of 1 and 3. Adults with the latter score had, according to our interpretation, still not learned that the route that took them to the

TABLE 4. Index score ( $\bar{x} \pm SE$ , with number of counts in parentheses) of immature White-crowned Sparrows when feeding in presence or absence of adults. Low score indicates feeding closer to cover.

Treatment	Immature index scores		<i>z</i> <sup>a</sup>	<i>P</i>
	Adults present	Adults absent		
1	1.50 $\pm$ 0.04 (182)	1.14 $\pm$ 0.03 (114)	6.87	0.0001
2	1.58 $\pm$ 0.05 (79)	1.39 $\pm$ 0.09 (29)	2.58	0.005
4	1.57 $\pm$ 0.03 (116)	1.26 $\pm$ 0.05 (72)	5.98	0.0001
5	1.60 $\pm$ 0.04 (98)	1.24 $\pm$ 0.05 (60)	5.49	0.0001

<sup>a</sup> Mann-Whitney *U*-tests using two-tailed probabilities.

TABLE 5. Kendall partial correlation coefficients ( $T_{xy.z}$ ) showing influence of adults on feeding position of immatures. Total number of birds on system held constant ( $z$ ), and tested for correlations between immature index scores ( $x$ ) and proportions of total number of birds on system that were adults ( $y$ ).

Treatment	$T_{xy.z}$	$n$	$z$	$P^a$
1	0.037	289	0.983	0.34
2	-0.10	112	-1.586	0.12
4	0.164	189	3.338	0.001
5	0.165	158	3.053	0.002

\* Two-tailed probabilities.

bowl closest to cover in treatment 1 no longer did so in treatment 2. In all the other treatments, the frequencies of adult index scores had a single mode, located at a score of 1.

### DISCUSSION

*Distance from cover.*—Other studies have also demonstrated that individuals feed closer to cover if given a choice (Grubb and Greenwald 1982, Schneider 1984, Lima 1987, 1990, Mullen 1990, but see Lima et al. 1987). The unique aspect of our study is that we tested the importance of cover per se by offering no cover, by switching the position of the cover, and by offering a simple perch as an alternative to cover. When the artificial bush was absent, very few individuals fed on the experimental food patch, despite a dense source of cover about 20 m away. Similarly, Lima (1990) found that foraging White-crowned Sparrows greatly increased their use of an open field after he provided a source of woody cover. When we provided the artificial bush, initial individuals moving onto the feeding patch almost always flew first to the bush, and then onto the patch, while later arriving individuals often moved directly onto the patch. This suggests that the probability that an individual is willing to risk directly approaching an exposed feeding position is directly proportional to the number of individuals already feeding. When there are no birds feeding, the less risky approach of first landing in the nearest source of cover may be traded off against feeding time lost by doing so. When we provided an alternative perch (but almost no cover) on the opposite side of the bowls from the bush, the sparrows used the bush almost exclusively, both as a point of origin before moving onto the bowls, and as a destination

when flushing from the bowls (under a presumed threat). Thus, we have demonstrated that White-crowned Sparrows strongly prefer a nearby source of cover before they will feed. The function of cover is more substantial than that of a perch and is probably to provide protection from predation.

*Time of day.*—Dark-eyed Juncos (*Junco hyemalis*) initiated feeding earlier in the day when food was provided under cover, than when food was away from cover, and individuals with reduced fat reserves initiated feeding earlier than control birds (Lima 1988). Lima concluded that there was a trade-off between starvation and predation risk. In the afternoon, juncos terminated their feeding at higher light intensities than when they initiated feeding, relinquishing up to 1 h of potential feeding time (Lima 1988). By contrast, we found that more birds fed in the afternoon than in the morning, but this may be an artifact of our observations. Our morning observations began relatively late, perhaps after an initial peak of feeding birds, while our evening observations ended just before the birds went to roost, resulting in our recording the afternoon peak and, thus, more birds. More studies such as Lima's (1988) are required to elucidate differences in foraging behavior at different times of day.

*Influence of social status.*—The mean duration of feeding bout found in our study (45.3 s) is considerably less than the 109 to 203 s found by Keys and Rothstein (1991) at a site 8.2 km away. However, the latter study involved a much larger feeding site and a smaller local population (136 to 188 sparrows trapped per year as opposed to 442 in the current study), which together should have resulted in less competition for feeding space. Strong competition for feeding space in our study was indicated by (1) the shorter feeding periods and (2) the increasing proportion of birds feeding further from cover as the total number of feeding birds increased.

In all four treatments with sufficient data for analyses, the index scores of immatures were higher when adults were present than when they were absent, which conformed to our *a priori* prediction. A partial correlation (holding number of birds constant) showed that immatures fed further from cover as the proportion of adults increased. Thus, immature birds fed further from cover than did adult birds, and dominant individuals apparently displaced



subordinates from the preferred feeding position (bowl closest to cover; Table 4). Several studies on other species have demonstrated that dominant individuals displace subordinates from feeding positions closest to cover. This occurs in small, stable flocks of less than 10 individuals (Black-capped Chickadees [*Parus atricapillus*], Desrochers 1989; and Willow Tits [*P. montanus*], Ekman and Askenmo 1984, Högs-tad 1988), as well as in larger less stable flocks (e.g. White-crowned Sparrows, Mullen 1990; White-throated Sparrows [*Z. albicollis*], Schneider 1984, Piper 1990). Numerous studies have shown that adult birds dominate immatures (e.g. White-crowned Sparrows; Fugle and Rothstein 1987, Keys and Rothstein 1991). One advantage of higher social status may be that it enables dominant birds to take lower risks of predation, because they feed closer to cover. This should give dominant individuals a lower escape time if the flock is attacked by a predator, and possibly even a lower probability that a predator will choose to direct an attack on them. Thus, dominant individuals should have a higher likelihood of surviving the winter even if food is not limiting, which may be the case in the mild winters of southern California.

We cannot eliminate the possibility that, in addition to active displacement by adults, immatures may also choose worse positions on their own (perhaps due to inexperience or because they are likely to be displaced from positions near to cover if adults arrive). Nevertheless, immatures do feed further from cover regardless of the proximate causation and, as discussed in the next subsection, this fact may influence the evolutionary control of cheating in a status-signalling system.

An unexpected finding of our study concerned the conditioning effect that adults seemed to show in the transition between treatments 1 and 2. Relative to immatures, adults were slower to switch from the bowl that used to be closest to cover in treatment 1 to the one that was closest in treatment 2. Although adults showed a significant tendency to switch over the four-day period of treatment 2, the results suggest that they may be less flexible in their behavior than immatures when confronted with a novel situation (i.e. a change in location of cover). Such inflexibility is what one might expect if adults are usually doing well (i.e. gaining access to preferred, safer feeding sites). By contrast, subordinate individuals such as immature

White-crowned Sparrows might be much more flexible in their behavior as their usual situation may be suboptimal. This apparent variation in degrees of behavioral flexibility needs further testing, but the results presented here indicate a heretofore unsuspected consequence of social dominance and subordination.

*Evolutionary control of status signalling.*—Previous experiments showed that cheating can increase the social status of subordinate White-crowned Sparrows because cheaters dominated noncheating members of their own age and sex class (Fugle et al. 1984, Fugle and Rothstein 1987). However, would an immature White-crowned Sparrow that cheats have greater overall fitness, measured as winter survival, than a noncheater? A critical answer to this question, and one that may solve the paradox of status signalling, is whether cheating subordinates feed closer to cover than noncheaters and, thus, reduce their predation risks (Mullen 1990). By definition cheaters possess brighter and (at least to humans) less-cryptic coloration than noncheaters, which may make them more conspicuous to predators. If cheaters feed no closer to cover than do noncheaters, then they are likely to experience a heightened risk of predation. Thus, we suggest that immatures do not cheat because increased access to food through heightened social status (a presumed benefit of cheating) may not outweigh increased predation risks due to brighter plumage.

Note that adult males dominated immature females painted as adults (Fugle and Rothstein 1987). Thus, cheaters may not feed closer to cover than noncheaters or may possibly feed at distances from cover that are between adults and noncheating immatures. Either of these possibilities might make cheaters more prone to predation than noncheaters and adults. Under this view, noncheaters have an advantage because their less conspicuous plumage makes it less likely that they will be targeted for an attack by a predator despite their relatively long distances from cover. Adults may be able to "afford" their brighter plumage because their higher intrinsic abilities to dominate other birds (see Collis and Borgia 1992) enable them to feed closer, on average, to cover than immatures. Also, predators may be unlikely to choose prey close to cover regardless of the prey's conspicuousness. A link between predation and the full expression of a status signal has been indicated in House Sparrows (*Passer domesticus*; Møller

1988) and suggested for Dark-eyed Juncos (Balph et al. 1979).

Our new hypothesis for the evolutionary stability of status-signalling systems depends on the widely held assumption that predation risk increases with distance from cover. Although we have no direct data on predation, we suggest that the birds' behavior shows the value of cover. Beside preferring to feed near cover, most birds first went to the bush before actually feeding. And more to the point, when entire flocks flushed in obvious fright situations, birds tended to dive into the bush. Thus, the hypothesis will receive very strong support if experimentally created cheaters (as in Fugle and Rothstein 1987) are found to feed as far from cover as noncheating immatures. If cheaters feed at distances intermediate between those of adults and noncheating immatures, the test will be inconclusive, but not inconsistent with our hypothesis (because the lesser distance may not outweigh any costs from increased conspicuousness). Our hypothesis will be invalidated if cheaters feed as close to cover as true adults.

The predation-risk hypothesis also will be invalidated if it is found that bright-colored White-crowned Sparrows are less prone to predation than dull ones. However, only one study has supported this unprofitable-prey hypothesis (Baker and Parker 1979) in birds. Furthermore, the factor most likely responsible for that support, much higher mass and lower maneuverability in duller individuals (Götmark 1992), does not apply to our study as adult and immature White-crowned Sparrows have identical masses (Fugle and Rothstein 1985). Nevertheless, we cannot at present exclude the possibility that adults are harder to catch than immatures because of their slightly longer wings (Fugle and Rothstein 1985) or greater experience, and that predators therefore prefer to attack immatures.

#### ACKNOWLEDGMENTS

Joe Alcock, Susan English, and Punam Mathur assisted in the field. Members of the behavioral ecology discussion group at the University of California at Santa Barbara (UCSB) gave valuable comments through all phases of this study. John Endler, Sidney Gauthreaux, Roland Knapp, Ellen Paxinos, Eric Schultz, Dave Ward, and Bob Warner gave valuable comments on drafts of the manuscript. Ted Mullen was kind enough to color band White-crowned Sparrows above and beyond the call of duty and made his

banding data freely available to us. Kris Burnell helped with the figures. The UCSB Vertebrate Museum provided essential pieces of equipment. R.H.S. received a University of California Regents Fellowship, and S.I.R. was supported by NSF grant 8616922 and by a UCSB Faculty Research Grant.

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