STATUS SIGNALING IS ABSENT WITHIN AGE-AND-SEX CLASSES OF HARRIS' SPARROWS

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ABSTRACT.—We tested the status-signaling hypothesis in two groups of same-age and same-sex Harris' Sparrows (*Zonotrichia querula*). Unlike flocks of mixed age and sex composition, badge size did not correlate with social status in these groups; thus, status signaling does not appear to occur within age-and-sex classes of Harris' Sparrows. Other predictions of the status-signaling hypothesis we tested were that (1) fighting ability and social status should be correlated, and (2) fighting ability and badge size should be correlated. We used a multivariate assessment of body size as an indicator of fighting ability and found no support for either prediction in the flock of adult females. In the flock of adult males, large birds were more dominant (Prediction 1) but fighting ability and badge size were not correlated (*contra* Prediction 2). *Received 21 May 1987, accepted 20 January 1988.*

THE status-signaling hypothesis, invoked to explain avian winter plumage variability (Rohwer 1975), comprises three relationships: (1) Individuals with superior fighting ability are able to defeat a greater number of opponents than individuals with inferior fighting ability. Good fighters therefore have higher social status than poor fighters (relationship A, Fig. 1). (2) Individuals should signal their fighting ability to other individuals (relationship B, Fig. 1). If good fighters can be recognized, they will be avoided by other birds and will gain resources without being contested. Individuals with inferior fighting ability do not cheat (i.e. display badges like those of better fighters) because they benefit either by associating with better fighters or by employing an alternative competitive strategy. Reliably signaling their ability and assuming a subordinate role presumably results in a higher payoff than cheating (Rohwer and Ewald 1981, Rohwer 1982). (3) Given the first two relationships, there should be a positive correlation between social status and the conspicuousness of the badge (relationship C, Fig. 1).

The status-signaling hypothesis has been analyzed in nine species and the results reviewed recently by Whitfield (1987). Plumage differences are often correlated with sex and age, so unless these correlated traits are controlled, it is unclear whether badges function as status signals within groups of same-sex and same-age individuals. Only two studies, on Great Tits (*Parus major;* Jarvi and Bakken 1984) and Pine Siskins (*Carduelis pinus;* Balph and Balph 1979), support the hypothesis fully by showing that plumage is correlated with social status even among birds of the same age and sex.

We investigated the status-signaling hypothesis in Harris' Sparrows (*Zonotrichia querula*) by examining dominance relationships among individuals of the same age and sex classes. We wanted to correlate social status and intrinsic fighting ability in controlled age and sex populations. We assumed that body size is a determinant, or at least an indicator, of fighting ability. If body size affected social status, then we predicted larger birds would have badges that were more conspicuous than those of smaller birds. The badge displayed by Harris' Sparrows, a black crown and bib on the throat and breast, varies among age-and-sex classes from being almost completely absent to covering almost all of this area. Badge size varies much less within age and sex classes. If better fighters are higher in status and and have larger badges, then we would expect a correlation between social status and badge size within these groups of same age-and-sex individuals. Rohwer (1985) showed that young birds dyed to resemble adults obtained higher social status than control birds within flocks of young males and young females. This demonstrated that status signaling occurs between age classes, and therefore cannot answer the questions posed here because badge size is correlated with age (Rohwer et al. 1981).

METHODS

Behavioral observations were conducted on females from 16 to 21 November 1982 and on males from 23 to 25 November 1982 in outdoor aviaries in north-central Kansas. Birds were captured in mist nets at a site in the flood plain of the Blue River, north of Tuttle Creek Reservoir, and banded with unique color combinations of plastic leg bands. Birds were assigned to sex and age (adult vs. subadult) classes by differences in wing length, plumage score, and tail shape (Rohwer et al. 1981). All 33 birds were later prepared as museum specimens (see below), and gonadal inspections and skull ossification data confirmed that all the birds were aged and sexed correctly at the time of the observations. The 17 adult females used in the experiment were caught at one locale on one occasion. The 16 adult males were from one locale but caught on two occasions (8 birds at a time) 4 days apart. After capture birds were transported about 50 km south to the Konza Prairie Research Natural Area near Manhattan, Kansas, where they were housed together with other birds of all age and sex categories. The females were housed together and allowed to habituate for 4 days until behavioral observations began. The males were also all housed together and habituated for 7 or 11 days.

All birds were transferred at the same time to a novel aviary out of sight of the holding cages, and observations were made immediately from a large wooden hide about 20 m from the aviary. Food was distributed profusely and evenly over the floor of the aviary. Two or three observers worked together; one or two dictated the interactions, and one person was recorder. After the initial observation period, during which more than half of the interactions were recorded, we attempted to fill empty cells in the dominance matrix; thus, interactions were recorded more or less randomly on each flock only during the first observation period. Observations were made throughout the day. Supplantings were scored as "active" or "passive." In active supplantings, the winning bird initiated the displacement by a short rush or other event indicative of aggression. In passive supplantings, the losing birds merely moved away at the passive approach of the "winner" without any overt indication of aggressive behavior on the part of the "winner."

We constructed dominance matrices by scoring each interaction to the right of the winner and below the loser. From these matrices we determined the number of subordinates each bird had. An individual was considered dominant to another if it won the greater number (i.e. simple majority) of contests between those two birds, or, when both birds won an equal number of contests, if it won the greater number of active contests. If both individuals won the same number of active and passive contests, the relationship was scored as a tie. We used the number of subordinates an individual had as the measure of social status.

All birds were prepared as flat-skin/skeleton combinations and deposited at the University of Washington Burke Museum. Body size was calculated by a principal components analysis on 9 body measurements (flattened wing length when captured and 8 bone measurements). Measurements of posterior skull width, humerus length, ulna length, synsacrum width, femur length, tibiotarsus length, and tarsometatarsus length were taken according to methods described by Rohwer (1972). Sternum length was measured as the distance from the anterior edge of the manubrial spines to the posterior edge of the mesial caudal process. The first principal component, PC1, is often interpreted as an indicator of body size (Ricklefs and Travis 1980, Schluter 1984, Watt 1986b). We used an orthogonal transformation solution (Varimax Solution, Stat View 512+), which resulted in a clear simple structure of the factors. The loadings of the five long-bone measures (humerus, ulna, femur, tibiotarsus, and tarsometatarsus) on rotated factor 1 ranged from 0.755 to 0.950 in both sexes. In females the other three bone measures had loadings on rotated factor 1 greater than 0.600; in males these loadings ranged from −0.157 to 0.137. Flattened wing length had small loadings in both females (0.230) and males (0.194). Because of the consistently high loadings of bone measures in females and the high loadings of long bones in males, we concluded that factor 1 of the orthogonal rotation was a good indicator of body size (the greater the rotated factor 1 score, the larger the bird).

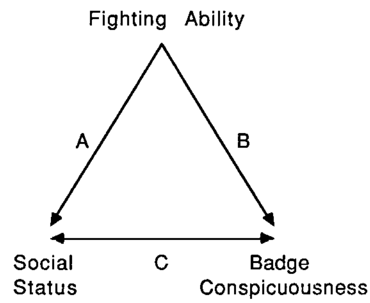

Fig. 1. Diagrammatic representation of the three relationships in the status-signaling hypothesis.

Plumage conspicuousness was assessed using the 14 categories pictured by Rohwer (1975). If a bird fell between two categories, the categories were averaged. The average plumage score of the males was 11.8 ± 1.5 (range 9–14), and that of the females was 9.3 ± 2.1 (range 5–12).

Spearman rank correlations were calculated for body size (rotated factor 1 score) and social status (number of subordinates) (relationship A), body size and plumage score (relationship B), and social status and plumage score (relationship C). The level of statistical significance used throughout was 0.05.

Results

Among the females no significant correlations were found for any of the three relationships involving body size, social status, and plumage score (r_s = 0.22, −0.20, and 0.34 for relationships A, B, and C, respectively). Among the males there was no significant correlation between body size and plumage score (r_s = 0.27) or between social status (number of subordinates, corrected for tied and undetermined dominance relationships) and plumage score (r_s = 0.08). Body size correlated significantly with social status (r_s = 0.61, $P < 0.05$). This relationship was manifested in two ways. Body size correlated positively with the number of times a bird was avoided by other birds (i.e. passive wins) (r_s = 0.62, $P < 0.05$) and negatively with the number of active aggressions a bird received (active losses) (r_s = −0.63, $P < 0.02$).

DISCUSSION

Our results do not support the hypothesis that status signaling occurs within age or sex classes of Harris' Sparrows. Badge score was uncorrelated with social status in both males and females. Rohwer et al. (1981) showed previously that badge score could not predict winners of encounters within age-and-sex classes at concentrated food resources but, unlike this study, that it could predict winners when food was distributed diffusely. The sample sizes in their study were small, however, and data from within each age-and-sex class were combined. Our work was based on a much larger sample size and dealt with overall dominance relationships, not simply isolated encounters. Watt (1986b) found a correlation between dominance rank and badge score in one group of adult female Harris' Sparrows. These females were members of a larger flock containing all age-and-sex classes, however, so their dominance ranks may have been affected by dominance relationships with other birds in the group.

Body size appeared to influence dominance in males, but not in females. Small males avoided large males and were the recipients of more aggression than large males. These findings may be explained in two ways: birds can assess their body size relative to their opponent's body size, or, because these birds were all familiar with one another, they can recognize individual birds. These explanations are not mutually exclusive. Although dominance status originally may have been based on body size, once a bird can recognize other individuals it may save time and energy when assessing the relative size of other birds.

It is not surprising that there was no correlation between body size and badge score. Badges are not signals of status within age-and-sex classes. We would have expected this correlation, at least in males, if the status-signaling hypothesis had been supported. Honest badges that signal body size would be expected because these should facilitate a bird's ability to assess the fighting ability of its opponents.

Because badges do not signal status, variability in badge size within an age-and-sex class either may function in individual recognition (Collias 1943, Shields 1977, Watt 1986a) or may not, in fact, be adaptive (Balph et al. 1979). If the former is true, manipulating a bird's appearance will make it unrecognizable to members of its own flock and therefore should increase the rate of aggression received by this bird, regardless of whether the plumage is made more or less "conspicuous." Whitfield (1987) performed plumage manipulations on Ruddy Turnstones (*Arenaria interpres*) and found that the rate of aggression toward experimental birds increased regardless of how the plumage was changed. This hypothesis could be tested in Harris' Sparrows by dying birds so that they still lie within the normal range of badge sizes for their own age-and-sex class. If manipulation results in a change in the rate of aggression toward those birds, the individual-recognition hypothesis will gain support. Watt (1986a) presented data on Harris' Sparrows consistent with the individual-recognition hypothesis. She found that increased plumage variability was related to increased relative avoidance levels in small groups. Her data are from flocks of mixed age-and-sex composition, however, so badges may be serving as indicators of age and sex classes.

Alternatively, variability may exist simply because there is no selection against it. Badges may serve as coarse indicators of fighting ability by identifying a bird's age-and-sex class, as in White-crowned Sparrows (*Zonotrichia leucophrys*; Fugle and Rothstein 1985, 1987) and as suggested for Harris' Sparrows (Watt 1986b). This would allow birds to avoid interacting with individuals they stand no chance of defeating. Fine-tuning of this signal, however, may not be possible because fighting ability can change on a day-to-day basis. It can be affected by condition of the individual and the individual's motivation to challenge an opponent. The lack of a correlation between body size and social status in females we found may have resulted from incongruities between body size and these other factors that may determine fighting ability.

We submit that the status-signaling hypothesis was not supported in Harris' Sparrows when age and sex are controlled. The individual-recognition hypothesis remains to be tested within groups of same-age and same-sex individuals.

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