The Condor 103:151–157

MALE BADGE SIZE PREDICTS DOMINANCE AGAINST FEMALES IN HOUSE SPARROWS[1]

ANDRÁS LIKER[2]
Behavioural Biology Research Group, Department of Ecology, Szent István University, Pf. 2, H-1400, Budapest, Hungary

ZOLTÁN BARTA[3]
Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Pf. 3, H-4010 Debrecen, Hungary

Abstract. We investigated dominance relationships and the use of male badge size as a status signal in a mixed-sex flock of House Sparrows (*Passer domesticus*). Specifically, we tested whether females differ from males in their fighting behavior or dominance status, and whether badge size predicts dominance and fighting success of males in male-female fights. We found that both sexes were involved frequently in aggressive encounters, and the mean dominance rank of males did not differ from the mean rank of females. Badge size was the only significant predictor of the dominance rank of males, and was a good predictor of their aggressiveness measured as the proportion of fights initiated. On the other hand, female dominance rank was correlated with body weight. In male-female fights, both the proportion of female-initiated aggressive interactions and the proportion of fights won by females decreased with increasing size of the opponent's badge. Large-badged males dominated more females in dyadic interactions than smaller-badged males. These correlational results suggest that male badge size may be used as a signal of dominance status between male and female House Sparrows in winter flocks.

Key words: badge size, dominance, House Sparrow, intersexual aggression, Passer domesticus, *social behavior, status signaling.*

INTRODUCTION

Several studies have investigated dominance relationships in captive House Sparrow (*Passer domesticus*) flocks, and have described their general characteristics. These studies found that captive sparrows frequently fight over resources, particularly for food and roosting places, and that it is often possible to identify a dominant individual within each pair of contestants (Watson 1970, Hegner and Wingfield 1987, Møller 1987). Individuals within the flocks can usually be arranged in a linear or close to linear dominance hierarchy, often with a despotic individual at the top, who clearly dominates other flock members and wins a high proportion (80–90%) of his or her fights (Watson 1970, Møller 1987, Solberg and Ringsby 1997). Dominance rank and aggressiveness are positively related to the circulating level of plasma testosterone at the time of the establishment of dominance relationships within the flocks (Hegner and Wingfield 1987). The best morphological predictor of dominance rank of male sparrows is the size of their black throat patch (i.e., badge), and males use their badge for signaling their status in aggressive encounters with other males (Møller 1987, Veiga 1993).

Our main aim is to investigate whether badge size is a predictor of dominance in male-female interactions. Although sparrows typically occur in mixed-sex flocks, earlier studies of male dominance status either excluded male-female interactions from the analyses (Møller 1987), investigated the correlates of male dominance rank in single-sex male flocks (Solberg and Ringsby 1997), or did not specify the types of interaction on which the results were based. To our knowledge, status signaling between the sexes has not been studied for any other bird species where one of the sexes lacks the signal, although the theory of status signaling (Rohwer 1975) predicts that signaling between the sexes may be adaptive in dimorphic species. For example, in House Sparrow flocks it may be advantageous for females to pay attention to the male's badge

---

[1] Received 9 March 2000. Accepted 11 September 2000.

[2] E-mail: aliker@univet.hu

[3] Present address: Centre for Behavioural Biology, School of Mathematics, University of Bristol, Bristol, BS8 1TW, UK.

size, because in this way they could avoid unprofitable fights against the most aggressive dominant males.

In this study we first investigate how much aggression occurs between the sexes and whether, on average, males and females differ in their dominance ranks in wintering flocks. The nature of dominance relationships between the sexes seems to be controversial based on the results of previous studies. For example, Watson (1970) and Møller (1987) suggested that females rarely participate in fights, and usually males are dominant to females during the winter. On the other hand, Hegner and Wingfield (1987) reported that females were dominant to males in some flocks, whereas there was no sex-related difference in dominance rank in other flocks. Second, we repeat and supplement some earlier tests of the status-signaling hypothesis which were carried out in male House Sparrows (Møller 1987, Solberg and Ringsby 1997), to demonstrate that badge size predicts dominance in male-male fights in our population. Finally, we test the following two predictions of the hypothesis that badge size has a signal function in intersexual fights: (1) females initiate fights less often against large-badged males than against males with smaller badges, (2) females retreat more often (i.e., win less often) in fights with large-badged males and, consequently, the number of females dominated by a male increases with increasing size of the male's badge.

METHODS

The study flock consisted of 10 male and 10 female House Sparrows captured from two neighboring flocks resident around the campus of the Szent István University, Faculty of Veterinary Sciences, Budapest. Sparrows were trapped by mist nets near feeding sites, during November–December 1997, except for one male which was trapped at the beginning of February 1998. Because more than 90% of the observations were done after the introduction of this latter male, and because he was a low ranking individual (17th of 20), we feel his introduction did not affect significantly the reported social organization of the flock. We captured females and males from both flocks; therefore, some males were unfamiliar to some females as well as to some males. After capturing the birds, we banded them with a metal band and a unique combination of two color bands, and measured their body weight to the nearest 0.1 g, tarsus length and beak length to the nearest 0.1 mm, and wing length to the nearest 1.0 mm. We measured weight again in February (in the middle of the study) and March (at the end of the observations) 1998. The maximum height (h) and maximum width (w) of the throat badge of each male also was measured to the nearest 1.0 mm. Badge size was estimated as the area of a circular sector with radius h and chord w (Veiga 1993). This estimate of badge size was highly repeatable (intraclass correlation: $r = 0.82$, $F_{1,32} = 10.6$, $P < 0.01$). The mean ± SE area of badge size was 302.8 ± 15.8 mm^2 (range 243.1–384.4 mm^2). All measurements were made by the senior author.

The flock was housed in an indoor aviary measuring $3.6 \times 4 \times 3$ (height) m. It contained two feeders, a dish for water, a dish for sand, several branches, and a small bush for roosting. One of the feeders (hereafter, ''the grid'') was a 0.8×0.8-m table that contained 48 shallow, 5-cm diameter holes for presenting food. The other feeder (hereafter, ''the feeder'') was a $10 \times 10 \times 20$-cm tank, with a 5×5-cm hole on the bottom of one side. A short wooden stick was fixed below the hole, from which the birds could reach seeds appearing in the hole of the feeder. Several birds could feed on the grid simultaneously, whereas only one bird could feed at the feeder. Between behavioral observations, food (a mixture of millet, sunflower seeds and wheat, mixed with vitamin powder) was provided *ad libitum* on the grid. Before observations, food was removed from the aviary for 2–3 hr, and it was provided again either on the grid (distributed in eight holes) or at the feeder at the start of the observations. Birds were housed under natural daylengths. The aviary provided enough space for the birds to retreat from aggressive encounters. Body weight decreased slightly during the study (mean ± SE at capture: 27.3 ± 0.4 g; at the end of the study: 26.3 ± 0.3 g; paired t-test: $t_{19} = 3.68$, $P < 0.01$), which may be related either to the favorable conditions (mild climate, predictable food) facilitating the loss of some fat, or to some kind of stress caused by disturbances during housing. All birds were released at the site of capture at the end of the study, and many of them have been regularly observed at an outdoor feeder subsequently.

Behavioral observations were conducted between January and March 1998. The duration of observation sessions varied between 1 and 2 hr, and started at various times during the day (between 06:00 and 18:00). During the observations, we recorded aggressive encounters between pairs of individuals if the following conditions were met: (1) both participants were identified, (2) one individual directly attacked the other bird by pecking at the opponent, and (3) the outcome of the contest was clear. An individual was considered to win a fight if he or she clearly supplanted the opponent. We also noted which participant of the contest initiated the fight. The birds were observed through a one-way window. In total, 44 observation sessions were conducted during the study (57 hr).

STATISTICAL ANALYSES

Dominance relationships were determined for each pair of individuals by the outcomes of repeated interactions: an individual was considered dominant in the dyad if it won more than 50% of the aggressive encounters, and the other member was considered subordinate. The dyad was tied if the participants won an equal number of fights. Dominance relationship was unknown in dyads with no aggressive encounters. Dominance rank of individuals within the flock was determined by de Vries' (1998) ''I and IS'' procedure, which allows the ordering of large flocks. This method seeks a rank order most consistent with a linear hierarchy by minimizing the numbers of inconsistencies (I) and the total strength of the inconsistencies (IS) in the hierarchy. The significance of linearity of the hierarchies was tested by a randomization test developed by de Vries (1995). This test can cope with tied and unknown relationships in the dominance matrix. We used 10,000 repeats to estimate the significance level for the unbiased Landau's linearity index (h'). To compare dominance ranks of males and females, a two-tailed, two-sample randomization test was applied (Manly 1991). To compare observed and expected number of fights between groups of male dyads with specific badge-size differences, we used Mantel's randomization test with 5,000 repetitions (Manly 1991). In other cases, we did not test the difference in frequency of fights between groups of dyads because we found no appropriate statistical procedure for such tests (e.g., for incomplete matrix of nonindependent observations). Because ranks of individuals were numbered from 1 (the most dominant) to 20 (the most subordinate), negative correlation coefficients involving dominance rank indicate dominants having higher values than subordinates for the variables examined. Ordinary statistical tests were conducted by SPSS for Windows 7.5 (SPSS, Inc. 1996). Mean ± SE and two-tailed probabilities are given throughout. In multiple statistical tests, Bonferroni correction was applied to adjust significance levels appropriately (Chandler 1995).

RESULTS

THE FREQUENCY OF FIGHTS AND THE RANKS OF MALES AND FEMALES

We observed 1,497 aggressive interactions among members of the sparrow flock. Males and females did not differ significantly in the number of fights they were involved in (males: 164.5 ± 22.7, females: 134.9 ± 20.9; Mann-Whitney U-test: $U = 36$, $P > 0.2$, $n_1 = n_2 = 10$). However, aggressive interactions were observed between males more often than expected by chance (observed/expected: 466/355), whereas they occurred less frequently between females (318/355) and between males and females (713/787). Expected frequencies were calculated as the product of total number of fights and the proportion of a given type of dyad; the proportion of female dyads and male dyads was 45/190 each, and the proportion of male-female dyads was 100/190. Similarly, the number of fights in male-male dyads tended to be higher (10.4 ± 1.5 fights per dyad, $n = 45$) than in either male-female dyads (7.1 ± 0.7, $n = 100$) or female-female dyads (7.1 ± 0.9, $n = 45$; Kruskal-Wallis test: $H_2 = 5.57$, $P = 0.06$).

A moderately linear dominance hierarchy was found in the sparrow flock ($h' = 0.580$, $P < 0.001$), with a relatively low number of inconsistencies (I = 19, IS = 136). The highest-ranking individual was a male who was clearly dominant over all other members of the flock and won a high proportion of his fights (92%). Nevertheless, neither sex was consistently dominant to the other in the flock: the mean rank of males (10.6 ± 1.9) did not differ from the mean rank of females (10.4 ± 2.0; two-sample randomization test: $P > 0.9$). There was no difference between the sexes in aggressiveness measured as the average proportion of their fights they initiated (males: 48.1 ± 4.3%, females: 47.8 ± 4.8%, Mann-Whitney U-test: $U = 47$, $n_1 = n_2 = 10$, $P > 0.8$). Overall, females initiated 327 (52%) of the 629 male-female fights for which we were able to identify the aggressor.

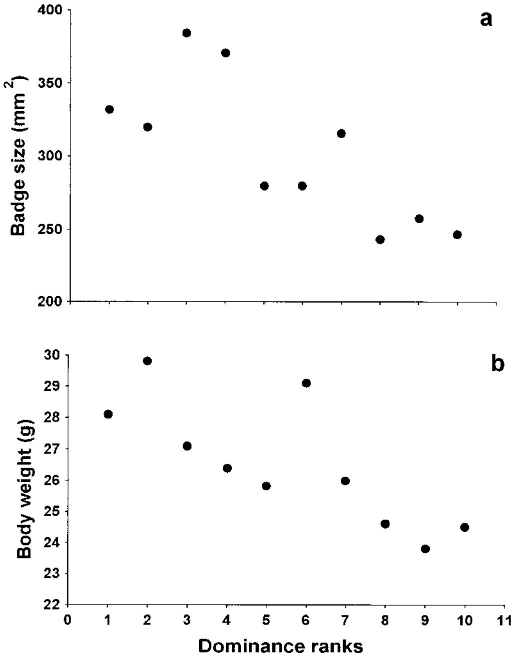

FIGURE 1. The relationships between (a) males' dominance rank and badge size ($n = 10$ males), and (b) females' dominance rank and body weight ($n = 10$ females). Dominance rank indicates the relative position of individuals within the entire flock. The most dominant individual has dominance rank 1.

There was no significant correlation between individuals' dominance rank and the number of fights in which the individuals were involved (entire flock: $r_s = -0.19$, males: $r_s = -0.35$, females: $r_s = -0.07$, all $P > 0.3$). Higher-ranking individuals initiated a higher proportion of their fights than lower-ranking individuals (entire flock: $r_s = -0.80$, males: $r_s = -0.82$, females: $r_s = -0.89$, all $P < 0.01$), and they also won a significantly higher proportion of the fights they initiated than did lower-ranking birds (entire flock: $r_s = -0.61$, males: $r_s = -0.77$, females: $r_s = -0.63$, all $P < 0.05$).

CORRELATES OF DOMINANCE IN MALES AND FEMALES

Of the measured morphological traits, only badge size was significantly related to the dominance ranks of males: high-ranking individuals had larger throat badges than low-ranking ones (Fig. 1a, Table 1). Although the badge size of males was not related to the number of fights in which they were involved ($r_s = 0.26$, $P > 0.4$, $n = 10$), the proportion of fights initiated by individual males was strongly correlated with their badge size ($r_s = 0.88$, $P < 0.01$, $n = 10$). Furthermore, fights occurred nonrandomly between males with respect to the badge size of participants. There was a greater number of aggressive encounters than expected by chance in pairs of males with closely matched badge size (Table 2). We also recorded more fights than expected in pairs with the largest badge-size differences. This was mostly due to a single pair of males that fought unusually frequently (53 fights). The

TABLE 1. Spearman rank correlations between dominance ranks of House Sparrows and their morphological traits and date of introduction into the aviary. A negative correlation coefficient indicates dominants having higher values for the trait than subordinates. Bonferroni correction was used to adjust significance levels for six (males) or five (females and entire flock) comparisons. * $P < 0.05$ at the adjusted significance level.

Variables	Males ($n = 10$)	Females ($n = 10$)	Entire flock ($n = 20$)
Badge size	−0.83*	—	—
Wing length	−0.28	−0.47	−0.16
Tarsus length	−0.22	−0.51	−0.41
Beak length	−0.59	−0.43	−0.55
Body weight	−0.29	−0.82*	−0.47
Date of introduction	−0.29	−0.42	−0.33

TABLE 2. Badge-size difference and frequency of fights among male House Sparrows. Observed numbers are the sum of fights recorded in dyads with the specified badge-size difference. Expected frequencies were calculated as the product of total number of fights and the proportion of a given type of dyad (8/45, 9/45, 16/45, and 12/45, respectively).

Difference in badge size (mm^2)	Number of fights[a]		Number of dyads
	Observed	Expected	
0–20	125	82.8	8
21–40	38	93.2	9
41–80	132	165.7	16
>80[b]	171	124.3	12
Total	466	466	45

[a] The observed frequencies differed significantly from the expected frequencies (Mantel's randomization test, $\chi^2_3 = 78.6$, $P < 0.05$).

[b] When the fighting frequency of one extreme dyad (53 fights) in the largest badge-size difference category was replaced by the average number of fights per dyad (10.36), the difference between observed and expected frequencies remained significant (Mantel's randomization test, $\chi^2_3 = 63.0$, $P < 0.01$).

reason for their exceptionally high aggressiveness toward each other is not clear. When we excluded that pair, the observed number of fights (118) approached the expected frequency (114) for this type of dyad. Within dyads of similar badge sizes (difference: 0–20 mm^2), fights occurred less often in pairs of small-badged opponents (200–300 mm^2: expected: 62.5, observed: 47, $n = 4$ dyads) than in pairs of large-badged males (301–400 mm^2: expected: 62.5, observed: 78, $n = 4$ dyads; no appropriate statistical test, see Statistical Analyses). Badge size was unrelated to other size variables ($r_s = 0.2$–0.4, all $P > 0.2$).

In females, dominance rank was strongly correlated with their body weight measured at capture (Fig. 1b), whereas it was not related to other morphological traits (Table 1). Dominance rank of females also was correlated with body weight measured in the middle and at the end of the study, although the relationships were somewhat weaker than that found for initial body weight (weight in February: $r_s = -0.75$; weight in March: $r_s = -0.71$; all $P < 0.05$, $n = 10$). Although a female's body weight did not relate to the number of female-female fights in which she participated ($r_s = 0.12$, $P > 0.7$, $n = 10$), the proportion of fights initiated by opponent females tended to decrease with increasing body weight of the focal female ($r_s = -0.56$, $P = 0.09$, $n = 10$). The frequency of fights did not vary with body-size difference of the opponents (weight difference $\leq$ 1.5 g: expected: 113.1 fights, observed: 110 fights, $n = 15$ dyads; weight difference 1.5–3 g: expected: 98.9 fights, observed: 88 fights, $n = 15$ dyads; weight difference > 3 g: expected: 106.0 fights, observed: 120 fights, $n = 15$ dyads; Mantel's randomization test, $\chi^2_3 = 3.1$, $P > 0.7$).

When we investigated the entire flock, no morphological trait was found to relate to the dominance rank of individuals (Table 1). Change in body weight during the study was not related to dominance rank (entire flock: $r_s = 0.32$, males: $r_s = 0.35$, females: $r_s = 0.27$, all $P > 0.1$). Because birds were released into the flock at different dates, we also tested whether the time of their introduction had an effect on their rank, but we did not find any significant effect (Table 1).

MALE-FEMALE FIGHTS

Males fighting successfully against male opponents also were successful against females: the number of males dominated by a male in dyadic interactions (i.e., the number of males against which he won more than 50% of the aggressive encounters) correlated positively with the number of females dominated by the male ($r_s = 0.68$, $P < 0.05$, $n = 10$). A similar but less strong tendency was found for females ($r_s = 0.57$, $P = 0.08$, $n = 10$).

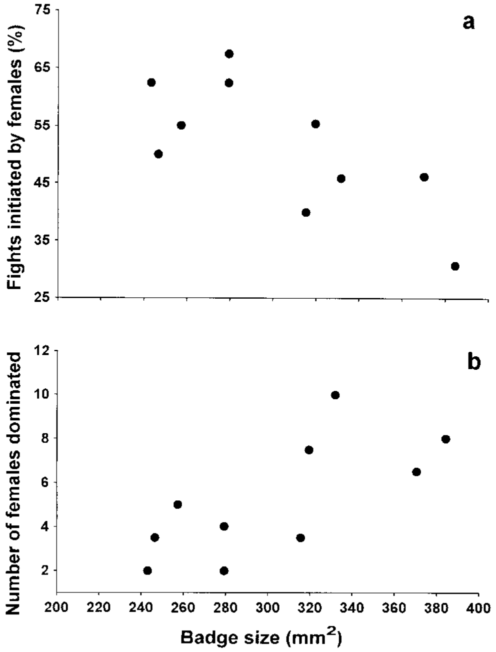

FIGURE 2. The relationships between male badge size and (a) the proportion of male-female fights initiated by females, and (b) number of females dominated by males in dyadic interactions.

The analyses of male-female fights suggest that male badge size predicts dominance between male and female opponents. Although the number of male-female fights a male was involved in did not relate to badge size ($r_s = 0.17$, $P > 0.6$, $n = 10$), the proportion of fights initiated by the females decreased with increasing badge size of the males ($r_s = -0.65$, $P < 0.05$, $n = 10$; Fig. 2a). The proportion of fights won by females also decreased with increasing badge size of the opponent male ($r_s = -0.84$, $P < 0.01$, $n = 10$). Finally, large-badged males dominated more females in dyadic interactions than small-badged males ($r_s = 0.77$, $P < 0.01$, $n = 10$, significant after Bonferroni correction for five comparisons; Fig. 2b). Body size and wing, tarsus, and beak lengths of males were not significant predictors of the number of females dominated (r_s = 0.3–0.6, n = 10, all $P > 0.05$ after Bonferroni correction).

The number of male-female fights that a female participated in did not relate to female body weight (r_s = 0.05, $P > 0.8$, n = 10). The proportion of fights initiated by males decreased strongly with increasing body weight of females ($r_s = -0.87$, $P < 0.001$, n = 10), and the success of males measured as the proportion of fights they won also decreased with increasing body weight of females ($r_s = -0.76$, $P < 0.02$, n = 10). These observations indicate that males avoid contests with large and dominant females.

DISCUSSION

The involvement of badge-size signaling systems in the establishment of dominance relationships has been shown for several bird species (Senar 1999). In the House Sparrow, status signaling by badge size among males has been reported for both captive and free-ranging birds, and from several geographically distinct populations (Møller 1987, Veiga 1993, Solberg and Ringsby 1997). In line with these studies, badge size was the only significant predictor of dominance rank and a good predictor of aggressiveness of male sparrows in our study. Our results imply that the badge-size–dominance relationship also is valid for mixed-sex flocks with frequent male-female interactions. Our results also corroborate Møller's earlier finding that fights occur especially often between large-badged males, giving further support to the status signaling hypothesis (Møller 1987).

We found correlational evidence that badge size predicts dominance relations between males and females. Females attacked large-badged males infrequently relative to smaller-badged males, and the number of females dominated by males correlated positively with badge size. Given that females' fighting success seems to decrease with increasing badge size of the opponent, females may reduce the costs of aggressive competition for resources by avoiding unprofitable contests with highly aggressive males. There are several alternative explanations, however, for the correlations we found. First, badge size may correlate with some unmeasured characteristics of males that affect female behavior. Second, females may use information from their previous contests, or observed contests of males, to adjust their fighting strategy in aggressive encounters with familiar males. In our flock, both males and females avoided fights with large and dominant females, against which they appeared to be unsuccessful, suggesting that badge-like status signals may not be necessary to assess dominance relations in stable flocks. Further experimental studies, involving badge size manipulations, are required to test whether female House Sparrows really pay attention to the badge size of males in intersexual aggression.

Dominance rank of females was positively related to body weight, a trait that may directly affect resource-holding power and may play a role in determining the outcomes of fights when status signals are absent (Maynard Smith and Harper 1988). This result is correlative and may be interpreted in alternative ways. For example, several current studies suggest that body weight is a strategic consequence of dominance rather than a determinant of it (Ekman and Lilliendahl 1992). In this study, however, dominance ranks of females were predicted by body weight measured before establishing the flock, and changes in body weight were not related to the dominance rank of individuals. Thus, higher body weight of dominant females could not be a short-term consequence of their better access to food in the aviary. On the other hand, females that were dominant in the captive flock might have been dominant individuals before capture; thus, their body weight could have been determined by their dominance prior to capture.

The lack of relationships between body weight and dominance rank for the entire flock (males and females combined) may be related to the fact that no significant correlation was found between body weight and dominance rank in males (Hegner and Wingfield 1987, Møller 1987, Solberg and Ringsby 1997). Although the correlations between body size variables and dominance were statistically nonsignificant for males and the entire flock (Table 1), this may be in part due to the low power of our tests (particularly in males). The direction of these correlations, however, uniformly suggests that body size may play a role in the establishment of dominance relationships in the case of males and, consequently, in the entire flock.

In our flock, females were frequently involved in agonistic encounters and they clearly achieved similar dominance ranks to that of males, suggesting that there may be less difference between the sexes in agonistic behavior and dominance status, at least under some conditions, than has been assumed by several previous studies (Watson 1970, Møller 1987). The differences between the studies may be related to at least three factors. First, male dominance may be most common during autumn and the first half of winter, when sexual activity is generally low; it may be less frequent during the early spring, when pairs form and males may have an interest in reducing their aggression towards females. Cink (1977) reported clear male dominance in flocks between September and January, female dominance after March, and a transitional period without sex-related dominance between January and March. However, some other studies reporting male dominance were conducted in late winter and spring (Watson 1970, Møller 1987), and female dominance has been reported in autumn flocks both for captive (Hegner and Wingfield 1987) and free-ranging House Sparrows (Johnston 1969, Kalinoski 1975). Second, intersexual behavior varies considerably among populations during the breeding season (Griffith et al. 1999), and population differences may persist during winter. Third, the availability of resources to flock members also may play an important role in determining the interactions between male and female sparrows. For example, in our study, females could not avoid aggressive encounters when gaining access to food, because only a limited number of birds could feed on the feeders we used. Under less competitive conditions, males may spend less time at feeding sites, allowing females to feed when males are absent. We suggest that both sex-specific seasonality in aggression and strength of competition for food may contribute to the variability of intersexual dominance in House Sparrows.

In conclusion, our results showed that badge size is a good predictor of male dominance rank in a mixed-sex House Sparrow flock, and that females may pay attention to their opponent's badge size in male-female interactions. We found that male and female House Sparrows may not differ in their dominance status as markedly as has sometimes been stressed. We suggest further experimental studies to test the significance of male badge size for male-female interactions.

ACKNOWLEDGMENTS

We thank János Kis, András Kosztolányi, Éva Mikics, Zsolt Pénzes, Anikó Seres and Gergely Zachar for their help in constructing the aviary and capturing birds, and Katherine Buchanan, Péter Kabai, János Kis, Szabolcs Lengyel, Tomas Pärt, Walter Koenig, and anonymous reviewers for their comments on earlier versions of the manuscript. Both authors were supported by János Bolyai Research Fellowship. The study was supported by an OTKA grant No. F026595 to AL.

LITERATURE CITED

CHANDLER, C. R. 1995. Practical considerations in the use of simultaneous inference for multiple tests. Anim. Behav. 49:524–527.

CINK, C. 1977. Winter behavior of the House Sparrow. Ph.D. diss., Univ. of Kansas, Lawrence, KS.

EKMAN, J. B., AND K. LILLIENDAHL. 1992. Using priority to food access: fattening strategies in dominance-structured Willow Tit (*Parus montanus*) flocks. Behav. Ecol. 4:232–238.

DE VRIES, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim. Behav. 50:1375–1389.

DE VRIES, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim. Behav. 55:827–843.

GRIFFITH, S. C., I. P. F. OWENS, AND T. BURKE. 1999. Female choice and annual reproductive success favour less-ornamented male House Sparrows. Proc. R. Soc. Lond. B 266:765–770.

HEGNER, R. E., AND J. C. WINGFIELD. 1987. Social status and circulating levels of hormones in flocks of House Sparrows, *Passer domesticus.* Ethology 76: 1–14.

JOHNSTON, R. F. 1969. Aggressive foraging behavior in House Sparrows. Auk 86:558–559.

KALINOSKI, R. 1975. Intra- and interspecific aggression in House Finches and House Sparrows. Condor 77:375–384.

MANLY, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London.

MAYNARD SMITH, J., AND D. G. C. HARPER. 1988. The evolution of aggression—can selection generate variability? Phil. Trans. R. Soc. Lond. 319:557–570.

MØLLER, A. P. 1987. Variation in badge size in male House Sparrows *Passer domesticus*: evidence for status signaling. Anim. Behav. 35:1637–1644.

ROHWER, S. 1975. The social significance of avian winter plumage variability. Evolution 29:593–610.

SENAR, J. C. 1999. Plumage coloration as a signal of social status. Proc. Int. Ornithol. Congr. 22:1669–1686.

SOLBERG, E. J., AND T. H. RINGSBY. 1997. Does male badge size signal status in small island populations of House Sparrows, *Passer domesticus*? Ethology 103:177–186.

SPSS, INC. 1996. SPSS for Windows 7.5. Chicago, IL.

VEIGA, J. P. 1993. Badge size, phenotypic quality and reproductive success in the House Sparrow: a study of honest advertisement. Evolution 47: 1161–1170.

WATSON, J. R. 1970. Dominance-subordination in caged groups of House Sparrows. Wilson Bull. 82: 268–278.