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LITERATURE CITED

- COKER, D. R., AND D. E. CAPEN. 1995. Landscape-level habitat use by Brown-headed Cowbirds in Vermont. *Journal of Wildlife Management* 59: 631–637.
- FINCH, D. M. 1991. Population ecology, habitat requirements, and conservation of Neotropical migratory birds. United States Forest Service General Technical Report RM-205.
- FRIEDMANN, H. 1929. The cowbirds: A study in the biology of social parasitism. C. Thomas, Springfield, Illinois.
- GATES, J. E., AND D. R. EVANS. 1998. Cowbirds breeding in the central Appalachians: Spatial and temporal patterns and habitat selection. *Ecological Applications* 8:27–40.
- GOGUEN, C. B. 1999. Brown-headed Cowbird movements, habitat use, and impacts on hosts in a grazed and ungrazed landscape. Ph.D. dissertation, University of Wisconsin, Madison.
- GOGUEN, C. B., AND N. E. MATHEWS. 1998. Songbird community composition and nesting success in grazed and ungrazed pinyon-juniper woodlands. *Journal of Wildlife Management*. 62:474–484.
- GOGUEN, C. B., AND N. E. MATHEWS. 1999. Review of the causes and implications of the association between cowbirds and livestock. Pages 10–17 in *Research and management of the Brown-headed Cowbird in western landscapes* (M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, Eds.). *Studies in Avian Biology* No. 18.
- GOGUEN, C. B., AND N. E. MATHEWS. 2000. Local gradients of cowbird abundance and parasitism relative to livestock grazing in a western landscape. *Conservation Biology* 14: in press.
- GUSTAFSON, E. J., AND T. R. CROW. 1994. Modeling the effects of forest harvesting on landscape structure and the spatial distribution of cowbird parasitism. *Landscape Ecology* 9:237–248.
- MAYFIELD, H. F. 1965. The Brown-headed Cowbird with old and new hosts. *Living Bird* 4:13–28.
- ORTEGA, C. P. 1998. Cowbirds and other brood parasites. University of Arizona Press, Tucson.
- RAIM, A. 1987. A radio transmitter attachment for small passerine birds. *Bird-Banding* 49:326–332.
- ROBINSON, S. K., S. I. ROTHSTEIN, M. C. BRITTINGHAM, L. J. PETIT, AND J. A. GRZYBOWSKI. 1995. Ecology and behavior of cowbirds and their impact on host populations. Pages 428–460 in *Ecology and management of Neotropical migratory birds: A synthesis and review of critical issues* (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- ROTHSTEIN, S. I., J. VERNER, AND E. STEVENS. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. *Ecology* 65:77–88.
- THOMPSON, F. R. III. 1994. Temporal and spatial patterns of breeding Brown-headed Cowbirds in the midwestern United States. *Auk* 111:979–990.
- VERNER, J., AND L. V. RITTER. 1983. Current status of the Brown-headed Cowbird in the Sierra National Forest. *Auk* 100:355–368.

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Female Dominance and Aggressive Behaviors in House Sparrow Flocks

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Some bird species display intersexual dominance at food resources (e.g. Bekoff and Scott 1989, Piper and Wiley 1989, Tarvin and Woolfenden 1997). Such interactions fall into three patterns: year-round fe-

male dominance, year-round male dominance, and alternating dominance wherein females dominate in the breeding season and males in the nonbreeding season (Smith 1980). Although Smith found alternating dominance to be the most common pattern in birds, she suggested that year-round female dominance should occur in socially monogamous, non-territorial species. In such species, no advantage would accrue to males who exhibit dominance in the

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nonbreeding season in preparation for territory acquisition for the breeding season.

House Sparrows (*Passer domesticus*) are socially monogamous and defend only small territories around their nest cavities (Lowther and Cink 1992). This makes them a candidate for year-round female dominance. Dominance relationships in House Sparrows have been investigated with conflicting results. Watson (1970) found that males in small captive flocks were dominant year-round, whereas Kalinoski (1975) noted that females were dominant only during winter. Cink (1977), working with free-ranging flocks, found that males were dominant during the nonbreeding season and females during the breeding season. Hegner and Wingfield (1987) found that females in small captive flocks were dominant during the nonbreeding season, but neither sex was dominant during the breeding season. Finally, a recent summary of dominance patterns in House Sparrows concluded that females are dominant during spring and summer and males during fall and winter (Lowther and Cink 1992). Because the claim of alternating dominance in House Sparrows is in opposition to the pattern that would be predicted by Smith (1980), I addressed sex-biased dominance in winter interactions of free-ranging flocks of House Sparrows.

Methods.—I observed interactions at three feeders during the winter (November to February) of 1997–98 in Muncie, Indiana. Feeders were separated by at least 3 km, and sparrows presumably were from three different flocks (typical home ranges separated by less than 2 km; Lowther and Cink 1992). Winter temperatures were typical for southeastern Indiana, although snowfall was below average (Ball State Weather Station). Thus, the interactions I observed likely were normal for the study area. House Sparrows often use feeders in this area and may not be adversely affected by snow cover when it occurs.

I observed interactions for one hour in the mornings (one hour after sunrise) from a blind set near each feeder. I made approximately 27 h of observation at feeder one, 25 h at feeder two, and 29 h at feeder three. Birds in the three flocks were not banded, but I assume the data at each feeder can be treated as an independent random sample for two reasons. First, flocks were large, with approximately 20 individuals (mean of point counts every 5 min) of each sex in each flock. Second, I frequently witnessed multiple interactions that involved different individuals. Thus, the data reported here are not attributable to a small number of individuals in each flock but rather reflect sampling from a variety of individuals of each sex in each flock.

For each intersexual interaction I recorded the sex of the initiator, whether the initiator won the interaction, and the type of aggression used. House Sparrows use three stereotypic aggressive displays (threat, lunge, and attack) that I used to categorize

TABLE 1. Number and outcome of intersexual interactions initiated by House Sparrows at three feeders and at three levels of aggression.

Initiator	Number won (%)	Number not won (%)	Total
Feeder One			
Male	48 (66)	25 (34)	73
Female	90 (79)	24 (21)	114
Feeder Two			
Male	105 (56)	84 (44)	189
Female	179 (75)	61 (25)	240
Feeder Three			
Male	97 (70)	42 (30)	139
Female	101 (82)	22 (18)	123
Low-level aggression			
Male	32 (42)	44 (58)	76
Female	73 (72)	28 (28)	101
Mid-level aggression			
Male	132 (72)	52 (28)	184
Female	202 (80)	51 (20)	253
High-level aggression			
Male	86 (61)	55 (39)	141
Female	95 (77)	28 (23)	123

aggression (see Summers-Smith 1963). Aggression levels were described as low, mid, or high corresponding to threats, lunges, and attacks, respectively. An individual was considered to have won the interaction if it caused the other individual to leave the feeder. An individual was considered not to have won the interaction (=no win) if the other individual did not leave the feeder, or if it displayed back at the initiator, who then left. I analyzed patterns in interactions using chi-square tests, with each interaction considered independent of the others.

Results.—Overall, I observed 187, 429, and 262 intersexual interactions at the three feeders (Table 1). Females initiated more interactions with males than vice versa at feeder one ($\chi^2 = 8.99$, $df = 1$, $P < 0.005$) and two ($\chi^2 = 6.06$, $df = 1$, $P < 0.025$) but not at feeder three ($\chi^2 = 0.98$, $df = 1$, $P > 0.10$; Table 1). An individual that initiated an interaction was likely to win that interaction, regardless of sex (initiator won 71% of interactions). Females won more of the interactions that they initiated than did males at feeder two ($\chi^2 = 16.3$, $df = 1$, $P < 0.001$) and three ($\chi^2 = 4.73$, $df = 1$, $P = 0.029$). The pattern also occurred at feeder one, but the difference was not significant ($\chi^2 = 3.35$, $df = 1$, $P = 0.067$). Note, however, that the two feeders where females won more interactions were not the same two feeders at which females initiated more interactions (i.e. in no case were data from one feeder clearly “different” from those at the other two feeders).

Based on the above results, I pooled data from the

three feeders to ask questions concerning levels of aggression in interactions initiated by one sex or the other. Both sexes used mid-level aggression most often (Table 1). Males and females, however, differed in their use of the three levels of aggression ($\chi^2 = 9.14$, $df = 2$, $P = 0.01$). Females initiated low- and mid-level aggressive interactions disproportionately, whereas males did so for high-level aggression (low vs. high, $\chi^2 = 4.24$, $df = 1$, $P = 0.039$; mid vs. high, $\chi^2 = 8.01$, $df = 1$, $P = 0.005$; Table 1), although only the mid vs. high comparison was significant after Bonferroni correction.

When comparing frequencies of initiated interactions won at the three levels of aggression, males did not experience consistent frequencies ($\chi^2 = 20.3$, $df = 2$, $P < 0.001$). In particular males lost more low-level interactions than mid- or high-level interactions (low vs. mid, $\chi^2 = 19.0$, $df = 1$, $P < 0.001$; low vs. high, $\chi^2 = 6.36$, $df = 1$, $P = 0.01$). Males lost similar frequencies of interactions at mid- and high-level aggression ($\chi^2 = 3.70$, $df = 1$, $P = 0.054$). Overall, males won 62% of the interactions they initiated. In contrast, females won similar frequencies of interactions that they initiated at all three levels of aggression ($\chi^2 = 2.38$, $df = 2$, $P > 0.10$) and won 78% of all interactions they initiated.

Discussion.—Females were the dominant sex at winter food resources in this study, as would be predicted by Smith (1980) but in contrast to Cink (1977). Smith cited several cases of species with known year-round female dominance that have a common link of lower prebreeding male dominance (compared with species with known year-round male dominance or alternating dominance). Lower prebreeding male dominance may be a result of lack of territorial behavior during the breeding and nonbreeding seasons in these species. House Sparrows maintain only a small territory around their nest site and do not defend foraging territories at any time. Thus, House Sparrows satisfy a requirement for exhibiting year-round female dominance (Smith 1980).

Cink (1977) found that female House Sparrows were dominant during the breeding season, the only study of free-ranging flocks that has been conducted at that time of year. Other studies of House Sparrows have either not addressed dominance relationships during the breeding season, or have found the sexes to be equally dominant in captive studies during the breeding season. By combining the findings of Cink (female breeding-season dominance) and of my study (female nonbreeding-season dominance), I argue that females are dominant year-round in the population that I studied.

Yet, discrepancies exist between the nonbreeding-season results of Cink and mine. Several factors may account for these differences. Sexual size dimorphism has been reported in House Sparrows, with an increase in the extent of dimorphism at more northern latitudes (Johnston and Selander 1973). All of the

populations in Cink's study occurred at higher latitudes than the population that I studied and thus should have had higher size dimorphism. Sexual dimorphism in northern House Sparrows may be maintained by several factors. First, smaller females may have a reproductive advantage over larger females by being able to begin breeding sooner (Downhower 1976). Second, House Sparrows near the population mean size (small males and large females) experience higher amounts of interspecific competition and lower overwinter survival (Johnston and Fleischer 1981). Third, smaller females may require less energy for daily survival than larger individuals and may be able to easily meet their energy requirements (see Johnston and Fleischer 1981). Smaller females may avoid interactions that they are unlikely to win owing to their size disadvantage and thus may be subordinate during the winter in northern populations.

Given these factors, I predict that a gradient exists from year-round female dominance in the climatically milder southern latitudes of the House Sparrow's range, to alternating dominance in the climatically harsher northern latitudes. Indeed, the same prediction holds for any nonterritorial socially monogamous species with a broad latitudinal range.

During intersexual interactions, both sexes used mid-level (lunge) aggression preferentially. This is consistent with the predictions of Enquist (1985) and the findings of Popp (1987) that displaying individuals use the level of aggression that is sufficient for securing the desired resource without taking on excessive costs. Mid-level aggression may be more costly than low-level aggression in terms of energy expenditure and the potential for retaliation, but it may be more effective in demonstrating the level of risk an individual is willing to take to obtain or hold a resource (Enquist 1985).

With this in mind, displaying individuals should make little use of expensive displays that potentially could trigger retaliation, such as high-level (attack) aggression. Males in my study were more willing to use high-level aggression than were females. Males may use high-level aggression based on their need to obtain resources. Popp (1987) found that individuals demonstrated higher levels of aggression based on the importance of the resource in question. Subordinate American Goldfinches (*Carduelis tristis*) preferentially used high-level aggression against dominant finches when the subordinates had been deprived of food. Female House Sparrows may be able to enforce their dominance to a point that males become desperate for access to the food resource and resort to costly high-level aggression to acquire it.

Females were as likely to win an interaction using low-level aggression as using mid-level aggression. Why they used mid-level aggression more often is not clear. I did not know ages of birds or numbers of juveniles within flocks, and females could have used

low-level aggression against young males while employing mid-level aggression against older males. Both sexes used mid- and high-level aggression against a same-sex opponent preferentially (Jawor 1998). This may indicate that separate dominance hierarchies exist for the sexes, and for intersexual interactions, and that different strategies exist for competing within these hierarchies, as has been observed in other species (e.g. Enoksson 1988, Bekoff and Scott 1989, Lahti et al. 1996).

Female dominance also may account for the high frequency of male loss during male-initiated low-level intersexual aggression. Low-level aggression may not be an effective display for males because females are unwilling to recognize it as a threat to their dominance status. Another possibility is that males use low-level aggression against females that are the same size or larger. In such cases, a female should not respond to low-level aggression by leaving the feeder. One could test the hypothesis that losses in male-initiated intersexual interactions depend on the female's response by examining male-male interactions. Specifically, the initiator in male-male interactions should win the interaction more often than not (see Jackson 1991). In any case, the question of why males use a level of aggression in interactions that they often lose will be better answered with banded individuals of known size in flocks with known histories of interactions.

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LITERATURE CITED

- Bekoff, M., and A. C. Scott. 1989. Aggression, dominance and social organization in Evening Grosbeaks. *Ethology* 83:177–194.
- Cink, C. L. 1977. Winter ecology and behavior of North American House Sparrow populations. Ph.D. dissertation, University of Kansas, Lawrence.
- Downhower, J. F. 1976. Darwin's finches and the evolution of sexual dimorphism in body size. *Nature* 263:558–563.
- Enoksson, B. 1988. Age- and sex-related differences in dominance and foraging behaviour of Nuthatches *Sitta europaea*. *Animal Behaviour* 36:231–238.
- Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behavior. *Animal Behaviour* 33:1152–1161.
- 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.
- Jackson, W. M. 1991. Why do winners keep winning? *Behavioral Ecology and Sociobiology* 28: 271–276.
- Jawor, J. M. 1998. Aggressive interactions and behaviors in House Sparrow (*Passer domesticus*) flocks. M.S. thesis, Ball State University, Muncie, Indiana.
- Johnston, R. F., and R. C. Fleischer. 1981. Overwinter mortality and sexual size dimorphism in the House Sparrow. *Auk* 98:503–511.
- Johnston, R. F., and R. K. Selander. 1973. Evolution in the House Sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. *American Naturalist* 107: 373–384.
- Kalinowski, R. 1975. Intra- and interspecific aggression in House Finches and House Sparrows. *Condor* 77:375–384.
- Lahti, K., K. Koivula, M. Orell, and S. Rytkönen. 1996. Social dominance in free-living Willow Tits *Parus montanus*: Determinants and some implications of hierarchy. *Ibis* 138:539–544.
- Lowther, P. E., and C. L. Cink. 1992. House Sparrow (*Passer domesticus*). In *The birds of North America*, no. 12 (A. Poole, P. Stettenheim and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Piper, W. H., and R. H. Wiley. 1989. Correlates of dominance in winter White-throated Sparrows: Age, sex and location. *Animal Behaviour* 37:298–310.
- Popp, J. W. 1987. Risk and effectiveness in the use of agonistic displays by American Goldfinches. *Behaviour* 81:141–156.
- Smith, S. M. 1980. Henpecked males: The general pattern in monogamy? *Journal of Field Ornithology* 51:55–63.
- Summers-Smith, J. D. 1963. *The House Sparrow*. Collins, London.
- Tarvin, K. A., and G. E. Woolfenden. 1997. Patterns of dominance and aggressive behavior in Blue Jays at a feeder. *Condor* 99:434–444.
- Watson, J. R. 1970. Dominance-subordination in caged groups of House Sparrows. *Wilson Bulletin* 82:268–278.

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