

VIGILANCE IN THE WHITE-BREASTED NUTHATCH: EFFECTS OF DOMINANCE AND SOCIALITY

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ABSTRACT.—Using captive pairs of White-breasted Nuthatches (*Sitta carolinensis*), I tested the nonexclusive hypotheses that the vigilance of social foragers has two components, (1) vigilance for predators and (2) vigilance for dominant conspecifics, and thus is mediated by the size of the foraging group as well as by an individual's dominance status. Evidence from pairs of nuthatches, tested while solitary and while together, revealed that males increased their vigilance when solitary, that females were subordinate to and more vigilant than males when both sexes were housed together in the aviary, and that the advantage of foraging socially in terms of a reduction in vigilance was greater for males. My results demonstrate that vigilance in White-breasted Nuthatches was sex specific and that male social dominance was the responsible mechanism. I suggest that subordinate social foragers have the additional constraint on their foraging time of keeping higher-ranking flock mates under surveillance.

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THE two commonly hypothesized advantages of foraging socially rather than solitarily are improved predator avoidance and enhanced foraging efficiency (reviewed by Wilson 1975, Moriarity 1976, Rubenstein 1978, Morse 1980, Krebs and Davies 1981). There is a growing realization that these two benefits are not independent. In fact, the size of a foraging group influences how individuals apportion their time budgets among such incompatible activities as scanning for predators and searching for food (e.g. Pulliam 1973; Powell 1974; Caraco 1979; Barnard 1980; Bertram 1980; Caraco et al. 1980a, b; Elgar and Catterall 1981; Lendrem 1983; Studd et al. 1983; Elgar et al. 1984). Several studies have demonstrated that as flock size increases, individual birds can allocate more time to foraging activities while the per capita vigilance level is maintained (e.g. Powell 1974, Siegfried and Underhill 1975, Caraco 1979, Jennings and Evans 1980, Sullivan 1984a).

A common shortcoming of these studies was their failure to consider that the costs and benefits associated with social foraging may be sex specific, dominance specific, or both [but cf. Moore 1972 (*in* Caraco 1979), Caraco 1979, Ekman and Askenmo 1984, Waite 1986]. Based partly on evidence that birds increased their vigilance in areas of higher predation risk (Barnard 1980, Caraco et al. 1980a) or when a predator was present (Caraco et al. 1980b), previous workers assumed that the principal function of vigilance was predator detection. Thus, these studies overlooked the possibility that the time

devoted to foraging was more constrained for subordinates because higher-ranking conspecifics interfered with their foraging (but cf. Robinson 1981, Knight and Knight 1986). I tested experimentally the possibility that females of a heterosexual pair are more vigilant than males because they must keep their dominant mate under surveillance while also maintaining a certain level of vigilance for predators. I used captive mated pairs of White-breasted Nuthatches (*Sitta carolinensis*) to examine the nonexclusive hypotheses that the vigilance of animals that forage in social groups is comprised of both vigilance for predators and vigilance toward other members of the foraging group, and, hence, is influenced by two proximate factors, sociality and dominance status. One prediction follows from each of these hypotheses, respectively. First, a male nuthatch should be more vigilant when alone than when with his mate. Second, a female nuthatch should be more vigilant than her (dominant) mate when they forage together. No prediction regarding the vigilance levels of solitary vs. social females is made because females, owing to their need to keep their dominant mates under surveillance, actually may be more vigilant when social than when solitary.

METHODS

Five pairs of wild-caught White-breasted Nuthatches were housed sequentially in a 4.8 m × 4.2 m × 2.7 m high indoor aviary between 25 November 1984 and

9 March 1985. Although *carolinensis* is slightly sexually dimorphic in plumage, to facilitate instant recognition of individuals I marked the cheek patches and breast of males with a waterproof felt-tip pen. To ensure that the nuthatches comprising each captive pair had actually been paired in nature, I captured a male and a female nuthatch that had arrived together repeatedly at a trapping station. The birds were held at $18.8 \pm 1.1^\circ\text{C}$ ($\bar{x} \pm \text{SE}$) on natural photoperiod and were maintained on an *ad libitum* diet of sunflower seeds (*Helianthus* sp.) and mealworms (*Tenebrio* sp. larvae). Two water sources were always available. Each pair of nuthatches had been used previously in other experiments and had been part of a captive mixed-species flock comprised of a male and a female Downy Woodpecker (*Picoides pubescens*), a male and a female White-breasted Nuthatch, three Tufted Titmice (*Parus bicolor*), and two Carolina Chickadees (*P. carolinensis*) (Waite 1986). Details concerning the aviary and the conditions under which the nuthatches were held are given by Waite (1986).

After the male and the female nuthatch of each captive pair had spent at least 3 days acclimating to the aviary environment, dominance-subordination interactions were recorded during 20 15-min observation sessions. I recorded all interactions in which one bird successfully used a supplanting attack (*sensu* Hinde 1952). To measure how much individuals capitalized on their dominance status to acquire or control access to food, I recorded whether the supplanted individual had a food item when it was supplanted; whether the supplanting individual obtained food as a result of the supplanting attack; whether the supplanting individual engaged in an apparent search for food or pecked at the substrate at the exact site of the supplanting attack, or both; and for all instances of social dominance, whether the interaction occurred at the feeder.

The general experimental procedure was as follows. On at least the eighth day of captivity for each mixed-species flock, I removed all birds except the male and female nuthatch from the aviary. Beginning between 0930 and 1030 the following day, I observed the two *carolinensis* in each of the following contexts: female solitary, male solitary, and social foraging (female with male present and male with female present). For each pair of birds, the order of these three contexts was generated from a random-numbers table. Observations of the male and the female foraging socially were made concurrently. Because White-breasted Nuthatches normally forage in cohesive heterosexual pairs during winter (McEllin 1979, Grubb 1982), the birds were kept in visual but not acoustic isolation from one another during the solitary treatments. This periodic visual isolation was accomplished by temporarily housing the bird not being tested behind opaque screens in a 1.6 m \times 4.2 m \times 2.7 m high annex to the main aviary (Waite 1986).

At the start of each session, a 0.6 \times 0.6 m feeding

tray was placed 1.5 m above the aviary floor. I watched each bird in each social context take 20 consecutive food items from the feeding tray in replicates 1, 2, and 3 and 15 food items in replicates 4 and 5. Each time a food item was taken by the focal bird, I recorded whether the food item was a mealworm or a sunflower seed, the time since the start of the trial when the food item was removed from the feeder, whether the food item was consumed or hoarded, and the time taken to eat (defined as the time spent pecking at a food item) or hoard the food item.

As an index of vigilance I recorded the number of head-cocks made by a bird while it ate a food item. The birds usually paused briefly at intervals, lifted the head, and often moved it from side to side; they thus appeared to scan the environment while shelling and eating sunflower seeds or tearing apart and eating mealworms, or while caching a food item in a bark crevice. For each food item consumed or hoarded, I counted the number of times a bird raised its head such that the axis of the bill was pointed even with or above an imaginary line parallel to the substrate at the bird's eye level. Head-scanning rates have been used as an index of predator vigilance in other studies (e.g. Caraco 1979, Sullivan 1984a), and increase at the expense of foraging efficiency after the presentation of a predator stimulus (Caraco et al. 1980b, Sullivan 1984b).

Records of scanning permitted the calculation of three measures of vigilance. These were head-cocks/min while handling a sunflower seed, head-cocks/min while handling a mealworm, and head-cocks/min while handling either a sunflower seed or a mealworm.

Statistical comparisons between the results from the two social contexts, social and solitary, for males and females were accomplished by paired *t*-tests using Bonferroni's probabilities with an experimental error rate of 0.05 (Snedecor and Cochran 1967). Records for a bird in a given social context were included in this statistical procedure only when at least three food items of a given type were consumed. During the five replicates the nuthatches hoarded 2.15 ± 1.24 ($\bar{x} \pm \text{SE}$) sunflower seeds and 1.45 ± 0.72 ($\bar{x} \pm \text{SE}$) mealworms $\cdot \text{bird}^{-1} \cdot \text{treatment}^{-1}$; records of food items that were hoarded were omitted from statistical analysis. Head-cocking rates are reported as means \pm SE. Statistical significance was set at the 0.05 level.

RESULTS

Males were unequivocally dominant to females, as they won all dominance-subordination interactions (Table 1). Moreover, even in the aviary, where food was superabundant, many of the interactions were contests for access to food. Thus, the assumption that males interfere with female feeding activities was sustained.

TABLE 1. Supplanting attacks and control of access to food by male White-breasted Nuthatches.^a

	Pair					$\bar{x} \pm \text{SD}$
	1	2	3	4	5	
Supplanting attacks ^b	28	34	12	33	16	24.6 \pm 10.0
Female had food ^c	13	3	2	7	11	7.2 \pm 4.8
Kleptoparasitism ^d	12	0	1	6	8	5.4 \pm 5.0
Male searched for food ^e	10	8	6	8	4	7.2 \pm 2.3
Occurred at feeder ^f	0	9	5	8	2	4.8 \pm 3.8

^a Observations taken during 20 15-min sessions.

^b Total number of supplanting attacks by the male against the female.

^c Number of supplanting attacks in which the female was handling a food item when displaced.

^d Number of times the male obtained food by supplanting the female.

^e Number of times the male engaged in an apparent search for food or pecked at the substrate, or both, at the exact site of the supplanting attack.

^f Number of times the male supplanted the female at the feeder.

Males head-cocked at a significantly greater rate (head-cocks/min) when tested alone than when tested with a female while handling sunflower seeds (11.73 ± 2.04 vs. 4.17 ± 0.37 ; $t = 4.438$, $P < 0.025$, $df = 3$, one-tailed) and while handling sunflower seeds and mealworms ($t = 3.568$, $P < 0.03$, $df = 4$, one-tailed; Fig. 1A), but not while handling mealworms (9.99 ± 3.75 vs. 4.80 ± 2.21 ; $t = 2.480$, $P < 0.09$, $df = 3$, one-tailed). These results provide support for the hypothesis that vigilance is predator directed and, thus, is influenced by the size of the foraging group.

When both sexes were housed together, females head-cocked at a significantly greater rate while handling sunflower seeds and mealworms than did males ($t = 2.978$, $P < 0.05$, $df = 4$, one-tailed; Fig. 1A). This result supports the hypothesis that vigilance is conspecific directed and, thus, is influenced by an individual's dominance status. However, the rates at which females and males head-cocked when housed together were statistically indistinguishable while handling sunflower seeds (9.48 ± 1.65 vs. 4.17 ± 0.37 ; $t = 2.640$, $P < 0.09$, $df = 3$, one-tailed) and mealworms (4.80 ± 2.21 vs. 6.44 ± 0.83 ; $t = 1.079$, $P > 0.1$, $df = 3$, one-tailed). Momentarily elevating the experimental error rate to 0.10 permits comparisons of head-cocking rates by solitary vs. social females and by solitary males vs. solitary females. Because neither comparison was statistically significant for any of the three measures of vigilance (P 's > 0.10 , two-tailed), it is difficult to reconcile the higher vigilance levels in social females compared with social males with the suggestion that male social dominance was not the proximate cause.

These failures to detect statistical differences

in head-cocking rates while handling mealworms prompted the following comparison of inter-head-cock intervals and handling times for mealworms and sunflower seeds. I reasoned that the time required to handle a mealworm might have been so brief that consuming a mealworm could have been done between head-cocks while maintaining the typical head-cocking rate. The mean inter-head-cock intervals while eating a mealworm were statistically indistinguishable (P 's > 0.05 , two-tailed t -tests) from the mean handling time per mealworm for both social (9.93 s vs. 7.68 s) and solitary (3.58 s vs. 5.73 s) males and both social (11.16 s vs. 6.18 s) and solitary (18.94 s vs. 7.07 s) females. Conversely, for sunflower seeds, although the comparison was not significant for social males (27.18 s vs. 24.66 s; $t = 0.188$, $P > 0.5$, $df = 4$, two-tailed), the mean inter-head-cock interval was significantly shorter than the mean handling time for solitary males (5.59 s vs. 27.37 s; $t = 6.688$, $P < 0.01$, $df = 3$, two-tailed), and for social (6.88 s vs. 29.21 s; $t = 4.462$, $P < 0.05$, $df = 3$, two-tailed) and solitary (9.66 s vs. 33.65 s; $t = 4.240$, $P < 0.025$, $df = 4$, two-tailed) females.

To examine more directly whether males had a greater advantage of foraging socially in terms of a reduction in vigilance than did females, I compared their changes in head-cocking rates (head-cocks/min) when solitary to when together. The percentage change in head-cocking rate when alone compared with when the male and female were housed together was significantly greater in males than in females while handling sunflower seeds (176.31 ± 26.96 vs. 1.52 ± 24.78 ; $t = 14.458$, $P < 0.0005$, $df = 3$, one-tailed), approached being significantly greater in males for mealworms (126.00 ± 83.87 vs.

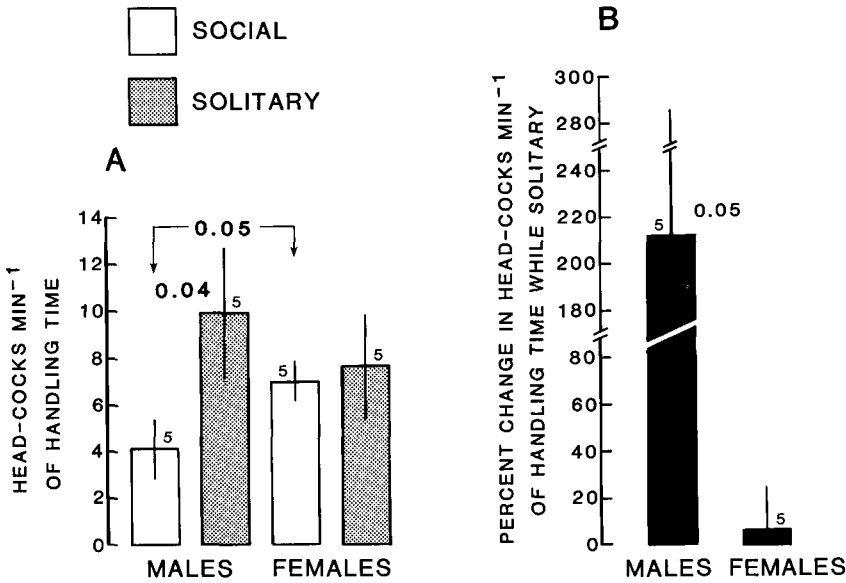


Fig. 1. (A) Frequency of head-cocking by male and female White-breasted Nuthatches while either shelling and eating a sunflower seed or eating a mealworm in the two social contexts, social and solitary. The bars represent the mean of the means; vertical lines are 1 SE. *P*-values are for one-tailed, paired *t*-tests using Bonferroni's probabilities with an experimental error rate of 0.05 (n 's = 5). (B) Percentage increase in the frequency of head-cocking by male and female White-breasted Nuthatches while either shelling and eating a sunflower seed or eating a mealworm when solitary relative to when social. The bars represent the means for five replicates; vertical lines are 1 SE. The *P*-value is for a one-tailed, paired *t*-test.

-40.92 ± 16.49 ; $t = 1.905$, $P < 0.09$, $df = 3$, one-tailed), and was significantly greater in males while handling seeds or mealworms ($t = 2.542$, $P < 0.04$, $df = 4$, one-tailed; Fig. 1B).

DISCUSSION

The results of this study generally support the hypotheses that vigilance is predator directed and conspecific directed and, thus, is influenced both by the tendency to be social and by an individual's dominance status within the social group. Both predictions were supported by at least one measure of vigilance, head-cocks/min while handling a sunflower seed or a mealworm. As predicted, males were more vigilant when tested alone than when tested with the female present, females were more vigilant than males when they were housed together, and, compared with males, females showed a smaller percentage reduction in vigilance when social than when solitary.

The vigilance measure, head-cocks/min while handling a mealworm, produced less clear-cut results. The lack of statistical differences in vig-

ilance levels in two of the three tests for this measure of vigilance was probably attributable to the short time required for the birds to consume mealworms. Such an interpretation is supported by the fact that, whereas the mean inter-head-cock intervals were significantly shorter than the mean handling times for solitary males and social and solitary females, the time required to handle mealworms did not differ statistically from the mean inter-head-cock interval for either males or females whether solitary or social. Thus, the time required to handle a mealworm apparently was so brief that it did not interfere markedly with a nuthatch's typical scanning frequency.

I demonstrated that males capitalized on their social dominance and controlled access to food. Male social dominance ensures priority of access to preferred resources (e.g. Gauthreaux 1978, Morse 1980) and has been demonstrated experimentally to be the proximate mechanism that causes differences in foraging behavior between male and female Downy Woodpeckers during the nonbreeding season (Peters and Grubb 1982). Admittedly, because the females

in this study were forced to stay within some maximum distance from the males, both the incidence of supplanting attacks and the females' vigilance levels might have been artificially high. This also may explain why males attacked females as often as they did when females did not have food (Table 1). However, it is common for the male and female White-breasted Nuthatches of a pair to forage within several meters of each other during winter in Ohio (pers. obs.). Alternatively, one might speculate that my results would have been even stronger had the nuthatches been acoustically, as well as visually, isolated in the solitary treatment. The birds of each pair made frequent contact calls while "solitary" and presumably were aware of each other's presence. Acoustic signals typically may be more important than visual ones, as White-breasted Nuthatches forage principally on large limbs and trunks (Grubb 1982, pers. obs.) and presumably often temporarily lose visual contact with one another while foraging together in nature. In any case, my results prompt the prediction that to avoid kleptoparasitic attacks while foraging near their mates, female White-breasted Nuthatches in Ohio probably incur the cost of increased time devoted to vigilance, at the expense of foraging time.

Other studies have demonstrated that the vigilance level of foraging birds increased with decreasing group size (e.g. Powell 1974, Caraco 1979, Barnard 1980, Bertram 1980, Elgar and Catterall 1981, Studd et al. 1983, Elgar et al. 1984), with increasing distance to cover (Caraco et al. 1980a), with the appearance of a predator (Caraco et al. 1980b, Hegner 1985), when foraging in microhabitats where the risk of predation was presumed to be high (Jansson 1982, Lendrem 1983, Ekman 1987), with increased distance from the center of a flock (Jennings and Evans 1980), and when an alarm call had been given (Sullivan 1984b). These studies assume that the primary function of vigilance is predator detection. Knight and Knight (1986) provided the only previous evidence that vigilance behavior of birds that feed in social groups has the additional function of detecting kleptoparasitic attacks made by conspecifics. They demonstrated a negative correlation between vigilance and group size in Bald Eagles (*Haliaeetus leucocephalus*) for groups of 1-4 eagles, but a positive correlation for groups of 8-14

eagles. My results constitute the first experimental demonstration that vigilance can be sex specific and that social dominance can be a mechanism responsible for differences in vigilance levels among flock mates.

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LITERATURE CITED

- BARNARD, C. J. 1980. Flock organization and feeding budgets in the House Sparrow (*Passer domesticus* L.). *Anim. Behav.* 28: 295-309.
- BERTRAM, B. C. R. 1980. Vigilance and group size in Ostriches. *Anim. Behav.* 28: 278-286.
- CARACO, T. 1979. Time budgeting and group size: a test of theory. *Ecology* 60: 618-627.
- , S. MARTINDALE, & H. R. PULLIAM. 1980a. Avian time budgets and distance from cover. *Auk* 97: 872-875.
- , ———, & ———. 1980b. Avian flocking in the presence of a predator. *Nature* 285: 400-401.
- EKMAN, J. 1987. Exposure and time use in Willow Tit flocks: the cost of subordination. *Anim. Behav.* 35: 445-452.
- , & C. E. H. ASKENMO. 1984. Social rank and habitat use in Willow Tit groups. *Anim. Behav.* 32: 508-514.
- ELGAR, M. A., P. J. BURREN, & M. POSEN. 1984. Vigilance and perception of flock size in foraging House Sparrows (*Passer domesticus* L.). *Behaviour* 90: 215-223.
- , & C. P. CATTERALL. 1981. Flocking and predator surveillance in House Sparrows: test of an hypothesis. *Anim. Behav.* 29: 868-872.
- GAUTHREAUX, S. A., JR. 1978. The ecological significance of behavioral dominance. Pp. 17-54 in *Perspectives in ethology*, vol. 3 (P. P. G. Bateson and P. H. Klopfer, Eds.). New York, Plenum Press.
- GRUBB, T. C., JR. 1982. On sex-specific foraging behavior in the White-breasted Nuthatch. *J. Field Ornithol.* 53: 305-314.
- HEGNER, R. E. 1985. Dominance and anti-predator behavior in Blue Tits (*Parus caeruleus*). *Anim. Behav.* 33: 762-768.
- HINDE, R. A. 1952. The behavior of the Great Tit (*Parus major*) and some related species. *Behaviour* Suppl. 2: 1-201.
- JANSSON, C. 1982. Food supply, foraging, diet and

- winter mortality in two coniferous tit species. Ph.D. dissertation, Gothenburg, Sweden, Univ. Gothenburg.
- JENNINGS, T., & S. M. EVANS. 1980. Influence of position in the flock and flock size on vigilance in the Starling, *Sturnus vulgaris*. *Anim. Behav.* 28: 634-635.
- KNIGHT, S. K., & R. L. KNIGHT. 1986. Vigilance patterns of Bald Eagles feeding in groups. *Auk* 103: 263-272.
- KREBS, J. R., & N. B. DAVIES. 1981. An introduction to behavioral ecology. Sunderland, Massachusetts, Sinauer Assoc.
- LENDREM, D. W. 1983. Predation risk and vigilance in the Blue Tit (*Parus caeruleus*). *Behav. Ecol. Sociobiol.* 14: 9-13.
- MCELLIN, S. M. 1979. Population demographics, spacing and foraging behaviors of White-breasted and Pygmy nuthatches in ponderosa pine habitat. Pp. 301-329 in *The role of insectivorous birds in forest ecosystems* (J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll, Eds.). New York, Academic Press.
- MOORE, N. J. 1972. The ethology of the Mexican Junco (*Junco phaeonotus palliatus*). Ph.D. dissertation, Tucson, Univ. Arizona.
- MORIARITY, D. J. 1976. The adaptive nature of bird flocks: a review. *Biologist* 58: 67-79.
- MORSE, D. H. 1980. Behavioral mechanisms in ecology. Cambridge, Massachusetts, Harvard Univ. Press.
- PETERS, W. D., & T. C. GRUBB, JR. 1982. An experimental analysis of sex-specific foraging in the Downy Woodpecker, *Picoides pubescens*. *Ecology* 64: 1437-1443.
- POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking in Starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* 22: 501-505.
- PULLIAM, H. R. 1973. On the advantage of flocking. *J. Theor. Biol.* 38: 419-422.
- ROBINSON, J. G. 1981. Spatial structure in foraging groups of wedge-capped Capuchin monkeys *Cebus nigrivittatus*. *Anim. Behav.* 29: 1036-1056.
- RUBENSTEIN, D. I. 1978. On predation, competition and the advantages of group living. Pp. 205-231 in *Perspectives in ethology*, vol. 3 (P. P. G. Bateson and P. H. Klopfer, Eds.). New York, Plenum Press.
- SIEGFRIED, W. R., & L. G. UNDERHILL. 1975. Flocking as an antipredator strategy in doves. *Anim. Behav.* 23: 504-508.
- SNEDECOR, G. W., & W. G. COCHRAN. 1967. Statistical methods. Ames, Iowa State Univ. Press.
- STUDD, M., R. D. MONTGOMERY, & R. J. ROBERTSON. 1983. Group-size and predator surveillance in foraging House Sparrows (*Passer domesticus*). *Can. J. Zool.* 61: 226-231.
- SULLIVAN, K. A. 1984a. The advantages of social foraging in Downy Woodpeckers. *Anim. Behav.* 32: 16-22.
- . 1984b. Information exploitation by Downy Woodpeckers in mixed-species flocks. *Behaviour* 91: 294-311.
- WAITE, T. A. 1986. Experimental studies of foraging and anti-predator behavior in some captive birds of a winter bark-foraging guild of temperate deciduous woodland. M.S. thesis, Columbus, Ohio State Univ.
- WILSON, E. O. 1975. *Sociobiology: the new synthesis*. Cambridge, Massachusetts, Belknap Press.