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Effects of Dominance on Vigilance in Avian Social Groups

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During winter, many temperate-zone animals must survive harsh environmental conditions of low ambient temperatures, long nights, and unpredictable food supplies. Two evolutionary forces are thought to affect an individual's survivorship during winter: risk of starvation and risk of predation (Lima 1986, McNamara and Houston 1990, Grubb and Pravosudov 1994a, Pravosudov and Grubb 1997). Foraging and vigilance for predators appear to be mutually exclusive forms of behavior that an animal must "trade off" (Lima 1986). To reduce the risk of starvation, an animal must maximize the rate of foraging and energy intake, but to reduce the risk of predation, it must maximize its vigilance. Social foraging has been thought to benefit all members of a group by allowing each member to increase its foraging efficiency while sharing vigilance with the rest of the group (Elgar 1989). Vigilance in social groups of birds may be directed at predators or dominant group members (Waite 1987a, b; Elgar 1989). Recent studies have suggested that vigilance toward dominant individuals could be directed at both conspecifics and heterospecifics in multispecies groups (Popp 1988, Carrascal and Moreno 1992, Sasvari 1992).

Ekman (1987) reported that subordinate Willow Tits (*Parus montanus*) were more vigilant than dominant individuals. Hogstad (1988a), on the other hand, reported the opposite trend, with dominant Willow Tits being more vigilant than subordinates. The latter report, however, was equivocal because in some instances juvenile females, which always have the lowest dominance rank, had the highest vigilance rates (Hogstad 1988a). However, the absolute rate of vigilance might not be the best measure of benefits for group members. Both studies of Willow Tits examined vigilance of group members within groups but did not provide comparative records for solitary individuals. Because parids seldom (if ever) are solitary in nature, only a manipulative study can provide records for solitary birds under controlled circumstances.

Although dominance-related vigilance within the same species occasionally has been studied in controlled experiments (Waite 1987a, b), the effect of heterospecific group members on vigilance has been

examined only within loose congregations of mixed-species flocks in uncontrolled circumstances around feeders (Carrascal and Moreno 1992, Sasvari 1992).

In a controlled environment, we tested three predictions about vigilance rates in multispecies social groups: (1) a bird's vigilance rate should be the highest when it is solitary; (2) in conspecific pairs, the subordinate should display a higher vigilance rate than the dominant, and the dominant should decrease its vigilance rate; (3) in heterospecific pairs, the subordinate species should display a higher vigilance rate than the dominant species, and the dominant species should decrease its vigilance rate. The first prediction is derived from the hypothesis that animals form social groups to decrease their risk of predation and to increase time available for activities other than vigilance (e.g. foraging). Thus, animals should be less vigilant in a social group than when they are solitary. The second and third predictions are derived from the hypothesis that vigilance consists of two components, vigilance for predators and vigilance for dominant group mates. Any animals in a group may spend less time scanning for predators, but socially subordinate individuals might have to be vigilant toward dominant conspecific or heterospecific group mates. Because dominant individuals (and/or species) in a social group can supplant subordinate individuals (and/or species) from a food source, increased vigilance for dominant group mates could benefit subordinate group members, whether conspecific or heterospecific.

Methods.—Carolina Chickadees (*Parus carolinensis*) and Tufted Titmice (*Parus bicolor*) form heterospecific social groups in winter in which titmice are always dominant over chickadees (Cimprich and Grubb 1994). From mid-November 1996 to late February 1997, we tested seven groups of these birds within a windowless indoor aviary 4 × 4 × 2 m high, each group consisting of two Carolina Chickadees and one Tufted Titmouse in all possible combinations of single and paired birds. We did not test groups consisting of two Tufted Titmice because: (1) such comparisons have already been made (Waite 1987b), and (2) we were most interested in interspecific dominance. The aviary contained a single open feeder with sunflower seeds and water provided *ad libitum*. Temperatures varied from -1 to 12.5°C (lower and upper quartile deviations were 3.2 and 7.1°C, respectively). Light from four 40-W fluorescent bulbs was maintained at LD 9:15 with lights on at 0800. The aviary contained four artificial trees fashioned from

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TABLE 1. The randomized position of each treatment within the six treatments of each replicate of the experiment.

Treatment	Replicate						
	1	2	3	4	5	6	7
Subordinate chickadee, alone	1	4	2	4	1	6	3
Dominant chickadee, alone	4	6	3	2	4	2	5
Dominant and subordinate chickadees, pair	3	5	1	3	3	1	4
Subordinate chickadee and titmouse, pair	2	3	6	5	2	5	2
Dominant chickadee and titmouse, pair	5	2	4	1	5	3	6
Titmouse, alone	6	1	5	6	6	4	1

sugar maple (*Acer saccharum*) branches on which the birds perched.

All birds were caught at different locations in central Ohio, and before being introduced to the aviary, all birds were kept individually for about a week in cloth-covered, 1-m³ holding cages. Within each replicate, we tested in randomized order the six possible combinations of a single bird of either species and pairs of birds consisting of either two chickadees or a chickadee and a titmouse. This randomization exercise resulted in no apparent bias across treatments (Table 1). Although we did not know the sex of any bird, because every replicate contained birds captured at random in different locations, we assume that we tested approximately equal numbers of males and females of both species. Dominance hierarchies occur both within and between sexes of Carolina Chickadees, and Tufted Titmice always dominate chickadees (pers. obs.).

Test subjects were placed in the experimental aviary between 1500 and 1600 on the day before each observation day. On an observation day, we recorded vigilance rates from 0900 to 1000 and from 1400 to 1500, and then changed the birds in preparation for the next day's observation sessions. Thus, each experimental replicate with three birds took six days to complete.

We determined dominance relationships of the two individually marked chickadees on the day they were released together into the experimental aviary. Aggressive confrontations were extremely rare, but the dominant often displaced the subordinate from the feeder and perching places. By contrast, the subordinate chickadee habitually moved from the path of the dominant. We also measured the wing length of both chickadees to determine whether body size was important for intraspecific dominance status. The dominance relationship in each case was extremely clear, and whether it was a titmouse or a chickadee, a dominant bird always displaced a subordinate one (more than 20 observations for each pair of birds).

We obtained a measure of vigilance by recording the number of times a bird "looked up" to scan its environment while perched on a horizontal branch

handling and eating a sunflower seed held between its feet. We considered a bird to be looking up when its bill was pointed above the horizontal plane (Cimprich and Grubb 1994, Pravosudov and Grubb 1995), and we calculated look-ups per second for all recorded intervals of more than 8 s. Sometimes birds may have looked up while swallowing food pecked from a seed, but they also looked up periodically while removing the shell to obtain access to the seed. Thus, we assumed that looking up while opening and eating a sunflower seed represented an interruption in food intake related to being vigilant. For parids such as chickadees and titmice, measuring vigilance while a bird is handling a food item seems to be more valid than while a bird is foraging when it could also be "looking up" to scan for prey items or another foraging site.

During the course of the 2 h of observation per treatment, we collected an average of 21.2 (range 14 to 28) records of vigilance per bird and then reduced these records to one mean vigilance rate per bird per treatment. Because vigilance can be sensitive to ambient temperature (Caraco 1979, Hogstad 1988b, Pravosudov and Grubb 1995), we also recorded ambient temperature for each observation period.

For each category of birds (i.e. dominant chickadee, subordinate chickadee, or titmouse), we performed a repeated-measures ANCOVA with treatment (alone, with dominant conspecific, with subordinate conspecific, or with dominant heterospecific) as a factor and ambient temperature as a covariate. Tukey honest significant difference (HSD) tests were used for post-hoc pairwise comparisons. We used paired *t*-tests to compare vigilance rates of dominant and subordinate chickadees when they were alone versus when they were together or in the presence of a Tufted Titmouse. Throughout the text we refer to dominant and subordinate chickadees in relation to intraspecific dominance only, because Tufted Titmice were always dominant to chickadees.

Results.—Ambient temperature was not significantly related to vigilance rates in any of the treatment groups (all *P*s > 0.6). In all seven experimental replicates, Tufted Titmice always dominated Carolina Chickadees, and the chickadee with longer

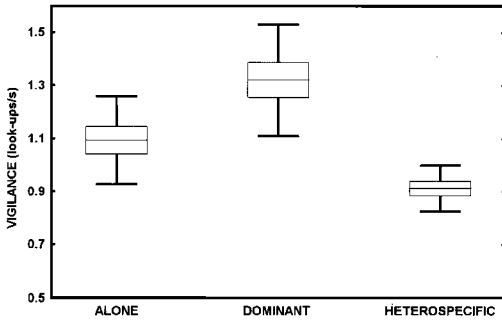


FIG. 1. Mean vigilance rates of seven subordinate Carolina Chickadees while solitary or with a dominant conspecific or heterospecific. Boxes are SE, and whiskers are SD.

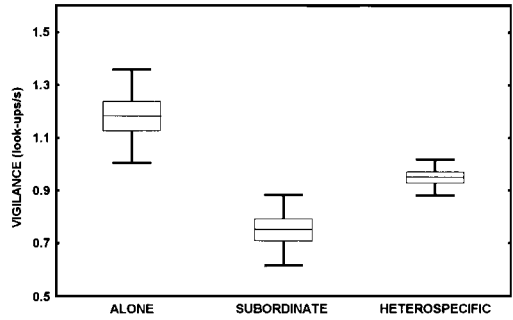


FIG. 2. Mean vigilance rates of seven dominant Carolina Chickadees while solitary or with a subordinate conspecific or dominant heterospecific. Boxes are SE, and whiskers are SD.

wings always dominated the chickadee with shorter wings irrespective of prior residency (dominant individual always displaced subordinate individual; $n > 20$ observations for each replicate).

When alone in the aviary, dominant and subordinate chickadees did not differ in their vigilance rates ($t = 0.96$, $df = 12$, $P = 0.35$). However, when two chickadees were housed together, vigilance rates of subordinate birds increased significantly ($F = 25.0$, $df = 2$ and 10 , $P < 0.001$; Tukey HSD test, $P = 0.004$; Fig. 1), and those of dominant birds decreased significantly ($F = 58.7$, $df = 2$ and 10 , $P < 0.001$; Tukey HSD test, $P < 0.001$; Fig. 2), compared with when they were alone. Vigilance rates of subordinate chickadees also were significantly higher than those of dominant chickadees (paired t -test, $t = 9.21$, $n = 7$, $P < 0.001$). When they foraged with a Tufted Titmouse, both chickadees reduced their vigilance significantly compared with when they foraged alone (Tukey HSD test, $P = 0.015$ for subordinate chickadee and $P = 0.001$ for dominant chickadee; Figs. 1 and 2). Vigilance rates between subordinate and dominant chickadees were not significantly different in the company of a Tufted Titmouse (paired t -test, $t = 0.92$, $n = 7$, $P = 0.39$). Although dominant chickadees reduced their vigilance rates when foraging with either a subordinate chickadee or a Tufted Titmouse, their vigilance rates were significantly lower in the presence of the subordinate conspecific than in the presence of the dominant heterospecific (Tukey HSD test, $P = 0.001$; Fig. 2).

Tufted Titmice reduced their vigilance rates significantly in the presence of a subordinate (Tukey HSD test, $P < 0.001$) and a dominant ($F = 856.5$, $df = 2$ and 10 , $P < 0.001$; Tukey HSD test, $P < 0.001$) chickadee compared with their vigilance rates when foraging alone (Fig. 3). However, titmouse vigilance was not affected by intraspecific dominance status of the chickadee with which they were housed (Tukey HSD test, $P = 0.931$; Fig. 3).

Discussion.—Our results fully supported the sec-

ond prediction, partially supported the first prediction, and disproved the third. Subordinate chickadees increased their vigilance and dominant chickadees decreased their vigilance when foraging in conspecific dyads compared with when they foraged alone. Relative to when they were alone, subordinate and dominant chickadees reduced their vigilance when foraging with the dominant heterospecific titmouse, and titmice also reduced their vigilance in two-bird heterospecific groups compared with when they were housed singly.

Foraging with a conspecific seemed to benefit only the dominant chickadee, whereas the subordinate chickadee had to spend increased time being vigilant for its dominant flock mate. Similar results have been obtained for monospecific groups of Tufted Titmice and White-breasted Nuthatches (*Sitta carolinensis*; Waite 1987a, b). From the results of our experiment, it appears that subordinate chickadees would be better off foraging alone if vigilance reduction were the only benefit of foraging in a group. It is possible that when a group consists of only two individuals, the difference in vigilance between dominant and subordinate individuals could be quite high.

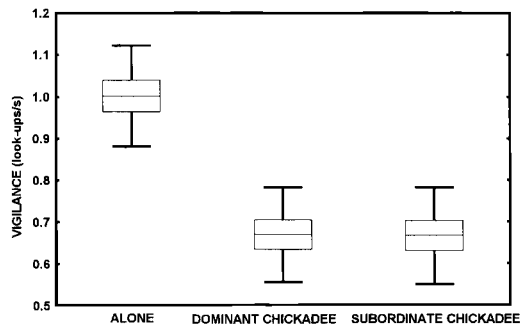


FIG. 3. Mean vigilance rates of seven Tufted Titmice while solitary or with chickadees. Boxes are SE, and whiskers are SD.

Individuals generally have the option to join a group of conspecifics and/or a group of heterospecifics, or to remain solitary. As mentioned previously, joining a group can be costly for both dominant and subordinate individuals (Pulliam and Caraco 1984, Caraco et al. 1989). For dominant individuals, these costs stem from sharing resources with subordinates, whereas subordinates must maintain higher vigilance and have more uncertain foraging success when in a group. However, for group-living to be favored by natural selection, the above-mentioned costs must be outweighed by the benefits of joining the group. Dominants benefit by increased foraging success and lower predation risk made possible by their decreased vigilance and the vigilance they parasitize from subordinates. However, subordinates do not seem to realize these benefits but must still accept the costs of higher vigilance. From an evolutionary perspective, such a scenario suggests that: (1) some benefits must exist from joining the dominant individuals, and (2) such benefits outweigh the costs of higher vigilance and uncertain foraging success. For example, subordinate birds could follow dominant conspecifics to better food patches. Hogstad (1989) showed that when dominant Willow Tits were removed from a group, the survivorship of subordinates was reduced significantly, clearly demonstrating that subordinates benefitted from the company of dominant conspecifics. In resident passerines, another benefit for a subordinate in a group of conspecifics could be the increased chance of replacing a same-sex dominant that disappears from the group, thus commanding the area as a breeding territory during the following reproductive season (Smith 1991). Such a chance should be much higher for a subordinate group member than for a solitary individual.

From a time-allocation perspective, flocking may be advantageous because individual group members can spend less time scanning for predators and more time foraging (Caraco 1979, 1980a, b; Barnard 1980; Caraco et al. 1980). Flocking may have two opposite effects on vigilance; i.e. lowering vigilance for predators while increasing vigilance for dominant individuals. However, it seems that a subordinate that joins a dominant conspecific nevertheless gains protection from predators. Although a subordinate may have to maintain higher vigilance in the presence of a dominant, the overall level of vigilance is higher for the group than for a solitary individual (Pulliam and Caraco 1984, Elgar 1989). Thus, lowered predation risk adds to the compensatory benefits mentioned above, making it adaptive for a subordinate individual to accept the costs of joining a group as opposed to remaining solitary.

On a heterospecific level, our results clearly demonstrated that Carolina Chickadees and Tufted Titmice shared vigilance interspecifically. Despite the fact that titmice were socially dominant to chicka-

dees, vigilance in the subordinate species always was lower in a mixed-species group than when birds foraged singly. Titmice did not discriminate in their vigilance between subordinate and dominant chickadees, and dominance status did not affect vigilance rates of chickadees grouped with a titmouse, a very consistent result showing that a species-specific response existed in vigilance. Although these results argue against the prediction that vigilance for dominants should work on both an intra- and an interspecific level, it is possible that some vigilance by subordinate species was directed toward the dominant species.

Our results suggest a direct advantage of forming multispecies social groups because individuals of all species can increase their foraging efficiency by sharing vigilance for predators. In previous experiments, birds were observed feeding from the same food source, leading to the conclusion that direct competition for food exists on both an intraspecific and an interspecific level (Carrascal and Moreno 1992). However, under natural conditions, use of different foraging niches (e.g. substrates for foraging, different food types, etc.) appears to reduce competition for food (Pravosudov 1986, Alatalo et al. 1987). Carolina Chickadees and Tufted Titmice have different foraging niches and diets (Grubb 1975, 1977; Pierce and Grubb 1981; Cimprich and Grubb 1994; Grubb and Pravosudov 1994b), and the chickadees' niche apparently remains unchanged even after titmice have been removed (Cimprich and Grubb 1994). Thus, chickadees may not direct much of their vigilance toward dominant heterospecific group members because they may be focused on different food sources, which would make joint flocking beneficial for both species as an antipredatory tactic. In mixed-species flocks, chickadees often seem to follow titmice rather than avoid them (pers. obs.), suggesting that some benefits must result from forming such groups (pers. obs.).

The vigilance of a dominant chickadee that was with a subordinate conspecific was different from that when it was with a titmouse. Although in both instances the vigilance of the dominant individual was lower than that of a single bird, the scanning rate was significantly lower in the presence of the subordinate conspecific. Thus, even though dominant chickadees may benefit from grouping with subordinate chickadees and Tufted Titmice, the degree of sharing vigilance between different species may vary because these individuals benefit more from their conspecific group members (Metcalf 1984).

Finally, our results support the idea that different adaptive functions exist when foraging in monospecific versus heterospecific groups. One of the benefits of heterospecific grouping could be reduced vigilance for predators and increased foraging efficiency. Different species of animals that form multispecies social groups often differ in their foraging niches,

and such differentiation could result in reduced competition for resources. Hence, members of a subordinate species might not be in danger of being supplanted from food resources, and animals of different species might realize the benefits of joining social groups to reduce the risk of predation, especially during the winter when obtaining food becomes highly unpredictable. Such an alliance of different species may significantly increase individual survival during the nonreproductive season through increased time for foraging and lowered risk of predation.

The function of foraging in monospecific social groups appears to be different for dominant and subordinate individuals, especially when group sizes are relatively small. Although dominants may garner increased foraging efficiency through reduced vigilance, subordinates might benefit from better foraging-patch selection or the chance to replace a dominant individual that has disappeared from the flock. To obtain such benefits, however, subordinates must pay the price of substantially increased vigilance directed toward dominant conspecifics. Despite such increases in vigilance, subordinates may still benefit through the increased net vigilance effect provided by the group. To reduce the effect of foraging with dominant individuals, subordinates would benefit from increased group size if the risk of being supplanted by a dominant is diluted among several subordinate group members. However, increased group size, in turn, might reduce foraging success of the entire group, and it appears that an optimal group size can be a tradeoff between gaining maximum foraging benefits and minimizing the rate of vigilance for dominant conspecifics. Including vigilance for dominant conspecifics in models of optimal group size could increase our understanding of the adaptiveness of sociality during the nonreproductive season.

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Maintenance Energy Costs of Two Partially Folivorous Tropical Passerines

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In homeotherms, residual variation of maintenance-energy costs around allometric curves can be related to factors independent of body mass, such as food habits (McNab 1986), taxonomic affiliation (Bennett and Harvey 1987), season (Kendeigh et al. 1977), habitat type (Hulbert and Dawson 1974), climate (Weathers 1979), and body composition (Daan et al. 1990). Food habits are important because the rate of energy acquisition might limit the rate of energy expenditure (McNab 1986, Weiner 1992). For mammals, McNab (1978, 1986) hypothesized that the processing of food with low metabolizable energy content, including the leaves of woody plants, requires a low basal metabolic rate (BMR). Hence, arboreal mammals that meet large portions of their energy requirement from leaves have lower BMRs than predicted from allometric equations (McNab 1978, 1980a). Some of the reduction of BMR in folivorous mammals seems to be related to properties of leaves,

such as their low metabolizable energy owing to the content of difficult-to-digest fiber and to the high content of secondary compounds (McNab 1978, 1986).

Food habits also influence rates of maintenance energy expenditure in birds (McNab 1988), but the relationship between folivory and avian BMR is not fully understood. To a large extent, this is because little is known about the energetics of folivorous species. Here, we report on the maintenance energy costs and thermal response to ambient temperature of two species of passerines that regularly include leaves and other plant tissues in their diets. Passerines are of interest because of their high mass-specific energy expenditure, because their small body size constrains the use of green tissues of plants, and because folivory is particularly scarce among them (Morton 1978, Parra 1978). Characteristics intrinsic to leaves should also affect avian consumers; therefore, it is of interest to determine if folivory is correlated with reduced BMR in birds, as it is in mammals.

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