

DOMINANCE, FORAGING AND PREDATION RISK IN THE
TUFTED TITMOUSE¹

THOMAS A. WAITE AND THOMAS C. GRUBB, JR.

Department of Zoology, The Ohio State University, Columbus, OH 43210

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Foraging animals often must make compromises between competing demands such as foraging efficiently and avoiding predators. Apportioning time between foraging and predator-directed vigilance (e.g., Pulliam 1973, Powell 1974, Caraco 1979, Barnard 1980, Lendrem 1983, Ekman 1987) is just one of several ways in which birds must compromise between foraging efficiently and avoiding predators. Other compromises involve the decisions made by individuals when (1) foraging in areas where predation risk is high or (2) when a predator has been detected. Recently, several authors (e.g., Stein and Magnuson 1976, Milinski and Heller 1978, Caraco et al. 1980a, Grubb and Greenwood 1982, Sih 1982, Werner et al. 1983, Lima 1985, Lima et al. 1985) have demonstrated that animals will use energetically profitable areas less for foraging if predation risk there is high.

The present study examines decisions made by the Tufted Titmouse (*Parus bicolor*) after an alarm call. Tufted Titmice and Carolina Chickadees (*P. carolinensis*) or Black-capped Chickadees (*P. atricapillus*) are the "nuclear" species (sensu Moynihan 1962) for mixed-species flocks of bark-foraging birds within temperate deciduous woods of North America during winter. Individuals of these species commonly give alarm calls when avian predators, such as Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*), are detected (Ficken and Witkin 1977, Gaddis 1980, pers. observ.). Generally, all birds of a mixed-species flock, including the most common "attendant" species, White-breasted Nuthatches (*Sitta carolinensis*) and Downy Woodpeckers (*Picoides pubescens*), go into a behavioral "freeze" for up to 15 min (\bar{x} = 4.8 min, SD = 3.2 min, n = 49; Gaddis 1980) when alarm calls are given by individuals of these three parid species (Sullivan 1984, unpubl. results). This tactic presumably decreases the probability of being detected by the predator.

After becoming immobile once an alarm call is given, each individual has to decide when to resume foraging, thereby exposing itself to the predator which still may be nearby. One might expect that the decision of when to resume foraging should be influenced by an individual bird's dominance status. Because socially dominant individuals have the capacity to procure food

via supplanting attacks launched against subordinates, they may be able to avoid exposing themselves to the predator by waiting until a lower-ranking bird has resumed activity. Therefore, subordinates might incur a greater risk of attack. One could argue also that the trade-off between these completely incompatible activities, remaining immobile and foraging, could be mediated by dominance status not solely because higher-ranking birds can kleptoparasitize subordinates, but also because dominants might be able to remain stationary longer than subordinates after an alarm call owing to their typically lower hunger levels. In any case, subordinates may be constrained by the need to minimize competition for food with dominants.

In this paper we describe a test of the prediction that the order in which flocking birds resume foraging after an alarm call is inversely related to dominance status. Our experiment is similar to those of Hegner (1985), who pulled a model Eurasian Sparrowhawk (*Accipiter nisus*) over captive flocks of Blue Tits (*Parus caeruleus*), and De Laet (1985), who recorded the responses of free-ranging Great Tits (*P. major*) to overflights of live Eurasian Sparrowhawks. The present experiment involved playing Tufted Titmouse alarm calls to captive groups of Tufted Titmice with known dominance hierarchies.

METHODS

Four groups of Tufted Titmice, each consisting of three individuals, were housed sequentially in an indoor aviary 4.8 m × 4.2 m × 2.7 m high between 19 December 1984 and 5 March 1985. Each cohort of three titmice had been used previously in other experiments (Waite 1986) with captive mixed-species flocks. To allow instant recognition of individuals, we marked the cheek patches of each bird a unique color with waterproof felt tip markers. The titmice could not be sexed reliably on the basis of external features, and since the birds in this study were neither laparotomized nor sacrificed, their sex remained unknown. Age was not determined but all of the titmice were presumably at least 6 months old. To ensure that the titmice had foraged together in the wild and thus had some familiarity with one another, we captured all three birds of a given group at a single trapping station. The birds in all captive groups also had considerable familiarity with one another owing to their relatively long period in captivity (i.e., ≥ 10 days) before the experiment was conducted. The birds were held at $18.7 \pm 1.4^\circ\text{C}$ ($\bar{x} \pm \text{SE}$) on natural photoperiod, and were maintained on an ad libitum diet of sunflower seeds (*Helianthus* sp.) and mealworms (*Tenebrio* sp.). Two water sources were always avail-

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able. Details concerning the aviary and the conditions under which the titmice were held as members of mixed-species flocks are in Waite (1986).

After the birds had been allowed at least 3 days to acclimate to the aviary environment, dominance hierarchies were determined. This was accomplished by recording, during 20 15-min observation sessions, all interactions in which one bird successfully used a supplanting attack. To measure how much individuals capitalized on their dominance status to acquire and/or control access to food, we recorded: (1) whether the supplanted individual had a food item when it was supplanted, (2) whether the supplanting individual obtained food as a direct result of the supplanting attack, (3) whether the supplanting individual engaged in an apparent search for food and/or pecked at the substrate at the exact site of the supplanting attack, and (4) for all instances of social dominance, whether the interaction occurred at the feeder.

The experimental procedure was as follows. After the ninth day of each flock's captivity, three experimental trials and one control trial were conducted in randomized order between 09:00 and 13:00. Experimental Alarm Call (AC) trials involved a playback of a three-note high-frequency Tufted Titmouse alarm call recorded in March 1984 when a stuffed male Cooper's Hawk was pulled on an monofilament line over three captive Tufted Titmice. This alarm call playback lasted approximately 1.5 sec. The control Contact Call (CC) trial involved a 2-min playback of Tufted Titmouse and Carolina Chickadee contact calls. For both AC and CC trials, the tape continued to run after the playback, but no recorded sound was broadcast. Playbacks were initiated only: (1) when all three birds were away from the feeder and none was handling a food item, (2) when all three individuals had consumed at least one sunflower seed or one mealworm during the previous 2-min period, and (3) when all three individuals were active (defined as having made at least one perch change during the preceding 3 sec). These procedures reduced the likelihood of the results being confounded by dominance-specific hunger states. Additionally, to minimize habituation to alarm calls over the three trials, we did not initiate a playback trial until at least 40 min had elapsed since the termination of the previous trial. While observing through a one-way window after the initiation of each playback, we recorded on a tape recorder: (1) whether a behavioral freeze was exhibited by each individual, (2) the first bird to move (defined as moving at least one body length), and (3) the first bird to return to the feeder (defined as landing on the feeding tray).

Parametric and nonparametric statistical tests were taken from Snedecor and Cochran (1967) and Hollander and Wolfe (1973), respectively. Multiple comparisons were accomplished by paired *t*-tests using Bonferroni's probabilities with an experimentwise error rate of 0.05. Statistical significance was set at the 0.05 level.

RESULTS

Hierarchies in all four flocks were linear and there were no reversals of dominance status during the period of captivity of any flock (Waite 1986). The assumption

TABLE 1. Dominance status within each flock and priority of access to food as indicated by asymmetries in contests involving food during 5 hr of observation.^a

Winner	Loser		
	Alpha	Beta	Gamma
Alpha	—	0.05 ^b	0.25 ± 0.15
	—	0.05 ^c	0.10
	—	0.40 ± 0.30 ^d	0.35 ± 0.15
	—	1.50 ± 1.31 ^e	1.05 ± 0.92
Beta	—	—	0.15
	—	—	0.05
	—	—	0.10
	—	—	1.75 ± 0.96
Gamma	—	—	—
	—	—	—
	—	—	—
	—	—	—

^a Records were taken during 20 15-min observation sessions. Data are reported with SE whenever $n \geq 5$.

^b Mean number of supplanting attacks hr^{-1} that occurred away from the feeder where supplanted bird was handling a food item when supplanted.

^c Mean number of times hr^{-1} that a supplanting individual obtained food as a direct result of the supplanting attack launched away from the feeder.

^d Mean number of times hr^{-1} that a supplanting individual engaged in a search for food and/or pecked at the substrate at the exact site of a supplanting attack that occurred away from the feeder.

^e Mean number of supplanting attacks hr^{-1} that occurred at the feeder.

that dominant titmice partially controlled access to food was sustained (Table 1). Dominants kleptoparasitized subordinates and won contests for access to food at the feeder. It follows, therefore, that after an alarm call subordinates might resume foraging before dominants to avoid interference at the feeder.

The titmice responded to the AC playback either by "scattering" to perches and then freezing or by freezing in place if already perched. The birds remained immobile for 250.2 ± 107.4 sec ($\bar{x} \pm \text{SE}$) after the alarm call playback. The AC, then, clearly was sufficient to elicit an alarm reaction and presumably communicated the message that a predator was in the vicinity. There was no alarm reaction (i.e., scattering, freezing, or alarm calling) during the CC trials, and the time lag between the onset of the contact call playback and the first movement was 1.2 ± 9.6 sec ($\bar{x} \pm \text{SE}$). Only once did a bird fail to move within 3 sec following the onset of the contact call playback; in that instance the most subordinate titmouse of Flock 2 remained stationary (viz., did not move at least one body length) for 58 sec while preening continuously. The latency to first movement for birds of each dominance rank was significantly greater during the AC trials than during the CC trials ($P_s < 0.025$, Fig. 1A). The mean latency to return to the feeder in the AC trials was significantly greater than in the CC trials for the intermediates ($t = 4.598$, $P < 0.01$, Fig. 1B), but the difference did not reach statistical significance for either the dominants ($t = 2.037$, $P < 0.08$) or the subordinates ($t = 1.785$, $P < 0.1$). Because the trial number and latency to first movement by any individual were not significantly correlated ($r = -0.138$, $P > 0.1$, two-tailed), indicating that the birds failed to habituate to the alarm calls, all three trials for each flock were included in all analyses.

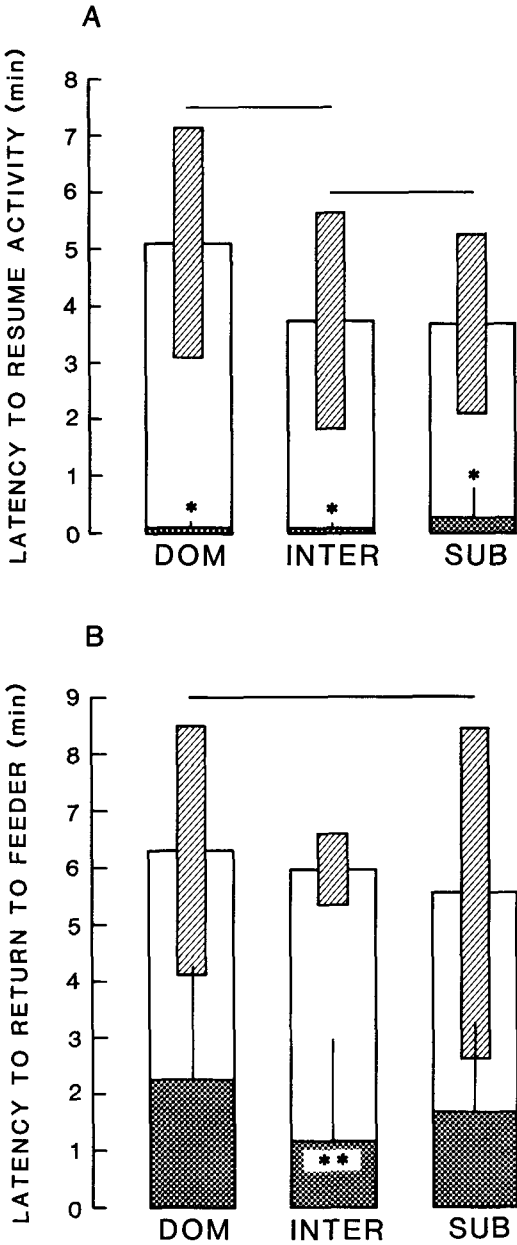


FIGURE 1. Relationship between dominance rank and (A) the latency to resume activity after the alarm call and (B) the latency to return to the feeder after the alarm call playback. Unshaded bars represent the mean of the means for all AC trials for each flock ($n_s = 4$). Wide stippled bars represent the means for the control trials. Narrow cross-hatched bars represent ± 1 SE for the AC (experimental) trials, and the vertical lines represent 1 SD for the CC (control) trials. Horizontal lines above the bars connect statistically indistinguishable AC means as determined by one-tailed paired t -tests using Bonferroni's probabilities. The results of one-

We compared, across dominance ranks, the mean time lag to resume activity and return to the feeder after the alarm call playback. Jonckheere's tests for an ordered relationship between a bird's dominance rank and the order in which it resumed activity or returned to the feeder failed to detect significant trends ($P_s > 0.05$). However, pairwise comparisons yielded a significant difference between dominants and subordinates in latency to resume activity (Fig. 1A; $t = 5.398$, $P < 0.02$), with dominants waiting an average of 84.6 sec longer than subordinates. Figure 1B shows that there were no statistically significant differences among birds of different dominance ranks in the mean time lag to return to the feeder after the alarm call playback.

DISCUSSION

Hegner (1985) clearly demonstrated that following the presentation of a Eurasian Sparrowhawk model there was a significant tendency for subordinate Blue Tits to precede dominants in returning to a feeder, and De Laet (1985) showed that after the overflight of a free-ranging Eurasian Sparrowhawk there was a significant inverse relationship between dominance rank and the sequence in which wild Great Tits returned to a feeder. The interpretation that dominants, owing to their superior ability to compete for food, could afford energetically to wait until subordinates had taken the predation risk associated with the resumption of activity is not without alternatives, as Hegner suggests. In Hegner's aviary study, there was (1) a tendency for dominants to spend more time than subordinates at the feeder before the presentation of the hawk model ($P = 0.12$, Jonckheere's test), and (2) a tendency for birds that spent more time at the feeder prior to the hawk model presentation to be later in the sequence of birds returning to the feeder ($P < 0.1$, Jonckheere's test). In De Laet's field study, dominant Great Tits tended to use the feeder earlier in the morning than did lower-ranking individuals (Binomial $P = 0.001$), and because the design of the feeder allowed only one bird to use it at a time, subordinates might have had restricted access to the superabundant food source. The results of these two studies taken together suggest that dominants might have been typically less hungry than subordinates. Thus, a reasonable alternative, though non-exclusive, interpretation of the negative correlation between sequence of return to the feeder and dominance status is that dominants outwaited lower-ranking birds after the predator stimulus not directly owing to their capacity for temporary preemption of the food resource, but rather, or also, because they were able to maintain a lower general hunger level than were subordinates.

In contrast to these previous studies (Hegner 1985, De Laet 1985), our results show that although subordinate Tufted Titmice, following an alarm call, resumed activity 84.6 sec before dominants, they did not typically precede dominants in returning to the feeder. Thus, in preceding dominants in activity resumption,

←
 tailed paired t -tests comparing means of AC and CC trials are shown by * if $P < 0.05$ and ** if $P < 0.01$.

and thereby incurring a presumably greater predation risk, subordinate Tufted Titmice did not seem to gain a foraging advantage. In this experiment, we attempted to eliminate any effects of dominance-specific hunger levels. Although hunger levels were not controlled independently for individuals of different dominance ranks in a rigorously quantitative manner in the present study, the conditions under which we initiated alarm call playbacks (see Methods) were designed to minimize differences among dominance-specific hunger levels. Additionally, because the feeder was large enough to allow access to more than one bird at a time, and because it proved impossible to keep the floor devoid of spilled food, subordinates apparently were disadvantaged only marginally in their ability to procure food (Table 1). Thus, it may be that even in the absence of dominance-specific hunger levels and priority of access to food, dominant Tufted Titmice exercise greater caution than do lower-ranking conspecifics.

Few studies have considered the effects of dominance on the trade-off between the need to forage efficiently and the conflicting demand of avoiding predators. Previous reports have demonstrated that dominant birds of the genus *Parus*, engaging in what resembles a "selfish herd" strategy (Hamilton 1971), force low-ranking conspecifics to occupy riskier microhabitats and/or the more vulnerable periphery of flocks (Glase 1973, Jansson 1982, Ekman and Askenmo 1984, Ekman 1987). Our results show that after a predator has been detected, high-ranking Tufted Titmice typically waited until subordinate individuals had resumed activity, thereby presumably incurring the brunt of the predation risk. Moreover, because subordinates appeared not to gain a foraging advantage as a result of resuming activity before dominants, our results are suggestive that dominant Tufted Titmice may be more averse to taking predation risks than are lower-ranking conspecifics irrespective of, or in addition to, lower hunger levels and their ability to out-compete subordinates for food. Unfortunately, however, because the birds in this study were not sexed, we cannot eliminate the possibility that the behavior observed was partly attributable to between-sex differences which were correlates of dominance status. Similarly, because the birds were not aged, we cannot rule out differences in experience as a proximate cause of the dominance-specific behavior observed. Thus, further experimentation is needed to test whether correlates of dominance (i.e., age, sex and hunger), rather than dominance differences per se, are responsible for dominance-specific antipredator behavior.

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COLONY DEPARTURE OF FAMILY GROUPS OF ANCIENT MURRELETS¹

IAN L. JONES² AND J. BRUCE FALLS

Department of Zoology, University of Toronto, 25 Harbord St., Toronto, Ontario M5S 1A1, Canada

ANTHONY J. GASTON

Canadian Wildlife Service, Ottawa, Ontario K1A 0E7, Canada

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The behavior of young seabirds at departure from the colony is critical for their survival and for the reproductive success of their parents. The young of several alcid species depart their nest site when partly grown and receive parental care on the sea later. Murres (*Uria* spp.) and the Razorbill (*Alca torda*) have semiprecocial young which are fed at the nesting ledge for 15 to 30 days (Gaston 1985), before leaving with the male parent (Scott 1973; Gaston and Nettleship 1981; S. Wanless and M. P. Harris, pers. comm.). The *Synthliboramphus* murrelets have precocial young which accompany their parents to sea a few days after hatching (DeWeese and Anderson 1976, Sealy 1976, Murray et al. 1983). Colony departure behavior of murre and Razorbill chicks has been described in detail (Tuck 1961, Greenwood 1964, Gaston and Nettleship 1981), but there is little information on the departure behavior of murrelets. In this note we describe the colony departure behavior of Ancient Murrelets (*S. antiquus*) at Reef Island, Queen Charlotte Islands, British Columbia. This island supports a colony of 5,000 pairs of Ancient Murrelets (Gaston, unpubl.).

METHODS

Fieldwork was carried out in May and June of 1984, 1985, and 1986. We monitored attendance of burrows

by adults by placing small rectangular plastic strips in the entrances of 45 burrows. These were displaced as birds entered. We marked 16 adults in burrows with fluorescent paint on their flank or back to measure incubation shifts. We checked the burrows regularly by feeling for the presence of pipping eggs or chicks. Vocalizations of adults and chicks were recorded using a Marantz PMS-220 cassette recorder and miniature microphones (Realistic 33-1052 and 33-1056). We monitored departure behavior near the burrow by listening to the vocalizations and other sounds of family groups from a blind in a dense part of the colony. Using a dim flashlight, we made brief observations of about 20 family groups just as they emerged from their burrows. We observed departures from several burrows using a Star-tron MK-303A night vision scope, though this was generally of little use in the extremely dark conditions within the colony. Using the scope we made extensive observations of the behavior of departing family groups on the sea below the colony, where viewing conditions were better.

RESULTS

Adult Ancient Murrelets tended to enter their burrows more frequently towards the end of their incubation period. Chicks began calling from at least the time of the first cracks in the eggs, which appeared 4 to 11 days before hatching ($\bar{x} = 6.20 \pm 1.58$ SD days, $n = 20$). However, parents normally did not vocalize while alone in the burrow with chicks. Complex vocalizations were normally restricted to the period just following the return of the off-duty member of the pair. Parents entered burrows several times ($\bar{x} = 2.55 \pm 0.76$ times, $n = 31$) and brooding changeovers occurred ($\bar{x} = 0.89 \pm 0.60$ times, $n = 9$) during the 1 to 4 days ($\bar{x} = 2.19 \pm 0.70$

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² Present address: Dept. of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada.