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Selective Alarm Calling by Downy Woodpeckers in Mixed-species Flocks

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Many species of birds and mammals give alarm signals when disturbed by predators. Although these alarm signals may appear altruistic, the alarm calls could benefit the caller. Individual fitness might be promoted by decreasing the probability of an attack, if the alarm call serves as a pursuit deterrent signal or discourages the predator from hunting in the immediate area (Smythe 1970, Trivers 1971, Woodland et al. 1980); by misdirecting the predator and increasing the probability that another individual is attacked (Perrins 1968, Charnov and Krebs 1977, Owens and Goss-Custard 1976); and by warning kin or a mate (Maynard Smith 1965, Williams 1966, Sherman 1977).

The balance between the risks and benefits associated with alarm calls presumably influences the conditions under which alarm calls are given. For example, the net benefit of alarm calling and the probability of giving an alarm call vary with age, sex, and reproductive status (Sherman 1977). The economics of alarm calling also may differ between species in mixed-species groups, so that one species is more likely to call than another in a given situation. Mixed-species winter flocks provide an opportunity to examine the situations in which several different species give alarm calls. During the winter, mixed-species flocks composed of Black-capped Chickadees (*Parus atricapillus*), Tufted Titmice (*Parus bicolor*), and several follower species [Downy Woodpeckers (*Picoides pubescens*), Hairy Woodpeckers (*Picoides villosus*), and White-breasted Nuthatches (*Sitta carolinensis*)] are common in eastern North America

(Morse 1970). All 5 species are vulnerable to predation by raptors and respond to each others' alarm calls (Bent 1937, 1938; Gaddis 1980). Yet within these flocks 2 of the species, chickadees and titmice, give almost all of the alarm calls (Gaddis 1980).

I examined the conditions eliciting alarm calls for 3 of these species (Black-capped Chickadees, Tufted Titmice, and Downy Woodpeckers) in winter flocks during encounters with naturally occurring predators (raptors) and predator models. Results indicate interspecific differences that can be interpreted in the context of benefit/cost logic.

Observations were made on alarm calling in mixed-species flocks during 3 winters from November 1979 to March 1982 at the Great Swamp National Wildlife Refuge in New Jersey. I recorded the flock composition and alarm calls during encounters with naturally occurring predators [Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*Accipiter cooperii*), and American Kestrels (*Falco sparverius*)] and predator models.

In the first predator-model tests, a stuffed Red-tailed Hawk (*Buteo jamaicensis*) was mounted on a pole and presented from a blind for 10 s to woodpeckers foraging 3–15 m away. I collected data only on woodpeckers with this model. I later replaced this model with a stuffed Sharp-shinned Hawk mounted on a pulley that ran down a wire between two trees. The model was released from a blind and immediately pulled back into the branches of the tree. In tests with this model, I collected data on woodpeckers, titmice, and chickadees foraging 2–15 m from the blind.

I presented predator models from blinds to 20 individually marked Downy Woodpeckers that were foraging with a mixed-species flock, with a conspecific, or alone. Two days generally were allowed be-

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tween tests on an individual woodpecker, although occasionally two woodpeckers foraging together were exposed to the predator model twice in the same day. Suet-filled traps and feeders were used to capture the woodpeckers for banding and to attract woodpeckers to the blinds. These feeders were set out sporadically throughout the winter and removed from a bird's territory at least two days prior to testing the bird with a predator model. Because squirrels were very successful at emptying the feeders, suet was never available to woodpeckers for more than two consecutive days.

The Black-capped Chickadees' high-frequency whistle ("high zees") and the Tufted Titmice's "seet" call were scored as alarm calls for these species (Morse 1970, Ficken and Witken 1977, Gaddis 1980). The loud "tichrr" call or rattle call was scored as an alarm call for the Downy Woodpeckers (Lawrence 1967, Winkler and Short 1978).

Downy Woodpeckers responded to the predator models, the naturally occurring predators, and the alarm calls of flock members in a similar manner (Sullivan in press). They froze for about 10 s, then exhibited a high level of vigilance (measured by headcocks/min) and ceased foraging for several minutes. Chickadees and titmice responded to the predator models, naturally occurring predators, and alarm calls by diving into bushes and remaining quiet for several seconds to several minutes.

Downy Woodpeckers gave alarm calls in only 3 of the 11 encounters (27%) with live raptors, in only 1 of the 19 tests (5%) with the Red-tailed Hawk model, and in only 3 of the 50 tests (6%) with the Sharp-shinned Hawk model. In contrast, chickadees and titmice frequently gave alarm calls. Chickadees gave alarm calls in all 7 encounters (100%) with live raptors and in 14 of the 16 tests (88%) with the Sharp-shinned Hawk model. Titmice gave alarm calls in 2 encounters (100%) with live raptors and in 3 of the 6 tests (50%) with the Sharp-shinned Hawk.

Downy Woodpeckers never gave alarm calls when foraging alone (0/46 instances), when with a flock that did not include another woodpecker (0/23 instances), or when with a Downy Woodpecker of the same sex (0/6 instances). This contrasts with the high frequency of alarm calls from woodpeckers foraging with a conspecific of the opposite sex (7/9 instances). Of the 7 alarm calls, 3 were given by females and 4 by males. On 6 of these 7 occasions the woodpeckers were foraging as a pair, and on the seventh occasion the pair was foraging with 2 chickadees and 2 nuthatches. The difference in propensity to give alarm calls when foraging with a member of the same or opposite sex was highly significant (Fisher Exact Probability test, $n = 15$ opportunities to alarm call, $P = 0.006$). The 2 instances when neither member of a heterosexual pair gave an alarm call occurred on the same day (18 March 1982) and involved the same

2 birds. The female was not banded, and I never saw her either before or after that day. I observed all other pairs foraging together at various times throughout the winter.

Chickadees and titmice gave alarm calls significantly more often in response to potential predators than did Downy Woodpeckers both in the absence of conspecifics ($\chi^2 = 71.57$, $n = 80$, $P < 0.01$) and in the presence of conspecifics (Fisher Exact Probability test, $n = 36$, $P = 0.01$). Black-capped Chickadees and Tufted Titmice gave alarm calls in 9 of 11 instances (82%; 5/5 for chickadees, 4/6 for titmice) when foraging without conspecifics and in 18 of 21 instances (86%; 17/19 for chickadees, 1/2 for titmice) when foraging with at least one conspecific. For the pooled chickadee and titmouse data the probability of alarm calling did not differ signfiicantly between when they were foraging with conspecifics and when they were foraging without conspecifics (Fisher Exact Probability test, $n = 32$, $P = 0.36$).

Both Downy Woodpeckers and Black-capped Chickadees (Witkin and Ficken 1979) appear to alarm call in the winter to protect their mates. Downy Woodpeckers give alarm calls less frequently and more selectively than Black-capped Chickadees or Tufted Titmice. What differences between parids and picids in the species-specific risks and benefits of alarm calls could account for this?

It is doubtful that kin selection can be used to fully explain the chickadees' and titmice's propensity to alarm call. The Black-capped Chickadees in these mixed-species flocks tend to be pairs from the previous season and unrelated young (Wallace 1941, Ficken et al. 1981), and pairs move from flock to flock during the winter (Ficken et al. 1981).

Chickadees and titmice fill different roles than woodpeckers in these flocks, which may affect the probability that they benefit from giving an alarm call. Chickadees and titmice constitute the nucleus of these mixed-species flocks and usually are found in the company of conspecifics (Morse 1970). Woodpeckers, on the other hand, are peripheral flock members and often drop out of the flock as the flock leaves the woodpecker's territory (Morse 1970, Sullivan 1984). Ficken et al. (1981) found strong associations between mated pairs of Black-capped Chickadees in winter flocks. I observed Downy Woodpeckers foraging with their presumed mates in only 82 of 250 (33%) sightings during 1979–1981. During the winter Black-capped Chickadees (and possibly Tufted Titmice) may spend more time foraging with their mates than woodpeckers spend with their respective mates, and therefore the parids' mates may be more likely to hear and benefit from the warning calls.

Differences in how these species evade predators may affect the cost of alarm calling. Chickadees and titmice immediately dove into low bushes when alarm calls were given or the predator model was pre-

sented. In contrast, Downy Woodpeckers froze on the side of a tree trunk or large branch, where they may be more vulnerable to predators than the chickadees and titmice. The predator models were presented at short distances from the birds. This may have affected the relative rates of alarm calls if woodpeckers had a longer flight distance than the parids and panicked during the tests.

There are also differences in the acoustic characteristics of the alarm calls among these species. High-frequency alarm calls may be difficult for predators to locate (Marler 1955, 1957; Perrins 1968). I found the chickadees' "high zee" call and the titmice's "seet" call more difficult to locate than the woodpeckers' lower-pitched "tichrrr" call, although I have no evidence that hawks also found these calls more difficult to locate.

While the relative costs and benefits of alarm calling for parids and picids are speculative, chickadees and titmice may experience greater benefits (the probability that a mate hears the warning call) and smaller costs (the probability of a predator locating and catching the alarm caller) when they give an alarm call than do Downy Woodpeckers. The chickadees' and titmice's propensity to give alarm calls can then be exploited by peripheral flock members, such as the Downy Woodpeckers. Greig-Smith (1981) found that flocks apparently formed around Stonechats (*Saxicola torquata*) because Stonechats gave alarm calls at longer flight distances than the other species. Downy Woodpeckers benefit from foraging with chickadee-titmouse flocks by decreasing the time they spend on vigilance, increasing their feeding rate, and responding to the other species' alarm calls (Sullivan 1984, in press). The conditions under which these mixed-species flock members give alarm calls suggest that the woodpeckers are exploiting chickadees and titmice as sentinels rather than participating in a cooperative situation.

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Daily Energy Expenditure by Female Savannah Sparrows Feeding Nestlings

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The adaptive significance of many life-history traits of birds presumably can be understood within the context of patterns of energy allocation (Cody 1966, King 1974). Yet precious few data exist for the energy expenditure of free-living birds during their reproductive period. In particular, little is known about the energy requirements of females while they are feeding their young.

Most extant information on the energetic cost of feeding young has been gathered indirectly by measuring the weight loss of parents as they feed different numbers of young (Hussell 1972) or from studies of caged parents (Brisbin 1969). With the advent of the doubly labeled water (DLW) technique (Lifson et al. 1955, Nagy 1975), reasonable estimates of the daily energy expenditure (DEE) of free-ranging birds now can be obtained (Nagy 1980). In essence, the technique involves isotopic labeling of an animal's body water with oxygen-18 and tritium or deuterium. From the difference between the turnover rates of the two isotopes, the rate of CO_2 production can be measured. When we concurrently compared CO_2 production in Savannah Sparrows (*Passerculus sandwichensis*) using DLW and standard laboratory techniques, we found a mean difference of +6.5% (range −0.2 to +11.0, $n = 7$), suggesting that acceptable estimates of CO_2 can be obtained while these birds are functioning in their normal environment (Williams and Nagy 1984a). Furthermore, Nagy and Costa (1980) have shown that water flux rates estimated with tritiated water vary within ±10% of actual flux rates in most situations.

Using the DLW method, Utter and LeFebvre (1973) calculated that female Purple Martins (*Progne subis*) with nestlings metabolized an average of 183.6 kJ/day ($n = 2$; mean wt = 47.7 g), which is somewhat higher than that of males during the same time period (142.9 kJ/day; $n = 2$). Males apparently did not feed nestlings as much as did females. Unfortunately, the number and age of the nestlings were not reported. Hails and Bryant (1979) found that female Common House-Martins (*Delichon urbica*, 20 g) feeding young metabolized 75.3 kJ/day, but the DEE of female birds was not correlated with brood mass.

In this study, we used DLW to measure the DEE of female Savannah Sparrows while they were feeding nestlings. Specifically, we wanted to compare the DEE of females while feeding a normal brood of 3 young with those feeding 2 young, late in the nestling period when energy demands presumably are greatest.

The study area and birds.—Our study area lay in the middle and upper littoral zone of a large salt marsh located on the Point Mugu Naval Air Station, Pt. Mugu, California (34°07'N, 119°07'W). The vegetation consisted of, in decreasing order of importance, *Salicornia virginica, Frankenia grandifolia, Batis maritima*, and *Monanthochloe littoralis*. Large, barren salt pans and shallow tidal channels intermixed with patches of vegetation to form a mosaic of sites used by Savannah Sparrows for foraging and nesting.

The breeding biology of the Savannah Sparrow at Pt. Mugu has been studied extensively by J. B. Williams and will be reported in detail elsewhere. In brief, these small, ground-nesting passerines reside there year-round and commence breeding in early April. Males defend territories (ca. 0.1 ha) and aid in provisioning the young, but only females incubate eggs. Of 83 nests found in 1978 and 1979, 78% contained 3 eggs, 18% held 4 eggs, and only about 4% held 2 eggs. Mean clutch size for these 83 nests was 3.16 ± 0.46 SD. In this study we removed a nestling from broods of 3 to make broods of 2 young several days prior to DLW measurement.

Field and laboratory methods.—We first determined the impact that capturing and handling females had on their subsequent behavior and the time required after disturbance for females to resume normal parental activities. To this end, we gave the birds sham injections of distilled H_2O and restrained them in a cloth bag for 1 h. We then released the female bird and watched from a blind for her return. In most cases, females handled 3–4 h before sunset resumed caring for young within 2–3 h after their release; however, about 20% of the females that we netted abandoned their young. All birds for which we present data in this study resumed feeding their young within 3 h after their release. Each female was color-banded to facilitate recognition.

We captured birds by placing mist nets around their