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MIXED FLOCKS, ACCIPITERS,
AND ANTIPREDATOR BEHAVIOR

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Predation has been frequently suggested as a major selective force leading to flocking by forest birds (reviewed by Moriarty 1976, Morse 1977), but encounters between flocks and their predators have rarely been witnessed. I report here my observations of encounters between mixed flocks and Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperi*).

The study area was located within San Felasco Hammock State Preserve near Gainesville, Alachua Co., Florida. The area contained primarily open woods of long-leaf pine (*Pinus palustris*) and turkey oak (*Quercus taeda*) surrounded by areas of second growth and mature woods containing such species as laurel oak (*Q. hemisphaerica*), pignut hickory (*Carya glabra*), and southern red oak (*Q. falcata*).

Between October 1977 and April 1978 I spent approximately 550 hours in the study area, of which 350 h were spent following and tape-recording mixed flocks. I recorded vocalizations on a Nagra IIN open reel tape recorder with a Dan Gibson P200 parabolic reflector microphone, and on a Superscope C105 cassette recorder with a Realistic electret condenser microphone. I analyzed the tapes on a Kay Electric Co. 7029A Sona-Graph.

Carolina Chickadees (*Parus carolinensis*) and/or Tufted Titmice (*P. bicolor*) in groups of two to seven each were "nuclear" (as opposed to "attendant") in that other species tended to join and follow them (terminology from Moynihan 1962). The most regular attendant species were the Black-and-white Warbler (*Mniotilta varia*), Yellow-throated Warbler (*Dendroica dominica*), and Brown Creeper (*Certhia familiaris*), all of which occurred at a density of one individual per flock and were seen only rarely away from the flocks. The Solitary Vireo (*Vireo solitarius*), Downy Woodpecker (*Picoides pubescens*), Red-bellied Woodpecker (*Melanerpes carolinus*), Pine Warbler (*Dendroica pi-*

nus), and Orange-crowned Warbler (*Vermivora celata*) were also regular attendant species, but they occurred at densities of one to three individuals per flock and were frequently seen away from the flocks. The Yellow-rumped Warbler (*Dendroica coronata*), American Goldfinch (*Carduelis tristis*), and Ruby-crowned Kinglet (*Regulus calendula*) occurred irregularly with the flocks in groups of four to more than 30 per flock.

On 55 occasions, a mixed flock gave an alarm response. On 21 of these occasions, the response was associated with the sudden appearance of an accipiter or other large bird with similar shape: eight times it was a Sharp-shinned Hawk, once a Cooper's Hawk, five times a Red-shouldered Hawk (*Buteo lineatus*), and once a Turkey Vulture (*Cathartes aura*). Five other responses were probably caused by attacks (from unknown predators) judging from the scattering of Yellow-rumped Warblers with sharp chipping calls as in other attacks. Three were responses to Sharp-shinned Hawks near roost sites (see below). I saw no likely cause for alarm in the remaining 26 responses. I observed no responses in 40 field hours in October, nor in 110 h in April. I estimate an overall average of one response per five hours observation time for the five months from November to March.

The response to the appearance of a predator began with a high frequency (9-11 kHz), whistle-like call given by a chickadee or titmouse and then chorused by others of these species. (These calls have been described in detail in Gaddis 1979.) All birds in the flock immediately became immobile or dove for cover if it was available. When the hawk actually attacked and flew into the midst of the flock, warblers scattered with outbursts of sharp chip-like calls. The hawk typically made a short chase of one of the fleeing birds but was never successful. It then perched amidst the flock and flew off in less than 10 s. The chorus of whistle-like calls continued for up to a minute after the hawk had left. The calls then gradually faded away.

The chickadees and titmice remained immobile for an average of 4.8 min (S.D. = 3.2, range = 1-15, N = 49) from the first high whistle call. Other species remained immobile for varying periods; the warblers and woodpeckers were usually the first to wander off. Before resuming activity, the chickadees and titmice be-

gan giving close-range contact calls ("tseet" notes) which increased in rate until one or more birds resumed activity and gave a "chick-ka-dee-dee" (by a chickadee) or "seejert" call (by a titmouse). These calls are probably homologous (Gaddis 1979). They were answered by several other parids as the flock moved away.

No significant correlation was found between the length of the suspended activity period and habitat density, flock size, time of day, cloud cover, or number of species in the flock (Spearman Rank Correlation tests, $P > .05$). Nor was a significant difference found in suspended activity period length following attacks vs. overflights (Mann-Whitney U-test, $P > .05$).

Morse (1973) observed 17 encounters between British parid flocks and Sparrowhawks (*Accipiter nisus*). The overall pattern of the flocks' responses was similar: a high whistle alarm call followed by a period of suspended activity lasting from one to more than five minutes. In a sample of 10 timed responses, he reported that "flocks usually returned to foraging . . . more rapidly after attacks" than after overflights. He found no significant correlations between suspended activity period and flock size, time of day, temperature, or cloud cover.

The flocks were very irregular in their movements in terms of both movement rate and direction while foraging; they followed no predictable routes. They frequently abandoned a feeding area only to return to it less than an hour later.

The location of the chickadees and titmice could be predicted only upon morning emergence from their roost holes. This emergence time varied with temperature and time of year. During the study, emergence occurred between one-half and one hour after sunrise.

On three occasions I saw a Sharp-shinned Hawk making short flights through the roost area at emergence time. Although still in their holes, the titmice and chickadees gave high whistle calls on all three occasions. In all other instances when accipiters were present, the hawks were either circling high above the forest or flying, nearly parallel to the ground, at high speed into the midst of the flock. Their unusual behavior in the roost area at emergence time gave the impression that they were looking for parids.

Irregularity in the movement patterns of mixed flocks has been reported by Odum (1941), Hinde (1952), Marler (1957), Moynihan (1962), Wallace (1970), and Austin and Smith (1972). Only Stanford (1947) and McClure (1967) have reported persistent routes in the movements of mixed flocks. The appearance of the Sharp-shinned Hawks in the roost area at emergence time on three occasions suggests that they were capable of learning regularities in the movement patterns of their prey. The flocks' irregular movements could therefore be interpreted as antipredator behavior. Humphries and Driver (1970) have termed this behavior "protean insurance" in that the irregularity probably helps to insure against predation.

In flocks with 10 or more species, only chickadees and titmice gave the high whistle alarm call, although all of the attendant species heeded its message (cf. Brewer 1961, Morse 1970). The exploitation of this element of the parids' communication system may be an incentive to other species to join their flocks. Moynihan (1962) and Winterbottom (1943) pointed out that

a prerequisite for the mixed species flock appears to be an intraspecifically social species that has developed certain adaptations to sociality which attract other species that have not necessarily developed these adaptations themselves. This intraspecifically social species becomes the nuclear species for a mixed species flock. Moynihan discussed plumage characteristics, reduced hostility, and "contact" call systems, but the critical component in the nuclear species' attractiveness may ultimately be its alarm calls and, in general, its complex of antipredator adaptations.

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