MOBBING BEHAVIOR OF A PAIR OF ELEGANT TROGONS¹

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Mobbing behavior among birds is considered a mechanism of predator deterrence; however, the benefits of mobbing to small or passively mobbing species is not clear (Cully and Ligon 1976, Curio 1978). Most species mob by giving loud calls combined with wing and tail flitting that, together, appear to attract additional birds of many species. I report here my observations on the mobbing behavior of a pair of Elegant Trogons (Trogon elegans) to a Great Horned Owl (Bubo virginianus). Although the trogons maintained a substantial distance between themselves and the owl, their calls quickly attracted other species, some of which mobbed very aggressively. By attracting more aggressive species to mob, small birds may be able to have predators driven away from their territories and derive the same benefits as the more aggressive species (the "move on" hypothesis of Curio [1978]).

On 4 July 1970 at the South Fork Campground in the Chiricahua Mountains, Chiricahua County, Arizona, I tethered a live Great Horned Owl 60 cm above the ground at the base of a small tree. It was immediately mobbed by a pair of Elegant Trogons. (I later discovered that the tree contained their nest.) I observed these birds for approximately 30 min before I terminated the session by moving the owl away from the area. After the owl was removed the trogons freely entered their nest. I watched the birds from behind some shrubs at a distance of about 10 m. Calls were recorded on a Uher 4000 Report-L tape recorder at 3.5 IPS using a Uher M514 microphone. The calls were analyzed on a Kay Electric Company Sonaraph 6061B. I did not attempt to count calls or flits, and I did not attempt to measure the duration of the response.

Within 1 min after I exposed the tethered owl, a male trogon began to mob from a distance of about 15 m. He was perched on a branch approximately 5 m high in full view of the owl and me. Within 2 min after the male trogon began mobbing he was joined by his mate. Although their calls were loud and attracted various other birds, no other trogons joined the mob.

The male trogon flew to a branch in view of the owl about 15 m away. He called and occasionally flitted his wings and tail. There was very little jumping or flying between perches. When the female arrived she took a perch with more cover about 6 m from the owl, and also began to call. Both trogons changed their perches during the mobbing session, but they never approached the owl closer than 6 m.

Elegant Trogons used a wing-tail flit while mobbing. The trogons first rapidly flicked the wings (duration about 0.1 sec), and then slowly raised and lowered the tail (duration approximately 1.0 sec). There was no bowing of the body associated with the flit.

Trogon mobbing calls consisted of a rapid series of loud staccato chucks given in phrases of 4 to 10 notes (Fig. 1). The male's calls sounded higher pitched than the female's,

The frequency range and amplitude characteristics of the calls of many species of mobbing birds are well suited to facilitate locating the calling birds, which makes it easy for more birds to join the mob (Marler 1955, Marler and Hamilton 1967, Martin and Marler 1977). The calls of Elegant Trogons are similar. High frequencies attenuate quickly, making a wide frequency range useful for determining the distance to the source (Martin and Marler 1977). The calls were repetitive and began and ended abruptly—characters that enhanced direction finding.

Trogon mobbing was passive compared to that of many other species. Gray-breasted Jays (Aphelocoma ultramarina), which joined the mob within 1 min after the male trogon began calling, jumped and flew constantly, often diving within 5 cm of the owl's head. Passerine mobbing is characterized by loud calls, numerous jumps and flights from perch to perch, and frequent tail flits (Hinde 1954; Cully and Ligon 1976, in press). In passerines, the tail flit

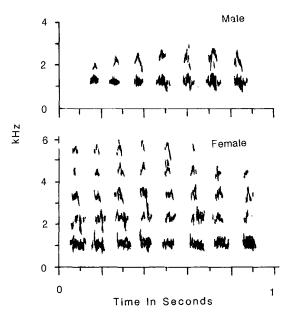


FIGURE 1. Sonograms of male and female Elegant Trogon mobbing calls.

but otherwise they were similar. Harmonics ranged in frequency from 1.0 to 2.5 kHz in the male and from 0.5 to 6.0 kHz in the female. The dominant harmonic of the male was centered at 1.5 kHz, that of the female at 0.8 kHz. Since high-frequency harmonics attenuate faster in woodlands than low frequencies (Martin and Marler 1977), the shorter frequency range recorded for the male may have resulted from my recording his calls at a greater distance. Mobbing call phrases ranged from approximately 0.5 to 1.2 sec in duration. The individual notes were regularly spaced at 0.1 to 0.12 sec intervals. Each note of the phrase was of similar duration (0.08 sec) and frequency range. The energy of the calls was given in a rapid burst.

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used in mobbing probably arose as a flight intention movement (Daanje 1950, Hinde 1954). A component of the evidence for its origin as a flight intention movement is the change in posture that accompanies the wing and tail movements; the movement is similar to the postural change that often precedes flight. This component of the flit (the change in posture) is missing from trogon mobbing tail flits. This suggests that in mobbing the important factor is movement, which enhances visibility to other birds and perhaps confusion of the predator (but see Curio 1978).

Trogon mobbing may illustrate the value of mobbing among small birds or other passively mobbing species. Although these species are not likely to drive large predators from their territories, their calls often attract other, more aggressive birds such as jays. Often when I placed a captive owl on a perch to observe the responses of other birds, the first species to mob were smaller species such as Plain Titmice (Parus inornatus) or Black-throated Sparrows (Amphispiza bilineata). When jays arrived they mobbed aggressively; on several occasions they startled the tethered owl sufficiently to cause her to fall off her perch. This suggests that mobbing may benefit the smaller species by attracting larger birds who can force owls, particulary small species, to flee.

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SPITEFULNESS, ALTRUISM, AND THE COST OF AGGRESSION: EVIDENCE AGAINST SUPERTERRITORIALITY IN TREE SWALLOWS¹

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Key words: Superterritory; aggression; hole-nesting; Tree Swallow.

Superterritoriality is a spiteful behavior in which an individual's relative fitness is improved by reducing the fitness of others through inhibiting them from breeding, rather than through an absolute increase in fitness (Verner 1977). Tree Swallows (Tachycineta bicolor) are obligatory hole-nesters, and a single pair can defend additional sites not essential for successful reproduction (Harris 1979, Muldal et al., 1985), thereby preventing conspecifics from using those nest sites. Harris (1979) suggested that the main function of surplus nest site defense in Tree Swallows is to depress the reproductive success of potential breeders. However, Robertson and Gibbs (1982) found that Tree Swallows do not orient their aggressive nest defense in relation to the location of surplus nest sites and concluded that Tree Swallows defend a circular radius around their nest site, which may encompass additional nest sites. A commentary by Harris (1985) indicates that the issue of superterritoriality in Tree Swallows is still unresolved. Here, we argue that the conditions under which superterritorial behavior would evolve do not occur in Tree Swallows.

For such spitefulness to evolve, the benefits to the superterritorial individual must exceed the costs. The exclusion of a potential breeder by an inhibitory individual results in an equal increase in relative fitness amongst all breeders, whether or not they inhibit others. In contrast, the costs of the extra aggression required to defend additional resources may be relatively great and are borne only by the inhibiting individual(s). It is therefore unlikely that the benefits of superterritoriality to the individual will exceed the costs. Colgan (1979:605) succinctly summarized this argument with his comment that "Colloquially, spitefulness has become altruism." Since the potential benefits of superterritoriality to the individual are low, the evolution of inhibitory behavior in Tree Swallows would require a very low cost to the aggression required to defend extra nest sites. We provide evidence against a low cost of aggression. This evidence includes injuries caused by aggressive encounters, and a seasonal decline in aggressive defense by residents, which suggests a trade-off between time and energy expended on intraspecific nest defense and other activities such as parental care.

Our study is based on two populations of Tree Swallows at the Queen's University Biological Station, Chaffey's Lock, 50 km north of Kingston, Ontario, Canada. The New Land (NL) population consists of about 60 pairs that breed in nest boxes which are distributed over several hayfields. The Northeast Sanctuary (NES) population has about 35 breeding pairs, with both artificial and natural nest sites over shallow water. During 1985 in the NL, we caught 9 birds with injuries that generally consisted of large bare areas on the back of the head and neck, and some-

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