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 atttracting 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 SWALLOWS[1]

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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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TABLE 1. Frequency of mild and strong responses by resident males and females to conspecific intruders throughout the breeding season. Mild responses include no response, circling the box, and brief chattering. Strong responses involve hole-guarding, hovering, loud chattering, chasing, and fighting.

Nest stage	Male response		Female response	
	Mild	Strong	Mild	Strong
Nest building/egg laying	251	132	182	141
Incubation	72	62	23	31
Nestling	64	18	37	16

times around the eye, where the feathers had been stripped off, exposing bruised skin. In one of these cases the injured bird was caught fighting inside a box with another bird. In the past two years, we have found three cases of a dead Tree Swallow with similar injuries inside a nest box. One instance of a female drowning while fighting has also been observed (Tozer, pers. comm.). In early May, fights involving a resident bird and an intruder near nest boxes are common. On three occasions after observing individuals fighting in the grass, we were able to capture the defeated bird by hand as it was unable to fly. Leffelaar and Robertson (1985) have described two cases of females seriously injured during fights. Although this evidence is anecdotal, it does indicate that Tree Swallows are capable of inflicting serious injury during aggressive interactions.

In 1984, we observed about 20 resident pairs in the NL and NES during 195 half-hour watches to record seasonal changes in resident aggression to intruders. An intrusion occurred when a nonresident Tree Swallow came within 15 m of the nest site. Intrusions which occurred while the resident was out of sight or inside the nest box were not included. For both male and female residents, the intensity of aggressive response declined in the nestling period (Table 1; Males: $\chi^2 = 13.56$, df = 2, $P < 0.01$; Females: $\chi^2 = 8.06$, df = 2, $P < 0.05$). This suggests that there could be a trade-off between aggressive defense and parental care, and therefore an energetic cost to aggressive behavior. An alternate explanation for the decline in aggression may be that there is a decrease in the benefits to be gained by inhibitory behavior because there are no longer potentially breeding individuals to be excluded late in the season. However, the intruder activity during the nestling period, and the presence of a floater population whose members can initiate nesting attempts late in the season (Stutchbury and Robertson 1985) indicate that this is not the case.

A low cost of aggression is a critical assumption of the superterritorial hypothesis (Harris 1979). However, aggressive nest defense in Tree Swallows is costly, and therefore a superterritorial function for surplus nest site defense is unlikely. The defense of surplus nest sites may directly increase the reproductive success of resident individuals by reducing the likelihood of usurpation (Robertson and Gibbs 1982), providing a second nest site if the first nesting attempt fails, or affording the male an opportunity for bigamy (Quinney 1983).

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