

## Interspecific Competition and Social Behavior in Violet-green Swallows

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Resource competition can lead to aggressive or territorial behavior among conspecifics or heterospecifics (Orians and Willson 1964). The demographic consequences of these interactions may also influence other life-history traits (Thornhill 1987). Competition for nest sites among cavity-nesting birds is a potent selective force that often prevents sexually mature individuals from breeding (Morse 1980). In populations of cavity nesters that breed in north-central Arizona (see Brawn and Balda 1988), I observed interspecific interactions between Violet-green Swallows (*Tachycineta thalassina*) and Western Bluebirds (*Sialia mexicana*), whose abundances are limited by nest-site availability. Here I describe these encounters and discuss the possible influence of interspecific resource competition on social behavior in Violet-green Swallows.

In 1980, I installed 60 nest boxes on each of two 8.5-ha areas in ponderosa pine (*Pinus ponderosa*) forest habitat where natural cavities were scarce (Brawn and Balda 1988). These areas are located south of Flagstaff, Arizona, in the U.S. Forest Service Coconino National Forest, Coconino County. Swallows and bluebirds within each area used nest boxes almost exclusively throughout the study (1981–1984, see Brawn 1988). Neither species is a permanent resident, but bluebirds arrive and begin to nest about a month before swallows.

I observed interspecific interactions along transects (5 per area) that permitted close observation of all boxes during each visit to an area. These observations were made during the morning (0530–1100) or late afternoon (1500–1830) from early April through mid-June. Upon detecting an interspecific encounter, I observed a disputed nest box until only one species was present for longer than 15 min. Beginning in early May, I periodically inspected all nest boxes to determine nesting activity. Boxes with nests were inspected twice weekly throughout the nesting cycle.

I observed 74 interactions between swallows and bluebirds at 33 different nest boxes. Bluebirds had begun nesting in all the disputed boxes and therefore always had priority. Fifty-nine of the encounters (80%) involved a single adult male bluebird and four or more swallows; the remainder were between a male bluebird and one swallow. Others have observed

swallow aggression toward female Western Bluebirds as well (e.g. Prescott 1982). Encounters commonly involved one or more swallows flying towards, but not striking, a bluebird perched on or near a box. Bluebirds remained perched, made frequent "rushing" flights at oncoming swallows, or left the vicinity. In 9 instances, as swallows "harassed" a bluebird, other swallows entered disputed boxes and deposited nest material (pine needles) or removed bluebird nest material (grass). I never observed swallow aggression toward bluebirds away from nest boxes.

Swallows were not marked individually, but I estimated groups to range from 4 to 12 individuals. These groups always included two or more brightly colored males and two or more dull colored individuals (probably females, but the phenology of swallow plumage characteristics is not reliably known [Pyle et al. 1987]). Solitary swallows were all brightly colored males.

Solitary swallows never displaced bluebirds ( $n = 15$ ), but groups drove bluebirds away from a box in 61% of the observed interactions ( $n = 59$ ). The proportion of group interactions that displaced bluebirds was significantly greater than that for bluebird vs. solitary swallow encounters (Chi-square test for proportions,  $\chi^2 = 24.2$ ,  $df = 1$ ,  $P < 0.001$ ). Of the 33 disputed nest boxes, 11 (33%) were used by swallows, bluebirds remained and nested in 18 (55%), and 4 (12%) were not subsequently used by either species. One member of six displaced bluebird pairs was color-banded, and two of these pairs nested in other boxes.

The rate of interspecific interactions per hour of field observation increased from 1981 through 1984. This trend was concomitant with annual increases in numbers of boxes occupied by bluebirds when swallows arrived at the study areas (Spearman rank test,  $\rho = 0.64$ ,  $df = 6$ ,  $P < 0.10$ , sample size based on number of breeding seasons per area when both species were present). At least 40% of the boxes on each area were unused each year, but these were probably unsuitable for swallows because they were either too low or in dense vegetation (see Brawn 1985). A relationship between variation in availability of contestable resources and frequency of interspecific interactions has been reported in other cavity nesters (Minot and Perrins 1986), among nectarivorous birds (Stiles and Wolf 1970), and among scorpionflies (Thornhill 1987).

Within a breeding season, swallow aggression was commonly directed at bluebird pairs in the early or preincubation stages of the breeding cycle. On average, 30% of the bluebird nests were more advanced when swallows began to select nest sites. I never ob-

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served attempts to usurp these boxes (but see Prescott 1982). Field experiments with other species have also demonstrated a positive association between phenological overlap in breeding activity and frequency of interspecific interactions at nest sites (Slagsvold 1978, Gowaty 1981). Gwinner et al. (1987) suggested a proximate explanation; simple physical association of a male cavity nester with a nest site can increase testes size and plasma levels of luteinizing hormone which, in birds, is associated with aggressive or territorial behavior. The magnitude of this effect increases as an individual is associated with a nest site. Thus, swallow aggression towards bluebirds may be more successful against relatively late breeders that offer lower resistance.

I suggest that social behavior in Violet-green Swallows enhances access to a vital resource. Interspecific dominance is often determined by body size (Murray 1981) and the average mass of male Violet-green Swallows ( $\bar{x} = 14$  g) is approximately half that of male Western Bluebirds ( $\bar{x} = 29$ ; Dunning 1984). Forming groups to overcome resource defense by larger-sized heterospecifics has been observed among other bird species that compete for access to food (Murray 1981) and among coral-reef fish (Robertson et al. 1976). Approximately 25% of all swallow nests ( $n = 47$ ) were in boxes previously occupied by bluebirds. Thus, social aggression towards heterospecifics is not mandatory to obtain a nest site. Nonetheless, interspecific competition (exploitative and interference) appears particularly strong for swallows in north-central Arizona because they arrive at breeding habitat and commence reproduction after all other sympatric species of cavity nesters ( $n = 5$ ; see Brawn and Balda 1988).

I frequently observed 2 or more individuals enter active swallow nests, but I could not ascertain whether or not all birds actually assisted the nest attempt. The question of whether the swallow groups that engaged in aggressive interactions were temporary aggregations or persistent social units is unanswered. If Violet-green Swallows are true cooperative breeders, my observations may indicate a rare example of interspecific resource competition that affected the evolution of a resource-based social system (see Thornhill 1987). Alternatively, Tree Swallows (*T. bicolor*) at active nests include a breeding pair and unrelated nest attendants that do not assist in reproduction, but seek to usurp nests from conspecifics (Lombardo 1986). Thus, social behavior in Violet-green Swallows could be functionally cooperative in the context of interspecific competition but, if successful, can lead to competitive interactions among conspecifics. Data on the identity, relatedness, and role of individuals at nests compared with those that participate in encounters with bluebirds would discriminate between these possibilities. Furthermore, manipulating the availability of usable nest sites and local abundances of interspecific competitors (*sensu*

Slagsvold 1978) would allow experimental evaluation of the relative importance of intra- vs. interspecific resource competition in avian social behavior.

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## Hurricane Damage to Red-cockaded Woodpecker (*Picoides borealis*) Cavity Trees

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The Red-cockaded Woodpecker (*Picoides borealis*) is a federally endangered species, which inhabits pine forests in the southeastern United States (Ligon 1970). Red-cockaded Woodpeckers excavate cavities for roosting and nesting in mature, living pine trees (Baker 1971), preferably longleaf pine (*Pinus palustris*) infected by redheart disease (*Fomes pini*) (Lennartz et al. 1983). Excavation of a single cavity may require a year or more, and it has been suggested that cavity trees are the primary ecological constraint that shaped the evolution of the cooperative breeding system of the Red-cockaded Woodpecker (Lennartz et al. 1987, Walters et al. 1988).

Natural disturbance is an important component of the southeastern pine forests inhabited by the Red-cockaded Woodpecker (Christensen 1977). Frequent surface fires maintain the open habitat favored by Red-cockaded Woodpeckers (Ligon et al. 1986). High winds and lightning associated with frequent summer thunderstorms and, less frequently, tornadoes and hurricanes are important sources of mortality among larger pines (Platt et al. 1988). In late summer and autumn 1985, three major storms struck the northeastern Gulf of Mexico: tropical storm Juan, and hurricanes Elena and Kate. The combination of heavy rain that saturated the soil and strong winds damaged some forests in northern Florida and southern Georgia. Trees were blown over and tree trunks snapped. During hurricane Kate, downbursts of wind gusting to 160 km per hour were estimated for Leon County, Florida (Clark 1986). We report the damage caused by these storms (mostly hurricane Kate) to Red-cockaded Woodpecker cavity trees in an old-growth longleaf pine forest in southern Georgia.

The Wade Tract, an 80-ha conservation easement managed by Tall Timbers Research Station in south-

ern Thomas County, Georgia, contains one of the largest remaining old-growth longleaf pine populations. As part of a long-term study of life history dynamics (Platt et al. 1988), all pines taller than breast height (1.5 m) on a 46-ha section of the Wade Tract were given identification numbers on metal tags in 1979. The diameter at breast height (DBH) of all tagged trees was recorded in 1979, and the surviving tagged trees were remeasured in 1984. Tagged trees were censused annually for mortality through 1987.

Red-cockaded Woodpeckers are common in the Wade Tract (Engstrom 1982). Some Red-cockaded Woodpecker nest trees were identified in 1979, but no systematic inventory of cavity trees was done before the storms in autumn 1985. In the spring of 1986, Engstrom visually inspected trees in the Wade Tract during a study of hurricane damage to the entire forest. All Red-cockaded Woodpecker cavity trees in the 46-ha study site were located at this time. Among nearly 7,800 marked and measured trees that were standing before the storms in the autumn of 1985, 33 were Red-cockaded Woodpecker cavity trees. These cavity trees ranged in size from 30 to 69.2 cm DBH ( $\bar{x}$  = 49.0 cm; Fig. 1).

Of 33 Red-cockaded Woodpecker cavity trees, 8 (24%) were killed during autumn 1985 (4 during hurricane Kate). Trunks of six of the eight trees snapped off at the site of the woodpecker cavity; trunks of the remaining two trees snapped below the cavity. Five of the eight Red-cockaded Woodpecker cavity trees that were snapped off had rotten heartwood most likely caused by redheart disease. The remaining three trees did not have obviously rotten heartwood at the point of the snapped trunk. Four additional cavity trees suffered a loss of large limbs or a gash in the trunk that may increase the chance of mortality over the next decade.

On the Wade Tract, age (measured with increment cores) and size (DBH) of 399 randomly selected longleaf pine trees are highly correlated (Platt et al. 1988). Trees of approximately 30 cm DBH in this random sample ranged from just under 40 to over 80 years old, and trees with diameters of approximately 60 cm DBH ranged from roughly 180 to 240 years old. Al-

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