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ATTENDANTS AT TREE SWALLOW NESTS. I. ARE ATTENDANTS HELPERS AT THE NEST?[1]

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Abstract. Adult and juvenile nest attendants of both sexes were common visitors at active Tree Swallow (*Tachycineta bicolor*) nests during the nestling period. Attendants were never known to be close genetic relatives of the parents at the nests they visited. Attendants never passed food to nestlings in 300 recorded interactions with nestlings. Attendants attempted to steal food from both parents and nestlings, but had no demonstrable effect on parental reproductive success. Attendants only passively mobbed potential predators. These results indicate that attendants were not helpers at the nest.

Key words: *Tree Swallow;* Tachycineta bicolor; *nest attendance; attendants; video observation.*

INTRODUCTION

Extra individuals have commonly been observed at active Tree Swallow (*Tachycineta bicolor*) nests during the breeding season. These attendants have sometimes been described as feeding the young at the nests they visit (Forbush 1929, Wetherbee 1933). Verner and Willson (1969) interpreted one account (Wetherbee 1933) as a case of polygyny. However, Sheppard (1977) rejected the polygyny hypothesis in favor of the "helpers-at-the-nest" alternative. Cash (1933), Hersey (1933), and Low (1933) all reported observing extra birds visiting nest boxes, but these visitors did not always feed young although young always begged from them. Burtt (pers. comm.) did not observe attendants feeding nestlings when he watched the interior of a nest box from an attached blind. However, if attendants commonly feed unrelated young, then attendants would appear to be altruistic.

Natural selection is the result of competition among individuals to have their genes represented in future generations. When individuals enhance the reproductive success of nonrelatives at the expense of their own reproductive success, they appear to violate the basic tenets of evolutionary theory (Darwin 1859, Hamilton 1964, Williams 1966, Alexander 1974, Power 1981). The seemingly altruistic acts of Tree Swallow attendants feeding the young of others pose a serious problem to the formulation of a general theory of social behavior that conforms to the Darwinian paradigm (Alexander 1975, 1979; Power 1981).

Reports of helping behavior in Tree Swallows are especially interesting, because Tree Swallows display few of the ecological and demographic characteristics (e.g., long life, low fecundity, subtropical or tropical distribution, and stable year-round territories) of typical cooperatively breeding species (see Brown 1978; Emlen 1978, 1982). In fact, Tree Swallows and typical cooperatively breeding species share only the characteristics of limited nest sites (Hersey 1933; Kuerzi 1941; Bent 1942; Erskine 1964, 1979; Holroyd 1975; Zeleny 1976; Boone 1982; Prescott 1982) and insectivory (Brown 1978).

This paper presents the results from a series of observations and experiments designed to determine (1) the identity (i.e., sex, age, and genetic relatedness to breeders) of attendants and (2) whether attendants are helpers at the nest (see Brown 1978 for criteria). A companion paper (Lombardo, unpubl.) reconciles the result that attendants have no apparent effect on parental reproductive success with an examination of the chronology of attendant visitation to provide an evolutionary explanation for this phenomenon.

METHODS

SITE DESCRIPTION

In 1980 I established a nest box trail of 22 boxes on the salt marshes of the John F. Kennedy Memorial Wildlife Refuge (JFKMWR) adjacent to Tobay Beach on the south shore of Long Island, New York (73°27′W, 40°37′N). The JFKMWR has a history of supporting Tree Swallow populations in nest boxes since the 1930s (D. Imhof, pers. comm.). The JFKMWR covers approximately 160 ha and contains coastal scrub vegetation, sand dunes, a large brackish pond, and an expansive *Spartina* salt marsh (see Schaeffer 1972 for a more complete description).

Boxes were added to the trail in 1981 (n = 18), 1982 (n = 30), and 1983 (n = 2) yielding a total of 72 boxes. Boxes were divided into two sub-colonies (A = 14 boxes, B = 58 boxes) separated by approximately 1,200 m. Each top-opening box was attached to a metal post driv-

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en into the mud of the salt marsh. Nest box holes were either 3.8 cm (n = 40) or 3.2 cm (n = 32) in diameter and were 1.5 m above the ground and faced south southeast.

MARKING

Every bird captured in nest boxes was banded with a U.S. Fish & Wildlife Service aluminum band. Breeding females were captured on the nest between 0500 and 0600 (Kuerzi 1941, DeSteven 1980, Burtt and Tuttle 1983) on the first day of incubation. Breeding males were banded one to two days after eggs hatched. Attendants were captured while visiting boxes during the nestling period. Males and attendants were captured at nest boxes using a radio-controlled trapping device (Lombardo and Kemly 1983). Birds were sexed by noting the presence of a well-developed brood patch in females or a cloacal protuberance in males. Nestlings were banded on Nestling Day 12 (ND12), where hatching equals ND1.

All captured birds were uniquely color-marked on their tails, wings, foreheads, throats, and breast feathers using a marking pen or Testors Airplane Dope (Samuel 1976). In 1983 the nestlings in six broods (n = 24) had their breast feathers painted before they fledged.

BASIC OBSERVATION TECHNIQUES

I define attendants as any additional birds (i.e., exclusive of the breeding pair) that visit nest boxes during the nestling period. In a previous publication (Lombardo 1985), I referred to attendants as nonbreeders. However, because some attendants had previously bred (see below), nonbreeder is an ambiguous and inaccurate term and has been abandoned.

During 137 hr of observations during the incubation period in 1980 and 1981, I observed little activity at boxes by birds other than the breeding pair. Therefore, there was little opportunity for attendants to help before eggs hatched, and observations were concentrated in the nestling period.

During 1980 to 1983, 39 randomly chosen breeding pairs were observed for 60 min at least every third day from the hatching of their eggs to the fledging of their young. Another 28 pairs that fledged young were observed less frequently. The order in which pairs were observed each day was determined by rolling a die. On average, four to six pairs were observed each day, mostly between 0600 and 1400. A total of 488 box-hr of observations were recorded during the nestling period ($\bar{x}$ = 12.5 hr/box; range, 1 to 19 hr/box). During observations I recorded the identity and activity of birds around the focal box. I observed boxes using both an 8 × 40 mm pair of binoculars and a 25× spotting telescope.

VIDEO OBSERVATION TECHNIQUES

To determine if attendants feed nestlings, I followed a design of H. W. Power (pers. comm.) and used a portable video system (Panasonic Portable Video Tape Recorder NV-3085; Panasonic Video Camera WV-3085; TV Zoom Lens 12.5–75mm, f/1:1.8, Sony Black and White Video Monitor CVM-960; Sony Video Tape V-30H; 35 m of coaxial video cable) to observe the interiors of nest boxes. The video tape recorder and camera were powered by two Panasonic Panalloid TY-361R, 6 volt 3 ampere/hr batteries. The camera was equipped with a microphone and the recorder with an audio earplug.

I cut holes in the sides of 40 nest boxes in 1981. The holes were normally covered by a piece of plywood. Two days before expected hatching, I replaced the piece of plywood with a piece of Plexiglas. A camera shroud of dark brown translucent plastic supported by a wooden frame was attached to boxes targeted for interior observations.

When parents or attendants approached the nest box hole, I noted behavior on the exterior of the box and then recorded behavior on the interior of the box when a bird entered. I later replayed the tape on the video monitor and transcribed the recorded behaviors. Observation periods lasted from 60 to 135 min of tape time. The interiors of 8 boxes were observed for 41 hr.

FRONTLET EXPERIMENT

To increase the number of observations of nonbreeder-nestling interactions, the nest box holes of 30 boxes (10 per year, 1981 to 1983) were made smaller with a tar paper "frontlet" tacked over the nest box hole. The frontlet kept nestlings from fledging and forced them to extend their heads out of the hole to be fed. Frontlets were placed on boxes on ND19 (fledging ≈ ND20) and boxes were observed for 60 min on ND20 before the frontlet was removed to allow the normal sequence of fledging behavior.

THE EFFECT OF ATTENDANTS ON NESTLING WEIGHT GAIN

The weight gain curve of Tree Swallows is characterized by a period of rapid growth to a maximum weight and a decline to fledging weight (Paytner 1954, Ricklefs 1968, Zach 1982, Zach and Mayoh 1982). I compared attendant attendance during the weight gain period with the average daily weight gain (g/day) of nestlings. Nestlings were weighed through-

out the nestling period with a Pesola spring scale (0 to 30 g) accurate to 0.5 g. Only boxes with observations spread throughout the weight gain period were included in the analysis.

MOBBING STUDIES

In 1982 I confronted breeding pairs with a stuffed Burrowing Owl (*Speotyto cunicularia*). The model was placed on a metal milk crate 3 m in front of nest boxes during the nestling period. After the model was in place, I retreated to my observation post and recorded the responses and identity of respondents (i.e., breeder or attendant) for 5 min after the first bird to approach the model appeared. I recorded the number and identity of birds mobbing the model every 60 sec until the 5 min trial period was over. Thirteen trials were performed between 15 June and 8 July 1982. After 9 July 1982 I recorded the number and identity of the birds that mobbed me during census visits to nest boxes.

TREE SWALLOW COLOR MORPHS

Tree Swallows are the only North American passerines in which females do not obtain full adult breeding plumage (iridescent blue-green) until at least their second breeding season (Dwight 1900, Kuerzi 1941, Cohen 1980, Rohwer et al. 1980, Hussell 1983). Before this time, females are brown with varying degrees of dorsal iridescent feathering (Cohen 1980, Hussell 1983). Males develop full breeding plumage in their first year. The annual molt is completed before the fall migration south (Dwight 1900).

Both sexes can breed in their first year (this study). Thus, there are two female plumage morphs in the breeding population: sub-adult and adult.

Throughout, "G-attendants" will refer to attendants in full iridescent green plumage. "SAF-attendants" will refer to female attendants in sub-adult plumage (Dwight 1900, Cohen 1980, Hussell 1983). "HY-attendants" were dusky gray-brown with no iridescent feathers (i.e., hatching year birds) and had a faint chest band. On the wing, HY-attendants appeared smaller and less robust than SAF-attendants. I was not able to sex HY-attendants by gross inspection. The term "attendants" will refer to the sum of G + BF + HY attendants.

STATISTICAL PROCEDURES

Before statistical analyses were performed, the data were tested for normality and homoscedasticity (Zar 1974) to determine the appropriate method of analysis (i.e., parametric or nonparametric analysis). Statistical tests were run using the Statistical Analysis Systems (SAS) statistical package (SAS 1982). Descriptions of the statistical tests used can be found in Hollander and Wolfe (1973) and Zar (1974). Unless otherwise noted, means and their standard errors are given as $\bar{x} \pm$ SE.

TABLE 1. Breeder, attendant, and nestling banding results.

	Returned as[2]			
	Male	Female	Attendant	Total banded
Banded as:[1]				
Male	17	—	0	70
Female	—	26	0	78
Nestling	3	7	1[3]	278
Attendant	1	0	1[4]	45

[1] Banded 1980 to 1982.
[2] Returns 1981 to 1983, including birds that returned to JFKMWR more than once after initial banding.
[3] Banded as a nestling in 1980, captured as a breeding male in 1981, and recaptured in an empty box in 1982. This bird did not breed at JFKMWR in 1982.
[4] Banded as a HY-nonbreeder in 1981 and recaptured as a male attendant in 1982.

RESULTS

OBSERVATION SUMMARY

Attendants were seen at every box that had young (n = 76). Attendants were observed 1,669 times (G-attendants 1,050 times, SAF-attendants 288 times, HY-attendants 331 times) from 1980 to 1983. Attendants were not seen every day at every box. Marked attendants (n = 45) were never seen again at the box where they were marked. Attendant presence varied daily over the whole study site. On some days attendants were not seen at the study site. On average, attendants significantly increased in number as the breeding season progressed. At the end of the breeding season, nearly all visitors were HY-attendants (Lombardo 1984).

BANDING AND MARKING

Table 1 summarizes banding, marking, and return data. None of the 45 birds captured as attendants were known close genetic relatives of the parents at the nests they attended. In fact, only two captured attendants were previously banded.

In 1,669 observations of attendants, only three sightings of banded attendants visiting nests were recorded. These sightings were at different boxes and none were observed revisiting the same box on subsequent days.

None of the birds banded as attendants returned to breed at JFKMWR (Table 1). However, one banded as a HY-nonbreeder in 1981 was found dead in a different box in April 1982 in sub-adult female plumage.

Of 278 birds banded as nestlings, 14 re-

turned to JFKMWR in subsequent years; none returned as attendants. However, marked fledglings were seen visiting other boxes days after they left their own.

None of the birds banded as breeders (males = 70; females = 78) returned as attendants in subsequent years. Only three of 1,669 observations of attendants were of birds that had successfully bred at other boxes (1 male and 2 adult females). Each bird visited another nest box several days after its own young had fledged. Another male visited several boxes over a period of several days more than 10 days after his breeding effort failed during incubation.

VIDEO OBSERVATIONS

In 41 hr of interior observations at 8 nest boxes, attendants were seen inside nest boxes 91 times. In only 20 instances did their behavior resemble feeding. All of these observations occurred in 1981 at 2 boxes (n = 26 box-hr of observation). In both 1982 and 1983 no attendants entered boxes during video observations. I observed 92 entries in 1980, 46 entries in 1981, 50 entries in 1982, and 14 entries by attendants in 1983 during normal exterior observations.

Before attendants entered a nest box they flew silently about the box before alighting at the hole. In most cases, the sound of the attendant landing on the hole caused the nestlings to begin loud begging with their heads straining upwards and their mouths wide open. The nestlings continued begging as the attendant entered. Once inside, the attendant stood on the rim of the nest cup and looked around the inside of the box, cocking its head one way then another. After several seconds of begging and not being fed, nestlings quieted down. Nestlings always begged from any bird that entered their box. Attendants often remained in boxes for several minutes before leaving.

In contrast, parents, especially males, emitted a "greeting" call as they approached their nests (Cohen 1984), entered quickly, delivered a single bolus of food to a single nestling and then exited. Parents may sometimes feed more than one nestling when nestlings are one to three days old (Burtt, pers. comm.). Approximately 3 times per hr, parents removed a fecal sac after feeding their nestlings. Attendants were never seen removing fecal sacs, although on one occasion a HY-attendant was observed ingesting one.

During those sequences that resembled feeding, attendants and nestlings matched bills at what appeared to be the nonbreeder's initiative, but no food was ever seen to pass to nestlings, and nestlings never seemed to swallow anything after these encounters. Frequently, nestlings continued begging even as the attendant withdrew its bill from the nestling's mouth. SAF-attendants were never observed exhibiting this "bill-matching" behavior. HY-attendants (n = 15) exhibited this behavior more often than G-attendants (n = 5).

On one occasion, two HY-attendants were in a box while the parents were feeding nestlings. After the parents exited, one attendant waited several seconds then tapped the bill of the last nestling fed. The nestling opened its mouth, and the attendant stuck its bill into the nestling's mouth. No food was seen being passed, and neither bird appeared to swallow anything when they separated. This behavioral sequence gave the impression that the attendant was attempting to take food from the nestling (L. Hodgkins, pers. comm.).

Attendants were never observed begging from parents while inside of nest boxes, although HY-attendants did beg from parents outside boxes. Parents ignored attendants inside their nest boxes, but sometimes parents chased attendants they encountered outside of their nest boxes (Lombardo 1984). This apparent lack of parental concern over attendants was quite unlike the violent responses by parent European Starlings (*Sturnus vulgaris*) to intruder starlings that they found inside of their nest boxes (E. Litovich, pers. comm.).

ATTEMPTS BY ATTENDANTS TO STEAL FOOD

Both HY-and G-attendants were seen intercepting parents on their flights back to their nests with their mouths filled with food. Attendants harassed the parents by flying directly at the parents' mouths in what appeared to be attempts to pirate food. During the instances (n = 20) when this behavior was seen, the parents always evaded the attendants and never lost food. However, parental deliveries of food were delayed due to this harassment.

HY-attendants did, on a few occasions, beg from parents while outside of nest boxes. Parents usually ignored attendants, but in one case a male parent passed a large moth to a begging HY-attendant perched on the nest box pole. At the time, the male's nestlings were 15 days old and incapable of leaving the box.

In 1982, I observed a SAF-attendant enter a box and beg for food from the parents. She was not fed. R. R. Cohen (pers. comm.) has reported similar behavior in HY-attendants at his study site in Colorado. Flux (1978) observed similar "scrounging" behavior in recently fledged starlings in New Zealand.

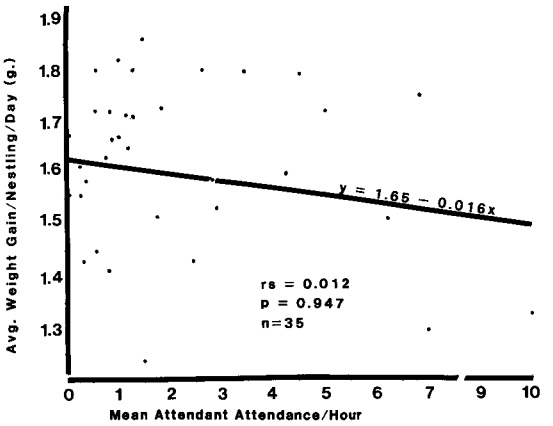

FIGURE 1. Average nestling weight gain/day vs. mean attendant attendance/hr. Only boxes with ≥5 hr of observations are included.

FRONTLET EXPERIMENT

During 30 hr of observations at 30 boxes, over 171 attendants were observed visiting boxes, but in only five instances did attendants appear to feed nestlings. At four boxes in 1982, attendants were constantly about the box preventing an exact count of their numbers. At the remaining 26 boxes, G-attendants represented 114/171 (66.67%), SAF-attendants 25/171 (14.62%), and HY-attendants 32/171 (18.71%) of all attendants observed.

Nestlings perched at the nest box hole for most of each observation period and begged vigorously from any bird that passed near the front of their box, including passing Barn Swallows (*Hirundo rustica*) and Sharp-tailed Sparrows (*Ammospiza caudacuta*). Parents passed food to nestlings while hovering in front of the nest box hole. Attendants usually ignored the begging nestlings even when the nestlings thrust their open mouths directly at them.

In the five instances of possible feedings, the attendants stuck their bills into the gaping mouths of begging nestlings. No food was seen being passed to the nestlings and nestlings did not react as though they had been fed because they kept on begging even as the attendants withdrew.

THE EFFECT OF ATTENDANTS ON NESTLING WEIGHT GAIN

There was no correlation between either total attendant attendance (Spearman $r_s = 0.012$, $n = 35$, $P = 0.947$; Fig. 1) or that of a particular attendant type with mean nestling weight gain during the period of maximum weight gain. This result was unaffected by breeding female plumage morph (sub-adult; $r_s = 0.502$, $n = 14$, $P = 0.068$; adult: $r_s = -0.229$, $n = 21$, $P = 0.318$).

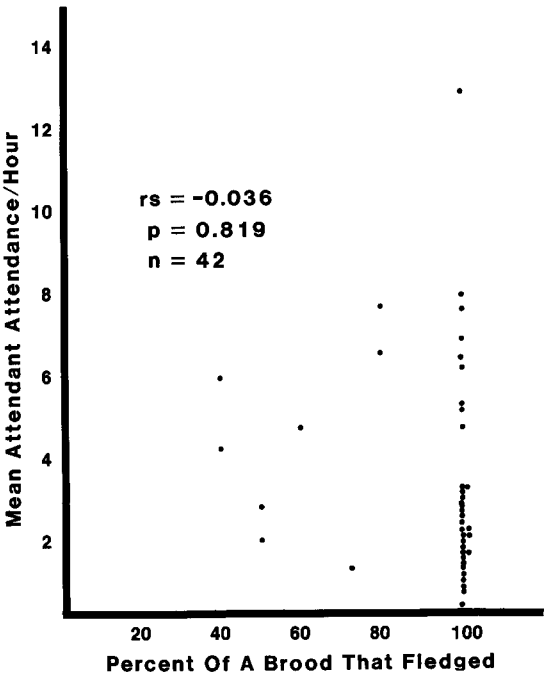

FIGURE 2. Mean attendant attendance/hr vs. the percent of a brood that fledged. Only boxes with ≥5 hours of observations are included.

THE EFFECT OF ATTENDANTS ON FLEDGING SUCCESS

There was no correlation between mean attendant attendance and the number of nestlings that fledged from a brood or the proportion of the brood that fledged (Fig. 2). This result was unaffected by breeding female plumage morph or attendant type.

MOBBING STUDIES

Both parents and attendants mobbed the owl model, but only parents made aggressive dives at it. Attendants hovered high above the model. It was not clear whether only parents emitted alarm notes. Shields (1984) reported that only parent Barn Swallows emitted alarm notes and dove at real and model predators. I elicited the same responses from the parents and attendants as the model did.

DISCUSSION

Tree Swallow nest attendants had no demonstrable effect on parental reproductive success. In 300 interactions (i.e., attendants and nestlings within touching distance of one another) between attendants and nestlings, no food was ever seen being passed from attendants to nestlings. During these interactions attendants either ignored begging nestlings or they thrust their bills, often repeatedly, into the gaping mouths of begging nestlings. This behavioral

interaction was most often observed when nestlings were between 17 and 20 days old and begged from their parents while perched in the nest box hole. That attendants did not feed nestlings disqualifies Tree Swallows as cooperative breeders under at least one criterion (Brown 1978).

There was no correlation between attendant attendance and parental reproductive success. The low frequency of attendant entries (e.g., only 14 entries in 120 box-hr of observation at 16 boxes in 1983) and their unpredictable and sporadic nature lend further support to the argument that attendants did not make a positive contribution to parental reproduction success by feeding nestlings.

In this study attendants did not hinder parental success. Attendants had no effect on nestling weight gain, the maximum weight of nestlings, or on the number or proportion of young that fledged from a brood.

A reevaluation of the behavioral interactions between attendants and nestlings led to the hypothesis that attendants were attempting to steal food from nestlings. Attendant attempts to steal food from parents and nestlings, while infrequent, may be especially detrimental to nestlings if the weather is bad (e.g., cold and wet) and nestlings are small. During cold and rainy weather, insect abundance is low (Williams 1961, Taylor 1963) and parents presumably have high energy demands in maintaining their body temperature and brooding young. The disruption of feeding schedules during this time could cause severe thermal stress in nestlings that have not yet become endothermic (e.g., see Dunn 1979) because parents must frequently leave them uncovered to forage, causing the nestlings' bodies to cool. Sheppard (1977) regularly found HY-attendants in boxes at her study site in central New York. She hypothesized that these attendants successfully outcompeted resident broods for the food delivered by parents because the attendants were larger than resident nestlings. She attributed the death of 10 nestlings in four broods to this behavior by attendants. There was no unequivocal evidence that attempts to steal food were more common during bad weather during the course of this study.

Attendants did appear to provide aid to parents in the form of passively mobbing potential predators. However, as Shields (1984) has suggested, passive mobbing is primarily a form of self defense and only secondarily affects the fitness of active mobbers (i.e., parents). Passive mobbers learn the location, identity, and probable behavior of the potential predator but take few risks in obtaining this information. Thus, if the intent of the passively mobbing attendants is selfish, Tree Swallows are further disqualified as cooperative breeders (Brown 1978).

In summary, these data indicate that Tree Swallow nest attendants are not helpers at the nest. They further support Burtt's (pers. comm.) observations that Tree Swallow attendants did not feed nestlings. The observations of attempts by attendants to pirate food from nestlings and parents suggest that attendants may not only be uncooperative but may also present a potential threat to parental success.

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