

## ATTENDANTS AT TREE SWALLOW NESTS. II. THE EXPLORATORY-DISPERSAL HYPOTHESIS<sup>1</sup>

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*Abstract.* Attendants (i.e., conspecific individuals exclusive of the breeding pair) are common visitors at active Tree Swallow (*Tachycineta bicolor*) nests during the nestling period. An examination of the chronology of attendant behavior revealed that attendants (i) visited several boxes, (ii) were especially attracted to preferred breeding locations, (iii) significantly increased in number as the breeding season progressed, (iv) were mostly young of the year by the end of the breeding season, and (v) chased nestlings as they fledged. Members of large, premigratory flocks of Tree Swallows examined nest boxes during late August. Attendants were not helpers at the nest and had no demonstrable effect on parental reproductive success (Lombardo 1986a).

Tree Swallows, because they are nonexcavating cavity nesters, face intense competition for a limited number of suitable nest sites. Sexually mature attendants at nests during the egg laying, incubation, and early nestling periods may be searching for exploitable breeding opportunities (e.g., see Leffelaar and Robertson 1985, Stutchbury and Robertson 1985). I hypothesize that hatching-year attendants, common during the late nestling period, are individuals in search of potential future nest sites. I call this the "exploratory-dispersal" hypothesis. Exploratory dispersal should be of special selective advantage to migratory, nonexcavating cavity nesters.

*Key words:* Tree Swallows; dispersal; migration; nest site selection; fledgling behavior.

### INTRODUCTION

Attendants (i.e., conspecific individuals exclusive of the breeding pair) are common at active Tree Swallow (*Tachycineta bicolor*) nests throughout the breeding season (e.g., see Kuerzi 1941, Tyler 1942, Sheppard 1977, Stutchbury 1984, Lombardo 1986a). Attendants include sexually mature individuals of both sexes and, late in the season, recently fledged birds (Tyler 1942, Stutchbury 1984, Leffelaar and Robertson 1985, Stutchbury and Robertson 1985, Lombardo 1986a). Leffelaar and Robertson (1985) and Stutchbury and Robertson (1985) have shown that attendants, especially second-year female attendants, are searching for exploitable breeding opportunities early in the breeding season. My observations indicate that attendants during the nestling period are not helpers at the nest (Lombardo 1986a).

In this paper I examine attendant behavior during the nestling period. I propose that the hatching year attendants present during this time are searching for potential future nest sites (R. R. Cohen, pers. comm.) because of the advan-

tages of premigratory dispersal (e.g., see Brewer and Harrison 1975, Baker 1978, Greenwood 1980, Adams and Brewer 1981, Cohen 1982, Shields 1982) in competition for a limited number of nest sites (Hersey 1933; Kuerzi 1941; Tyler 1942; Erskine 1964, 1979; Zeleny 1976; Boone 1982; Prescott 1982, 1983; Cohen 1985; Robertson et al. 1986). I call this the "exploratory-dispersal" hypothesis. The antecedent to this hypothesis can be found in Chapman (1935).

Because these data were collected during a study that determined that attendants were not helpers at the nest (Lombardo 1986a), the data necessary to make a direct test of the critical prediction of the exploratory-dispersal hypothesis (i.e., hatching-year attendants return the following spring to breed in the areas they explored) are not available. However, the data do provide enough information to explore the corollaries of this hypothesis. Such an examination provides a direction for future study and the means of designing experiments that provide the critical data necessary to test the hypothesis.

Because searching for potential future nest sites by attendants probably involves first searching widely for nest sites in suitable habitat and then assessing nest site quality within those habitats

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(R. J. Robertson, pers. comm.), attendants should, (i) disperse from their natal area soon after independence, (ii) visit, and enter, several nest sites within suitable habitat in order to assess nest site quality, (iii) be most attracted to active nests because nest site occupancy implies high nest site quality when vacant sites are also present, (iv) be especially attracted to the generally preferred Tree Swallow nest sites (i.e., old cavities in the middle of open habitat; Austin & Low 1932, Low 1933, Chapman 1935, Kuerzi 1941, Tyler 1942, Sheppard 1977, Muldal et al. 1985), (v) behave agonistically toward parents and their offspring because of the conflict of interest between attendants and breeders and their offspring, and (vi) examine potential future nest sites during the premigratory period because it is a period of little stress (Baker 1978). Observations of attendant behavior were consistent with these predictions.

## METHODS

The study was conducted from 1980 to 1983 at a nest box trail located on the salt marshes of the John F. Kennedy Memorial Wildlife Refuge (JFKMWR) at Tobay Beach on the south shore of Long Island, New York. The trail grew from 22 boxes in 1980, to 40 boxes in 1981, 70 boxes in 1982, and 72 boxes in 1983. Boxes were approximately 30 m apart and were erected in three parallel rows with nest box holes facing south-southeast. Boxes were divided into two subcolonies (A = 14 boxes, B = 58 boxes) in identical habitat but separated by ca. 1,200 m. Sites A and B were established in 1980. The study site has been described in detail elsewhere (Schaeffer 1972).

## MARKING

Breeding females ( $n = 78$ ) were captured on the nest between 05:00 and 06:00 on the first day of incubation (Kuerzi 1941, DeSteven 1980, Burt and Tuttle 1983). Breeding males ( $n = 70$ ) were usually captured and banded one to two days after eggs hatched. Some males were banded earlier when they were fortuitously captured in boxes during regular nest censuses. 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 ( $n = 278$ ) were banded on Nestling Day 12 (hatching equals ND 1).

All captured birds were banded with a U.S. Fish and Wildlife Service aluminum band and uniquely color-marked on their tails, wings, foreheads, throats, or breast feathers using a marking pen or Testors Airplane Dope (Samuel 1976). In 1983, 24 nestlings from six broods had brood specific patterns painted on their breast feathers before they fledged.

## BASIC OBSERVATION TECHNIQUES

Attendants are any swallows exclusive of the breeding pair that visit nests during the nestling period. Observations were concentrated during the nestling period because I never observed nest attendants before the nestling period during 137 hr of observations at 26 nests during 1980 and 1981 (see below). Because some attendants had previously bred (Lombardo 1986a), *nonbreeder*, the former designation for these individuals (Lombardo 1985), is inaccurate and has been abandoned.

From 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 daily, mostly between 06:00 and 14:00. A total of 488 hr of observations of 39 pairs were recorded during the nestling period ( $\bar{x} = 12.5$  hr/pair; range 1 to 19 hr/pair). During observations I recorded the identity (e.g., parent or attendant) and the behavior of birds around the focal nest box. I used both an 8 × 40 mm pair of binoculars and a 25 × 50 mm telescope to observe birds.

## DEFINITIONS OF ATTENDANT BEHAVIOR

Attendant visits were defined as flying about the nest box (i.e., circling or hovering within 3 m), perching on the box, or entering the nest box interior. Entries are analyzed separately when they provide insight into the significance of attendant behavior. Attendant visits and entries are expressed as  $\bar{x} \pm SE/hr$  throughout.

## PLAYBACK OF NESTLING BEGGING CALLS

On about Nestling Day 6, nestlings became more active and began to produce sounds that were audible outside of the nest box. To test the hypothesis that nestling begging calls alone attract-

ed attendants, I recorded the begging calls of a 16-day-old brood of five nestlings on a Uher Model 4000 portable tape recorder in 1981. During recording, the microphone was attached to an inside wall of a nest box and the tape recorder was placed on the ground below the nest box. A 7 min sequence of continuous begging calls was recorded and played back during nine trials at two different empty nest boxes on three different days. Each experimental box was located next to an active box that contained nestlings. I recorded the number, identity, and behavior of birds that approached within 3 m of the nest box during each trial. As a control, I left the speaker and recorder in place and recorded the number, identity, and behavior of any birds that approached within 3 m of the box during 7 min of silence. Control and experimental trials were alternated at the same nest box.

#### TRANSLOCATION EXPERIMENT

Because I rarely observed attendants at empty boxes, I tested the hypothesis that attendants were attracted by parental activity. In both 1982 and 1983, I randomly selected 10 pairs with nestlings between 8 and 15 days old for inclusion in the experiment. Between 06:00 and 07:00 on experimental days, I removed one-half of the nestlings from the brood (e.g., three of six nestlings) in an experimental nest box and moved them to a nearby empty nest box. Two hours later I returned and simultaneously observed the experimental box, the box with the translocated nestlings, and a nearby empty box. I recorded the identity and behavior of any birds that approached within 3 m of any of the three nest boxes for 60 min. At the end of the observation period I returned the nestlings to their natal nest box. Twenty sets of three nest boxes were observed.

#### TREE SWALLOW COLOR MORPHS

The breeding population consisted of (i) subadult females: mostly yearling and some older females in brown plumage with varying amounts of iridescent feathering, (ii) green females: most third year and all older females in full iridescent plumage, and (iii) green males: all males are in full iridescent plumage before their first winter (Dwight 1900, Cohen 1980, Hussell 1983). The iridescent plumage of swallows at my study site appeared to be more green-blue than blue-green.

Forty-nine percent of breeding females were subadult females (Lombardo 1986b).

Throughout, "G-attendants" refers to attendants in full iridescent plumage and includes both males and females; "SAF-attendants" refers to female attendants in subadult plumage; "HY-attendants" refers to attendants with a dusky gray-brown plumage with no iridescent feathers (i.e., hatching-year birds) and 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 examination. However, banding data showed that HY-attendants were of both sexes (Lombardo 1986a). The term "attendants" refers to the sum of G- + SAF- + HY-attendants.

#### RESULTS

During 488 hr of observations at 39 nests from 1980 to 1983, attendants were observed singly or in groups 1,669 times (G-attendants 1,050 times, SAF-attendants 288 times, and HY-attendants 331 times). Parents visited their nests 6,872 times (males,  $n = 3,134$ ; females,  $n = 3,738$ ) during the same observation periods. Parental visits included both brooding and feeding visits. Video observations of nest box interiors (Lombardo 1986a) revealed that nearly 100% of parental visits after ND 3 resulted in the feeding of a single nestling.

Once eggs hatched, attendants were seen at every nest ( $n = 76$ ) that had young. Attendants were not necessarily seen every day at every nest. Attendant abundance varied from day to day and within observation periods at each nest. I sometimes observed as many as 15 to 20 attendants, especially HY-attendants, around a nest at one time. Marked attendants ( $n = 45$ ) were never seen again at the nest where they were originally marked. I saw attendants, both singly and in small flocks of five to ten birds, going from box to box as though they were using a "trapline." Attendants were seen at both empty and active boxes.

#### ATTENDANT ENTRIES INTO NEST BOXES

Attendant entries accounted for 293 of 1,669 (17.6%) observations of attendants. Four of 39 (10.3%) nests were responsible for 109 of 293 (47.1%) of entries. At 5 of 39 (12.8%) nests, attendants were observed visiting but not entering nest boxes. At 8 of 39 (20.5%) nests only single entries were recorded. In sum, 279 of 293 (95.2%)

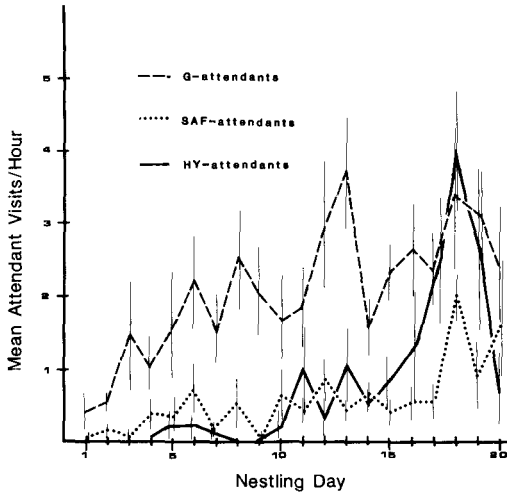


FIGURE 1. Mean attendant visits/hr vs. nestling day. Hatching is equal to day 1. Attendant visitation rates at subadult and green female nests combined. Only nestling days 1 to 20 used in determination of correlation.  $\bar{x} \pm SE/hr$  are indicated. G-attendants,  $r_s = 0.770$ ,  $P < 0.001$ ; SAF-attendants,  $r_s = 0.714$ ,  $P < 0.001$ ; HY-attendants,  $r_s = 0.873$ ,  $P < 0.001$ ; Attendants,  $r_s = 0.895$ ,  $P < 0.001$ .

entries were recorded from 1980 to 1982. The extremely uneven distribution of attendant entries (i.e., 10% of observed nests were responsible for 47% of the observed entries), and the observation that attendant entries had no demonstrable effect on parental reproductive success (Lombardo 1986a), make the determination of their biological significance difficult.

#### ATTENDANT AND PARENTAL VISITS IN RELATION TO NESTLING AGE

There was a highly significant correlation between mean attendant visits/hr and nestling age (Spearman rho [ $r_s$ ] = 0.895,  $P < 0.001$ ,  $n = 20$  days; Fig. 1). A statistically significant positive relationship also existed between each attendant type and nestling age (Fig. 1). Mean attendant entries/hr significantly increased with nestling age ( $r_s = 0.716$ ,  $P < 0.001$ ,  $n = 20$  days). I did not observe attendant entries before ND 6 (100 hr of observations) or after ND 20 (13 hr of observations). Analyzing these data for the nests of subadult and green females separately produced the same results.

In contrast to attendant visits, parental visits increased to a plateau between ND 6 and ND 15 before declining (Fig. 2). In general, parental vis-

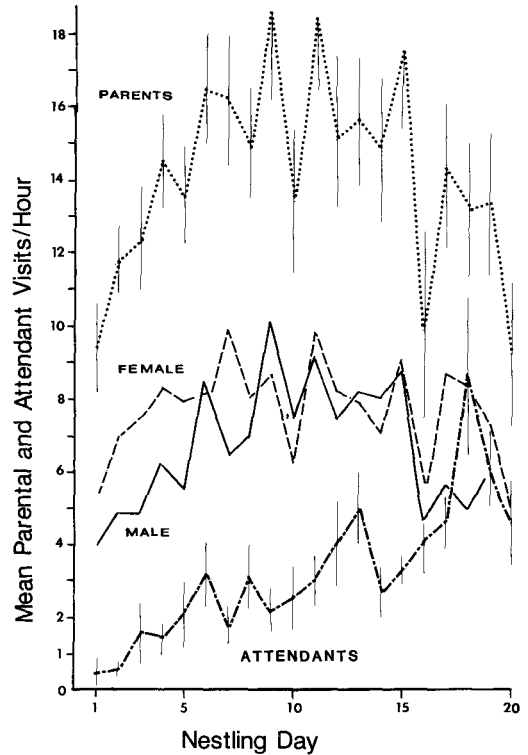


FIGURE 2. Mean parental and attendant visits/hr vs. nestling day. Parental and attendant visitation rates for subadult and green female nests combined. Parents = sum of male and female visits.  $\bar{x} \pm SE/hr$  are indicated. Only nestling days one to 20 used in determination of correlation. Parents,  $r_s = 0.029$ ,  $P = 0.905$ ; Males,  $r_s = 0.052$ ,  $P = 0.828$ ; Females,  $r_s = 0.054$ ,  $P = 0.821$ ; Attendants,  $r_s = 0.895$ ,  $P < 0.001$ .

its followed nestling weight gain curves: Tree Swallow nestlings gain weight until about ND 14 then lose weight until fledging (Paynter 1954, Ricklefs 1968, Zach 1982, Zach and Mayoh 1982, this study).

#### ATTENDANT AND PARENTAL VISITS IN RELATION TO BROOD SIZE

Although both male and female parents responded to larger brood sizes with higher visitation rates (Fig. 3) (see Leffelaar and Robertson 1986, Quinney 1986), attendant visitation rates were not correlated with brood size ( $r_s = 0.543$ ,  $P = 0.266$ ,  $n = 6$ ; Fig. 3).

#### ATTENDANT VISITS AND BREEDING FEMALE COLOR

There was no difference between mean attendant visits/hr at the nests of subadult and green female

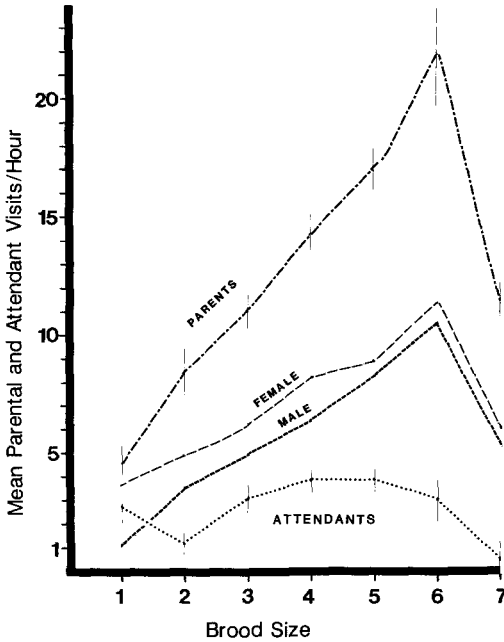


FIGURE 3. Mean parental and attendant visits/hr vs. brood size. Attendant visitation rates for subadult and green female nests combined. Only brood sizes one to six were used in correlation analysis because of less than 10 hr of observations at brood size seven.  $\bar{x} \pm SE/hr$  are indicated.

parents ( $3.08 \pm 0.28$ ,  $n = 191$  hr of observations vs.  $3.72 \pm 0.32$ ,  $n = 297$  hr of observations; Wilcoxon's two-sample test,  $Z = -0.285$ ,  $P = 0.775$ ). There were no differences between breeding green and subadult females in the mean visitation rates of each attendant type at their nests during each breeding season.

PLAYBACK OF NESTLING BEGGING CALLS

Although there were attendants within 200 m of the experimental box during all trials, neither attendants nor parents of broods in nearby boxes approached within 3 m of the experimental box during either the broadcast ( $n = 9$ ) or control ( $n = 9$ ) trials. I observed attendants at other boxes in the vicinity of the experimental box during some trials.

TRANSLOCATION EXPERIMENT

There was a significant difference between the mean number of attendants observed at each of the three different categories of nests during the Translocation Experiment (Table 1). A nonpara-

TABLE 1. Translocation experiment that tested the null hypothesis that mean attendant visits at nests with parents and nestlings = attendant visits at nests with only nestlings = attendant visits at empty nests. The null hypothesis was rejected with a Kruskal-Wallis test,  $H = 12.06$ ,  $P < 0.005$ ,  $df = 2$ . Nonparametric multiple comparison (Zar 1974): Parents and nestlings > nestlings only > empty,  $P < 0.05$ .

Parents and nestlings	Nestlings only	Empty
$1.60 \pm 0.34^1$	$0.85 \pm 0.08$	$0.45 \pm 0.14$
32 <sup>2</sup>	17	9

<sup>1</sup> Attendant visits  $\bar{x} \pm SE/hr$ ,  $n = 20$  boxes observed for 60 min each.  
<sup>2</sup>  $n$  = number of attendants observed.

metric multiple comparison of means (Zar 1974) revealed that (i) boxes with both parents and nestlings attracted the most attendants, (ii) boxes with only nestlings attracted the second most, and (iii) empty boxes attracted the least. All differences were significant at  $P < 0.05$ . Although translocated nestlings begged loudly for food, their parents did not respond to their calls.

ATTENDANT VISITS AND PARENTAL ACTIVITY

There was a significant correlation between parental visits and attendant visits ( $r_s = 0.232$ ,  $P < 0.001$ ,  $n = 488$  hr of observations). Extra birds around nest boxes were never observed during the incubation period during late May and early June from 1980 to 1982 ( $n = 137$  hr of observation at 26 boxes). In 1982, because of nest failures and subsequent renestings, five females were incubating after 1 July and attendants were observed at those nests. However, nests with nestlings ( $n = 11$ ) attracted more attendants than concurrently active nests with incubating females ( $n = 5$ ) ( $3.27 \pm 1.0$ ,  $n = 36$  attendants vs.  $1.64 \pm 0.39$ ,  $n = 18$  attendants; one-tailed paired sample  $t$ -test,  $t = -4.57$ ,  $P < 0.002$ ,  $df = 9$ ;  $n = 22$  hr of observation).

PHYSICAL PARAMETERS OF THE NEST BOX

Aside from those parameters associated with breeding activity that may have affected attendant behavior (e.g., nestling age, nestling or parental activity, brood size, and breeding female color), there are a host of other, abiotic parameters defined by the attributes of the nest box itself and its position that may be attractive to attendants.

The null hypothesis that each of the 36 boxes from which young fledged was equally attractive

to attendants was rejected (Kruskal Wallis  $\chi^2 = 122.64$ ,  $P < 0.0001$ ,  $df = 34$ ). In the analyses that follow, only those boxes ( $n = 22$  boxes) with 10 or more hours of observation are included to ensure a more accurate measure of attendance at each box. Mean attendant and parental visitation rates were used for the analysis of boxes with multi-year occupancy. Insufficient data from separate years precluded a yearly analysis of the same parameters.

Sheppard (1977) showed that Tree Swallows preferred to breed in cavities located near the center of a group of suitable nest cavities. Boxes positioned within a group attracted more attendants ( $4.95 \pm 1.04$ ,  $n = 7$  boxes) than those on an edge ( $2.59 \pm 0.51$ ,  $n = 15$  boxes) (Mann-Whitney U Test,  $U = 87.5$ ,  $P < 0.05$ ). However, there was no difference ( $t = -0.007$ ,  $P = 0.994$ ,  $df = 110$ ) in the mean date of clutch initiation between edge boxes (date  $24.71 \pm 0.91$ ,  $n = 69$  clutches) and those within a group of boxes (date  $24.72 \pm 1.21$ ,  $n = 43$  clutches) boxes where 1 May = date 1.

When given a choice between old and new nest boxes, Tree Swallows preferred to breed in older, more weathered boxes. While there was no difference ( $t = 0.216$ ,  $P = 0.829$ ,  $df = 110$ ) in the mean date of clutch initiation between boxes erected in 1980 (date  $24.85 \pm 1.07$ ,  $n = 62$  clutches) and those erected after 1980 (date  $24.54 \pm 0.92$ ,  $n = 50$  clutches), females preferred to lay eggs in boxes erected in 1980 and 1981. Ninety-seven of 112 clutches (86.7%) that were initiated (i.e., at least one egg laid, original clutches only) from 1980 to 1983 were initiated in boxes erected in 1980 ( $n = 64$ ) and 1981 ( $n = 33$ ). Boxes erected in 1980 ( $n = 22$ ) attracted more attendants than those erected after 1980 ( $n = 50$ ) ( $4.24 \pm 0.70$ ,  $n = 15$  boxes vs.  $2.17 \pm 0.56$ ,  $n = 7$  boxes; Mann-Whitney U Test,  $U = 81$ ,  $P < 0.05$ ). However, attendants may have been attracted to parental activity rather than box age because parents visited boxes erected in 1980 ( $15.64 \pm 1.29$ ,  $n = 15$  boxes) more often than those erected after 1980 ( $10.54 \pm 1.63$ ,  $n = 7$  boxes) (Mann-Whitney U Test,  $U = 83$ ,  $P < 0.05$ ). Insufficient data precluded testing the null hypothesis of equality of mean attendant attendance for the year boxes were erected for each year separately.

Tree Swallows prefer to nest in cavities that are in open habitat (Austin and Low 1932, Low 1933, Chapman 1935, Kuerzi 1941, Tyler 1941,

Sheppard 1977). Of the 72 boxes available for breeding, 28 (38.9%) were erected within 30 m of coastal scrub vegetation (see Schaeffer 1972 for a description of vegetation types), and 44 (61.1%) were erected on the open expanse of the salt marsh. Boxes that were more than 30 m from scrub attracted more attendants than did boxes nearer scrub ( $4.47 \pm 0.72$ ,  $n = 13$  boxes vs.  $2.31 \pm 0.64$ ,  $n = 9$  boxes; Mann-Whitney U Test,  $U = 90.5$ ,  $P < 0.05$ ). There was no difference ( $t = -0.293$ ,  $P = 0.769$ ,  $df = 110$ ) in the mean date of clutch initiation between boxes near (date  $25.00 \pm 1.21$ ,  $n = 40$  clutches) or far (date  $24.55 \pm 0.91$ ,  $n = 72$  clutches) from vegetation. Parental visitation rates were equal at boxes near and far from scrub ( $12.86 \pm 2.39$ ,  $n = 9$  boxes vs.  $14.77 \pm 1.08$ ,  $n = 13$  boxes; Mann-Whitney U Test,  $U = 82$ ,  $P > 0.05$ ).

#### ATTENDANT AND PARENTAL VISITS IN RELATION TO CALENDAR DATE

There was a highly significant correlation between attendant visitation rates ( $r_s = 0.430$ ,  $P < 0.001$ ,  $n = 61$  days) and calendar date for each day of the breeding season when considered from the date the first egg hatched until the date the last nestling fledged. This was due to the sharp increase in mean HY-attendant visits/hr as the season progressed ( $r_s = 0.780$ ,  $P < 0.001$ ,  $n = 61$  days). The visitation rates of both G-attendants ( $r_s = -0.145$ ,  $P = 0.264$ ,  $n = 61$  days) and SAF-attendants ( $r_s = -0.056$ ,  $P = 0.666$ ,  $n = 61$  days) did not change. These patterns were the same at the nests of subadult and green females with one exception: G-attendant visitation rates at subadult female nests significantly declined ( $r_s = -0.349$ ,  $P = 0.012$ ,  $n = 61$  days) as the breeding season progressed.

In Figure 4 the breeding season is divided into blocks of 10 days each, starting on 31 May. This method simplifies the analysis by lessening the importance of daily fluctuations in attendant number. In general, G-attendants dominated observations and increased their mean visits/hr until the first week in July (Fig. 4). SAF-attendant visitation rates showed no significant relationship with date when analyzed in this fashion (Fig. 4), although observations of them also increased until early July.

During late June and early July of each year (except 1980 when no HY-attendants were observed), I recorded an influx of HY-attendants at the study site. In 1980 the influx was made

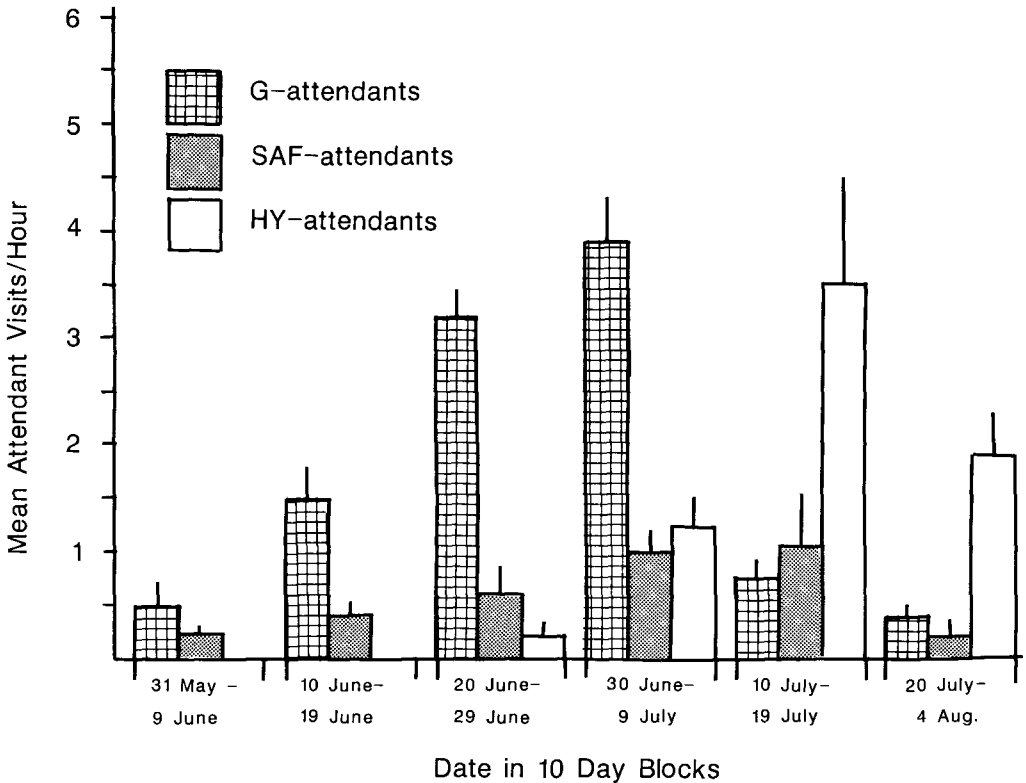


FIGURE 4. Mean attendant visits/hr vs. date in 10-day blocks. Date 1 = 1 May.  $\bar{x} \pm SE/hr$  are indicated. G-attendants,  $r_s = -0.200$ ,  $P = 0.704$ ; SAF-attendants,  $r_s = 0.086$ ,  $P = 0.872$ ; HY-attendants,  $r_s = 0.926$ ,  $P = 0.008$ , Attendants,  $r_s = 0.600$ ,  $P = 0.208$ .

up of mostly G-attendants. I never observed an HY-attendant before 22 June. HY-attendants accounted for the majority of observations from 10 July to early August. By 1 July most breeding

pairs were in the second half of the nestling period and 32 of 76 (42%) successful broods had already fledged young. Only three of the 218 (1.4%) HY-attendants observed in 1981 and 1982 were birds that fledged at JFKMWR, and only one of the 24 (4.2%) color-marked fledglings in 1983 was observed attending another nest. These results indicate that the origin of HY-attendants in the influx was outside of my study site.

In addition, in only three (one male and two adult females) of the 1,338 (0.22%) times sexually mature attendants were observed were they birds that had already completed breeding at other boxes. Each visited a different box several days after their own young had fledged. This result indicates that the origin of sexually mature birds in the influx was from outside of my study site.

Attendant visitation rates did not follow the visitation rates of parents (Fig. 5). Parental visits decreased daily as the breeding season progressed because by late in the breeding season most young had already fledged and the remaining active

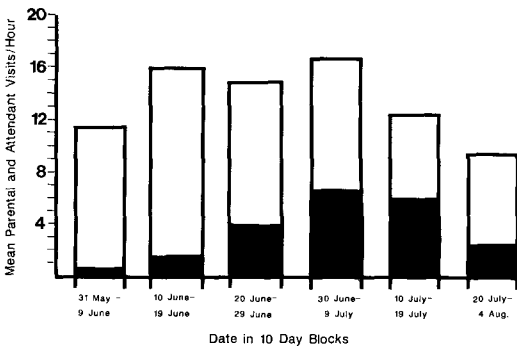


FIGURE 5. Mean parental and attendant visits/hr vs. date in 10-day blocks. Date 1 = 1 May. Parents are indicated by open bars and attendants by shaded bars. Parents = sum of male and female visits. Parents,  $r_s = -0.257$ ,  $P = 0.623$ ; Attendants,  $r_s = 0.600$ ,  $P = 0.208$ .

boxes were in the later stages of the nestling period and parental visitation rates were declining (Fig. 2). The seasonal patterns of attendant and parental visits were the same at the nests of both subadult and green females.

#### OBSERVATIONS DURING THE PREMIGRATORY PERIOD

Immense flocks of Tree Swallows (Childs 1900), sometimes numbering in the millions, form along the Atlantic coast during late summer prior to their migration south (Kuerzi 1941, Tyler 1942). I observed Tree Swallow activity around nest boxes during visits to the study site in late August of 1981, 1982, and 1983. Often subflocks of ca. 100 birds (some subflocks were smaller) broke off from the main flock flying above the marsh and swirled around a nest box. Many birds landed on the nest box top, pole and hole while others hovered in front of the hole. Sometimes birds pushed one another from perches at the hole in what appeared to be attempts to gain access to a view of the box interior. I never saw a bird enter a box during this activity. Individuals left and rejoined the main flock constantly during this activity. Subflocks appeared to move randomly from box to box. There was no evidence of greater activity around boxes that had been active during the previous breeding season.

#### DISCUSSION

Given that Tree Swallows require a nest cavity to breed and that suitable cavities are limited in number (Holroyd 1975), all individuals not in possession of a nest site should search for them. Sexually mature attendants of both sexes were observed throughout the breeding season, but they were most abundant when they still had an opportunity to breed (see Fig. 4). In four years of study at JFKMWR, the latest date of clutch initiation that resulted in fledged young was 25 June. Therefore, by late June it was probably too late for a pair to initiate breeding and successfully rear young to fledging at JFKMWR and accordingly, attendant visits at nests declined precipitously in early July (Fig. 4).

Sexually mature attendants are expected to be opportunistic in their search for nest sites and to attempt to use cavities in which pairs have already failed and deserted. Observations of previously unbanded birds initiating breeding during mid-June at JFKMWR ( $n = 2$ ) at previously unsuccessful nests are consistent with this pre-

dition. Other studies (e.g., Leffelaar and Robertson 1985, Stutchbury and Robertson 1985) have also shown that sexually mature attendants are opportunistic when they have a chance to breed.

A critical prediction of the exploratory-dispersal hypothesis is that HY-attendants should return to breed at sites they "prospected" the previous year. For example, Eadie and Gauthier (1985) showed that "nest prospecting" females in cavity nesting ducks (*Bucephala* spp.) returned to breed near the sites they visited the previous year. Shields (pers. comm.) reported six cases of young Barn Swallows (*Hirundo rustica*) breeding where they had prospected the previous year rather than their natal area.

During this study, none of the 45 birds banded as attendants returned to breed at the study site. This result is not fatal to the prediction because it may very well be that when attendants were handled during banding they "judged" the site as unacceptable due to a high predation risk. However, one bird banded as an HY-attendant in 1981 returned as a male, G-attendant in 1982. Another bird was captured as an HY-attendant in 1981 and found dead in a box in April 1982 in subadult female plumage. Together these two examples indicate that HY-attendants were capable of returning to the sites they had visited in the past. The first example suggests that the male may have been excluded from breeding when he returned to the study site.

The study site is within the primary migratory route of most northeastern populations of Tree Swallows and it is probable that many of the attendants that visited JFKMWR also visited many other breeding areas. The fact that 40 to 50% of the nest boxes at the study site were unoccupied each year despite the presence of potentially breeding attendants of both sexes implies that JFKMWR was marginal quality breeding habitat and thus was judged unacceptable by many visiting attendants. Additionally, there may have been a biased operational sex ratio favoring females (see Leffelaar and Robertson 1984, 1985) that may have contributed to low occupancy rates. That only 268 of 638 (42%) eggs produced fledged young lends further support to my contention that JFKMWR was of marginal breeding quality because this was a much lower success rate than those reported for other sites (e.g., see Wedemeyer [93.7%] 1935, Kuerzi [70.5%] 1941, Paynter [79.8%] 1954,



Chapman [60%] 1955, Sheppard [80.7%] 1977, DeSteven [55.3%] 1978). It is also likely that millions of Tree Swallows passed through JFKMWR during each fall migration, thereby precluding the possibility of banding a significant number of potential returning birds. Thus, it is possible that the immigrant birds that bred at JFKMWR each year, had in fact visited it during the previous summer. However, insufficient data are available to either satisfy or falsify this prediction. The true test of this prediction awaits a marking procedure that does not subject birds to the trauma of handling (Burt and Tuttle 1983). The remainder of this discussion considers the corollaries to the exploratory-dispersal hypothesis.

That color-marked ( $n = 1$ ) or banded ( $n = 3$ ) nestlings were rarely seen acting as HY-attendants in their natal area after fledging from nests at the study site supports the prediction that recently fledged birds should disperse from their natal area soon after independence.

Attendants, especially HY-attendants, were observed visiting several nest boxes, whether occupied or not, on their flights through the study site. In three cases, color-marked HY-attendants visited nest boxes other than the ones in which they were originally captured. However, I never observed color-marked attendants ( $n = 45$ ) revisiting the same nest where they were originally captured, probably because of the trauma associated with handling (see above, Burt and Tuttle 1983). These observations support the prediction that attendants should visit several nest sites in order to assess nest site quality. It is more difficult to determine if they were assessing site quality. If nest site occupancy is a reasonable criterion of nest site quality when empty sites are nearby, then nest site occupancy, and hence quality, can easily be determined by observing parental breeding activity.

Results from the broadcast of nestling begging calls and the translocation experiment indicate that attendants were, at least initially, attracted to parental activity around nests. Indeed, there was a significant correlation between parental and attendant visits ( $r_s = 0.232$ ,  $P < 0.001$ ,  $n = 488$  hr of observations). Neither breeding female color morph nor brood size significantly affected attendant behavior. That attendant visitation rates steadily increased with nestling age and did not parallel parental visits suggests that attendants were neither (i) sensitive to nestling de-

mands nor (ii) solely attracted to parental activity. That attendants did not feed nestlings (Lombardo 1986a; Burt, pers. comm.) satisfactorily disproves the alternative hypothesis that attendants augmented parental feedings and thereby allowed parents to decrease their feeding rates. The increase in HY-attendant visits throughout the breeding season suggests that the correlation between attendant visitation rates and nestling age was an artifact of the increase in HY-attendants visiting the study site as the breeding season progressed.

All categories of attendants were especially attracted to the generally preferred breeding sites of this species (i.e., old cavities, in the middle of groups and out in the open) (Austin and Low 1932, Low 1933, Chapman 1935, Kuerzi 1941, Sheppard 1977), although breeders at JFKMWR did not always show these preferences. HY-attendant behavior upon arrival at a nest box was very similar to the behavior exhibited by breeding birds when box examination occurred in the spring (R. R. Cohen, pers. comm., pers. observ.): the birds flitted hesitantly around a box, landing at the hole several times before entering. The entire sequence from arrival to entry often took several minutes. Entering nest boxes and monitoring parental activity are probably important components in the assessment of nest site quality.

Interactions between parents and attendants should be hostile because of the conflicts of interest between them. Parent-attendant interactions are detailed elsewhere (Lombardo 1984). In summary, parental responses to both stuffed model and live attendants at their nests indicated that there was a temporal component to parental aggression that correlated with the potential threat that attendants presented to parental reproductive success. Parents were most aggressive toward model and live G- and SAF-attendants early in the breeding season (Lombardo 1984) when live attendants presented a real threat to parental reproductive success (e.g., see Leffelaar and Robertson 1984, 1985). Attendants occasionally chased parents. An experiment that examined the dynamics of parent-attendant interactions (Lombardo 1985) revealed a delicate balance between parental aggression and restraint that was based on reciprocity (Axelrod and Hamilton 1981).

If attendants were searching for potential future nest sites, they should have viewed fledglings

as potential nest site competitors and behaved aggressively toward them, thereby discouraging recently fledged young from imprinting upon the nest site and thus decreasing the probability that fledglings will return the following year to compete with the attendants (Brown and Bitterbaum 1980). This behavior should be of special selective importance to nest site limited species and it may be a general phenomenon in nonexcavating cavity nesting swallows. Brown and Bitterbaum (1980) and Lofton and Robertson (1983) observed juvenile Purple Martins (*Progne subis*) being attacked before, and chased after, fledging by nonparental birds. Cohen (pers. comm.) observed fledgling Tree Swallows being chased as they left the nest by a nest site competitor, the Violet Green Swallow (*Tachycineta thalassina*).

Sheppard (1977) observed fledgling Tree Swallows being chased, often hostilely, by conspecific nonparental birds. In this study, I saw five nestlings fledge naturally from four nests and they were hostilely chased from view by attendants. Attendants snapped their bills at the fledglings' tails as fledglings flew from view. In contrast to Brown and Bitterbaum's (1980) finding that mature martins harassed fledglings, HY-attendants chased fledglings in my Tree Swallow population. The parents of these fledglings were not in view during these observations.

Predicting precisely when young will fledge is difficult. I increased the probability of observing attendant behavior toward fledglings by hand fledging 13 nestlings from five broods during 1981, 1982, and 1983. I prevented the nestlings from fledging by restricting the size of the nest box hole until the nestlings were 22 days old and then released them one at a time. Nine of the released fledglings (69%) were chased from view by attendants. On the two occasions that parents were present during the release of their young they did not chase their young or the attendants that were chasing them. Some chases were aggressive and attendants snapped at the tails of fledglings as they fled. Because parents may feed their young for several days after fledging (Burt 1977; Cohen, pers. comm.), this harassment behavior could have a negative effect on fledgling survival if the harassers can effectively separate fledglings from their parents. However, there is no unequivocal evidence that the lack of yearling philopatry in Tree Swallows (Kuerzi 1941, Chapman 1955, this study) is due to harassment by attendants after fledging.

The mass examination of nest boxes by Tree Swallows during the late summer is (i) consistent with the hypothesis that the location of suitable future breeding sites during the premigratory period is favored because this period is one of little stress (Baker 1978), and (ii) consistent with the prediction that individuals should visit multiple breeding sites in order to assess site quality. Because the direction of migration in the fall is toward the south, it is likely that the great majority of birds taking part in this mass examination of boxes bred or fledged from areas north of JFKMWR and thus were visiting and examining the study site for the first time. During both mass examinations and normal attendant activity, my general impression was that examination behavior by one or a few individuals attracted more examiners. This suggests that nest site examination is an important social phenomenon in Tree Swallows. I have also observed mass examination of nest boxes by European Starlings (*Sturnus vulgaris*), another nonexcavating cavity-nesting species, in March (Lombardo and L. C. Romagnano, unpubl. data).

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