

SEXUAL DIFFERENCES IN PARENTAL EFFORT DURING THE NESTLING PERIOD IN TREE SWALLOWS (*TACHYGINETA BICOLOR*)

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ABSTRACT.—I investigated the nestling feeding, nest sanitation, and brood defense components of parental effort during the nestling period at 46 Tree Swallow (*Tachycineta bicolor*) nests to test the hypothesis that males contribute less parental effort than females in monogamous bird species. I observed sexual differences in parental effort during the nestling period. Females fed young and removed fecal sacs more frequently than did males. Within pairs, sexual differences in feeding nestlings and removing fecal sacs were associated with female plumage class. Parents with larger broods fed young and removed fecal sacs more often than did parents with smaller broods. However, feeding rates were not always proportional to brood size. Breeding female plumage class and parent sex both influenced the feeding rate per nestling at different brood sizes. During the nestling period the patterns of feeding and fecal-sac removals by males and females resembled a nestling weight-gain curve.

Males chased conspecific intruders more often than did females. Within pairs, sexual differences in brood defense were associated with breeding female plumage class. Brood size had no effect on the rate at which parents chased intruders in pairs where the breeding female was in adult plumage. Mates of females in subadult plumage that were tending larger broods chased intruders more often than did males with smaller broods. Parents chased intruders more often when their nestlings were older. Received 8 December 1989, accepted 21 November 1990.

IN MONOGAMOUS bird species that rear altricial young, it is often assumed that male parental effort (*sensu* Low 1978) is substantial and nearly equal to female parental effort (Trivers 1972, Emlen and Oring 1977, Wittenberger 1979). However, because of the fundamental sex differences in initial parental investment that are consequences of anisogamy (Trivers 1972), and uncertain paternity (e.g. see Gowaty and Karlin 1984, McKinney et al. 1984, Hoffenberg et al. 1988, Sherman and Morton 1988, Payne and Payne 1989), male parental effort should be less than female parental effort in putatively monogamous species (Alexander and Borgia 1979).

My purpose was to test the hypothesis that males make less parental effort than females in a monogamous bird species. I compared the parental efforts made by male and female Tree Swallows (*Tachycineta bicolor*) during the nestling period. I estimated parental effort by measuring the rates at which parents fed their nestlings, removed nestling fecal sacs from nests, and defended their broods from conspecific intruders.

Tree Swallows are almost exclusively monog-

amous, although polygyny has been reported in areas of superabundant food resources (Quinney 1983). Females do most of the nest building (Kuerzi 1941, Sheppard 1977), but males add most of the feathers that line the nest cup (Sheppard 1977, Cohen 1985). Only females incubate eggs and brood nestlings (Kuerzi 1941, Sheppard 1977, Dunn 1979). Both males and females feed aerial insects to their nestlings (Kuerzi 1941, Sheppard 1977, Leffelaar and Robertson 1986, Lombardo 1986, Quinney 1986), remove nestling fecal sacs (Sheppard 1977, Lombardo 1986, Quinney 1986), and defend the nest from predators and conspecific nest intruders during the nestling period (Lombardo 1985, 1986, 1987b). Leffelaar and Robertson (1986) argued that biparental care contributed to the maintenance of monogamy in Tree Swallows, except in areas of superabundant food resources (Quinney 1986).

I observed sexual differences in nestling feeding (*contra* Leffelaar and Robertson 1986, Quinney 1986), nest sanitation (*contra* Quinney 1986), and brood defense against conspecific intruders during the nestling period. These sexually different patterns of parental effort were influenced by brood size, total brood mass, brood

age, and the plumage class of the breeding female.

METHODS

This study was conducted from 1980 to 1983 at a nest-box trail at the John F. Kennedy Memorial Wildlife Refuge (JFKMWR) adjacent to Tobay Beach on the south shore of Long Island, New York (40°37'N, 73°27'W) (see Schaeffer 1972 for a complete description of the ecology of the study area). I established my study trail with 22 boxes in 1980, and by 1983 it contained 72 boxes. All boxes were located on the open expanse of a *Spartina* sp. salt marsh. Nest boxes were erected in three parallel rows, with boxes ca. 30 m apart (see Robertson and Gibbs 1982, Muldal et al. 1985).

Breeding females were captured on their nests between 0500 and 0600 EDT on the first day of incubation. Breeding males were captured and banded 1–2 days after the eggs in their nests hatched. Birds were sexed by the presence of a well-developed brood patch in females or a cloacal protuberance in males. Using a water-proof marking pen or acrylic paint, we uniquely color-marked all captured birds on their tails, wings, foreheads, throats, and breast feathers. Each bird was banded with a numbered USFWS aluminum band.

I determined rates of parental feeding, fecal-sac removal, and nest defense in 46 pairs of swallows during the nestling period. I observed under all weather conditions except heavy rain, when feeding activity was rare. For 60 min at least every third day, I observed 37 pairs from the hatching of their eggs until their nestlings fledged. Another 9 pairs were observed less frequently. The order in which pairs were observed each day was determined by rolling a die. On average, 4–6 pairs were observed daily, most often between 0600 and 1400 EDT. Parental effort was observed during 409 one-hour observation periods. During observations I recorded the identity and activity of all birds around the focal nest box. To determine whether or not parents that entered nest boxes actually fed nestlings, I observed the interiors of 8 nest boxes for 41 h with a portable video system (described in Lombardo 1986) from 1981 to 1983. Williams (1988) found that the energy expended by Tree Swallow parents feeding their nestlings was positively correlated with the number of feeding visits that they made, and he suggested that feeding frequency is a good measure of parental effort in this species (see also Nur 1988). Feeding and fecal-sac removal rates were calculated for all 409 observation periods.

I examined parental defense against conspecific intruders at the nest because this is a costly behavior. Nest defense takes away the time and energy that might be devoted to parental effort or self-maintenance.

Conspecific nest intruders are common at active nests during the nestling period (e.g. see Lombardo 1985, 1986, 1987a, b). Intruders do not cooperate with parents in the rearing of nestlings (Lombardo 1986) and are probably individuals in search of potential future nest sites (Lombardo 1987b). An intruder *visit* was recorded when an intruder flew about the nest box (i.e. circling or hovering within 3 m), perched on the box, or entered the box. A parent-intruder *encounter* was recorded as any time a parent (alone or with its mate) and one or more intruders were simultaneously present at a nest box or within 3 m of it. A parental *chase* was recorded any time a parent actively chased an intruder or supplanted it from a perch. Parental chase rates were calculated only for the 267 of 409 (65%) observation periods when intruders were present.

Breeding female Tree Swallows were categorized as either adult (AF) or subadult (SAF) based on plumage characteristics (Hussell 1983). Most females in subadult plumage are second-year birds, whereas most females in adult plumage are after-second-year birds. Males develop the monomorphic full adult breeding plumage before their first winter (Dwight 1900). Both sexes can breed in their first year, but SAFs differ from AFs in several reproductive variables (DeSteven 1978, 1980; Stutchbury and Robertson 1988). *Adult female pairs* are defined as breeding pairs in which the breeding female was in adult plumage. *Subadult female pairs* are defined as breeding pairs in which the breeding female was in subadult plumage.

Nestlings were weighed throughout the nestling period according to different weighing schedules each year. Nestlings were weighed to the nearest 0.5 g with a spring scale.

For most statistical analyses, observations of different individuals and repeated observations of the same individuals were pooled. However, some of the confounding problems in interpreting pooled data associated with pseudoreplication in design (Hurlbert 1984) were avoided in this study. Observation periods were assumed to be independent because (1) individuals were observed only once each day, (2) individuals of the same sex at different nests were not observed simultaneously, and (3) each observation period was unique in that brood size, total brood mass, and brood age were different for each daily observation period and for the repeated observations of each pair. Thus, although repeated observations of the same individuals were pooled, each observation period was independent. Data from different years were pooled because preliminary analyses showed no between-year effects on parental effort.

The data were tested for normality and homoscedasticity to determine the appropriate method of analysis (Zar 1974). Unless otherwise noted, regression analyses used square-root transformed data (Zar 1974). Statistical tests were performed using MIDAS (Fox and Guire 1976). Unless otherwise noted, the

TABLE 1. Sexual differences in parental effort by Tree Swallows. Components are reported as $\bar{x} \pm SD$ per hour. The numbers of feeding visits, fecal-sac removals, encounters with intruders, and chases of intruders are in parentheses; n = the number of 1-h observation periods. A Wilcoxon matched-pairs test was used to compare male and female components; ** = $P < 0.01$, *** = $P < 0.001$.

Type of effort	Male	Female	n	P
Feeding visits	6.93 \pm 5.65 (2,835)	8.33 \pm 5.62 (3,405)	409	***
Feeding visits/nestling	1.72 \pm 1.29	2.20 \pm 1.49	409	***
Fecal-sac removals	0.51 \pm 0.96 (208)	0.95 \pm 1.47 (387)	409	***
Fecal-sac removal/nestling	0.12 \pm 0.23	0.25 \pm 0.37	409	***
Encounters with intruders	1.81 \pm 1.76 (485)	1.53 \pm 1.82 (410)	267	**
Chases of intruders	0.55 \pm 0.89 (147)	0.32 \pm 0.68 (86)	267	**
Chases/nestling	0.31 \pm 0.39	0.19 \pm 0.25	267	***

components of parental effort are reported as $\bar{x} \pm SD$ per hour and the slopes of regression equations are reported as $b \pm SE$.

RESULTS

There were no statistically significant differences between adult female pairs and subadult female pairs in any component of parental effort or in mean intruder visits per hour.

There were statistically significant sexual differences in all components of parental effort (Table 1). Females made significantly more feeding visits and removed significantly more fecal sacs than did males. Males encountered and chased intruders significantly more often than did females (see also Lombardo 1987a). The same patterns of sexual differences in parental effort were found for AF pairs and SAF pairs when analyzed separately.

Within breeding pairs, sexual differences in parental effort were associated with breeding female plumage class. To examine sexual differences within pairs, I used the Wilcoxon matched-pairs test to compare the relative proportions of feeding visits, fecal-sac removals, encounters with intruders, and chases of intruders made by each parent in each pair observed for at least 5 h during the nestling period. In SAF pairs ($n = 23$), males made significantly smaller proportions of feeding visits (0.436 ± 0.126) and fecal-sac removals (0.312 ± 0.184) than their mates did, but encountered (0.556 ± 0.084) and chased (0.589 ± 0.214) intruders more often than their mates did (all $P < 0.05$). In contrast, in AF pairs ($n = 14$) the

relative proportions of feeding visits (0.434 ± 0.130), fecal-sac removals (0.415 ± 0.346), encounters (0.574 ± 0.176), and chases (0.667 ± 0.332) of intruders made by males were not significantly different from those made by their mates (all $P \geq 0.10$).

Patterns of feeding and fecal-sac removal.—Male and female feeding frequency of broods (Spearman's ρ , $r_s = 0.461$, $n = 409$, $P < 0.001$) and per nestling ($r_s = 0.326$, $n = 409$, $P < 0.001$) were significantly correlated with each other. The relative amounts of effort expended by mates in feeding frequency appear positively associated. Male and female fecal-sac removal rates from broods ($r_s = 0.326$, $n = 409$, $P < 0.001$) and per nestling ($r_s = 0.280$, $n = 409$, $P < 0.001$) were significantly correlated, which suggests that the relative amounts of effort expended by mates in nest sanitation were positively associated as well. These results were unaffected when these data were separately analyzed for AF pairs and SAF pairs.

Within each observation period a serial randomness test (Zar 1974) showed that males and females made feeding visits at random with respect to one another. These results were unaffected by separately analyzing these data for AF pairs and SAF pairs.

The temporal pattern of feeding visits differed for AF pairs and SAF pairs. Parental feeding visits were categorized as how many visits were made by one parent before the other parent made a feeding visit (Table 2). In AF pairs, males were just as likely as their mates to make runs of ≥ 2 consecutive feeding visits (males, 235 of 698 [34%] visit types were runs of ≥ 2

TABLE 2. The patterns of feeding visits to nestlings by Tree Swallows. Visit types are categorized by the number of food deliveries made by one parent before the other parent made a delivery. Nest types are categorized by the plumage class of the breeding female; AF = adult female ($n = 252$ 1-h observation periods), SAF = subadult female ($n = 157$ 1-h observation periods).

Nest type	Parent sex	Visit type					
		1	2	3	4	5	>5
All pairs	Male	785	218	75	24	15	23
	Female	734	236	66	32	11	58
AF pairs	Male	463	147	47	15	11	15
	Female	478	130	33	18	6	23
SAF pairs	Male	322	71	28	9	4	8
	Female	256	106	33	14	5	35

visits; females, 210 of 688 [31%] visit types were runs of ≥ 2 visits; $\chi^2 = 1.57$, $df = 1$, $P > 0.10$). In contrast, males in SAF pairs were less likely than females to make runs of ≥ 2 consecutive feeding visits (males, 120 of 422 [27%] visit types were runs of ≥ 2 visits; females, 193 of 449 [43%] visit types were runs of ≥ 2 visits; $\chi^2 = 24.51$, $df = 1$, $P < 0.001$).

Feeding and fecal-sac removal rates and brood size.—Parents with larger broods made more feeding visits per hour to broods and removed more fecal sacs per hour from broods than did parents with smaller broods (Fig. 1). There were sexually different patterns in this type of parental effort in relation to brood size (Fig. 1).

Males mated with AFs increased their effort at making feeding visits to broods at a rate greater than their mates' over brood sizes 1–6 (Fig. 1a, male slope = 0.49 ± 0.06 , $r^2 = 0.233$, $P < 0.001$; female slope = 0.28 ± 0.05 , $r^2 = 0.131$, $P < 0.001$, $t = 12.49$, $df = 490$, $P < 0.001$). Males and females in AF pairs with brood sizes 1–6 increased their fecal-sac removal rates from broods at similar rates (Fig. 1a, $t = 0.35$, $df = 490$, $P > 0.50$).

With no data for brood sizes 1 and 2, I related feeding and fecal-sac removal rates for SAF pairs only to brood sizes 3–6 (Fig. 1b). Males mated with SAFs increased feeding and fecal-sac removal rates at a rate greater than their mates' from brood size 3–6 (Fig. 1b, male slope = 0.47 ± 0.10 , $r^2 = 0.127$, $P < 0.001$; female slope = 0.33 ± 0.11 , $r^2 = 0.059$, $P < 0.01$; $t = 6.17$, $df = 308$, $P < 0.001$).

Pairs with brood sizes 3–6 were the most commonly observed (91% of observation periods for all pairs), and similar male and female patterns of feeding and fecal-sac removal rates from brood sizes 1–6 for AF pairs were observed from

brood sizes 3–6 (Fig. 1a). The data from brood size 6 were obtained from only one pair each of AF pairs and SAF pairs.

Male and female increases in feeding and fecal-sac removal rates were not proportional to brood size, and they were different (Fig. 1). In AF pairs, males with larger broods made more feeding visits/h/nestling ($b = 0.04 \pm 0.01$, $r^2 = 0.030$, $P < 0.001$) and removed more fecal sacs/h/nestling ($b = 0.04 \pm 0.01$, $r^2 = 0.033$, $P < 0.001$) from brood sizes 1–6. Adult female feeding visits/h/nestling are best described by a quadratic equation ($y = 0.07x^2 - 0.06x + 2.46$, $r = 0.11$) that significantly departs from linearity ($P < 0.001$). Female feeding visits/h/nestling declined from brood size 1 to 3, but increased from brood size 3 to 6 ($b = 0.08 \pm 0.03$, $r^2 = 0.030$, $P < 0.05$). Adult female fecal-sac removals/h/nestling are also best described by a quadratic equation ($y = 0.04x^2 - 0.03x + 0.70$, $r = 0.043$, $P < 0.01$) and followed the same pattern as feeding visits/h/nestling. In contrast to their mates, males mated with AFs did not provide more feeding visits/h/nestling or remove more fecal sacs/h/nestling in larger broods from brood sizes 3–6 (Fig. 1a, both slopes, $P > 0.05$).

In SAF pairs, neither females nor males made more feeding visits/h/nestling or removed more fecal sacs/h/nestling in larger broods from brood sizes 3–6 (Fig. 1b, all slopes, $P > 0.05$).

Parental nest defense and brood size.—The patterns of nest defense were different for AF pairs and SAF pairs (Fig. 2). In AF pairs, parents with larger broods did not chase intruders more often than did parents with smaller broods (both slopes, $P > 0.10$; Fig. 2a). In SAF pairs, males with larger broods chased intruders more often ($b = 0.20 \pm 0.09$, $r^2 = 0.04$, $P < 0.05$), whereas

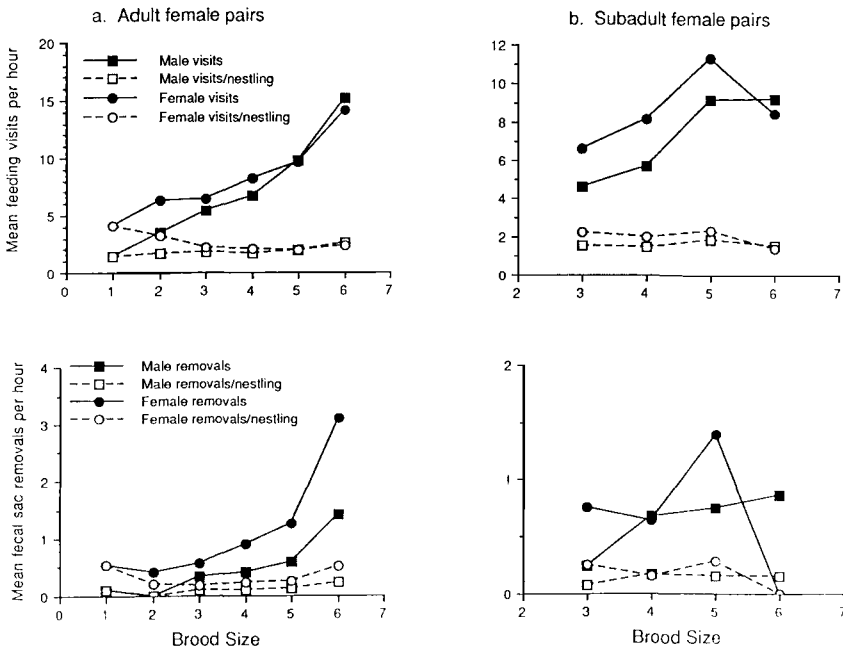


Fig. 1. Rates of Tree Swallow parental feeding visits and fecal-sac removals for brood size. The slopes of the regressions are given in the text. (a) Adult female pairs. Sample size of brood size (BS) 1 = 20 1-h observation periods. BS3 = 54, BS4 = 74, BS5 = 77, and BS6 = 10. (b) Subadult female pairs. Sample sizes of BS3 = 37, BS4 = 59, BS5 = 52, and BS6 = 8.

their mates did not ($b = 0.03 \pm 0.08, r^2 = 0.0009, P > 0.75$) (Fig. 2b).

Over brood sizes 1-6, neither male nor female chases/h/nestling in AF pairs was affected by brood size (both slopes, $P > 0.10$, Fig. 2a). With-in both AF pairs and SAF pairs, there was a lack of relationship between the parental chases/h/nestling and brood size over brood sizes 3-6 (all slopes, $P > 0.10$).

Feeding and fecal-sac removal rates and brood age.—Male and female patterns of feeding visits to broods (Fig. 3a) and fecal-sac removals from broods during the nestling period were similar (Fig. 3b). Both feeding visits and fecal-sac removals increased from hatching, plateaued from nestling day 6 to day 15 (the day the first egg in a clutch hatches = nestling day 1), then declined to fledging (Fig. 3; also see fig. 2 in Lombardo 1987b). In general, feeding visits and fecal-sac removals followed a typical Tree Swallow nestling weight gain curve. Tree Swallow nestlings gain weight until about nestling day 14 and then lose weight until fledging (Paynter 1954, Ricklefs 1968, Zach 1982, Zach and Mayoh 1982, this study). Note that females made more

feeding visits per hour and removed more fecal sacs per hour each day of the nestling period (with the exceptions of nestling days 9 and 10) than did males. These differences between sexes were especially pronounced from nestling day 15 to day 21 (Fig. 3), but daily differences in mean rates were not statistically significant. The same patterns of feeding visits and fecal-sac removals during the nestling period were found when pairs were separately analyzed.

Feeding visits/h/nestling did not change significantly with brood age (male slope, $b = -0.0050 \pm 0.0049, r^2 = 0.0026, P = 0.31$; female slope, $b = -0.0024 \pm 0.0046, r^2 = 0.0007, P = 0.60$; Fig. 3a). The same patterns of feeding visits/h/nestling were found when AF and SAF pairs were separately analyzed.

As broods got older, both males ($b = 0.0089 \pm 0.0025, r^2 = 0.031, P < 0.001$) and females ($b = 0.018 \pm 0.003, r^2 = 0.077, P < 0.001$) removed more fecal sacs/h/nestling (Fig. 3b). This same pattern of fecal-sac removals/h/nestling was found when AF pairs and SAF pairs were analyzed separately except that the elevation of the AF regression line ($b = 0.019 \pm 0.003, r^2 =$

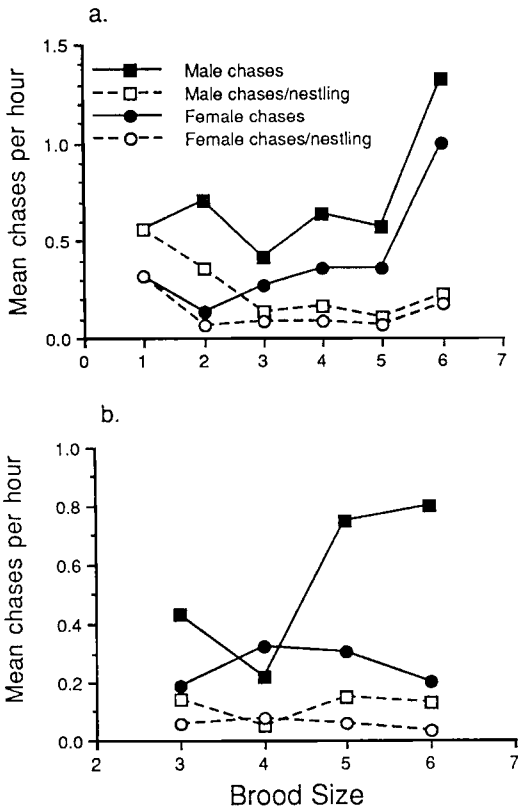


Fig. 2. Rates of Tree Swallow parental chases of conspecific intruders and brood size. The slopes of the regressions are given in the text. (a) Adult female pairs. Sample size of brood size (BS) 1 = 16 1-h observation periods, BS2 = 7, BS3 = 33, BS4 = 45, BS5 = 53, and BS6 = 6. (b) Subadult female pairs. Sample size of BS3 = 21, BS4 = 41, BS5 = 40, and BS6 = 5.

0.077, $P < 0.001$) was significantly higher than the male regression line ($b = 0.0090 \pm 0.0025$, $r^2 = 0.031$, $P < 0.001$) ($t = 2.80$, $df = 491$, $P < 0.01$). Adult females removed more fecal sacs/h/nestling each day of the nestling period than did their mates.

Parental nest defense and brood age.—There was a significant correlation between mean parental (male + female) chases per hour and brood age ($r_s = 0.61$, $P < 0.05$, Lombardo 1987a). These results were unaffected by separately analyzing these data for AF pairs and SAF pairs. A subset of the Lombardo (1987a) data against brood age is included (Fig. 4).

Neither males ($b = -0.003 \pm 0.003$, $r^2 = 0.003$, $P > 0.30$) nor females ($b = 0.005 \pm 0.003$, $r^2 =$

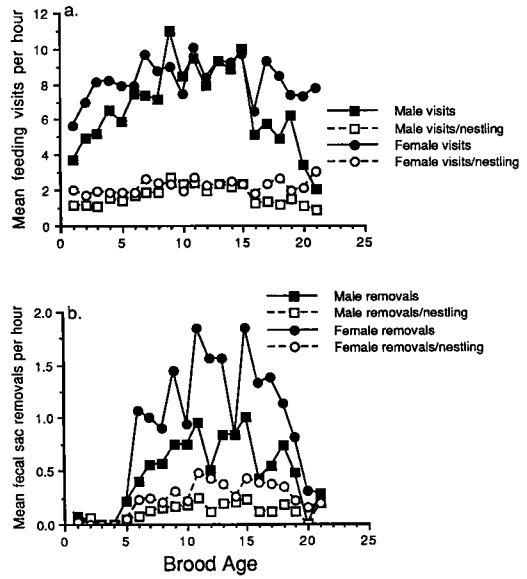


Fig. 3. Rates of Tree Swallow parental feeding visits and fecal-sac removals versus brood age (days). All brood sizes are included. The slopes of the regressions are in the text. (a) Mean feeding visits per hour and brood age. (b) Mean fecal-sac removals per hour and brood age.

0.01, $P > 0.10$) chased intruders more often as nestlings got older. This result was unaffected when data were analyzed separately.

Feeding and fecal-sac removal rates and total brood mass.—There were sexual differences in feeding and fecal-sac removal rates and total brood mass, and these patterns were different for AF pairs and SAF pairs. Within AF pairs, rates of male and female feeding visits and fecal-sac removals from broods and per nestling significantly increased with total brood mass (all slopes, $P < 0.01$). For AF pairs, female feeding visits/h/nestling did not significantly increase with total brood mass. Within SAF pairs, only male fecal-sac removals per hour from broods and per nestling significantly increased with total brood mass (both slopes, $P < 0.05$).

DISCUSSION

I found significant sexual differences in parental effort during the nestling period in Tree Swallows. These differences were associated with the age-correlated plumage class of the breeding female. These results differ from Lefelaar and Robertson (1986) and Quinney (1986),

who found that male and female Tree Swallows fed nestlings at very similar rates. Quinney (1986) also found that males removed a disproportionately large number of nestling fecal sacs, which is the opposite of my observation (Table 2). Leffelaar and Robertson's study was restricted to pairs at nests where the breeding female laid a clutch of 6 eggs, and thus their sample was probably biased in favor of AF pairs (see DeSteven 1978, Stutchbury and Robertson 1988). Quinney (1986) studied only pairs with females in adult plumage.

The differences between my observations and those of Leffelaar and Robertson (1986) and Quinney (1986) may reflect geographic variation in the costs associated with providing parental care. In addition, the sexual differences in feeding rates I observed contrast with the equality of feeding roles in other species of swallows (Moreau 1947, Allen and Nice 1952, Bryant and Westerterp 1980, Ball 1982).

The analyses of patterns of sexual differences in parental effort within pairs suggest that males mated with subadult females are less competent than their mates at feeding nestlings and removing fecal sacs. Further, the relative abilities of males and females in adult female pairs at feeding nestlings and removing fecal sacs were comparable. In addition to differences in feeding frequency, there can also be differences in the amount of prey delivered to nests during each visit (*load size*) (e.g. Biermann and Sealy 1982, Wittenberger 1982, Simmons 1986, Grunzel 1987, Jones 1987) or the type of prey delivered to young (Pinkowski 1978). Quinney (1986) reported no differences between male and female Tree Swallows in load size and prey types captured. However, Stein (1986) reported that male Tree Swallows delivered larger items than females. It is not known whether adult and subadult females differ in load size and prey type. Because of their relative inexperience, subadult females may be less competent aerial foragers than adult females (DeSteven 1978, Stutchbury and Robertson 1988). Foraging ability increases with age (e.g. Orians 1969, Recher and Recher 1969, Dunn 1972, Buckley and Buckley 1974, Schreiber and Young 1974, Morrison et al. 1978, Searcy 1978, Burger 1981, MacLean 1986). I did not determine load sizes and prey type in this study. Given the different results obtained by Quinney (1986) and Stein (1986), the questions of sex- and age-related differences in load size

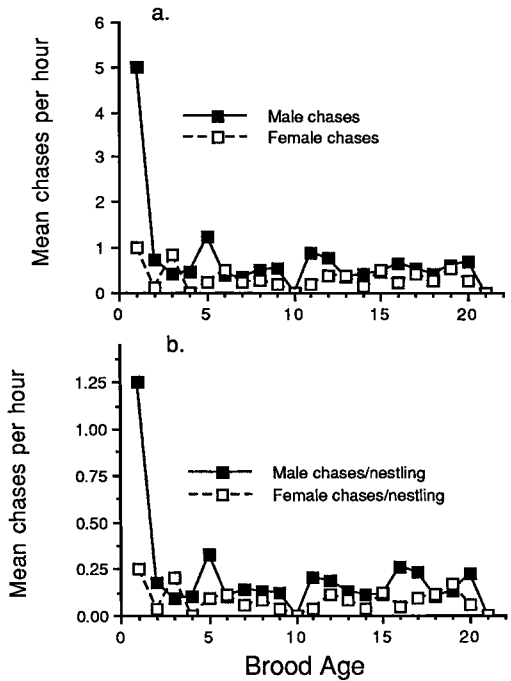


Fig. 4. Rates of Tree Swallow parental chases of conspecific intruders and brood age. All brood sizes are included. The slopes of the regressions are in the text. (a) Mean chases per hour. (b) Mean chases per hour per nestling.

and foraging ability in Tree Swallows require further study.

Male and female feeding rates were positively associated with one another, which implies complementarity between feeding roles (Grunzel 1987). Individual behavioral differences among cooperators may be advantageous (Clark and Ehlinger 1987), and parent Tree Swallows can only partially compensate for mate loss by increasing their own food delivery rates (Leffelaar and Robertson 1986).

The patterns of feeding visits showed no significant tendency for males and females to alternate visits. Litovich (1982) showed that parental feeding rates were influenced directly by nestling begging rates in the European Starling (*Sturnus vulgaris*). It is likely that in Litovich's study parental efforts were influenced by the efforts of their mates only as those efforts affected the demands nestlings made for food (see Hussell 1988). For example, Whittingham (1989) showed that male Red-Winged Blackbirds (*Agelaius phoeniceus*) did not assist their mates in

feeding nestlings when female provisioning met nestling demands.

The temporal patterns of feeding visits were different for adult and subadult pairs. Adult females were as likely as their mates to make ≥ 2 consecutive feeding visits before being spelled by them. In contrast, subadult females were more likely than their mates to make ≥ 2 consecutive feeding visits. This difference in foraging behavior in subadult female pairs remains unexplained.

Parents with larger broods fed more frequently and removed more fecal sacs per hour (Fig. 1). Leffelaar and Robertson (1986) obtained similar results. Parent birds commonly increase their feeding rates of nestlings at larger brood sizes (e.g. see Moreau 1947, Lack 1954, Gibb 1955, Royama 1966, Robertson and Biermann 1979, Power 1980, Biermann and Sealy 1982, Johnson and Best 1982, Nur 1984, Grundel 1987). The patterns of response to increases in brood size differed in adult and subadult female pairs (Fig. 1).

Tree Swallow subadult female pairs are as capable as adult female pairs in rearing experimentally enlarged broods (DeSteven 1980). Nestlings in enlarged broods, however, were lighter than those in control broods reared by subadult pairs. No such difference occurred between enlarged and control broods reared by adult female pairs. DeSteven's (1980) results support the hypothesis that parents in subadult female pairs are less capable than adult female pairs in feeding nestlings.

Sexually different patterns of energy expenditure in parental effort through the entire nesting cycle may place greater energetic stress on females than on males. Except for the energetically expensive and risky acts of adding feathers to the nest cup and nest defense, male Tree Swallows appear to expend little on parental effort until hatching (ca. 30 days). Their mates do most of the nest building and add nest feathers, lay eggs, incubate eggs, brood nestlings, and defend the nest. Male and female parents in adult female pairs expended energy at statistically indistinguishable levels while feeding nestlings (Williams 1988). Williams (1988) did not compare the energy expenditure levels of male and female parents in subadult female pairs.

Although parental feeding rates generally increase with brood size, the increase is often not

proportional to brood size (e.g. see Moreau 1947; Gibb 1950, 1955; Lack 1954; Royama 1966; Morehouse and Brewer 1968; Best 1977; Walsh 1978; Zammuto et al. 1981; Johnson and Best 1982; Nur 1984; Leffelaar and Robertson 1986). Gibb (1950, 1955) and Lack (1954) hypothesized that the inability of parents to sustain high feeding rates accounted for this pattern. The Gibb-Lack hypothesis predicts that feeding rate per nestling should remain relatively constant at small brood sizes but decline as brood size increases beyond the average brood size (fig. 6 in Nur 1984). Nur (1984) challenged this widely held view and argued that parental feeding rates represent a trade-off between fledgling and parental survival so that at each brood size parents feed nestlings at a rate that maximizes parental fitness. Studies on the Blue Tit (*Parus caeruleus*; Nur 1984) and Great Tit (*Parus major*; Smith et al. 1988) support Nur's hypothesis.

Leffelaar and Robertson (1986) reported that Tree Swallow parental feeding rates per nestling decreased linearly as brood size increased. I found both breeding female plumage class and parent sex influenced patterns of feeding visits/h/nestling at different brood sizes (Fig. 1). This may be explained partially by the hypothesis that males, because of sexually different patterns of parental effort over the nesting cycle, may devote relatively more energy to parental effort during the nestling period than their mates and thus increase their feeding visits/h/nestling in proportion to brood size. The equation that describes adult female feeding visits/h/nestling resembles the curve for Blue Tits (fig. 2 in Nur 1984). Because the constant parental effort during the nesting cycle is energetically draining, adult female Tree Swallows may have made a trade-off to enhance offspring survival and reduce their own survivorship through adjusting their feeding visits/h/nestling. In contrast, in subadult female pairs the patterns of feeding visits/h/nestling (Fig. 1b) suggest that each nestling was fed a fairly constant number of feedings per hour regardless of brood size. More data on feeding rates at brood sizes 1, 2, and 6 are needed to adequately test the Gibb-Lack hypothesis for subadult female pairs.

Male and female patterns of feeding visits and fecal-sac removals over the nestling period were very similar (Fig. 3). The pattern resembled the shape of a typical Tree Swallow nest-

ling weight-gain curve. In contrast, Leffelaar and Robertson (1986) found that parental feeding rates increased linearly from nestling day 1 to day 10 and then leveled off for the remainder of the period. Although only females brood newly hatched nestlings, males did not increase feeding during this period as has been found in other species (e.g. Royama 1966, Seel 1969, Best 1977, Pinkowski 1978, Power 1980, Breitwisch et al. 1986).

Males defended nests against intruders more often than females did (Table 1; Lombardo 1987a). This pattern is common in birds (e.g. see Slack 1976, Merritt 1984, Shields 1984, Breitwisch et al. 1986, Buitron 1988, Knight and Temple 1988). Males that provide paternal care but have uncertain paternity should specialize in the type of parental care, *shareable care*, that can be consumed by more than one offspring at a time (e.g. brood defense). The costs of shareable care are less influenced by the number of offspring than are the costs of the nonshareable components (Wittenberger 1979, 1981; Lazarus and Inglis 1986). *Nonshareable care* is consumed by only one offspring at a time (e.g. a bolus of food delivered to one begging nestling). Specializing in providing shareable care lowers the costs to males of providing care to nongenetically related offspring (H. W. Power pers. comm.). Approximately 24% of male Tree Swallows may be commonly cuckolded (Morrill and Robertson 1990).

The different patterns of sexual differences within pairs in brood defense suggest that subadult females are less competent nest defenders than their mates. Further, the relative brood defense abilities of mates within adult female pairs are comparable. Brood size had no effect on parental defense in adult female pairs (Fig. 2a). In subadult female pairs, males with larger broods made more chases per hour (Fig. 2b). Because intruder visitation and parental feeding rates are positively correlated (Lombardo 1986) and male feeding frequency increased with brood size (Fig. 1b), male responses may have been a secondary effect of increased encounters with intruders at larger brood sizes rather than increased effort independent of intruder abundance. Other investigators have shown various relationships between brood defense and brood size (e.g. Ricklefs 1977, Gottfried 1979, Robertson and Biermann 1979, Grieg-Smith 1980, Regelman and Curio 1983, Curio

et al. 1984). I found no clear support for Lazarus and Inglis' (1986) prediction that parental effort at providing nonshareable care should increase with brood size.

Parents chased intruders more often when their nestlings were older (Fig. 4). Parental chase rates during the nestling period corresponded to increased intruder visits per hour with brood age ($r_s = 0.26$, $n = 267$, $P < 0.001$). This increase in intruder visits with brood age was an artifact of the increase in intruder abundance at the study site as the breeding season progressed (Lombardo 1987b). The apparent increase in parental effort at nest defense against conspecifics may have been an artifact of the increase in conspecific nest-intruder visits to nests as the season progressed rather than increased parental effort that was independent of intruder abundance.

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