

EFFECTS OF FOOD ABUNDANCE AND MALE PARENTAL CARE ON REPRODUCTIVE SUCCESS AND MONOGAMY IN TREE SWALLOWS

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ABSTRACT.—We examined the roles of food abundance and male parental care in the maintenance of monogamy in Tree Swallows (*Tachycineta bicolor*). Mated, male Tree Swallows were removed from territories to simulate the lack of male parental care that would be incurred by secondary females. Removals took place in lakeshore and roadside habitats in central Alberta, Canada. Insect sampling over three breeding seasons indicated that the lakeshore had greater biomass of insects than the roadside during egg laying, but there was no difference during the nestling period. Both our male removal experiment and natural cases of polygyny suggested that loss of male parental care had little effect on reproductive success or survival of females or their offspring. Unaided females increased their per-capita nest-visit rate in two of three years, so the rate of visitation per nestling did not differ significantly between unaided females and both the male and female at control nests. Control females at the lakeshore produced more fledglings than control females at the roadside. This difference in productivity was due to earlier laying and larger clutches at the lakeshore than at the roadside and not to differences in brood reduction or insect abundance during the nestling period. In both habitats, male parental care was relatively unimportant to female reproductive success and, therefore, within a given habitat secondary females did not incur a reproductive cost. All natural cases of polygyny occurred at the lakeshore. We suggest that polygyny occurred at the lakeshore, and not at the roadside, because food abundance was greater during laying at the lakeshore, and this allowed secondary females to lay more eggs and produce more fledglings than females mated to monogamous males at the roadside. Received 11 March 1991, accepted 10 February 1992.

THE ABUNDANCE and distribution of food are thought to affect the mating systems of birds (Emlen and Oring 1977, Oring 1982). For example, some models of avian mating systems (Orians 1969, Emlen and Oring 1977) predict higher levels of polygyny on territories that have higher food abundance. These models assume that females prefer to settle on territories with more food because they will be able to produce relatively more offspring. Food abundance may influence mating systems and reproductive success in species with biparental care via two mechanisms. First, food abundance may affect the cost to females of feeding their nestlings, and this may influence whether they choose unmated or already-mated males as mates. In many birds secondary mates of polygynous males receive little or no assistance with feeding nestlings and, as a consequence, raise fewer young than either primary or monogamous females (reviewed in Dyrce 1988).

Under these conditions, females should choose monogamy more frequently in habitats with less food because male parental care should be relatively more important to female reproductive success. Second, females may choose mating situations based on food conditions during settlement or laying if reproductive success is influenced more strongly by laying date or clutch size than by male assistance with feeding nestlings. If, early in the season, food abundance is greater on the territories of already-mated than unmated males, then females may choose secondary mate status because they can produce more offspring by laying earlier or by laying larger clutches. These two mechanisms are not exclusive, but they suggest different ways that food abundance can affect both reproductive success and mating behavior in bird populations.

Many previous studies have suggested that monogamy in birds is maintained by the importance of male parental care to female reproductive success (Winkler and Wilkinson 1988). This interpretation is based on a large number of male-removal studies that indicate that male parental care improves female reproductive

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success (see reviews in Wolf et al. 1988, Bart and Tornes 1989, Dunn and Hannon 1989). However, most male-removal studies cannot estimate the relative importance of male parental care to the maintenance of monogamy, because they rarely control for other factors, such as food abundance, that also influence female reproductive success and mate choice. In contrast to the male-removal experiments, studies that have supplied supplemental food suggest that the level of food early in the breeding season influences reproductive success and mating behavior (Ewald and Rohwer 1982, Davies and Lundberg 1984). To understand the relative importance of food abundance and male parental care to the maintenance of monogamy it will be necessary to control for the effects of both of these factors on female reproductive success.

In this paper, we investigate the influence of variation in food abundance and male parental care on the reproductive success and mating behavior of female Tree Swallows (*Tachycineta bicolor*). We removed mated male swallows to simulate the lack of male parental care incurred by secondary females. This was a valid assumption in our study, because secondary females rarely received male assistance with feeding nestlings (P. Dunn, unpubl. data). The removals were done at two sites (lakeshore and roadside) that differed in insect abundance during the laying, but not the nestling, period. Therefore, if male parental care was not important to female reproductive success in either habitat, then any differences between the lakeshore and roadside in female reproductive success or mate choice probably would be due to differences between the sites in conditions during the laying season.

METHODS

Study animal.—Tree Swallows are aerial insectivores that nest readily in nest boxes. They are usually monogamous, but polygyny occurs occasionally (5–8% of males; Quinney 1983, this study). At our study area in central Alberta, Tree Swallows have a single brood of altricial nestlings each year. Eggs are incubated by the female for 13 to 15 days and young fledge at 18 to 20 days of age. During incubation the male guards the nest, but does not incubate. In monogamous pairs both parents feed the nestlings. Polygynous males usually feed young in the nest of their primary female (the first female to settle), so the secondary female receives little or no male parental care. Foraging occurs both on and off the territory, which

is a small area around the nest box. We considered males polygynous only if they were seen copulating with two females and they defended the nest boxes occupied by these females throughout the season. All females in our cases of polygyny were marked individually. Copulations in Tree Swallows occur on the nest box or on nearby perches.

Study area.—Tree Swallows were studied at Beaverhill Lake, Tofield, Alberta (53°38'N, 112°36'W) during May through July 1986–1988. Beaverhill Lake is a large (130 km²), shallow lake surrounded by pastures and aspen (*Populus* spp.) parkland. The lakeshore is characterized by large emergences of midges (Chironomidae) in mid-May. Adult swallows often forage low over the lake surface at this time. The roadside habitat that we studied was 1.5 km southwest of the lakeshore site. The roadside site did not have large emergences of midges because it was 1 km south of the lake and the prevailing winds during the study were from the southwest (i.e. not from the lake; Environment Canada 1986–1988). Individually marked swallows usually foraged less than 300 m from the nest box and marked birds from one habitat were never observed foraging in the other habitat.

We placed 80 nest boxes in lakeshore habitat and 40 nest boxes in roadside habitat in 1986. These numbers were increased to 100 nest boxes at the lakeshore in 1987 and 1988, and to 55 and 52 boxes at the roadside in 1987 and 1988, respectively. All nest boxes were of the same dimensions and all faced east. Most nest boxes were spaced 24 m apart at the lakeshore and roadside. As part of another experiment (Dunn and Hannon 1991), some nest boxes at the lakeshore had additional boxes placed around them in a spiral at 1, 4, 8 and 16 m, and some boxes at the roadside had additional boxes placed 1 m east and 4 m west. This difference in number and spacing of boxes between the lakeshore and roadside did not confound our analysis of reproductive success, because nest density did not affect fledging success (Dunn and Hannon 1991); however, it may have affected the frequency of polygyny in each habitat. We address this potential effect in the discussion. All boxes were in the same location each year except at the roadside where boxes were moved 700 m west after 1986 (to keep boxes away from a temporary pond).

Estimation of insect abundance.—To estimate a relative index of insect abundance, we used "tow nets" that have proven effective for sampling insects eaten by Tree Swallows (Quinney and Ankney 1985). The insect sampling technique and equipment were identical to those described by Hussell and Quinney (1987). There is a significant positive correlation between clutch size and insect abundance as measured by these nets (Hussell and Quinney 1987). These nets collect all of the taxa and size classes of insects delivered to nestlings, although not in the same proportion as in the nestlings' diet (Dunn 1989). Therefore, we believe that these nets provide an index of relative food avail-

ability. We emphasize that our results are based on relative indices, and any potential biases in sampling are likely to be similar between habitats. Insects flew or were blown into the tow nets and were collected in a jar of 70% ethanol attached to a sleeve at the end of the net. Two nets were used in each habitat each year. Nets were 2 m above the ground and many birds foraged near this height at our study area. In southern Ontario, Holroyd (1972) found that Tree Swallows spent 47% of their foraging time below 4.6 m. The nets were opened manually at dawn and closed at dusk on almost every day from 6 to 12 May (depending on the year) through 2 July. Nets were not operated on two days in each of 1986 and 1987 and one day in 1988 because of high winds or snow. Hourly wind speeds were calculated for each net at each site to correct for variation in the amount of air sampled per day by each net. These hourly wind speeds were estimated from regressions based on wind-speed measurements made at each net with hand-held anemometers and wind speeds recorded at Environment Canada weather stations (Elk Island National Park, 30 km northwest and Edmonton International Airport, 80 km west). A correction for low wind speed was made following Hussell and Quinney (1987). Insect biomass was calculated by counting the number of insects in different size and taxon categories and multiplying that number by the mean dry biomass of each size and taxon category. An insect biomass index (IBI) was calculated for each day by dividing the daily insect biomass by the kilometers of wind passing through the net while it was operating that day. We did not include insects over 13 mm long in the insect biomass index calculation, because they are rarely fed to nestlings (0.7%, Quinney and Ankney 1985, this study). Insects less than 1 mm were excluded for the same reason.

Capture, marking, and determination of age and sex.—Swallows were caught in the nest box (Cohen and Hayes 1984, Magnusson 1984), banded and individually color-marked on the breast with felt-tipped ink markers. We individually color marked 86% and 19% of all breeding females and males, respectively. For behavioral observations, we only used breeding pairs in which at least one member was individually color-marked. Birds were classified to sex by the presence of a brood patch in females or cloacal protuberance in males. Females that were yearlings (SY = second calendar year of life) and older (ASY = after second calendar year) were distinguished by plumage differences (Hussell 1983). Other studies have found differences between yearling and older females in clutch size and fledging success (DeSteven 1978); however, we found no such differences in this study. Nevertheless, we have generally excluded data from yearling females to facilitate comparisons with other studies. Data from yearlings ($n = 6$) were only included in the analysis of return rates where samples sizes were small. There was no difference between the lake-

shore (20% SY females; 31/156) and roadside (14% SY females; 12/86) in the proportion of yearling females that nested at each site ($G = 1.35$, $P = 0.2$, $df = 1$).

Male-removal experiment.—In each habitat, control and male-removal nests were chosen randomly from monogamous pairs. Over three years, males were collected from 47 nests: 7 nests during laying; 25 nests during incubation; and 15 nests between hatch and seven days of age (nestlings can fledge after 16 days). This total does not include unaided females that gained a replacement mate ($n = 2$ females; these mates killed the young at hatch). Six of the 47 unaided females were yearlings. The number of visits to nests by observers was similar for nests of control and unaided females. We examined the data from nests of unaided females for differences in timing of male removal that may have biased our analyses. Mean date of male removal (relative to hatch date) did not differ between lakeshore and roadside habitats ($P = 0.16$; two-way ANOVA). However, timing of male removal did differ among years ($P < 0.001$) because males were removed from laying through the early nestling period in 1987, while we removed males only around the time of hatch in 1986 and 1988. If male parental assistance had a cumulative effect on fledging success, then one would expect to see a positive correlation between the timing of male removal and subsequent fledging success. However, no such relationship was found in this study ($r^2 = 0.001$, $P > 0.5$). Therefore, male removal data from throughout the breeding season were pooled within years, but we controlled for year effects in all analyses.

Estimation of female settlement date.—We estimated when pair bonds were established: (1) to determine which birds were the primary and secondary mates of polygynous males; and (2) to compare the fledging success of monogamous and secondary females from different territories that paired at the same time. Settlement date and date of nest initiation were used to estimate the date pair bonds formed. Settlement date was the first date of three consecutive days during which two birds were seen on or near a nest box (methods similar to Stutchbury and Robertson 1987). Ten 1-min scans were made daily at each nesting area in 1988 to determine if a nest box was occupied. Nest initiation was estimated as the first day that pieces of grass were found in the nest box. Settlement date was significantly correlated with date of nest initiation in 1988 ($r^2 = 0.58$, $df = 63$, $P = 0.001$). Stutchbury and Robertson (1987) did not find a significant correlation, but the breeding season is shorter and more synchronous in our study population (Dunn and Robertson in press). In 1986 and 1987 settlement data were not collected on a daily basis, so we estimated the date of pair formation from nest initiation date. This procedure allowed us to unambiguously assign females to primary or secondary status in five of seven cases of polygyny. In the remaining two cases, the primary and secondary females settled on the same

date, so we assigned secondary status to the female that did not receive male assistance with feeding nestlings. Our results remained unaffected when data from primary and secondary females were switched in these two cases.

Estimation of reproductive success and survival.—Each nest box was visited every two to three days around the time of clutch initiation to determine date of laying the first egg (laying date) and clutch size. Nests were checked starting one or two days before the calculated hatch date to determine hatching date (day the first egg hatched was nestling day 0). Nestlings were weighed with a Pesola scale just before fledging (at 16 days of age) to assess body condition. Fledging success was the number of nestlings in the nest at 16 days of age minus birds found dead in the box on visits after 20 days after hatch. The percentage of nests that produced at least one young (successful nests) and fledging success of successful nests were used to determine if male parental care made a significant contribution to the reproductive success of the pair.

For the purpose of comparing insect abundance with timing of breeding, we defined three periods during breeding: egg-formation/laying; incubation; and nestling. The laying period was defined as four days before the date of the 10th percentile of clutch initiation to two days before the date of the 90th percentile of clutch completion. These values were chosen based on studies of egg formation (Schifferli 1976) and timing of fertilization (Leffelaar and Robertson 1984). The nestling period was from 15 days (approximate length of incubation) after the 10th percentile of clutch completions to 30 days (approximate length of incubation and nestling periods) after the 90th percentile of clutch completions. The incubation period was the period between the laying and nestling periods.

Females could compensate for loss of male parental care by increasing their rate of food delivery to nestlings. This may result in lower body mass or return rate of unaided than control females. We weighed females between 1500 and 1800 when their nestlings were 16 days old to determine if unaided females weighed less than control females. Rate of return to the study area was analyzed from banded swallows nesting in 1986 and 1987 to determine how many offspring and parents recruited into the breeding population.

Observations of parental care.—Observations of individually marked females at control and male-removal nests were made at each nest every two to three days. An initial nest was chosen randomly for observation every two to three days (at the start of a new series of observations), after which nests were picked systematically. Observation sessions were 20 min long and were spread as evenly as possible among three periods of the day: morning (sunrise to 0900), midday (0900 to 1500), and late afternoon (1500 to 2000). During each observation session, observers recorded all

visits by the female and male inside the nest box and, for the females, the time engaged in particular behaviors: inside the nest box; perched on the box or post; flying; and perched at the entrance hole looking into or out of the nest box.

During the nestling period in 1986–1988, 31 control and 27 unaided adult females were observed for a total of 264 and 266 h, respectively. Because the same individuals were observed several times, we used averages of each behavior calculated from multiple observations of the same bird (only nests with at least three observation sessions were analyzed). This reduces the problem of nonindependent samples. However, it assumes that: (1) brood size and age have the same relative effect on the behavior of unaided and control females (i.e. similar slopes); and (2) observations of unaided and control females were distributed similarly. These were valid assumptions in our case. Slopes of the regression lines for nest visit rate and all other behaviors did not differ between unaided and control females ($P > 0.05$; ANCOVA for each year and behavior, with brood size or age as the covariate and treatment as the grouping variable). There was also no difference between unaided and control females in the distribution of brood sizes or ages when our observations were made (Kolmogorov-Smirnov tests for each year; $P > 0.32$). Therefore, although brood size and age may have influenced parental behavior (Lombardo 1991), they did not have different effects on control and unaided females. There was also no significant correlation between the number of observations/nest and the mean value of any behavior we measured (separate Pearson correlations for control and unaided females, $P > 0.28$).

We collected food boluses from nestlings fitted with pipe-cleaner collars (e.g. Walsh 1978) to examine whether mass of food boluses given to nestlings differed between unaided and control females and between habitats. Each nest was sampled once to reduce potential effects on nestling growth, and we made no parental care observations at a nest on the day we sampled food boluses. Collars were placed on all young in a nest during sampling. Collars were removed after the female made three to four trips inside the nest box. Boluses were retrieved from nestlings and dried to constant mass in an oven at 95°C prior to weighing.

Statistical analyses.—We used analysis of variance (ANOVA) to examine insect abundance, laying date, clutch size, fledging success, and various behaviors. Interaction terms from ANOVA were nonsignificant unless noted otherwise. Values for the insect biomass index were log-transformed prior to analysis. All tests of independence in two-by-two tables were performed with the G-test and William's correction (Sokal and Rohlf 1981). Tests of independence with three-way tables were performed using log-linear models in the CATMOD procedure of SAS (SAS Institute 1985). Means are presented with standard errors. All statistical tests were two-tailed unless noted otherwise.

TABLE 1. Insect biomass index (mg/100 km wind)^a at Beaverhill Lake, Alberta, 1986–1988.

Site	Laying			Incubation			Nestling		
	\bar{x}	(95% CI)	<i>n</i> ^b	\bar{x}	(95% CI)	<i>n</i>	\bar{x}	(95% CI)	<i>n</i>
1986									
Lakeshore	68.0	(30.3–152.9)	16	9.0	(4.0–20.2)	9	11.7	(7.2–19.0)	19
Roadside	36.2	(18.7–70.1)	16	17.5	(6.2–49.3)	9	18.7	(12.0–29.2)	17
1987									
Lakeshore	28.7	(15.9–52.1)	17	7.5	(1.6–34.0)	6	8.9	(5.9–13.5)	21
Roadside	12.4	(6.6–23.5)	12	14.2	(8.5–23.5)	12	9.8	(5.8–16.6)	18
1988									
Lakeshore	14.4	(7.1–28.7)	14	10.1	(6.4–15.7)	10	7.6	(5.0–11.5)	22
Roadside	10.6	(5.5–20.1)	17	12.0	(7.4–19.5)	7	10.2	(6.4–16.2)	23

^a Mean IBI estimated by calculating arithmetic mean of log-transformed IBI and then converting back to mg/100 km wind by taking antilog of transformed mean. Calculation of 95% CI from Sokal and Rohlf (1981:420–421).

^b Days of insect sampling.

RESULTS

Insect abundance.—Mean insect biomass index (IBI) did not differ between the lakeshore and roadside when data from the entire breeding season were analyzed (Table 1; $P = 0.37$, three-way ANOVA). However, there were significant interactions between nesting period and year, between habitat and year, and between habitat and nesting period. Year effects were probably caused by greater mean IBI in 1986 than in 1987 or 1988 (Table 1). The habitat-year and habitat-nesting-period interactions probably were caused by a greater mean IBI during laying at the lakeshore than at the roadside in 1986 (Table 1). When analyzed by nesting period, mean IBIs only differed between the lakeshore and roadside during the laying period (Table 1; $P = 0.027$, two-way ANOVA). In general, the mean IBI was 1.4 to 2.3 times greater at the lakeshore than at the roadside during the laying period (yearly means; Table 1).

Natural polygyny.—All six cases of polygyny occurred at the lakeshore. There were two cases of natural polygyny in 1986 (6% of males at the lakeshore), four cases in 1987 (7% of males at the lakeshore) and none in 1988. Secondary females settled from 7 to 13 May (10 May \pm 1.3, 5 ASY, 1 SY), while monogamous ASY females at the lakeshore settled from 5 to 14 May (8 May \pm 0.4, $n = 35$; $t = 1.55$, $P = 0.13$). Data from 14 monogamous ASY females at the lakeshore were excluded to compare the fledging success of monogamous and secondary females that settled concurrently. For females that settled concurrently and nested successfully, the fledging success of secondary females (5.4 ± 0.7 young, n

$= 5$) was as high as the fledging success of monogamous ASY females at the lakeshore (5.9 ± 0.2 young, $n = 21$; $t = 0.92$, $P = 0.37$) and roadside (5.0 ± 0.7 , $n = 8$; $t = 0.6$, $P = 0.58$). Therefore, secondary females did not suffer a reproductive cost from loss of male parental care.

Male-removal experiment.—Reproductive success was analyzed from three years of data on 41 unaided and 149 control ASY females. Males were removed from 16 nests at the lakeshore and 25 nests at the roadside. There were no differences in laying date or clutch size between control and unaided females (Tables 2 and 3). However, the earliest male removals were made late in the egg-laying period, so we did not expect an effect. There were significant interactions between treatment and site and between year and site in the analysis of laying date (Table 2). However, these interactions were not present in the analysis of clutch size (Table 3), or in the subset of data used to analyze fledging success (see below).

Sample sizes were too small to compare the frequency of nest failure of control and unaided females between habitats. After pooling study sites, there was no difference between control (32% failures, 41/128) and unaided (29%, 12/41) females in the frequency of nests that produced no fledglings (log-linear model; $P = 0.66$ for treatment effect). The rate of nest failure was higher in 1988 (46%) than in 1987 (16%) or 1986 (19%), because of predation by weasels (*Mustela ermina*) on almost one-half of the nests at the lake ($P = 0.01$ for year effect). Only one to two nests were depredated in 1986 and 1987, when most nest failure was due to starvation or abandonment. Since the rate of nest failure was sim-

TABLE 2. Laying date at nests of control and unaided female Tree Swallows, Beaverhill Lake, Alberta, 1986–1988.^a Only includes adult birds with known clutch size. Does not include data from nests of primary or secondary females, or renests.

Site	1986	1987	1988
	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$
Control			
Lakeshore	26 May \pm 0.6 (8)	23 May \pm 0.7 (27)	24 May \pm 0.4 (48)
Roadside	28 May \pm 1.1 (10)	27 May \pm 0.7 (11)	24 May \pm 0.8 (20)
Unaided			
Lakeshore	26 May \pm 2.2 (3)	20 May \pm 0.8 (5)	22 May \pm 0.4 (6)
Roadside	28 May \pm 1.5 (7)	28 May \pm 0.7 (9)	25 May \pm 1.1 (6)

^a P-values for each effect in three-way ANOVA: treatment, $P = 0.28$; year, $P = 0.0001$; site, $P < 0.001$; treatment \times site, $P = 0.047$; year \times site, $P = 0.007$; treatment \times year, $P > 0.60$.

ilar between control and unaided females, but different among years, we only analyzed fledging success for successful nests.

Fledging success at successful nests.—Mean fledging success of unaided and control females did not differ within a habitat or among years (Table 4). The interaction between treatment and habitat was also not significant ($P = 0.43$), which suggests that the effect of male removal did not differ between the lakeshore and roadside. Overall, females nesting at the lakeshore produced more fledglings than females at the roadside (Table 4). This occurred probably because mean clutch size of monogamous adult females was greater at the lakeshore than at the roadside (Table 3) and fledging success was related positively to clutch size at both sites (lakeshore, $r^2 = 0.48$, $P = 0.004$; roadside, $r^2 = 0.75$, $P < 0.001$). Brood reduction (loss of eggs or young) was similar between the two sites. Assuming that experimental male removal simulates secondary mate status, it appeared that secondary mates at the lakeshore would produce more young than females mated to monogamous males at the roadside. Fledging success

was greater for unaided females at the lakeshore (6.2 ± 0.3 young, $n = 11$) than control females at the roadside (5.2 ± 0.3 young, $n = 38$; $t = 2.5$, $P = 0.02$). For a given clutch size, adult females produced similar numbers of fledglings at the lakeshore and roadside (ANCOVA with clutch size as the covariate; P for intercept = 0.97; $df = 1$ and 84). However, there was a significant difference between the slopes of the lakeshore and roadside regression lines ($P = 0.014$), because in one year (1988) females with the most common clutch sizes of five and six eggs tended to produce fewer fledglings at the road than at the lake. Therefore, in at least two of three years the difference in fledging success was probably due to differences in laying date or clutch size and not due to differential loss of eggs or nestlings.

Body mass of nestlings.—We used body mass as an index of nestling body condition just prior to fledging (16 days after hatch). In this analysis a mean nestling mass was calculated for each brood to reduce dependence among samples. Prior to examining the effect of male removal on mean nestling mass, we tested for and found

TABLE 3. Clutch size at nests of control and unaided female Tree Swallows, Beaverhill Lake, Alberta, 1986–1988.^a Does not include data from nests of primary or secondary females or renests. Five nests with unknown laying dates are included.

Site	1986	1987	1988
	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$
Control			
Lakeshore	6.8 \pm 0.2 (8)	6.6 \pm 0.3 (27)	6.5 \pm 0.1 (43)
Roadside	5.9 \pm 0.3 (12)	5.8 \pm 0.3 (12)	6.4 \pm 0.2 (20)
Unaided			
Lakeshore	7.0 \pm 0.0 (3)	7.2 \pm 0.2 (5)	6.8 \pm 0.2 (6)
Roadside	6.1 \pm 0.3 (9)	5.9 \pm 0.4 (9)	6.3 \pm 0.2 (6)

^a P-values for each effect in three-way ANOVA: treatment, $P = 0.16$; year, $P = 0.79$; site, $P = 0.0001$; all interactions, $P > 0.16$.

TABLE 4. Number of fledglings at successful nests (fledged at least one young) of control and unaided female Tree Swallows, Beaverhill Lake, Alberta, 1986-1988.^a

Site	1986	1987	1988
	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$
Control			
Lakeshore	5.8 \pm 0.2 (6)	5.7 \pm 0.2 (25)	5.8 \pm 0.4 (17)
Roadside	5.5 \pm 0.2 (10)	4.0 \pm 0.7 (9)	5.7 \pm 0.3 (19)
Unaided			
Lakeshore	6.0 \pm 0.6 (3)	6.4 \pm 0.4 (7)	5.0 (1)
Roadside	4.7 \pm 0.4 (6)	4.3 \pm 0.8 (6)	4.7 \pm 0.7 (6)

^a *P*-values for each effect in three-way ANOVA: treatment, *P* = 0.60; year, *P* = 0.62; site, *P* < 0.014; all interactions, *P* > 0.05.

no effect of timing of male removal, year or habitat on mean nestling mass. We also found no correlation between mean nestling mass and percent brood reduction. A positive relationship would be expected if there were greater mortality among lighter nestlings. Only brood sizes of five, six and seven young had more than three samples in each treatment category (Fig. 1). Among these broods, mean nestling mass was not affected significantly by male removal (two-way ANOVA; *P* = 0.15; *df* = 2 and 70). Brood size tended to have an effect on fledging mass (*P* = 0.059).

Body mass of female parents.—Control and unaided ASY female parents weighed 16 days after hatch had similar body mass (ANOVA; *P* = 0.17 for treatment effect, *P* = 0.49 for site effect). At the lakeshore, control and unaided females weighed 21.0 \pm 0.3 g (*n* = 24) and 20.8 \pm 0.2 g (*n* = 7), respectively; while at the roadside, control and unaided females weighed 21.1 \pm 0.4 g (*n* = 9) and 20.2 \pm 0.5 g (*n* = 9), respectively. Mean body mass of ASY females also did not differ between unaided and control females at either the lakeshore (*P* = 0.30) or roadside (*P* = 0.64) after controlling for brood size with ANCOVA.

Return rate of fledglings and parents.—Ten fledglings were recaptured on the study area in subsequent years, and all but two (from control nests) subsequently bred. Eight of the 10 returning birds were from control nests (1.24% returning), and two were from nests of unaided females (1.18% returning). These return rates were not significantly different (*G* = 0.003, *df* = 1, *P* > 0.95). Mean nestling mass of control broods that had at least one individual return in subsequent years (22.5 \pm 0.7 g, *n* = 4) did not differ from broods that had no individual return (23.5 \pm 0.2 g, *n* = 49; *P* = 0.07). Only 1

of the 10 returning fledglings was the heaviest nestling in its brood on day 16. Among ASY females that nested in 1986 or 1987, 28% (18/65) of control and 28% (8/29) of unaided females returned to the study area the next year (*G* = 0.0001, *df* = 1, *P* = 0.99). For all females nesting in 1986 or 1987, 29% (24/84) of control and 26% (9/35) of unaided females returned the next year (*G* = 0.05, *df* = 1, *P* > 0.8). For females that did not change breeding habitats, fledging success in the next year was not affected by male removal in the previous year (*F* = 0.03, *P* = 0.87, *df* = 1 and 23; data included 10 unsuccessful nests and 5 SY females).

Nest-visit rate of control and unaided females.—Rate of nest visitation did not differ significantly between control and unaided females, although unaided females tended to make more visits than control females (*P* = 0.11; Table 5). The nest-visit rate of all females was greater at the roadside than at the lakeshore (*P* = 0.04 for site effect; Table 5). In contrast, the rate of nest visitation was higher for control pairs (male and female combined) than for unaided females, and the difference between sites was not significant (Table 5). Interaction terms were not significant in these analyses, which suggests that the relative effect of male removal on nest visitation did not differ between unaided females at the lakeshore and roadside. Although unaided females did not increase significantly their total number of nest visits, from the perspective of individual nestlings (per-capita visits) it appeared that, in two of the three years, unaided females visited them as often as control pairs (Fig. 2; *P* > 0.27 for 1987 and 1988). However, in 1986 the per-capita nest-visit rate was lower for unaided females than control pairs (Fig. 2, a difference of 1.1 visits nestling⁻¹ h⁻¹; *P* = 0.04).

Other behaviors were examined for differ-

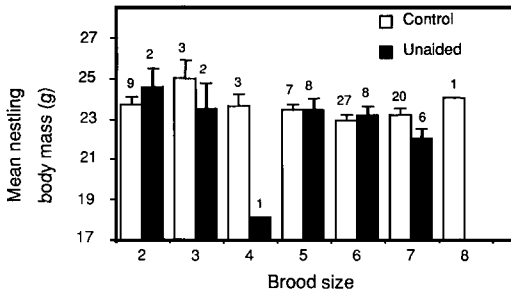


Fig. 1. Mean body mass (g) and SE of Tree Swallow nestlings on day 16 (just before fledging) at nests of control (paired) and unaided females, Beaverhill Lake, Alberta, 1986-1988. Data from nests of ASY females. Numbers above bars are number of nests sampled.

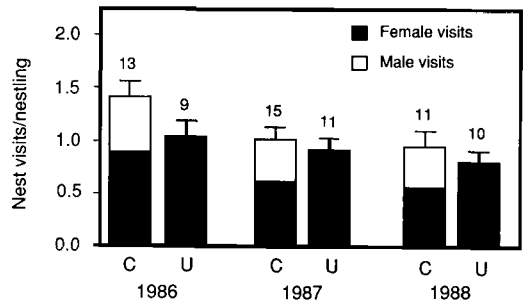


Fig. 2. Mean nest visits per nestling and SE (during 20-min observation periods) at nests of control (C) and unaided (U) female Tree Swallows, Beaverhill Lake, Alberta, 1986-1988. Numbers above bars are number of nests sampled.

ences between unaided and control females using ANCOVAs with brood size as the covariate. There were no differences between the lakeshore and roadside, so habitats were pooled in these analyses (Table 6). Unaided females spent less time perched at their nest boxes than did control females. However, it was not obvious what other behaviors unaided females were spending more time doing, if they were spending less time perched (Table 6).

Food bolus mass at the roadside and lakeshore.— Females might be able to compensate for the loss of the male by increasing the mass of each food bolus fed to nestlings. We examined mean dry biomass/bolus by collecting food boluses ($n = 42$) from collared nestlings in nests of seven control (five lakeshore and two roadside) and nine unaided (five lakeshore and four roadside)

females in 1987 and 1988. There was no difference between control and unaided females in the mean brood size or brood age during the days that these nests were sampled (t -tests, $P > 0.24$, $df = 14$). Mean dry biomass/food bolus did not differ between unaided (0.054 ± 0.008 g) and control (0.040 ± 0.007 g) females at the lakeshore, or between unaided (0.037 ± 0.006 g) and control (0.050 ± 0.004 g) females at the roadside ($P = 0.82$ for treatment effect; $P = 0.56$ for habitat effect; two-way ANOVA).

DISCUSSION

Male parental care did not improve the reproductive success or survival of females breeding at Beaverhill Lake. There was no significant effect of male removal on nest success, fledging

TABLE 5. Mean nest visits of adult Tree Swallows per 20-min observation period during the nestling period, Beaverhill Lake, Alberta, 1986-1988.^a

	1986	1987	1988
	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$
Lake			
Pairs	7.2 ± 0.7 (6)	5.8 ± 1.5 (7)	5.9 ± 0.6 (5)
Females only			
Control	4.5 ± 0.3 (6)	3.4 ± 0.8 (7)	3.1 ± 0.3 (5)
Unaided	5.6 ± 0.8 (3)	4.8 ± 0.5 (6)	4.3 ± 1.0 (4)
Road			
Pairs	9.3 ± 0.4 (4)	8.1 ± 1.7 (3)	4.9 ± 0.8 (6)
Females only			
Control	6.4 ± 0.6 (4)	3.9 ± 1.0 (3)	3.4 ± 0.8 (6)
Unaided	6.1 ± 1.1 (5)	6.6 ± 0.4 (3)	3.6 ± 0.6 (6)

^a P -values for comparison of nest visits of control versus unaided females in three-way ANOVA: treatment, $P = 0.11$; year, $P = 0.0004$; site, $P = 0.038$. P -values for comparison of total nest visits at nests of control versus unaided females: treatment, $P = 0.005$; year, $P = 0.003$; site, $P = 0.14$.

TABLE 6. Behavior of control and unaided adult female Tree Swallows during the nestling period, Beaverhill Lake, Alberta, 1986–1988. Sample sizes are number of nests. Times are out of 20-min observation periods (in seconds).

	1986	1987	1988	P-values from two-way ANOVAs		
	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$	$\bar{x} \pm SE (n)$	Treatment	Year	Interaction
In box						
Control	278 ± 51 (10)	238 ± 57 (10)	404 ± 44 (11)	0.35	0.02	0.82
Unaided	300 ± 78 (8)	318 ± 32 (9)	425 ± 55 (10)			
Perched						
Control	28 ± 13 (10)	8 ± 9 (10)	84 ± 26 (11)	0.001	0.001	0.16
Unaided	3 ± 2 (8)	8 ± 4 (9)	46 ± 19 (10)			
Flying						
Control	840 ± 48 (10)	806 ± 59 (10)	600 ± 43 (11)	0.92	0.0001	0.91
Unaided	871 ± 78 (8)	792 ± 39 (9)	596 ± 54 (10)			
At hole						
Control	54 ± 13 (10)	116 ± 37 (10)	113 ± 23 (11)	0.34	0.005	0.33
Unaided	23 ± 6 (8)	67 ± 14 (9)	134 ± 31 (10)			

success, female body mass, nestling body mass at fledging or rates of return of adults or fledglings to the study area. These results indicate that females were not choosing monogamous mating situations because of the importance of male parental care to female reproductive success or survival. Therefore, we suggest that the importance of male parental care mechanism was not a likely explanation for the maintenance of monogamy in this population. The most important influence on female reproductive success appeared to be food abundance (mean IBI) during the laying season. Nestling season food abundance did not differ between the lakeshore and roadside sites, and in two of three years there was also no difference in brood reduction between sites. This suggests that the lakeshore and roadside sites were of equal quality during the nestling season. During the laying season, however, mean IBI was 1.4 to 2.3 times greater at the lakeshore than at the roadside. This difference in food abundance was associated with clutches that averaged 0.5 eggs greater at the lakeshore than at the roadside. As a consequence of the greater clutch size, fledging success was also greater at the lakeshore than at the roadside (mean = 0.7 more fledglings at the lakeshore). These differences in food abundance and reproductive success were also associated with a difference in mating behavior. All six cases of polygyny occurred at the lakeshore. The absence of polygyny at the roadside could have been due to differences between sites in the number and spacing of nest boxes (see

methods). However, in another experiment in which we added nest boxes to some territories (Dunn and Hannon 1991), we found that males increased their probability of becoming polygynous when they had two or more nest boxes on their territories that were over 5 m apart. Additional nest boxes at the roadside were placed a maximum of 5 m apart, and this could have limited the potential for polygyny to occur at the roadside. However, five males at the roadside defended extra boxes 24 m apart yet did not become polygynous. At the lakeshore, 25% (3/12) of males with similar territories (two or more boxes 24 m apart) became polygynous. This suggests that polygyny occurred at the lakeshore, and not at the roadside, because of female choice of breeding locations with more food rather than limited numbers of extra nest sites. In summary, we suggest that polygyny occurred because of female choice of better laying season conditions at the lakeshore, and not because secondary females at the lakeshore were compensated somehow for their loss of male parental care.

Most other male-removal studies in typically monogamous species have found that male parental care is helpful, but not a necessity (reviewed in Wolf et al. 1988, Bart and Tornes 1989, Dunn and Hannon 1989). In these cases monogamy may be maintained in the population, because the loss of male parental care associated with secondary mate status makes monogamy almost always more advantageous to females than polygyny (Wittenberger and Tilson 1980).

However, some male-removal studies have found that loss of male parental care had little or no effect on reproductive success (Richmond 1978, Gowaty 1983, Hannon 1984, Martin et al. 1985, Martin and Cooke 1987, this study). In these cases, monogamy cannot be explained by the polygyny-threshold model or other models that assume polygyny is costly to the reproductive success of females (see reviews in Davies 1989, Searcy and Yasukawa 1989). The mating behavior of Tree Swallows at Beaverhill Lake is probably best characterized under the Searcy and Yasukawa (1989) classification as female-directed choice, when there is no cost or benefit associated with polygyny. That is, females are choosing mates based on the quality of the breeding situation (laying season food abundance in our case), and mating status has little or no effect on female reproductive success.

It is important to know the mechanism used by females to choose mates, because this information may help us to understand the relative importance of male parental care in the maintenance of monogamy (Dunn and Hannon 1989). In the past, it has generally been assumed that the importance of male assistance with feeding nestlings determines the choice of mates. However, there is evidence that both laying and nestling season conditions may influence female reproductive success and mate choice. For example, Pleszczyńska and Hansell (1980) increased levels of polygyny in Lark Buntings (*Calamospiza melanocorys*) by increasing the number of shaded nest sites. Greater nesting cover increased the proportion of nestlings that fledged, presumably because of greater protection from hyperthermia. Female buntings also appeared to show directed choice of better quality nesting locations, but in this case nesting season conditions appeared to influence reproductive success most strongly. Food supplementation experiments that have examined mating behavior (Ewald and Rohwer 1982, Davies and Lundberg 1984) are more difficult to interpret, because in these studies food was supplied throughout the breeding season. Nevertheless, in Red-winged Blackbirds (*Agelaius phoeniceus*), supplemental feeding generally advanced egg laying and increased male mating success (Ewald and Rohwer 1982), suggesting an effect of early season conditions on female mate choice. In female Dunnocks (*Prunella modularis*), food supplementation led to a decrease in female home-range size early in the breeding

season and, as a consequence, males were better able to defend more than one mate. In a five-year study of Northern Harriers (*Circus cyaneus*), Simmons et al. (1986) found that microtine-rodent abundance was correlated with female reproductive success and male mating success. They suggested that male provisioning of food was important to female reproductive success throughout the breeding season. However, females may base their mating decisions on male courtship feeding and condition, which appear to be influenced by food abundance early in the nesting season (Simmons et al. 1986). Studies of mating systems and parental care should ask why male parental care is important (Dunn and Hannon 1989), not just whether it is important to female reproductive success.

If male parental care does not improve female fledging success in Tree Swallows, then: (1) Why do males provide any parental care? (2) Why are not more males polygynous? Bart and Tornes (1989) presented three hypotheses for the maintenance of monogamous pair bonds in cases where the value of male parental care is low. Only one of these hypotheses is applicable to Tree Swallows. They suggested that, if male parental care is generally not costly to males, then there might not be strong selection against providing male parental care. This hypothesis may have some application in Tree Swallows because, although male parental care does not measurably improve female fledging success, there do not appear to be any better alternatives for males during the nestling period (such as finding another mate), and assisting the female with feeding appears to improve the condition of nestlings in larger broods (e.g. Dunn and Robertson in press). A high rate of nest failure during the nestling period (from predation or weather) may also favor remaining with one's mate and assisting with feeding if it facilitates re-nesting (Martin and Cooke 1987). It is also possible that male parental care could be important in years of very low insect abundance and that because of fluctuations in food abundance monogamy maximizes the long-term fitness of females (Lyon et al. 1987, Bart and Tornes 1989). During our three-year study, insect abundance was relatively high (Table 7) and constant (Table 1) during the nestling period, so we could not examine the role of uncertainty in maintaining monogamy (see Rubenstein 1982).

Food abundance and intraspecific competition for nest boxes probably limit polygyny to

TABLE 7. Insect biomass index (IBI) in Ontario and Alberta. Values are arithmetic means, standard errors, ranges, and sample sizes of back-transformed yearly means for 1977-1984 in Ontario and 1986-1988 in Alberta. Data collected in same way in Ontario and Alberta.

Location	Laying season	Nestling season	Source
	$\bar{x} \pm SE$ (range, n^a)	$\bar{x} \pm SE$ (range, n)	
Ontario			Hussell and Quinney (1987)
Sewage lagoon	39.1 \pm 7.6 (7.2-77.2, 8)	17.9 \pm 3.3 (7.2-38.2, 8)	
Backus field	3.1 \pm 0.4 (1.6-5.2, 8)	3.3 \pm 0.3 (1.7-4.5, 8)	
Alberta			This study
Lakeshore	37.0 \pm 6.0 (14.4-68.0, 3)	9.4 \pm 1.5 (7.6-11.7, 3)	
Roadside	19.7 \pm 8.3 (10.6-36.2, 3)	12.9 \pm 2.9 (9.8-18.7, 3)	

^a Number of years of sampling.

varying degrees in different populations of Tree Swallows. In many locations, polygyny may be uncommon because food abundance is relatively low and, as a consequence, male parental care may be more important to female reproductive success and mate choice. For example, in previous studies of Tree Swallows in Ontario (Lefelaar and Robertson 1986, Quinney 1983, 1986), male parental care appeared to be important to female reproductive success. Compared with Ontario sites, food abundance was relatively high at Beaverhill Lake (Table 7; Dunn and Robertson in press). This may explain why male parental care did not appear to be important to female reproductive success or survival at our study area. In areas where food abundance is relatively high and polygyny is advantageous to some females, polygyny might still be uncommon because intrasexual competition for nest boxes prevents most males from gaining a territory large enough that two females can breed without one female excluding the other (see Dunn and Hannon 1991, Dunn and Robertson in press).

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