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Is reproduction by Tree Swallows (Tachycineta bicolor) Cost-Free?

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Citation Details

IS REPRODUCTION BY TREE SWALLOWS COST FREE?

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ABSTRACT.—We manipulated brood sizes of Tree Swallows (*Tachycineta bicolor*) in 1996 and 1997 to test for the existence of intra- and intergenerational costs of reproduction. Modal clutch size was six eggs, but experimental brood sizes ranged from two to nine young. Nestling starvation was higher in 1996 (and dependent on brood size) than in 1997, but in both years enlargement of brood size resulted in increased productivity. Nestling mass near fledging was negatively correlated with brood size, but tarsus length and wing chord were not. Food deliveries by parents increased steadily between broods of two to six young but then remained constant between broods of six to nine young. The loss of female mass between incubation and the end of the nestling period was positively related to the pair's total feeding effort, and female mass near fledging declined with increasing brood size. The latter decline disappeared, however, when broods of nine were omitted. Adult return rate (1996 to 1997) was highest among birds that raised enlarged broods. Our results, and a review of other studies of Tree Swallows, suggest that broods of seven or eight young can be raised without costs to the parents or young, and it appears that costs associated with feeding young have not influenced annual fecundity of Tree Swallows. Rather, egg production is most likely limited by energy availability to laying females. A major cost of reproduction for Tree Swallows probably arises from nest-site competition in that early arrival in spring to obtain nest sites exposes adults to high risks of death from starvation. *Received 26 July 1999, accepted 20 February 2000.*

COSTS OF REPRODUCTION are widely assumed to be fundamentally important to the evolution of life-history strategies (Roff 1992, Stearns 1992). The basic premise is that time and energy expenditure are limited such that compromises must be struck between competing activities such as self maintenance, production and incubation of eggs, feeding of young, frequency of breeding, and parental survival. Costs may be passed to offspring (intergenerational costs; Mauck and Grubb 1995, Svensson and Nilsson 1997), absorbed by parents (intragenerational costs; Daan et al. 1996), or shared (Jacobsen et al. 1995, Maigret and Murphy 1997). Ultimately, parental ''decisions'' that balance competing demands determine the production of offspring and the survival of parents. Intergenerational costs often have been documented as an inverse relationship between the number and size of young (see Stearns 1992), and small young often have poorer prospects of survival (e.g. Pettifor et al. 1988, Lindén et al. 1992; but see Hochachka and Smith 1991).

We are less certain, however, of the importance of intragenerational costs for the evolution of life histories because the measurement and interpretation of data have proved difficult and controversial. For instance, several early studies found positive rather than negative correlations between reproductive effort and parental survival (e.g Smith 1981). These paradoxical results led to the realization that costs can be measured only through experimental change of breeding effort because individuals may optimize their reproduction (Hogstedt 1980, Gustafsson and Sutherland 1988, Pettifor et al. 1988, McNamara and Houston 1996). In addition, the difficulty of measuring survival in the wild with the small sample sizes typical of most studies probably has resulted in the failure to reject false null hypotheses of no difference in survival among adults that raised reduced or enlarged broods (type II error; Hegner and Wingfield 1987).

In lieu of assessing costs by measuring sur-

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vival, researchers have used negative associations between parental body mass and reproductive effort as evidence for the existence of reproductive costs (Bryant 1988, Hillstrom 1995). A problem with this approach is that loss of mass may be an adaptive response to reduce stress on parents in anticipation of increased workloads (Norberg 1981, Freed 1981, Sanz and Moreno 1995). Moreover, manipulations of reproduction in altricial species have focused largely on the brood-rearing period because it has been assumed that feeding young is more energetically taxing than laying eggs, incubating, or caring for fledglings. However, Monaghan et al. (1995; see also Heaney and Monaghan 1996) showed that the cumulative costs of laying and incubating different numbers of eggs may result in large differences in parental effort that affect a parent's ability to care for young. Research has also shown that parental care may peak after the young leave the nest (Morehouse and Brewer 1968) and that clutch size may be limited by the demands of this period (Murphy 2000).

Despite more than 30 years of research on costs of reproduction to adults, the surprising fact is that few studies of passerines have experimentally examined survival or fecundity costs across years. A recent survey of the literature showed that experimental data exist for only nine species (16 studies), three of which were parids (7 of 16 studies; Murphy 2000). Thus, much remains to be learned about the existence of intragenerational costs of reproduction and the potential role that they have played in the evolution of avian life histories. Therefore, we attempted to test for the existence of inter- and intragenerational costs of reproduction in Tree Swallows (*Tachycineta bicolor*) using brood-size manipulation experiments that tested for a negative effect of brood size on (1) nesting productivity, (2) nestling size/quality, (3) parental body condition, and (4) adult survival. In addition, we analyzed parental feeding responses to changes in brood size to evaluate if provisioning was constrained by the environment (Lack 1947, Gibb 1955) or reflected tradeoffs between current and future offspring (Nur 1984, Conrad and Robertson 1993).

Study Area and Methods

Study area.—We conducted our study in 1996 and 1997 at three sites in Delaware County, New York.

The main site was in a meadow along Charlotte Creek (42°27′N, 74°47′W). Nest boxes ($n = 48$) were arranged in two grids and were spaced at 20-m intervals. Two other nearby sites (Pine Lake, 4 boxes; Bob and Flossie's farm, 6 boxes) were also located in fields near Charlotte Creek. Standard methods for determining date of first egg, clutch size, egg mass, and hatching success were followed (see Ramstack et al. 1998). We combined data from all sites because no differences were found for the basic breeding statistics (Ramstack et al. 1998), and neither age structure nor morphological measures of adult size and condition differed between the main colony and the two smaller colonies (M. T. Murphy unpubl. data).

Brood-size manipulations and nestling measurements.—Brood-size manipulations have followed one of two approaches: (1) modifying brood size by a set number of young, or (2) randomly assigning nests to different brood sizes without regard to original clutch size. The first approach assumes that individuals may optimize clutch size and attempts to adjust parental effort by the same amount in all individuals, whereas the latter approach assumes that all parents are of equal quality. Previous manipulations of Tree Swallow brood size involved increases or decreases of two young, and none of these studies detected significant costs to breeding adults (see below). Thus, we chose to impose a greater range of potential costs and manipulated broods without regard to original clutch size.

Most females in the Charlotte Valley lay six eggs (Ramstack et al. 1998). We transferred between one and four young among broods, resulting in nests that contained between two and nine nestlings (some broods were 80% larger than the number of eggs laid). Transfers were made quickly (<10 min) one to two days posthatching, and young were always moved to a nest with nestlings within one day of their age. Transfers occurred among all experimental categories so that even some of the control and reduced broods contained foreign young. In summary, we had 13 control (clutch size = brood size), 21 enlarged (brood size > clutch size), and 19 reduced broods (brood size < clutch size); within our sample, clutch size and experimental brood size were negatively correlated ($r = -0.264$, df = 51, $P = 0.056$). That none of the nests was abandoned indicates that parents accepted the experimental manipulations and our disturbances at their nests.

Broods were checked every few days during the nestling period and daily during feeding observations (see below) so that we knew brood size and whether young had starved. We measured tarsus length, wing chord, and body mass of young between 1200 and 1500 EDT for all nestlings on day 13 (hatching = day 0). The number of young to fledge (= productivity) was determined by revisiting the nest after the young had left. All dead nestlings found within or outside the nest box were subtracted

from brood size at day 13 to determine the actual number fledged. If no dead bodies were found, and no young disappeared during our observation periods, we assumed that all young had fledged.

Adult body mass and survival.—In both years, we captured as many adults as possible during the nestling period when young were 12 to 14 days old. We used a combination of mist nests and trap doors at the nest cavity to capture adults as they fed their young. In 1997, we also captured nearly all females during the first half of incubation by blocking the box entrance and lifting the females off the nest. All adults were banded at first capture with a U.S. Fish and Wildlife Service band. Sex was determined based on the presence of an incubation patch (female) or cloacal protruberance (male), and age of females was determined using plumage characters (Pyle et al. 1989). Measurements of body mass (with a 50-g Pesola scale), wing chord, exposed culmen, and tarsus were made for all adults. Bill and tarsus lengths were measured using dial calipers, and wing chord was measured using a stopped ruler.

Observations of parental feeding behavior.—In 1997, we observed parental feeding trips at 24 nests during three 1-h periods when young were 9 to 13 days old. Data were collected on three consecutive days at each nest, with observation times rotated to remove variation associated with time of day. Most observations were made between mid- to late morning and only during periods of dry weather or very light rain. We assumed that all trips to a box represented a visit to feed one nestling. Given the highly synchronized breeding of Tree Swallows, the decision to characterize each pair's feeding effort using three 1-h periods spread over three days represented a compromise between maximizing the number of pairs sampled and thoroughly sampling each pair's effort. We made most of our observations from a small hill along the main colony. The hill afforded unobstructed views of nests from distances of 50 to 150 m. Observers used binoculars to simultaneously watch two to three nests. We did not differentiate between the sexes and report the pair's total average feeding rate over the three observation periods.

Predictions and analyses.—We analyzed data using version 4.1 of STATISTIX (1994). Throughout, we treated the nest as the sample unit, limited ourselves to first nests of the season, used two-tailed tests with parametric statistics unless the assumptions of normality and homoscedasticity of variances were violated, and used $P \leq 0.05$ to establish significance. We first compared basic breeding statistics from 1996 and 1997 with data from the two previous years (Ramstack et al. 1998). Our purpose was to determine whether conditions during our two-year study were within the ''normal'' range of variation. We then tested predictions of the hypothesis that elevated reproductive effort brought about by enlarging broods increased costs to young, adults, or both. The

intergenerational-cost hypothesis predicts that if adults opt to maintain their own condition at the expense of their young, then productivity would decline, nestling starvation would increase, or the overall size and quality of young would decline when brood size was enlarged. We further predicted that brood size would have no effect on adult body mass, loss of female mass between incubation and the nestling period, and adult survival between breeding seasons.

The alternative, that adults absorbed most of the costs of raising enlarged broods, predicts that productivity would increase with brood size, whereas the number of starved young and the size and quality of young would be independent of brood size. However, the critical predictions of this hypothesis are that enlargement of brood size would bring about a decline in adult condition, a greater loss of female body mass between incubation and the nestling period, and reduced parental survival between breeding seasons.

We tested for differences in productivity, proportion of nestlings to starve (arcsine transformed), and nestling size using least-squares regression with brood size as the independent variable. We also tested for possible confounding effects of other variables (e.g. year, breeding date) using multiple linear regression in which type III sums of squares were used to evaluate significance. To test for costs to the adults, we regressed adult body mass (measured when the young were between 12 and 14 days of age) and loss of female body mass (between incubation and day 13 of the nestling period) against brood size. We assumed that all birds that survived between breeding seasons were equally likely to return to the breeding colonies, and we used Fisher's exact tests to compare the number of individuals that returned versus did not return in relation to the manipulation category (reduced + control vs. enlarged). Unfortunately, the land on which the main colony was located changed ownership between 1997 and 1998, and we were not allowed to determine return rates in 1998.

We also made observations of feeding behavior to test predictions of the cost hypothesis. Analyses were conducted on the total number of trips per hour and the per-capita hourly feeding rate (trips per nestling per hour). Lack's (1947) original model of food limitation (which assumes that feeding rates are constrained by the environment) predicts that the number of food deliveries will reach a maximum at the population's modal clutch size and that larger broods will receive the same total number of feeding trips (Gibb 1955). In contrast, the evolutionary-restraint hypothesis assumes that feeding a brood that is the same size as the normal clutch does not burden parents because selection has favored smaller clutches that limit stress and improve the prospects that parents survive to breed in future years. Enlargement of brood size thus removes the evolutionary restraint

TABLE 1.   Reproductive statistics for Tree Swallows breeding at Charlotte Creek, New York, from 1994 to 1997. Values are $\bar{x} \pm$ SD, with n in parentheses. Breeding date (day 0 = 1 May) was the only variable that differed significantly among years (1995 earlier than all other years).

Variable	1994	1995	1996	1997	F	P
Breeding date	25.0 ± 6.60 (14)	14.2 ± 3.63 (24)	24.7 ± 4.11 (34)	22.5 ± 5.06 (35)	29.95	<0.001
Clutch size	5.8 ± 0.70 (14)	5.7 ± 0.74 (25)	5.5 ± 0.71 (34)	5.6 ± 0.77 (30)	0.90	0.448
Egg mass (g)	1.8 ± 0.16 (14)	1.8 ± 0.14 (23)	1.8 ± 0.13 (32)	1.8 ± 0.17 (29)	0.67	0.573
No. hatched	4.9 ± 0.83 (11)	5.5 ± 0.78 (24)	5.3 ± 0.85 (33)	5.4 ± 0.75 (27)	1.47	0.228
No. fledged[a]	5.2 ± 0.75 (6)	5.3 ± 1.50 (18)	4.2 ± 1.30 (5)	5.4 ± 0.52 (8)	2.55	0.072
No. starved[a]	0.7 ± 0.82 (6)	0.1 ± 0.88 (18)	0.8 ± 1.79 (5)	0.0 ± 0.00 (8)	2.45	0.081

[a] Only control broods (brood size = clutch size) were compared (n = 13 for 1996 and 1997).

on parental behavior, and parents are expected to increase their feeding rates to provision the extra young (Nur 1984). The asymptotic pattern predicted by Lack's food-limitation model predicts a significant quadratic term in a second-order polynomial regression of feeding rate against brood size, whereas the evolutionary-restraint model predicts a strictly linear relationship between feeding rate and brood size (Nur 1984). We tested for both patterns using linear and polynomial regression.

RESULTS

Annual comparisons.—Most pairs began laying during the fourth week of May in 1994, 1996, and 1997. Although the start of breeding was significantly earlier in 1995 than in the other three years (Table 1), clutches of six eggs predominated in all years, and we found no annual differences in clutch size, egg mass, or number of young hatched (Table 1). In contrast, the number of young that fledged or starved tended to vary among years. For these analyses, we restricted our comparisons to control nests (clutch size = brood size). Within this reduced data set, 1996 appeared to be a difficult year for rearing young (on average, most pairs lost one nestling before fledging), whereas 1997 appeared to be average or above average for breeding.

Experimental nests: Starvation, productivity, and nestling quality.—Significantly more young starved in 1996 than 1997 (t = 2.60, df = 51, P = 0.015). In 1996, the number to starve increased significantly with brood size (r^2 = 0.229, P = 0.014), and the proportion of young to fledge declined with brood size (r^2 = 0.278, df = 22, P = 0.008). Nonetheless, the largest broods were the most productive (b = 0.558, r^2 = 0.321, P = 0.003). The number of young to starve was very low in 1997 and was independent of brood size (r^2 = 0.001, P = 0.95), as was

the proportion of young to fledge (r^2 = 0.000, df = 26, P = 0.95). As a result, productivity increased linearly with brood size (b = 0.959, r^2 = 0.875, P < 0.001), and although 1996 was a poor year, the largest broods (8 and 9 young) fledged the most young in both years.

Nestling mass declined significantly with brood size in 1996 (P = 0.001; Fig. 1) and 1997 (P = 0.014; Fig. 1) and in the combined sample for both years (r^2 = 0.270, P < 0.001). Nestlings were heavier in 1997 than in 1996 (P = 0.045; Fig. 1), and after accounting for the effect of year, 26% of the variation in nestling mass was related to brood size (P < 0.001). Nestling tarsus length (t = 7.15, P < 0.001) and wing chord (t = 2.36, P = 0.024) also were longer in 1997, but neither variable exhibited significant variation with brood size in 1996, 1997, or in the combined sample (Fig. 1).

The longer tarsi of nestlings in 1997 might have resulted from better foraging conditions (as suggested by the significantly lower frequency of starvation and significantly higher body mass and wing chord of birds in 1997), but different observers measured nestlings in the two years, which may have contributed accidentally to the annual variation that we detected. However, the fact that tarsus length was positively and significantly correlated with nestling mass in 1996 (r = 0.500, df = 24, P = 0.009) but not in 1997 (r = −0.081, df = 25, P = 0.69) suggests that the short tarsi in 1996 at least in part were related to low food availability. Wing chord tended to increase with hatching date (r^2 = 0.095, df = 51, P = 0.025), and after controlling for the effects of date and year, we still found that wing chord was independent of brood size (P = 0.51). Body mass and tarsus length did not increase with hatching date.

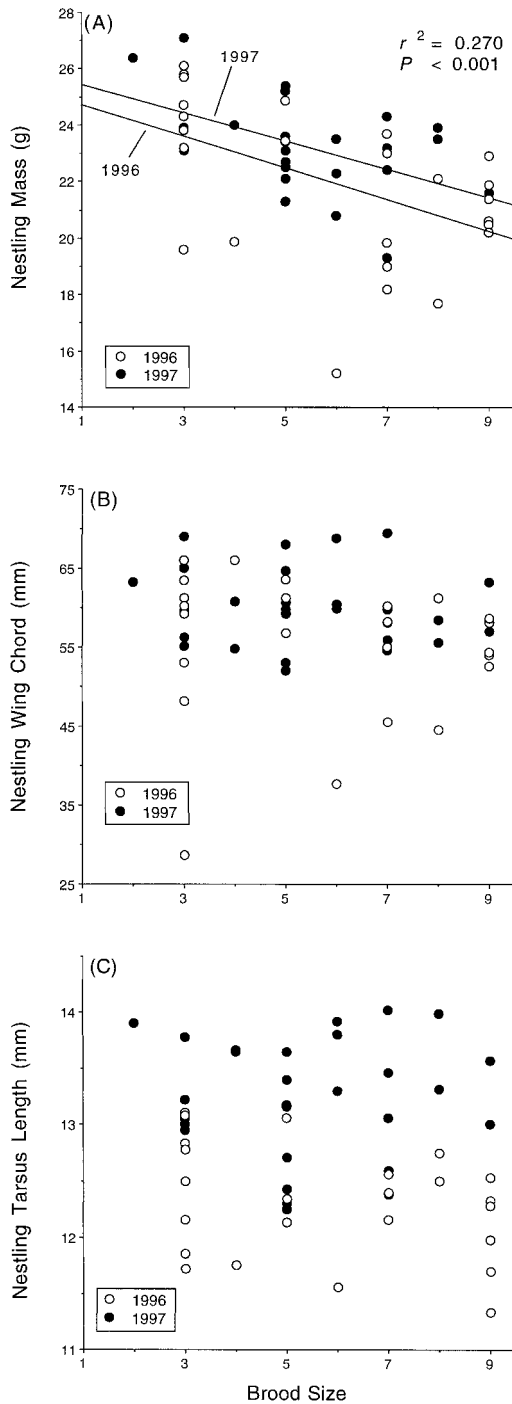*Parental feeding behavior.*—We eliminated

FIG. 1. Variation in body mass (A), wing chord (B), and tarsus length (C) of Tree Swallow nestlings on day 13 (hatching = day 0) in relation to experimental brood size. Date from 1996 (open circles) and 1997 (filled circles) were analyzed separately (as shown for mass) and as a single data set, and in all

three nests from analyses, one that was a statistical outlier (more than 3 SDs beyond the predicted value) and two where unexpected human activity during observations caused the parents to stay away from the nests. Based on the remaining 21 nests, a linear regression showed that 65% of the variation in feeding rate was related to the number of young in the nest ($P < 0.001$). However, feeding rate appeared to reach an asymptote beyond broods of six young (Fig. 2), and a second-order polynomial regression increased the explained variation to 75.3% and showed that the quadratic term (brood size^2) was significant ($P = 0.01$). Parents thus reached a maximum feeding rate at broods of six to seven young (Fig. 2). Not surprisingly, per-capita feeding rate declined with increasing brood size ($b = -0.326$, $r^2 = 0.652$, $P < 0.001$), indicating that individual nestlings were fed less frequently as brood size increased (Fig. 2).

Brood size never accounted for more than about 25% of the variation in nestling size. A possible additional contributor to differences in nestling mass or linear dimensions was parental feeding rate. However, regressions of total parental feeding rate in 1997 with nestling mass ($r^2 = 0.125$, $P = 0.098$), wing chord ($r^2 = 0.001$, $P = 0.87$) and tarsus length ($r^2 = 0.000$, $P = 0.993$; df = 19 in each case) were nonsignificant. Conclusions were unchanged after we controlled for possible confounding effects of brood size and breeding date (all $Ps > 0.35$).

Adult mass: Effects of brood size and feeding rate.—We combined data on body mass from the two years because mass did not differ between 1996 and 1997 (males, $t = 1.06$, df = 31, $P = 0.30$; females, $t = 1.79$, df = 44, $P = 0.08$), and mass tended to decline with brood size in both years. Body mass of both sexes at day 13 of the nestling period declined with increasing brood size, but the pattern was significant only for females (Table 2). The decline in female mass with brood size was stronger in 1996 ($r^2 = 0.411$, df = 21, $P = 0.001$) than in 1997 ($r^2 =$

cases results were the same. For mass, coefficients for the regression lines did not differ significantly ($P > 0.05$) between 1996 ($b = -0.558$, SE = 0.203) and 1997 ($b = -0.497$, SE = 0.150).
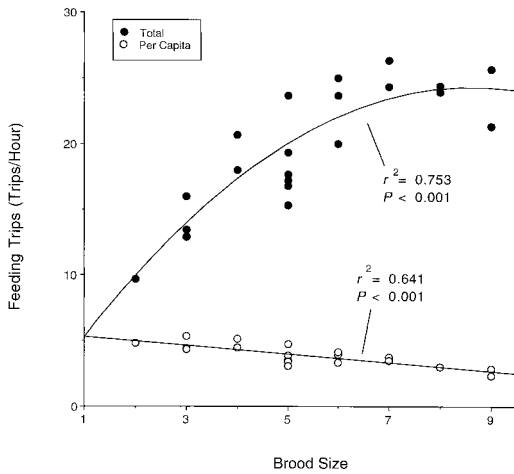
FIG. 2. Feeding rate versus broods size for Tree Swallow broods in 1997. Filled circles denote total feeding rate versus brood size, and open circles denote feeding rate per nestling.
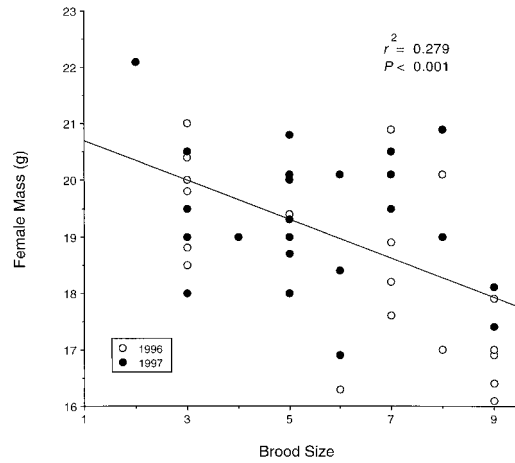

FIG. 3. Relationship between body mass of female Tree Swallows and brood size between days 12 and 14 of the nestling period (hatching = day 0). The analysis is based on the combined samples for 1996 and 1997.

0.096, df = 23, P = 0.141), again suggesting that 1996 was a stressful year.

Most of the negative relationship between body mass and brood size resulted from the very poor condition of females that raised broods of nine young (Fig. 3). Indeed, mass did not vary with brood size among females that raised between two and eight young (r^2 = 0.059, df = 37, P = 0.142). Likewise, loss of female body mass between early incubation and day 13 of the nestling period was unrelated to brood size (Table 2). Feeding rate also may have contributed to variation in body mass. Body mass tended to decline with increasing feeding effort in both sexes, but in neither case was the decline significant (Table 2). In contrast, loss of mass by females between incubation and day 13 of the nestling period was directly related to the total feeding rate of the pair (Table 2, Fig. 4).

Adult return rate.—Of the banded females from 1996, 5, 4, and 12 raised reduced, control, and enlarged broods, respectively. All five of the females that returned in 1997 had raised enlarged broods in 1996 (41.7% return rate). A significantly higher proportion of females that raised enlarged broods returned in 1997 compared with the combined sample of nine females that had raised control or reduced broods (Fisher's exact test, P = 0.045). Males showed a similar pattern, but the difference was not statistically significant (P = 0.462). The difference in return rate between parents of reduced and control broods versus enlarged broods for the combined female and male samples also was significant (P = 0.009), indicating that at least one parent of enlarged broods was more likely to return to the colony in the next breeding season. Body mass of adults at cap-

TABLE 2. Relationship between adult body mass versus the independent variables brood size and total feeding rate, and per-capita feeding rate for Tree Swallows at Charlotte Creek, New York, 1996 and 1997 data combined.

Variable	Female mass at day 13				Male mass at day 13				Loss of female mass[a]			
	b	r^2	n	P[b]	b	r^2	n	P[b]	b	r^2	n	P[b]
Brood size	−0.346	0.279	46	<0.001	−0.148	0.100	33	0.074	0.107	0.020	18	0.573
Feeding rate	−0.075	0.090	21	0.186	−0.059	0.090	17	0.243	0.151	0.372	16	0.012
Per-capita rate	0.430	0.089	21	0.188	0.146	0.019	17	0.599	−0.001	0.000	16	0.999

[a] Data for 1997 females only.
[b] Critical P-value after Bonferroni correction for multiple comparisons is 0.017.
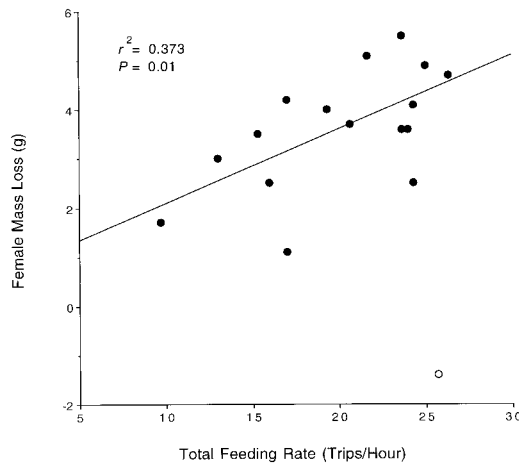
FIG. 4. Loss of mass of female Tree Swallows between the first half of incubation and days 12 to 14 of the nestling period in relation to average feeding rate of the pair between days 9 and 13 of the nestling period. The open circle in the lower right represents one female that was omitted from the analysis. Her mass during incubation (16.5 g) was extremely low compared with all other females.

ture in 1996 did not differ between individuals that returned versus did not return in 1997 (females, $t = 0.86$, df $= 19$, $P = 0.40$; males, $t = 0.00$, df $= 12$, $P = 1.0$).

Discussion

Comparisons with other studies.—Our results are in broad agreement with those of previous studies that have tested for costs of reproduction in Tree Swallows by manipulating brood size. For instance, productivity increased (significant in four or four studies), nestling mass decreased (three of four studies), and tarsus length (three of three studies) and wing chord (two of three studies) were independent of experimental increases of brood size (Table 3). Loss of female mass between incubation and the end of the nestling period tended to increase with brood size (nonsignificant trend in two of two studies), and female body mass showed a nonsignificant tendency to decline with brood size in DeSteven's (1980) study. However, we found a significant decline but again note that the significance in our study depended on including broods of nine young (Fig. 3), which is a substantial (50%) increase in brood size over the modal clutch size.

Because sample sizes for adult survival were small in all studies, the statistical power to detect a negative effect of brood size on adult survival was low. Nonetheless, a consistent pattern emerged: females in all four studies (and males; data not shown) tended to return at a higher rate when they raised enlarged broods (Table 3). Enlarging broods also appeared to have no effect on juvenile survival in the two studies where it was measured. Finally, Wheelwright et al. (1991) failed to find a negative effect of elevated current reproductive effort on future fecundity of females (Table 3). Thus, all four studies provided no evidence that Tree Swallows experienced long-term intra- or intergenerational costs when raising enlarged broods.

TABLE 3. Results of four studies in which brood size was enlarged to measure costs of reproduction in Tree Swallows. All traits were compared with experimentally enlarged brood sizes. Symbols indicate pattern of variation of each trait with brood size (P in parentheses).

Trait	DeSteven 1980	Wiggins 1990	Wheelwright et al. 1991	This study
Productivity	+ (<0.001)	+ (<0.001)	+ (<0.001)	+ (<0.001)
Nestling mass	− (0.19)	− (<0.01)	− (<0.05)	− (<0.001)
Nestling tarsus	—[a]	+ (>0.05)	− (>0.05)	− (0.45)
Nestling wing	− (0.36)	—	− (<0.05)	− (0.65)
Offspring survival[b]	− (0.46)	—	+ (>0.70)	—
Adult female mass	− (0.33)	—	—	− (<0.001)[c]
Loss of female mass	+ (0.24)	—	—	+ (0.57)
Adult female survival	+ (0.57)	+ (0.41)	+ (0.26)	+ (0.04)
Future fecundity	—	—	NS[d]	—

[a] Data not available.

[b] Return rate of nestlings between fledging and the next breeding season.

[c] Significant decline in mass dependent upon inclusion of broods of nine. Pattern was not significant when broods of nine were dropped from analysis ($P = 0.142$).

[d] Neither future breeding date nor clutch size affected by brood manipulation ($P > 0.40$).

Jacobsen et al. (1995) suggested that the failure to detect costs of reproduction in studies of adult passerines was a consequence of the difficulty of measuring small changes in survival when annual survival was already low. The fact that all four studies of Tree Swallows revealed a tendency toward higher survival among females that raised enlarged broods argues against this interpretation of our results, suggesting instead that raising enlarged broods has no long-term ill effects on females. We suspect that the tendency toward low return rates by females that raise smaller broods most likely reflects a failure to return to sites where previous reproductive success was perceived as low (Murphy 1996, Haas 1998); if true, this violates the assumption that all surviving birds were equally likely to return to the study site.

The negative relationship between nestling body mass and brood size in our Charlotte Valley population (and elsewhere; Table 3) might cause one to question the conclusion that no intergenerational costs were expressed. Nonetheless, we feel confident that this was the case because neither tarsus length nor wing chord showed a tendency to vary inversely with brood size. Furthermore, closer inspection of Figure 1 shows that nestling body mass at nearly all nests was above adult mass (19 to 21 g). Thus, even broods that were relatively light seemed to be well fed. Stored fat may account for the extra one or two grams of mass carried by young from smaller broods (Fig. 1), which may have helped them to offset their low foraging success in the three to five days after they became independent. However, results from studies by DeSteven (1980) and Wheelwright et al. (1991) suggest that the slightly smaller young that fledge from enlarged broods do not experience reduced survivorship.

Provisioning behavior.—The asymptotic pattern in parental feeding rate in our study (Fig. 2) was unusual. Most studies have found a strictly linear relationship between feeding rate and brood size when broods were enlarged (see Rytkönen et al. 1996), but Tree Swallows appeared to reach a maximum feeding rate at broods of six young. The asymptotic feeding pattern and the lower mass of young in large broods (Fig. 1) are consistent with Lack's food-limitation hypothesis. However, the failure of female mass to decline with brood size in the range of two to eight young suggests that females were not working maximally to feed the extra young in broods of seven and eight. Not until females were forced to raised broods of nine (three to four more young than their clutch size) did female body mass decline. Broods of seven and eight did not appear to have required substantially greater effort to raise than broods of six, and parents seemed to limit their effort by passing the slight (but inconsequential) costs of the one to three extra nestlings to their young. Broods of nine appeared to represent a true threshold of parental care, but we note that broods of this size exceeded typical clutch sizes by 50 to 80%. We view our results as being consistent with models of parental care that assume that clutch size and parental behavior reflect a balance between the value of current and future broods (Nur 1984, Winkler 1987, Conrad and Robertson 1993).

Neither female body mass nor loss of mass were associated with brood size in the range of two to eight young, but the pair's total feeding effort accounted for much of the variation in the amount of mass females lost between incubation and the late brood-rearing period. Experimental analyses of feeding behavior in Blue Tits (*Parus caeruleus*; Nur 1984), Great Tits (*P. major*; Smith et al. 1988) and Eastern Kingbirds (*Tyrannus tyrannus*; Maigret and Murphy 1997) have also shown that high parental feeding effort has a negative effect on body condition. Given that parents could not anticipate their future brood size and feeding effort, these four studies suggest that loss of body mass by adults during reproduction was a function of an increased work load and not an adaptive adjustment downward to reduce stress. Maigret and Murphy (1997) also showed that male kingbirds that failed to return between years were in poorer condition at the end of the nestling period than males that returned. Although large broods clearly required more work from adult Tree Swallows (Fig. 2; see also Leffelaar and Robertson 1986, Lombardo 1991), brood size per se may not be a good surrogate for more direct measures of parental effort such as feeding rate. Unfortunately, we could not determine whether high feeding effort affected survival because we were prevented from checking our nest boxes in 1998, but we suggest that future studies attempt to link survivorship to more direct measures of parental effort.

Constraints on clutch size?—The apparent ''cost-free'' ability of parents to raise seven and even eight young begs the question ''why don't females lay larger clutches?'' The failure to do so becomes even more perplexing when viewed in the context of the limited breeding opportunities that most females would have faced historically. Among altricial species, secondary cavity nesters like Tree Swallows generally lay the largest clutches and produce the most young (Martin and Li 1992), presumably because of limited breeding opportunities that result from competition for scarce nesting cavities (Martin 1993, 1995; Beissinger 1996). Tree Swallows arrive on the breeding grounds very early in the spring, presumably to acquire nest sites (Robertson et al. 1992). Early arrival can be quite risky. For instance, we found 10 and 11 dead adults in our boxes before the beginning of egg laying in 1996 and 1997, respectively. All birds appeared to have starved. That Tree Swallows take such risks suggests that competition for nest sites is intense, and Tree Swallows lose nests to larger species of cavity nesters (e.g. Rendell and Robertson 1989).

Food limitation to egg-laying females seems to be the most parsimonious explanation for the failure of Tree Swallows to lay larger clutches despite their ability to raise enlarged broods of seven or eight young with no apparent added costs. Indeed, Tree Swallow clutch size and food availability during laying are positively correlated (e.g. Hussell and Quinney 1987, Dunn and Hannon 1992, Dunn et al. 2000). Experiments by Winkler and Allen (1995) also have shown that handicapped females laid later, and for their laying date produced smaller clutches, than did unmanipulated females. Tree Swallows apparently are ''income breeders'' (i.e. they produce eggs from daily food intake; Drent and Daan 1980). The availability of aerial insects usually is lower in the prelaying period than in the nestling period of Tree Swallows (Hussell and Quinney 1987; McCarty 1995 *in* Winkler and Allen 1996), and thermoregulatory costs probably are higher before laying because of lower air temperatures early in the breeding season. Thus, it appears that females cannot produce enough eggs to match their later ability to feed young.

Dunn and Hannon's (1992) experimental removal of male Tree Swallows supports our conclusion. Unaided females fledged as many young as control pairs, and survival to the next year by adult females and juveniles was unaffected by male removal. We agree with Dunn and Hannon's (1992:496) conclusion that ''The most important influence on female reproductive success appeared to be food abundance during the laying season.'' Our conclusions thus echo the call for a renewed focus on possible energetic constraints to reproduction that take place prior to the brood-rearing period (Monaghan et al. 1995, Heaney and Monaghan 1996, Monaghan and Nager 1997). For other species, special attention may need to be directed toward understanding events that transpire during the postfledging period of parental care (e.g. Murphy 2000).

We propose that costs of reproduction in Tree Swallows are expressed mainly as a high risk of starvation in the early spring when adults return to compete for nest sites. Tree Swallows must possess a cavity for breeding, and clutch sizes decline seasonally (Winkler and Allen 1996, Ramstack et al. 1998). Declining prospects of recruitment for young that fledge late in the season apparently drive the seasonal decline in clutch size (Winkler and Allen 1996). A failure to acquire a cavity, or even a delay in breeding, result in reduced fitness. Thus, early arriving Tree Swallows face a tradeoff between the risk of starvation and the benefits of breeding as early as possible.

LITERATURE CITED

BEISSINGER, S. R. 1996. On the limited breeding opportunities hypothesis for avian clutch size. American Naturalist 147:655–658.

BRYANT, D. M. 1988. Energy expenditure and body mass changes as measures of reproductive costs in birds. Functional Ecology 2:23–34.

CONRAD, K. F., AND R. J. ROBERTSON. 1993. Brood size and the cost of provisioning nestlings: Interpreting Lack's hypothesis. Oecologia 96:290–292.

DAAN, S., C. DEERENBERG, AND C. DIJKSTRA. 1996. In-

creased daily work precipitates natural death in the Kestrel. Journal of Animal Ecology 65:539–544.

DeSteven, D. 1980. Clutch size, breeding success, and parental survival in the Tree Swallow (*Iridoprocne bicolor*). Evolution 34:278–291.

Drent, R. H., and S. Daan. 1980. The prudent parent: Energetic adjustments in avian breeding. Ardea 68:225–252.

Dunn, P. O., and S. J. Hannon. 1992. Effects of food abundance and male parental care on reproductive success and monogamy in Tree Swallows. Auk 109:488–499.

Dunn, P. O., K. J. Thusius, K. Kimber, and D. W. Winkler. 2000. Geographic and ecological variation in clutch size of Tree Swallows. Auk 117: 215–221.

Freed, L. A. 1981. Loss of mass in breeding wrens: Stress or adaptation? Ecology 62:1179–1186.

Gibb, J. A. 1955. Feeding rates of Great Tits. British Birds 48:49–55.

Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the Collared Flycatcher *Ficedula albicollis.* Nature 335:813–815.

Haas, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: An experimental approach. Auk 115:929–936.

Heaney, V., and P. Monaghan. 1996. Optimal allocation of effort between reproductive phases: The trade-off between incubation costs and subsequent brood rearing capacity. Proceedings of the Royal Society of London B 263:1719–1724.

Hegner, R. E., and J. C. Wingfield. 1987. Effects of brood-size manipulation on parental investment, breeding success, and reproductive endocrinology of House Sparrows. Auk 104:470–480.

Hillstrom, L. 1995. Body mass reduction during reproduction in the Pied Flycatcher *Ficedula hypoleuca*: Physiological stress or adaptation for lowered costs of locomotion? Functional Ecology 9: 807–817.

Hochachka, W., and J. N. M. Smith. 1991. Determinants and consequences of nestling condition in Song Sparrows. Journal of Animal Ecology 60: 995–1008.

Hogstedt, G. 1980. Evolution of clutch size in birds: Adaptive variation in relation to territory quality. Science 210:1148–1150.

Hussell, D. J. T., and T. E. Quinney. 1987. Food abundance and clutch size of Tree Swallows *Tachycineta bicolor.* Ibis 129:243–258.

Jacobsen, J.-O., K. E. Erikstad, and B.-E. Saether. 1995. An experimental study of the costs of reproduction in the Kittiwake *Rissa tridactyla.* Ecology 76:1636–1642.

Lack, D. 1947. The significance of clutch size. Ibis 89: 302–352.

Leffelaar, D., and R. J. Robertson. 1986. Equality

of feeding roles and the maintenance of monogamy in Tree Swallows. Behavioral Ecology and Sociobiology 18:199–206.

Lindén, M., L. Gustafsson, and T. Pärt. 1992. Selection on fledging mass in the Collared Flycatcher and the Great Tit. Ecology 73:336–343.

Lombardo, M. P. 1991. Sexual differences in parental effort during the nestling period in Tree Swallows (*Tachycineta bicolor*). Auk 108:393–404.

Maigret, J. L., and M. T. Murphy. 1997. Costs and benefits of parental care in Eastern Kingbirds. Behavioral Ecology 8:250–259.

Martin, T. E. 1993. Evolutionary determinants of clutch size in cavity-nesting birds: Nest predation or limited breeding opportunities? American Naturalist 142:937–946.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65:101–127.

Martin, T. E., and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. Ecology 73:579–592.

Mauck, R. A., and T. C. Grubb, Jr. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. Animal Behaviour 49:999–1008.

McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. Nature 380:215–221.

Monaghan, P., M. Bolton, and D. C. Houston. 1995. Egg production constraints and the evolution of avian clutch size. Proceedings of the Royal Society of London B 259:189–191.

Monaghan, P., and R. G. Nager. 1997. Why don't birds lay more eggs? Trends in Ecology and Evolution 12:270–274.

Morehouse, E. L., and R. Brewer. 1968. Feeding of nestling and fledgling Eastern Kingbirds. Auk 85:44–54.

Murphy, M. T. 1996. Survivorship, breeding dispersal and mate fidelity in Eastern Kingbirds. Condor 98:82–92.

Murphy, M. T. 2000. Evolution of clutch size in the Eastern Kingbird: Tests of alternative hypotheses. Ecological Monographs 70:1–20.

Norberg, R. Å. 1981. Temporary weight decrease in breeding birds may result in more fledged young. American Naturalist 118:838–850.

Nur, N. 1984. Feeding frequencies of nestling Blue Tits (*Parus caeruleus*): Costs, benefits and a model of optimal feeding frequency. Oecologia 65:125–137.

Pettifor, R. A., C. M. Perrins, and R. H. McCleery. 1988. Individual optimization of clutch size in Great Tits. Nature 336:160–162.

Pyle, P., S. N. G. Howell, R. P. Yunick, and D. F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.

Ramstack, J. M., M. T. Murphy, and M. A. Palmer.

1998. Comparative reproductive biology of three species of swallows in a common environment. Wilson Bulletin 110:233–243.

RENDELL, W. B., AND R. J. ROBERTSON. 1989. Nest-site characteristics, reproductive success and cavity availability for Tree Swallows breeding in natural cavities. Condor 91:875–885.

ROBERTSON, R. J., B. J. STUTCHBURY, AND R. R. COHEN. 1992. Tree Swallow (*Tachycineta bicolor*). *In* The birds of North America, no. 11 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia and the American Ornithologists' Union, Washington, D.C.

ROFF, A. D. 1992. The evolution of life histories. Chapman and Hall, London.

RYTKÖNEN, S., K. KOIVULA, AND M. ORELL. 1996. Patterns of per-brood and per-offspring provisioning efforts in the Willow Tit *Parus montanus*. Journal of Avian Biology 27:21–30.

SANZ, J. J., AND J. MORENO. 1995. Mass loss in brooding female Pied Flycatchers *Ficedula hypoleuca*: No evidence for reproductive stress. Journal of Avian Biology 26:313–320.

SMITH, H. G., H. KÄLLANDER, K. FONTELL, AND M. LJUNGSTROM. 1988. Feeding frequency and parental division of labour in the double-brooded Great Tit *Parus major*. Effects of manipulating brood size. Behavioral Ecology and Sociobiology 22:447–453.

SMITH, J. N. M. 1981. Does high fecundity reduce survival in Song Sparrows? Evolution 35:1142–1148.

STATISTIX. 1994. Version 4.1, analytical software, Tallahassee, Florida.

STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

SVENSSON, E., AND J. A. NILSSON. 1997. The trade-off between molt and parental care: A case of sexual conflict in the Blue Tit? Behavioral Ecology 8:92–98.

WHEELWRIGHT, N. T., J. LEARY, AND C. FITZGERALD. 1991. The costs of reproduction in Tree Swallows (*Tachycineta bicolor*). Canadian Journal of Zoology 69:2540–2547.

WIGGINS, D. A. 1990. Clutch size, offspring quality, and female survival in Tree Swallows: An experiment. Condor 92:534–537.

WINKLER, D. W. 1987. A general model for parental care. American Naturalist 130:526–546.

WINKLER, D. W., AND P. E. ALLEN. 1995. Effects of handicapping on female condition and reproduction in Tree Swallows (*Tachycineta bicolor*). Auk 112:737–747.

WINKLER, D. W., AND P. E. ALLEN. 1996. The seasonal decline in Tree Swallow clutch size: Physiological constraint or strategic adjustment? Ecology 77:922–932.

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