The costs of reproduction in tree swallows (*Tachycineta bicolor*)[1]

NATHANIEL T. WHEELWRIGHT,[2] JOANNA LEARY, AND CARAGH FITZGERALD

Department of Biology, Bowdoin College, Brunswick, ME 04011, U.S.A.

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We investigated the effect of brood size on nestling growth and survival, parental survival, and future fecundity in tree swallows (*Tachycineta bicolor*) over a 4-year period (1987–1990) in an effort to understand whether reproductive trade-offs limit clutch size in birds. In addition to examining naturally varying brood sizes in a population on Kent Island, New Brunswick, Canada, we experimentally modified brood sizes, increasing or decreasing the reproductive burdens of females by two offspring. Unlike previous studies, broods of the same females were enlarged or reduced in up to 3 successive years in a search for evidence of cumulative costs of reproduction that might go undetected by a single brood manipulation. Neither observation nor experiment supported the existence of a trade-off between offspring quality and quantity, in contrast with the predictions of life-history theory. Nestling wing length, mass, and tarsus length were unrelated to brood size. Although differences between means were in the direction predicted, few differences were statistically significant, despite large sample sizes. Nestlings from small broods were no more likely to return as breeding adults than nestlings from large broods, but return rates of both groups were very low. Parental return rates were also independent of brood size, and there was no evidence of a negative effect of brood size on future fecundity (laying date, clutch size). Reproductive success, nestling size, and survival did not differ between treatments for females whose broods were manipulated in successive years. Within the range of brood sizes observed in this study, the life-history costs of feeding one or two additional nestlings in tree swallows appear to be slight and cannot explain observed clutch sizes. Costs not measured in this study, such as the production of eggs or postfledging parental care, may be more important in limiting clutch size in birds.

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Nous avons étudié l'effet de la taille de la couvée sur la croissance et la survie des oisillons au nid, sur la survie des parents et sur la fécondité future chez des hirondelles bicolores (*Tachycineta bicolor*) au cours d'une période de 4 ans (1987–1990) afin d'établir si des compromis dans la reproduction viennent limiter le nombre d'oisillons par couvée chez les oiseaux. Outre les observations en nature de nichées de différentes tailles chez une population de l'île Kent, Nouveau-Brunswick, Canada, nous avons aussi modifié la taille des nichées en ajoutant ou en retirant deux rejetons, augmentant ou allégeant ainsi le fardeau reproducteur des femelles. Contrairement à ce qui a prévalu dans les études antérieures, ces expériences d'augmentation et de diminution ont été répétées durant 3 années successives chez les mêmes femelles afin d'évaluer les coûts cumulatifs de la reproduction, facteurs qui pourraient passer inaperçus par une manipulation unique des couvées. Contrairement à ce qu'indiquent les prédictions théoriques, ni les observations, ni les manipulations expérimentales n'ont indiqué l'existence d'un compromis entre la qualité et le nombre d'oisillons. La longueur des ailes, la masse et la longueur du tarse des oisillons se sont avérés indépendants de la taille de la couvée. Bien que les écarts entre les moyennes aient suivi les prédictions, peu de différences étaient significatives statistiquement, malgré l'importance des échantillons. Les oisillons des portées réduites n'étaient pas plus susceptibles de revenir se reproduire au même endroit une fois adultes que les oisillons des grandes couvées, mais les taux de retour des oiseaux des deux groupes étaient très faibles. Les taux de retour des parents étaient également indépendants de la taille des couvées; la taille des couvées ne semblait pas non plus avoir d'effet négatif sur la fécondité future (date de ponte, nombre d'oeufs par couvée). Le succès de la reproduction, la taille des oisillons et la survie ne différaient pas d'une année à l'autre chez les femelles dont les couvées sont été manipulées pendant plusieurs années successives. À l'intérieur des limites couvertes par cette étude, on constate que les coûts reliés à l'alimentation de un ou deux oisillons additionnels chez les hirondelles bicolores semblent peu élevés et ne peuvent expliquer les tailles de couvées observées. Les coûts non évalués dans cette étude, tels ceux reliés à la production d'oeufs ou aux soins parentaux après l'apparition des plumes, limitent peut-être davantage le nombre d'oisillons dans une couvée chez les oiseaux.

[Traduit par la rédaction]

Introduction

The influential papers of Lack (1947) and Williams (1966) focused attention on two critical concepts in life-history theory: the factors limiting the number of offspring produced and the costs of reproduction. Lack (1947) envisaged that natural selection would favor the evolution of intermediate clutch sizes in birds because of a trade-off between nestling number on the one hand and fledgling quality and survival on the other, owing to limitations on parental feeding rates. Williams (1966) noted that a trade-off may also exist between (*i*) present reproductive effort and (*ii*) future fecundity and parental survival, which he termed the cost of reproduction. Recently, researchers have searched for evidence for both types of trade-off by manipulating clutch and brood size in birds (e.g., De Steven 1980; Wiggins 1990*b*; references in Lessells 1986; Nur 1988*a*). The last few years in particular have seen a flurry of published experiments and some controversy about the generality of reproductive trade-offs (Reznick 1985; Bell and Koufopanou 1986; Murphy and Haukioja 1986; Winkler and Wilkinson 1988; Stearns 1989), although Nur (1988*a*) concluded that most research published as of 1987 demonstrated at least some costs of reproduction. The picture has become cloudy since Nur (1988*a*) wrote his review, with the publication of several studies that provide only weak or inconsistent support for traditional predictions of reproductive trade-offs with increasing brood size (e.g., Lessells 1986; den Boer-Hazewinkel 1987; Finke et al. 1987; Reid 1987; Korpimäki 1988; Orell and Koivula 1988; Smith et al. 1989).

Nur (1988*b*) made several valid criticism of earlier studies. He stressed that nonexperimental studies allowed only weak inference, that the measurement of reproductive costs has often been incomplete because it focused on fledgling quality and survival but overlooked effects on parental survival and future fecundity, that brood size specific dispersal can lead to biased estimates of survival, and that short-term studies may miss important between-year variation in environmental conditions.

In this paper we report the results of observations and brood manipulations designed to uncover constraints on clutch size and to quantify the costs of reproduction in tree swallows (*Tachycineta bicolor*). Unlike previous studies of birds (for plants, see Primack and Hall 1990), the same individual females were manipulated in the same manner (broods either enlarged or reduced) and by the same amount (two offspring) in up to 3 years to determine the existence of subtle costs of reproduction that may only be exposed when females repeatedly exert large reproductive efforts. We sought to avoid the pitfalls listed by Nur (1988*b*) by examining the effects of brood size experimentally and interpreting them against a background of natural variation. We also attempted to measure costs as completely as possible by considering the effect of brood manipulations on parental survival and future fecundity and by including measures of offspring quality among the costs of reproduction because of its direct relationship to parental fitness. Confounding adult mortality and dispersal is not a problem in this study because adults are philopatric and our study site is an isolated island on which practically every nest can be found, although the problem potentially remains for fledglings (see Methods). Our study was repeated in 3 successive years during which we also quantified the abundance of aerial insects in an effort to relate food availability to growth and survival in tree swallows.

Methods

Study site and species

Our study was conducted at the Bowdoin Scientific Station, located on Kent Island, an 80-ha island in the Bay of Fundy, New Brunswick, Canada (44°35'N; 66°46'W). Since 1935, tree swallows have nested on Kent Island in artificial nest boxes distributed at 30-m intervals across an abandoned hay field (Paynter 1954; Harris 1979; Williams 1988). During the period of the study the breeding population fluctuated between 82 and 101 pairs. A few additional pairs probably nest on the island in natural cavities in dead spruce trees (*Picea glauca*), but such nesting opportunities are rare because there are no breeding woodpeckers on Kent Island to create cavities. Nearby Sheep Island has neither trees nor nest boxes, and Hay Island, which is part of the same three-island archipelago, has a small spruce-fir (*P. glauca, Picea rubens, Abies balsamea*) forest but no nest boxes. The nearest other breeding locations for tree swallows are located on Grand Manan Island, 9 km away, or on the Maine mainland, more than 20 km away. Almost all nestlings and incubating females at Kent Island, as well as most adult males, have been banded with Canadian Wildlife Service aluminum bands annually since 1966.

The natural history of tree swallows at Kent Island has been described in detail by Paynter (1954; see also Kuerzi 1941). Each summer breeding females lay a clutch of 3–8 eggs. Mean clutch sizes in 1947–1948 and 1987–1989 ranged from 5.2 to 5.9 eggs (Paynter 1954; N. T. Wheelwright and A. R. Lewis, unpublished data), which is a typical clutch size for the species at that latitude (D. J. T. Hussell, T. E. Quinney, P. O. Dunn, et al., in preparation). The cool climate of the Bay of Fundy tends to delay clutch initiation until late May or early June, which is a week or so later than comparable mainland sites (D. J. T. Hussell, T. E. Quinney, P. O. Dunn, et al., in preparation). Incubation normally takes 15–16 days, a period extended by the cool climate: most nestlings fledge 21–22 days after hatching (Paynter 1954; cf. Table 3).

Working with tree swallows has certain advantages for the study of clutch size and the costs of reproduction. Because the species nests semicolonially at Kent Island, sample sizes (especially for nonexperimental studies) can be large. The island is isolated, and virtually all nests can be located, so differential dispersal and biases in the probability of recapture with respect to brood size (e.g., Breitwisch 1989) are unlikely in this system unless brood size specific dispersal distances exceed 9 km. Unlike house martins (*Delichon urbica*; Bryant 1979), female tree swallows almost never raise two broods in one season (Paynter 1954; but see Hussell 1983), so one can ignore the effects of reproductive effort on subsequent breeding attempts within the same season (intraseasonal costs of reproduction: Nur 1990). Tree swallows are aerial insectivores, feeding mostly on patchy swarms of 3- to 5-mm midges (Diptera: Chironomidae) on Kent Island (N. T. Wheelwright and A. R. Lewis, unpublished data). Consequently, they do not defend feeding territories, and because the colony is relatively dense and restricted to rather homogeneous habitat, there is little problem of bias caused by variation in territory quality (e.g., Högstedt 1980). Interindividual differences in reproductive abilities remain, of course, potentially obscuring the relationship between brood size and reproductive success (e.g., Perrins and Moss 1975), but the problem can be minimized by controlling for parental age and previous reproductive performance (see later).

Nonexperimental procedures

Clutch size may be constrained when nestling growth is negatively affected by brood size, assuming that small fledglings are less likely to survive than large ones (Perrins and Moss 1975). We regressed the mass, wing length, and tarsus length of offspring late in the nestling period against the size of the brood in which they had been raised as a nonexperimental approach to understand how brood size might affect the quality of offspring produced. Only unmanipulated nests were included in the analyses. Nestling mass was recorded in 1987; in subsequent years we measured mass (using an electronic balance to the nearest 0.1 g), wing length (unflattened, using a wing ruler to the nearest millimeter) from the bend of the wing to the tip of the longest primary, and tarsus length (using calipers to the nearest 0.1 mm from the tibiotarsal joint to the proximal base of the hallux). We also examined the relationship between fledging success (fledglings/egg) and brood size in the same samples. In addition, we examined whether the size of the brood in which a nestling had been raised had any effect on the likelihood that it subsequently joined the breeding population, although nestling return rates are too low for tree swallows at Kent Island to permit a meaningful statistical test.

Large broods receive more frequent food deliveries than small broods (Quinney 1986; C. Schultz, unpublished data), which elevates metabolic costs of parents (Williams 1988). To determine whether raising large broods diminished long-term survival, we compared the clutch sizes of adults that reappeared the next year with those of adults that disappeared. To explore whether raising large broods negatively affected future fecundity, we assessed the relationship between brood size and the number of fledglings produced in successive years.

Experimental procedures

Because nonexperimental analyses may be confounded by genetic and environmetnal correlations (females capable of laying large clutches may also be proficient at raising large broods: Nur 1988*a*), we experimentally modified brood sizes (cf. De Steven 1980; Wiggins 1990*b*). For females that returned, we performed similar manipulations (adding or subtracting offspring) in successive years. In 1988 we selected 15 pairs of nests matched for anticipated hatching date, clutch size, and as closely as we could, location within the colony. Hereafter we refer to these as matched nests. Within each matched nest pair, one nest was randomly determined by the toss of a coin to be enlarged by two eggs; the other nest, which served as the source of the supplemental eggs, was accordingly reduced by two eggs. Previous researchers have disagreed about whether experimental brood size should be randomly assigned (e.g., Nur 1984; Lessells 1986) or whether brood size should be adjusted relative to a female's original brood size (e.g., De Steven

1980; Røskaft 1985; Finke et al. 1987; Korpimäki 1988). Given that individual differences in parental abilities are often invoked to explain negative results and that initial clutch size has been interpreted to reflect maternal quality (Perrins and Moss 1975; Nur 1990), the latter seemed to us a preferable procedure as a way to control for differences in parental abilities. Such an approach also allows a comparison with De Steven's (1980) and Wiggins' (1990a, 1990b) studies of the same species.

Control nests were visited as often as experimental nests, and in some cases their eggs were removed and replaced, but their brood sizes were not changed. When the nestlings from control and experimental nests were 11 days old, we weighed them and measured their wing and tarsus lengths as described earlier. Measuring nestlings at this stage gave a good indication of nestling size at age 15 days, which is about the last day that nestlings can be handled without risking premature fledging (Paynter 1954; De Steven 1980) ($r^2 = 0.37$ (wing), 0.75 (mass), and 0.47 (tarsus); $P < 0.0001$ for all linear regressions). It should be noted, however, that mass, in particular, is a highly plastic character (see Wiggins 1990a; Wheelwright and Dorsey 1991). We identified female parents by capturing them several times during incubation. Male parents were more difficult to determine; using the procedure of Hussell and Quinney (1987) we were able to trap males when they entered the next box at 27% of the nests in 1988 and 72% in 1989.

In 1989 and 1990, we located all returning females involved in earlier brood manipulations. Birds whose broods had been enlarged the previous year were once again assigned to the enlargment treatment; those whose broods had previously been reduced were again assigned to the reduction treatment. By the end of the experiment, three surviving females had their broods enlarged and four females had their brood reduced in 3 successive years (Table 3). In each year, we attempted to match each nest with another for premanipulation (natural) clutch size and hatching date, as well as colony location where possible. Because of mortality and differences between nests in hatching dates in the later years of the experiment, we could not always pair a 1988 "brood-enlarged" female with a 1988 "brood-reduced" female, so we included some new birds in the experiment. Some experimental birds returned and were captured in mist nets but apparently did not breed or bred unsuccessfully, so sample sizes vary between analyses. In total, we performed 54 brood manipulations.

Procedures were similar in all years (and like those of De Steven 1980) except that in 1989 and 1990 we exchanged hatchlings (day 1) rather than almost-hatched eggs in order to minimize nest desertion and variance in hatching dates within broods. Because eggs were exchanged a day or so before hatching in 1988, the additional cost of incubating enlarged clutches was assumed to be trivial (Biebach 1981; Moreno and Carlson 1989; Smith 1989). We refer to the experiments in all years as brood manipulations to emphasize that reproductive costs of the experiment were concentrated on the nestling period rather than on the incubation period.

In 1989 we measured nestlings when they were 12 days old, rather than 11. The correlations between nestling measurements at 11 and 12 days of age for a subset of 74 nestlings measured at both ages were highly significant ($r^2 = 0.77$ (mass), 0.25 (tarsus), and 0.86 (wing); $P < 0.01$ for all linear regressions). In 1988 and 1990 we observed nests daily after the nestlings had been measured to determine the length of the nestling period.

There were no significant differences in any year between enlarged and reduced nests in the premanipulation clutch size, hatching date, female age, female wing length, female mass, male age, or male wing length (Mann–Whitney U-test, $P > 0.75$ except male wing length, $P = 0.07$). Unlike De Steven (1980), we did not maintain constant brood sizes by replacing nestlings that died, but brood reductions occurred at relatively low rates, independent of treatment. Enlarged broods remained large until the end of the nestling period, fledging significantly more young than controls or reduced broods (Table 3).

Although we refer to survival of birds associated with different-sized broods, we actually measured recapture rates. Recapture rates probably approximate survival rates despite the fact that they potentially underestimate survival when individuals survive but disperse or go undetected. Such problems are probably of only minor importance for adult females at Kent Island, given the scarcity of natural cavities in the open habitats preferred by swallows, the repeated censuses of nest boxes, the strong philopatry of adult females, and the isolation of the site (see earlier). Additionally, we made an effort to catch nonbreeding swallows while operating mist nets in the middle of the tree swallow colony for thousands of net-hours each summer as part of a separate study of Savannah sparrows (*Passerculus sandwichensis*). Return rates of adult females, at least, proved to be in line with survival rates of other passerines. We found no evidence of brood size dependent dispersal.

We quantified aerial insect abundance by capturing insects on a daily basis throughout June and July in 1988–1990 (except on days with heavy rain), using passive sampling nets suspended at a height of 2 m at two locations near the center of the colony (see Hussell and Quinney 1987). Nonparametric and, where appropriate, parametric analyses were performed using Statview SE + Graphics (Abacus Concepts 1988). Two-way ANOVAs were performed with nestling body size (wing length, mass, or tarsus length) as the dependent variable, year of the study as one factor, and natural brood size (1–4 nestlings vs. >5 nestlings) or experimental brood size (enlarged vs. reduced) as the other factor. Except where noted otherwise, descriptive statistics are given as ± 1 SD.

Results

Unmanipulated nests

Brood size, fledgling quality, and survival

In only 1 year of the study was nestling body size at age 11 or 12 days significantly correlated with brood size in unmanipulated nests (Table 1). Wing length, mass, and tarsus length differed among years, but they did not differ between broods of 1–4 nestlings vs. >5 nestlings (two-way ANOVA; $P > 0.05$). Both clutch size and number of fledglings were significantly correlated with brood size (Spearman rank; $P < 0.01$), and therefore the relationships between these variables and nestling body size were generally similar to those between brood size and mean nestling body size. Clutch and brood size vary with laying date in tree swallows (Stutchbury and Robertson 1988), as do insect abundance, climate, and other factors (Hussell and Quinney 1987; N. T. Wheelwright and A. R. Lewis, unpublished data), so we performed a multiple regression with brood size and hatching date as the independent variables and mean nestling body size as the dependent variable. When we controlled for hatching date, only nestling mass in 1988 correlated negatively with brood size ($P < 0.05$).

Natal philopatry and survival are rather low among Kent Island tree swallows; only 26 of 1157 nestlings banded between 1987 and 1989 have subsequently returned (2.2%). Although such small samples do not permit a rigorous statistical test, yearlings that had been banded as nestlings and were recaptured the following year did not differ as nestlings from those that were not recaptured in terms of their wing length, mass, or tarsus length in any year of the study (Mann–Whitney U; $P > 0.05$).

Reproductive success (fledglings/egg) was not correlated with brood size in unmanipulated nests (1987: $r_s = 0.12$, $P = 0.25$, $N = 92$; 1988: $r_s = 0.23$, $P = 0.054$, $N = 72$; 1989: $r_s = 0.14$, $P = 0.23$, $N = 71$; 1990: $r_s = -0.32$, $P = 0.13$, $N = 23$). (Similar results are obtained if reproductived success is defined as fledglings/nestling.) Survival of fledglings (as inferred from the few recaptures in subsequent years) was not affected by how many nest mates they had had (Table 2). The few nestlings that returned to Kent Island as yearlings had been raised in broods that were no different in size than those of nestlings that were not seen again (Mann–Whitney U; $P > 0.18$ for all years).

TABLE 1. Spearman rank correlations (r_s) between brood size and three measures of nestling size (averaged across the brood) in unmanipulated nests measured when nestlings were 11 or 12 days old

	Rank correlation			
	Mass	Wing length	Tarsus length	
1987	−0.26			12
1988	−0.29*	0.02	−0.28*	55
1989	−0.21	0.17	0.00	52
1990	0.12	−0.06	0.26	21

[a] Number of broods.
*$P < 0.05$.

TABLE 2. Fraction of all individuals that returned in a given year as a function of clutch size the previous year

	Rate of return		
		6–8 eggs[a]	P^b
1987 to 1988			
Nestlings	0.035 (114)	0.027 (328)	0.89
Females	0.400 (30)	0.538 (65)	0.30
Males	0.222 (18)	0.086 (35)	0.33
1988 to 1989			
Nestlings	0.011 (93)	0.011 (177)	~1.00
Females	0.308 (26)	0.457 (46)	0.32
Males	0.500 (10)	0.143 (35)	0.06
1989 to 1990			
Nestlings	0.033 (60)	0.026 (222)	~1.00
Females	0.364 (22)	0.453 (64)	0.63
Males	0.105 (19)	0.462 (52)	0.01

NOTE: Sample (in parentheses) excludes individuals involved in experimental brood manipulations.
[a] Clutch size in previous year.
[b] Results of Fisher's exact tests (nestlings and males) and χ^2 tests (females).

Brood size, parent survival, and future reproductive success

Females that produced small clutches were no more likely to return the following year than females that produced large clutches in any year (Table 2). Even when samples from all years were combined (a questionable practice in recognition of the importance of year to year variation in environmental conditions) or when probabilities were combined (Sokal and Rohlf 1980, p. 779), female survival was independent of previous clutch size. Males were more likely to return if they had been associated with smaller than average clutch sizes in 1988, but they showed the opposite trend the following year (Table 2).

There was no indication that laying a large clutch or raising a large brood had a negative effect on a female's future fecundity, although once again the shortcomings of nonexperimental approaches should be kept in mind. Brood size was correlated positively, rather than negatively, with the number of eggs laid the following year among nonexperimental females (1987–1988: $r_s = 0.43$, $P = 0.02$, $N = 32$ females; 1988–1989: $r_s = 0.39$, $P = 0.04$, $N = 28$). The number of fledglings produced also tended to be correlated positively between years (1987–1988: $r_s = 0.34$, $P = 0.08$; 1988–1989: $r_s = 0.14$, $P = 0.33$).

Experimental nests

Effects of brood size on fledgling size

Brood size had no significant effect on nestling wing length, mass, or tarsus at age 11 or 12 days in experimental nests (Table 3; combining probabilities from independent tests of significance (Sokal and Rohlf 1980); $P < 0.30$). Paired t-tests comparing matched nests (pairs of nests where both successfully produced 11-day-old young) showed that wing length and tarsus length did not differ significantly between treatments in any year; nestlings from reduced broods were heavier only in 1988 ($P < 0.05$). A two-way ANOVA, however, suggested that nestlings from experimentally enlarged broods were significantly lighter and had shorter wings than nestlings from reduced broods (19.8 ± 3.3 g vs. 22.2 ± 2.0 g; 42.8 ± 8.0 mm vs. 46.5 ± 6.1 mm, respectively; $N = 18$ enlarged and 21 reduced broods; $P < 0.05$). There were also significant year effects, due mostly to slightly different methods employed each year (see Methods). When the analysis was restricted to those females whose broods were manipulated in 3 successive seasons (Table 3), there were no significant differences between treatments in nestling wing length, mass, or tarsus (two-way ANOVA; $P > 0.05$) or in any 1 year (Mann–Whitney U test; $P > 0.05$). Enlarged and reduced broods did not differ in the length of the nestling period (the time between hatching and fledging) or fledging success (fledglings/egg) (Table 3).

One factor rarely controlled for in clutch or brood manipulation studies is parental quality, although it is often invoked to explain variation between females in reproductive success (e.g., De Steven 1980; Pettifor et al. 1988; Nur 1990). A female's reproductive success in earlier years may provide a measure of her present parental quality. We found no difference between experimental females in the number of fledglings produced in the year preceding manipulations of their brood. Females whose broods were enlarged in 1988 had produced 3.9 ± 2.3 fledglings in 1987, compared with 4.9 ± 1.8 fledglings produced in 1987 by females whose broods were reduced in 1988. Control females in 1988 had produced 4.0 ± 2.6 fledglings in 1987 (Kruskal–Wallis test; $P > 0.50$). If the direction of these differences were meaningful, we would have expected an even greater handicap for nestlings raised in enlarged broods (expressed as decreased nestling size or fledging success) because their mothers had earlier proven themselves inferior parents.

Effects of brood size on parent survival and future fecundity

Adult females whose broods had been enlarged returned the following year at about the same rate as control females or females with reduced broods (Table 4). Of the 30 females involved in the original experiment in 1988, 6 were alive in 1990 (3 whose broods were enlarged each year, and 3 whose broods were reduced each year). Brood manipulations had no obvious effect on female fecundity 1 year later: neither brood size nor hatching date differed among females whose broods were manipulated the previous year (Table 5).

The few adult males who returned in successive years after having their broods manipulated showed no obvious long-term effects of brood manipulations, in terms of either survival or the brood size of the females with whom they were mated (Table 5), although as De Steven (1980) pointed out, it is difficult to detect subtle costs of reproduction with such small sample sizes.

Insect abundance

About 90% of all insects sampled were 3- to 5-mm midges ($N = 5876$ insects). Midges, which also make up the major part of the diet of tree swallows on Kent Island, were far more

TABLE 3. Effects of brood-size manipulations on nestling size and fledging success

| | Treatment | | | |
	Brood enlarged by 2 offspring	Control	Brood reduced by 2 offspring	P^a
1988				
Wing length (mm)	39.0 (6.6)	43.3 (5.9)	43.4 (3.4)	0.44
Mass (g)	18.5 (2.7)	20.9 (2.7)	21.4 (1.3)	0.07
Tarsus length (mm)	12.0 (0.4)	12.3 (0.3)	12.3 (0.2)	0.27
Nestling period (days)	22.0 (1.8)	—	21.0 (1.2)	0.27
Fledglings/egg	0.85 (0.11)	0.77 (0.26)	0.93 (0.12)	0.12
No. of fledglings	6.6 (1.1)	4.3 (1.6)	3.6 (0.5)	:0.01
N^b	9	55		
1989				
Wing length (mm)	49.5 (6.9)	52.8 (5.1)	51.8 (6.7)	0.52
Mass (g)	21.6 (3.3)	22.7 (2.4)	23.6 (1.6)	0.60
Tarsus length (mm)	10.7 (0.4)	11.1 (0.4)	10.8 (0.3)	0.05
Fledglings/egg	0.85 (0.10)	0.89 (0.17)	0.85 (0.27)	0.55
No. of fledglings	6.7 (1.0)	5.3 (1.2)	3.3 (1.2)	:0.01
N^b	6	53	6	
1990				
Wing length (mm)	40.9 (7.0)	43.0 (4.6)	47.1 (6.8)	0.20
Mass (g)	20.4 (4.0)	20.7 (2.2)	22.4 (3.1)	0.67
Tarsus length (mm)	12.1 (0.5)	12.2 (0.3)	12.3 (0.5)	0.84
Nestling period (days)	22.0 (1.0)	22.0 (1.3)	21.5 (1.7)	0.27
Fledglings/egg	0.57 (0.43)	0.87 (0.13)	0.75 (0.35	0.35
No. of fledglings	4.0 (3.0)	4.4 (0.8)	2.5 (1.3)	0.02
N^b	3	21	4	

NOTE: All values are brood means (1 SD in parentheses). Nestlings were measured at 11 days of age in 1988 and 1990 and at 12 days in 1989. Slightly different methods of measuring wings and tarsi were used each year, but within a year all measurements were standardized (see Methods).

[a]Results of Kruskal–Wallis tests comparing enlarged, control, and reduced broods.

[b]Number of broods, including only those raised by females whose broods were enlarged or reduced in 3 successive years.

TABLE 4. Fraction of all individuals that returned in a given year as a function of brood-size manipulations the previous year

| | Rate of return | | | |
	Brood enlarged by 2[a]	Control[a]	Brood reduced by 2[a]	P^b
1988 to 1989				
Nestlings	0.033 (61)	0.011 (270)	0.00 (39)	0.74
Females	0.500 (14)	0.426 (54)	0.400 (15)	0.87
Males	0.750 (4)	0.350 (20)	0.330 (3)	0.49
1989 to 1990				
Nestlings	0.000 (35)	0.027 (291)	0.00 (19)	
Females	0.625 (8)	0.418 (91)	0.375 (8)	0.62
Males	0.250 (4)	0.397 (63)	0.00 (6)	0.80

[a]Treatment in previous year.

[b]Results of Fisher's exact tests comparing return rates for enlarged and reduced broods

abundant in 1988 than in 1989 or 1990, as estimated by passive samples (Hussell and Quinney 1987). Over the 30-day period during which 75–95% of all tree swallow nests hatched young, we collected an average of 65.6 ($\pm$100.3) midges per sample in 1988, 10.8 ($\pm$17.3) in 1989, and 14.1 ($\pm$17.1) in 1990.

Discussion

The costs of reproduction and reproductive trade-offs in general have proven exceedingly difficult to pinpoint, despite

their intuitive appeal (Lack 1947; Williams 1966; Charnov and Krebs 1974; Bell and Koufopanou 1986; Stearns 1989). In this study, we searched for several types of costs associated with large brood sizes: (i) short-term costs, such as reduced nestling size and prolonged nestling periods, and (ii) long-term trade-offs, such as diminished survival rates, delayed future reproduction, and reduced future clutch sizes. We examined nestlings, female and male parents, and we took several approaches: (i) nonexperimental correlation of brood size with growth, survival, and future fecundity; (ii) experimental manipulations of brood size; and (iii) compounding the effect of the manipulations by imposing a similar reproductive burden on the same individual females in successive years.

Neither observation nor experiment supported the existence of an important trade-off between offspring quality and quantity within the range of brood sizes in this study, in contrast with the predictions of Lack (1947) and reports for other species (Perrins and Moss 1975; Nur 1984; Orell and Koivula 1988; Smith et al. 1989). Many of the correlation coefficients (Table 1) and differences between means for all nestling size variables (Table 4) were in the direction predicted, but few differences were statistically significant, despite large sample sizes. There was great variability between broods of the same size in the average size of nestlings, as indicated by low absolute values of r_s (Table 1). Possibly, the experimental enlargement of brood size did not elevate foraging costs. Although Williams (1988) showed an increase in metabolic costs associated with raising more young in the same tree swallow colony, preliminary data

ABLE   Eff   brood manipulations on fecundity in subsequ   'ear   ale tree swallows

| | Treatment in previous year | | | |
	Brood enlarged by 2 offspring	'ontrol	Brood reduced by 2 offspring	p
989				
Clutch size				
Clutch initiation				
date (Julian)	49.3 (7.8)	48.7 (8.4	46.6 (2	
N	7	30	6	
1990				
Clutch size		5.4 (0.9)	6.0	
Clutch initiation				
date (Julian)	156.0	60.6 (5		
N	4			

NOTE: All values are means (1 SD in parentheses), with sample sizes below.
[a]Results of Kruskal–Wallis tests comparing enlarged, control, and reduced brood

on control nests showed no relationship between parental feeding rate and brood size (over the range of 2–4 nestlings) during 2-h observation periods ($N = 11$ nests; Spearman rank test; $P > 0.30$ (C. Schultz, unpublished data)). In any event, parents with enlarged broods were able to raise their young adequately on abundant swarms of midges, with no obvious adverse effects. Some parents that lay large clutches are presumably characterized by superior parental abilities in other respects as well (Högstedt 1981; Smith 1981), which illustrates the problem of relying on nonexperimental approaches for uncovering costs of reproduction and raises the possibility of individual optimization of clutch size (Nur 1988a). The absence of more dramatic consequences for nestlings that have to share food within increasingly large broods may be explained in part by the fact that parents with few offspring may actually have to spend more time brooding them (and less time foraging) because the homeothermic capacity of the brood is positively correlated with its size (Clark 1984).

Any effect of brood size on nestling size may have been short-lived, for the lower mass of offspring from large broods did not noticeably reduce their likelihood of survival (see also Wiggins 1990a). Fledgling survival (as inferred from recaptures) appeared to be unrelated to the size of the brood in which they were raised in both nonexperimental and experimental analyses, although low return rates made it difficult to draw conclusions about the effect of brood size on offspring recruitment.

There was no significant relationship between brood size and survival in parents with unmanipulated broods. Similarly, females and males who were forced to raised enlarged broods survived as well as control parents or parents with reduced broods. Furthermore, adults suffered no clear costs in terms of future fecundity. De Steven's (1980) brood-size manipulations with the same species yielded equally equivocal results: enlarged broods did not differ from controls in nestling wing length, fledgling success, fledgling survival, or adult survival.

As Primack and Hall (1990) emphasize, the costs of reproduction may be subtle or delayed. To unmask them, they recommend that investigators should repeatedly impose the same treatment on the same individuals. Accordingly, we expected to witness negative effects of brood enlargements in the 2nd year of the experiment, and perhaps even greater effects in the 3rd year. Nonetheless, the effect of brood manipulations on nestling wing length, mass, and tarsus length was less in 1989 than in

1988, and less still in 1990; and there was no effect of repeated brood manipulations on parent survival or future fecundity.

Even though tree swallows have high energy requirements because of the demands of aerial foraging (Williams 1988), our results as well as those of De Steven (1980) suggest that food availability during the breeding season does not directly limit brood size, although it may constrain egg formation (Hussell and Quinney 1987). Consistent with this conclusion is that increasing brood size had its most evident negative effect during a year (1988) when insects were extraordinarily abundant. Male-removal experiments (Wolf et al. 1988; Bart and Tornes 1988; P. Dunn, personal communication) and observations under natural conditions (Quinney 1986; although see Leffelaar and Robertson 1986) have demonstrated that unaided adults can raise nestlings, thereby casting doubts on Lack's (1947) emphasis on nestling food as the central factor explaining the evolution of clutch size. No experimental study has so far been successful in recreating two important components of the cost of reproduction, namely the energy, nutrients, and time involved in egg production and postfledgling parental care (Moreno 1984). On Kent Island tree swallows continue to feed and guard their young for several days after they leave the nest (A. R. Lewis, unpublished data). It may turn out that one or both of these are truly the factors that limit clutch size in birds. Other factors that may confound studies of reproductive trade-offs include year to year variation in results (Clobert et al. 1987; Korpimäki 1988; Orell and Koivula 1988), variation between habitats (Paynter 1954; Hussell and Quinney 1987), variation between age groups (De Steven 1980; but see Bryant 1979; Lessells 1986), and variation in time of year (Finke et al. 1987).

One wonders about the fact that most studies involving clutch- or brood-size manipulations have concentrated on introduced species (e.g., Lessells 1986) or on species whose population densities have been hugely inflated by the provision of predator-proof artificial nest boxes (e.g., this study; Perrins and Moss 1975; Askenmo 1979; De Steven 1980; Ekman and Askenmo 1986; Quinney 1986; den Boer-Hazewinkel 1987; Boyce and Perrins 1987; Finke et al. 1987; Korpimäki 1988; Smith et al. 1989; see East and Perrins 1988). Clutch size in tree swallows evolved under conditions when nest cavities were isolated, uncommon, and perhaps vigorously contested and when the densities of conspecific foragers were much lower.

In conclusion, we found little support for a cost of reproduc-

tion in tree swallows over the range of brood sizes that we studied. The question of what factors limit clutch size remains. Experimental manipulation of brood sizes makes the "individual optimization" hypothesis for a positive correlation between clutch size and reproductive success less plausible in this case because enlarged and decreased broods were matched for initial clutch size (and presumed parental quality). Fluctuating selective pressures (as indicated by fivefold differences in insect prey abundance between years in this study) may partly account for variation in clutch size within populations (see also Boyce and Perrins 1987), but they do not explain the minor responses to brood manipulations. Future research should concentrate on constraints and trade-offs during the periods of egg laying and fledgling care. Despite the difficulty of demonstrating statistically significant differences between treatments with very similar survival rates, and the requirements of impracticably large sample sizes (De Steven 1980; Nur 1988a), the sample size of experimental studies of the consequences of clutch and brood size has grown to the point where we can begin to draw reliable conclusions about the existence of costs by statistically analyzing the direction of the outcome of the studies themselves (cf. Nur 1990). Although we agree with Nur (1988a) that negative results do not disprove the existence of reproductive costs, the accumulation of studies, especially recent work, suggests that experimentally enlarging broods by one or two young might temporarily and slightly reduce nestling growth, but will have little or no effect on fledgling survival, parental survival, or future reproduction, except perhaps in years when resources are limiting.

Acknowledgements

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