

TIME AND RECRUITMENT COSTS AS CURRENCIES IN MANIPULATION STUDIES ON THE COSTS OF REPRODUCTION

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Abstract. Life history theory predicts that parents will have lower Darwinian fitness if they tend clutches that are above or below the size they naturally produce. We experimentally tested for relationships between fitness and clutch size in Tree Swallow (*Tachycineta bicolor*) offspring and parents. Over 130 trios of nests initiated on the same day were randomly divided among reduce (−3 eggs), control (3 eggs picked up and replaced), or add (+3 eggs) manipulations. Pre-manipulation modal clutch size was six eggs (range before manipulations was 1–10; afterwards, it was 1–11). Hatching took longer in larger clutches, but the proportion of eggs hatching and fledging was similar for clutches from 4 to 10, so that clutches of 10 produced the maximum number of fledgling. Parental feeding rates were higher for larger broods, but per capita feeds to nestlings were fewer, and nestlings were smaller. Nonetheless, survival of both young and adults, based on recaptures in subsequent years, was not significantly affected by manipulations. Manipulations also had no significant effect on subsequent reproduction, including the number of fledglings produced by either local recruits or returning breeders. Collectively, our results failed to detect fitness costs associated with tending larger clutches for either parents or the offspring reared and suggested directional selection for larger clutch size. However, because clutches that hatch later produce fewer recruits, the extra days required to lay more eggs and to fledge extra young may eliminate a large part of the advantage that would accrue to parents producing enlarged clutches. For example, our data suggest that there may be less than a 16% benefit to producing nine instead of six eggs, rather than 50%, as is suggested by experimentally manipulated egg numbers alone. Thus, time, rather than costs of reproduction, may be the crucial constraint selecting against Tree Swallows laying larger clutches.

Key words: lifetime reproductive success; recruitment; reproduction costs; *Tachycineta bicolor*; Tree Swallows.

INTRODUCTION

Life history theory is predicated on trade-offs (Roff 1992, Stearns 1992). Interest in the trade-off between current and future reproductive effort arose from the hypothesis that, at each breeding event, female birds lay the optimum number of eggs to maximize their lifetime reproductive success (a hypothesis modified from Lack 1947 by Williams 1966, Charnov and Krebs 1974, Perrins and Moss 1975). Although some experimental studies have supported the modified hypothesis, several others have failed to find evidence of such a trade-off (reviews in Lessells 1986, Nur 1988a, Partridge and Harvey 1988, Dijkstra et al. 1990, Monaghan and Nager

1997). In particular, no previous studies have found this trade-off in Tree Swallows *Tachycineta bicolor* (De Steven 1980, Wiggins 1990, Wheelwright et al. 1991, Murphy et al. 2000). Wheelwright et al. (1991) even failed to find evidence of costs of reproduction in female Tree Swallows raising enlarged broods for three successive years. One reason many such studies have not detected costs is that only the effort in raising broods has been assessed; the substantial costs of incubation (e.g., Yom-Tov and Hilborn 1981, Gloutney et al. 1996, Heaney and Monaghan 1996) have been overlooked. To address this, we manipulated Tree Swallow clutches shortly after laying was completed, so that parents experienced both increased costs of incubation and increased costs of brood and fledgling provisioning.

A second reason the hypothesis may not have been supported is that sample sizes have been insufficient to detect putative costs. To address this, we used 14 years of data from over 1500 nests to test for fitness consequences to nestlings and parents of manipulated and natural clutch sizes. A third reason may be that the costs of reproduction are not a major constraint for Tree

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Swallows; here we evaluated the importance of time as a constraint on recruitment.

Tree Swallows are cavity-nesting passerines that readily use nest boxes (Robertson et al. 1992). In our population, modal clutch size is six, and parents are single-brooded. We removed three eggs from some clutches and added three to others. We then compared the number of days required to hatch clutches, proportion of eggs hatching and producing fledglings, parental feeding rates and nestling size, subsequent return rates of young and apparent survival of parents, and subsequent reproductive success of young and parents.

METHODS

General methods

Our study site was the St. Denis National Wildlife Area, 40 km east of Saskatoon, Saskatchewan, Canada (described in Clark and Shutler 1999, Shutler and Clark 2003). We report on observations from the 1991–2004 breeding seasons. In the colony, there were 50 Tree Swallow boxes (following the design in Hussell and Quinney 1987) in 1990, 75 in 1991, 100 in 1992, and 115 thereafter. Boxes were 1.5 m above ground on metal posts that were spaced a minimum of 30 m apart. We minimized differences among nest box environments by orienting all box entrances southeast, erecting boxes away from shade, and removing old nesting material at the end of each breeding season. All procedures involving birds were approved by the University of Saskatchewan Animal Care Committee (Saskatoon, Saskatchewan, Canada). Individuals were captured opportunistically or trapped (when nestlings were ~4 days old) inside nest boxes, and banded with numbered aluminum Canadian Wildlife Service bands. Statistical analyses were performed in SAS version 8.02 (SAS Institute 2002). Except where indicated, we report means \pm SE.

Nest monitoring and manipulations

Beginning in mid-May each year, boxes were visited daily to record initiation date (date of first egg) and the date of the laying of the last egg (which we deemed had occurred if clutch size remained consistent for three consecutive days). Visits thereafter were timed to determine hatching success (number of eggs hatching/clutch size \times 100) and fledging success ([number of nestlings at 12 days – young found dead in the nest at 20 days]/clutch size \times 100).

To measure investment in incubation, in 1991 through 1995, daily visits began a day before estimated hatch (14 days after the last egg was laid). Under the null hypothesis that clutch size does not influence incubation time, all eggs would hatch at 14 days. We calculated surplus egg-incubation days as

$$1a + 2b + 3c + 4d$$

where *a* through *d* are the number of eggs hatching on

days 15 through 18 days after clutch completion, respectively.

In each of 1991, 1992, 1993, 1994, 1996, and 1998, between 18 and 31 trios of nests that were initiated on the same day were randomly assigned to reduce, control, or add manipulations. Three eggs were removed from a reduce nest and placed in an add nest. Three eggs in a control nest were picked up and replaced. Because manipulations were done within three days of clutch completion, costs borne by parents in add manipulations included ~12 days of incubation and ~20 days of feeding. Due to predation before fledging, final sample sizes were 134 reduce (*N* = 4, 9, 65, 52, and 4 for clutches of 1 to 5, respectively), 144 control (*N* = 2, 3, 12, 76, 46, and 8 for clutches of 3 to 8, respectively), and 143 add (*N* = 3, 15, 68, 48, and 9 for clutches of 7 to 11, respectively) clutches.

Feeding rates and nestling size

To test whether brood size influenced parental effort, we monitored parental feeding rates in 1992. After the first nestling had hatched in a box, adults were captured and marked individually by bleaching (with commercial hair products) tail feathers in distinct patterns. Based on asymptotic standard deviations, we settled on 20 min as providing stable estimates of parental feeding rates (based on an analysis of observation periods of up to 90 minutes; C. Fehr, *unpublished data*). Each box was watched with a 20 \times spotting scope from at least 30 m away. Observations were repeated both before and after noon when nestlings were 8, 12, and 16 days of age, for a total of six observation periods per nest. To control for the initial disturbance caused by our arrival, observation periods began when the first feeding was observed. The number of trips to the box explains >95% of total food delivery in Tree Swallows, and quality of food is independent of brood size (McCarty 2002).

From 1991 to 1994, most nestlings were measured at 16 days post-hatch. From 1996 on, most young were measured at 12 days post-hatch, but in some cases we measured nestlings at other ages because of time constraints arising from synchronous breeding. We thus controlled for age by including it as a covariate in general linear models that used these data. Measurements taken in all years included unflattened wing length (\pm 0.5 mm using a stopped wing ruler), and body mass (\pm 0.5 g using a spring balance). In some years, we also measured length \pm 1 mm of the ninth primary, maximum tail length, bill length, and head length. Because of variation in weather and consequent food availability, we also included year as a covariate in analyses of growth. Because nestmates are not independent, we computed average growth indices for each nest.

Survival and reproductive success subsequent to manipulation

Survival was estimated by recapturing birds in years subsequent to banding and constructing encounter

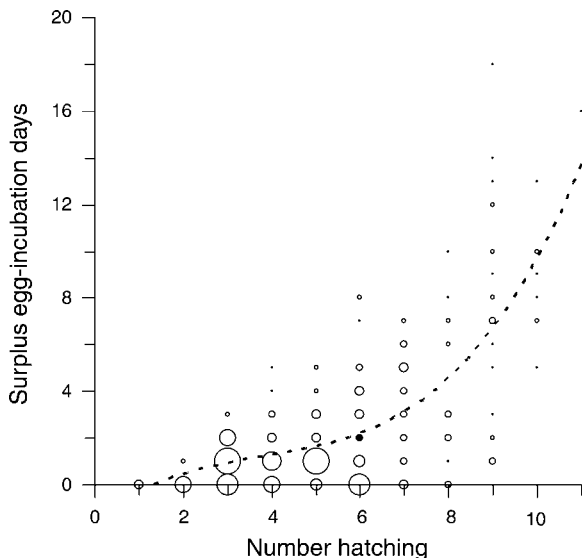


FIG. 1. Additional incubation time required for larger Tree Swallow clutches ($N = 238$). (See *Methods: Nest monitoring and manipulations* for the calculation of surplus egg-incubation days.) Symbol size denotes the number of overlapping points, ranging from 0 to 16. The dotted curve denotes the third-order polynomial fitted to data ($R^2 = 0.51$, $P < 0.0001$).

histories for each individual. For consistency, we excluded birds that received more than one treatment, and only included encounter histories beginning in the year in which a bird was subjected to its first (and only) clutch manipulation. Apparent survival rates were estimated using standard Cormack-Jolly-Seber models in Program MARK (White and Burnham 1999). Apparent survival was initially modeled to include effects of clutch manipulation, sex, and year, and then we considered 15 models that represented simpler explanations for variation in survival and recapture probabilities. Models included constant survival and recapture probabilities for some or all three main effects, as well as separate recapture probabilities for 1992 and 1993 pooled vs. all other years (for a description of weather impacts on recapture rates see Shutler and Clark [2003:623]). Akaike's Information Criterion adjusted for sample size (AIC_c) was calculated; the difference (ΔAIC_c) between AIC_c of the best model, that with the lowest AIC_c value, and other models was used to determine each model's relative plausibility (Burnham and Anderson 1998).

Subsequent reproductive success of birds following manipulation was also compared and summed over their lifetime. For these comparisons, 21 individuals experiencing both an add and a reduce manipulation were pooled with controls. Five individuals were in reduce manipulations twice, and seven were in add manipulations twice; these birds were pooled with individuals experiencing single reduce or add manipulations, respectively.

RESULTS

Hatching and fledging

Most (83%) clutches that were eventually manipulated and retained for analysis began with six or seven eggs, so that the most common reduce clutches were three or four eggs, and the most common add clutches were nine or 10 eggs (see data presented in *Nest monitoring and manipulations*; sample sizes may differ slightly from Shutler and Clark [2003] because data were missing for different variables). Thus, there was little overlap in clutch size among manipulations.

Hatching took longer to complete in larger clutches (general linear model where the explanatory variable was [manipulated] number hatching and the response variable was surplus egg-incubation days, $F_{1,236} = 171.2$, $P < 0.0001$; Fig. 1). Despite the delays, hatching success (excluding depredated nests) was $>70\%$ for clutches of between four and 10, regardless of whether or not they had been manipulated (Fig. 2). Clutches of three or fewer were abandoned in many cases, suggesting that either females were less motivated to incubate clutches with unusually low reproductive value or, in the case of unmanipulated clutches, that egg-laying was interrupted (e.g., by death or injury of one member of a breeding pair). At the other extreme, females were capable of incubating some artificially large clutches, including some containing 11 eggs (Fig. 2). Similarly, fledging success was $>50\%$ for clutches of between four and 10, regardless of whether or not they had been manipulated (Fig. 2). Hence, on average, parents produced the most fledglings from clutches of 10 eggs (Fig. 3).

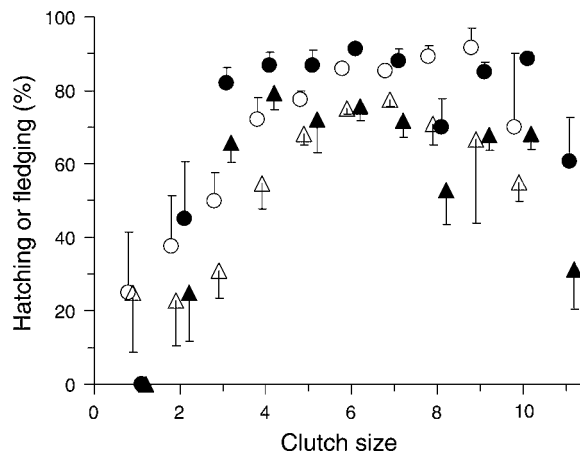


FIG. 2. Success in relation to clutch size. Excluding depredated nests, in both unmanipulated clutches (open symbols, $N = 967$) and manipulated clutches (solid symbols, $N = 421$), hatching success (circles) and fledging success (triangles) were fairly consistent for clutches and broods of 4–10. Note that we had a small number of unmanipulated clutches that exceeded clutch sizes involved in the manipulations. For clarity, data for unmanipulated vs. manipulated clutches are laterally offset, and only positive standard errors for hatching success and negative standard errors for fledging success are shown.

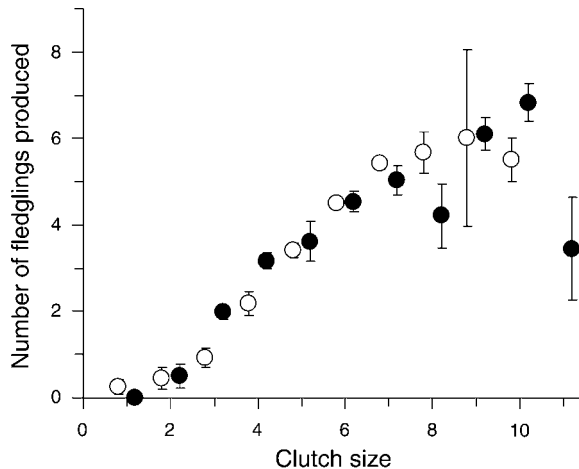


FIG. 3. Production of fledglings in relation to clutch size. For 10 or fewer eggs, there was a linear relationship between the number of young that parents fledged and (manipulated) clutch size (general linear model $F_{1,444} = 168.4$, $R^2 = 0.27$, $P < 0.0001$; a model with a linear and second-order polynomial term ($F_{2,443} = 91.6$, $R^2 = 0.29$, $P < 0.0001$) and a model with a linear and second- and third-order polynomial terms ($F_{3,442} = 61.1$, $R^2 = 0.29$, $P < 0.0001$) did not explain significantly more variation. Data are means \pm SE; open symbols are unmanipulated clutches, and solid symbols are manipulated clutches.

In 1993, >90% of embryos and young perished in the nest because of an extended damp, cold spell (R. G. Clark, unpublished data). If we excluded this year, hatching success was >80% for clutches of between four and 10, and fledging success was >70% for broods of between four and 10, and SES were smaller for both these variables, but the general patterns seen in Fig. 3 remained consistent. In sum, parents were capable of hatching and fledging clutches larger than those they laid, although some pairs were possibly limited to a maximum of 10 (Fig. 3).

Feeding rates and growth

During 234 observation periods at 45 different boxes (15 reduce, 15 control, 15 add), we saw 739 feedings by males and 891 feedings by females (similar to Leffelaar and Robertson 1986). Because of occasional poor weather, sampling effort was not equal among nest boxes. However, after regressing against brood size, residual feeding rates at nests did not vary relative to brood age, time of day, nest initiation date, or date of observation (all absolute values of $r < 0.10$, all P values > 0.30 ; also see McCarty 2002). Hence, we pooled data from the six observation periods to avoid pseudoreplication, using a single average feeding rate for each box. Both males and females increased feeding rates to larger broods (combined feeding rate $r = 0.66$, $P < 0.0001$; Fig. 4). However, per capita feeding rates decreased as brood size increased ($r = -0.55$, $P = 0.0001$; Fig. 4). Hence, costs in parental effort and in food delivery to nestlings were significantly related to brood size. Lower per capita

feeding rates were associated with smaller nestlings in larger broods (Table 1, Fig. 5). This may have translated into delayed fledging from larger broods (but see Wheelwright et al. 1991), but we avoided visiting nests at this stage so that we did not provoke premature fledging. A second feature of growth within larger broods was greater variation among nestlings in body size (Table 1), although this variation could have arisen from mixing eggs from different clutches (which varied in precise stage of incubation and in parentage) rather than from consequences of clutch size.

Survival, recruitment, and lifetime fledgling production

Apparent recruitment of 1836 nestlings from manipulated clutches was 4.7% (87 individuals), and did not vary relative to manipulation (Table 2). None of the body size measures predicted recruitment (logistic regressions; all P values > 0.12). However, nestlings with lower mass were less likely to be recaptured ($N = 1835$, Wald $\chi^2 = 6.8$, $P = 0.009$). This result held if we added manipulation (reduce, control, or add; Wald $\chi^2 = 0.1$, $P = 0.98$) to the model. We had few data to compare lifetime fledgling production of young recruiting from manipulated clutches because many of these individuals had their clutches manipulated, but we did not detect consequences to parameters strongly correlated with recruits' subsequent fledgling production, namely, clutch initiation date and clutch size (Table 2). Another influence on recruitment was time of year at which birds left the nest; late-fledged young were less likely to recruit locally (likelihood ratio $\chi^2 = 4.4$, $P = 0.04$; Fig. 6), and this result was not biased by late-fledging young dispersing greater distances (r between fledging date and natal dispersal distance = 0.02, $P = 0.71$, $N = 418$).

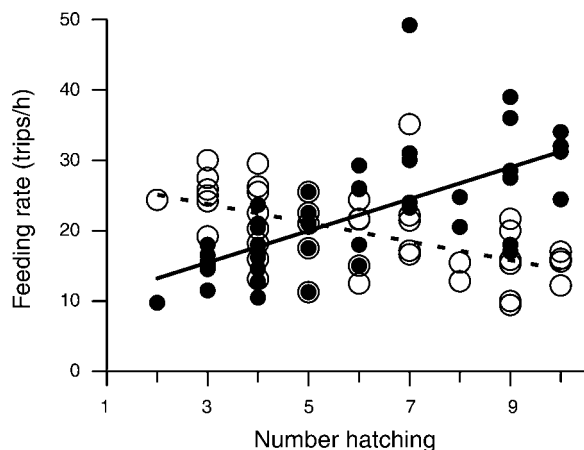


FIG. 4. Feeding rate relative to number hatching. Parents (combined trips of female and male) increased feeding rates to larger broods (solid symbols, solid line), but not sufficiently to maintain per capita feeding rates to nestlings (open symbols, dotted line). Data for per capita feeding rates are multiplied by 5, so that the negative slope of this relationship is more easily compared to that of parental feeding rates.

TABLE 1. Results of general linear models for Tree Swallow brood development relative to brood size.

Morphological measure	Model				Year			Age		Brood size	
	df	<i>N</i>	<i>R</i> ²	<i>P</i>	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Mean for brood											
Wing	7, 330	337	0.64	<0.0001	5	41.5	<0.0001	122.1	<0.0001	48.0	<0.0001
Ninth primary	3, 142	145	0.77	<0.0001	1	9.7	0.002	103.7	<0.0001	25.8	<0.0001
Tail	4, 142	146	0.78	<0.0001	2	73.3	<0.0001	82.1	<0.0001	29.6	<0.0001
Bill	4, 142	146	0.25	<0.0001	2	9.3	0.0002	34.2	<0.0001	2.3	0.13
Head length	3, 142	145	0.56	<0.0001	1	5.4	0.02	32.7	<0.0001	13.5	0.0003
Mass	7, 330	337	0.22	<0.0001	5	5.3	0.0001	0.3	0.60	47.6	<0.0001
Standard deviation for brood†											
Wing	7, 320	327	0.09	<0.0001	5	0.8	0.54	0.1	0.77	26.6	<0.0001
Ninth primary	3, 139	142	0.18	<0.0001	1	3.2	0.07	1.8	0.18	28.8	<0.0001
Tail	3, 139	142	0.15	<0.0001	1	2.3	0.13	0.9	0.35	22.6	<0.0001
Bill	3, 139	142	0.12	0.0005	1	5.5	0.02	4.7	0.03	10.7	0.001
Head length	3, 139	142	0.08	0.008	1	1.5	0.22	0.7	0.40	9.6	0.002
Mass	7, 320	327	0.10	<0.0001	5	3.3	0.007	1.5	0.21	19.3	<0.0001

Notes: Larger broods grew more slowly, and there was more variation in nestling size within larger broods (results shown are from general linear models controlling for year and age in days at which nestlings were measured). Because some measures were not taken in some years, degrees of freedom vary for year, but there is one degree of freedom for the other variables in models.

† Excludes broods <3.

Approximately 80% of adults were captured from active nests, and dispersal distance was not affected by manipulation (Shutler and Clark 2003). Apparent return rate of 255 adult females raising manipulated clutches was 54% (138 individuals) and for 193 adult males was 54% (104 individuals), but was not related to manipulation (Table 2). After excluding individuals experiencing more than one manipulation (which biases survival estimates downward because it excludes individuals that survived the initial manipulations), the most plausible model in Program MARK suggested that apparent survival rate varied annually ($AIC_c = 876.6$). The highest ranked model in the model set that incorporated treatment as a predictor was not well supported ($\Delta AIC_c = 7.6$); this model estimated apparent survival rates for reduce and control females combined to be 42.3% (95% confidence interval [CI] = 37.5–47.2%) and that of add females to be 45.2% (95% CI = 30–54.8%).

Data did not support predictions of impaired reproduction following add manipulations (Table 2). In fact, both females and males had the most young fledge from their nests if they experienced add manipulations and the least if they had experienced reduce manipulations (Tukey studentized range tests revealed significance [$P < 0.05$] for females in add vs. reduce manipulations, and for males in both add and control vs. reduce manipulations; Table 2). Hence, adults would apparently do better raising larger clutches than they actually produced.

DISCUSSION

We observed many of the predicted or commonly observed relationships for experimentally enlarged clutches. Larger clutches took longer to hatch (Nur 1984a, Conrad and Robertson 1992) and were associated with increased parental feeding rates, although not

enough to maintain per capita feeding (Drent and Daan 1980, Leffelaar and Robertson 1986, Nur 1988b, Martins and Wright 1992). Thus, parents passed some of the costs of large clutches on to their young (Hochachka 1992), and this was reflected in smaller nestlings (Bryant and Gardiner 1979, Cronmiller and Thompson 1980, Burness et al. 2000). Slower growth and greater variance in growth rates among nestlings can, in turn, delay fledging (De Steven 1980, Cresswell 1997); if not, smaller size at fledging may reduce survival (Perrins 1965, Nur 1984a, Magrath 1991). Accordingly, we observed lower return rates for young with lower mass. Despite these apparent costs, on the whole, hatching and fledging success were unaffected in supra-modal clutches as large as 10 (Murphy et al. 2000 suggest a threshold of nine for their population of Tree Swallows). As a consequence, parents fledged more offspring from larger broods (Wheelwright et al. [1991] added or removed two nestlings from their nests, and did not find that manipulated reproductive success was affected). Moreover, not only were subsequent survival and reproductive effort unaffected by manipulations, lifetime fledgling production was higher for individuals associated with clutches larger than those produced naturally (Table 1; also see VanderWerf 1992, Tinbergen and Sanz 2004).

If their lifetime reproductive success would be higher, why do parents not produce larger clutches? Something that appears to have been largely overlooked in the literature on the costs of reproduction is that clutch and brood manipulations do not completely mimic the benefits for a bird naturally producing an enlarged clutch (also see Pettifor et al. 1988). To illustrate, consider that a female needs at least one extra day to form and lay each extra egg (Nur 1984b, 1988b). These delays may be greater if females attempt to acquire

nutrients before local productivity is sufficiently high (Nilsson 1994, Brown and Brown 1999). There is substantial evidence that food availability influences laying date and clutch size in Tree Swallows (Hussell and Quinney 1987, Dunn et al. 2000). Moreover, Tree Swallows do not always lay an egg a day (R. G. Clark, *unpublished data*), so that naturally produced larger clutches are more likely to include days when no eggs are laid. Longer total laying time, longer hatching times, and slower nestling growth all delay the date on which young eventually will fledge. Because late-fledged young were less likely to recruit locally (also see Pettifor et al. 1988, Blums et al. 2002, Winkler et al. 2005), a large part of the potential benefits from laying larger clutches would be lost to costs in time (Pettifor et al. 1988, Winkler and Allen 1996). To quantify this in our population, we assume that local recruitment is correlated with total recruitment. Control females raising clutches of six fledged, on average, 78.1% of their young, whereas females with clutches enlarged to nine fledged, on average, 67.2% of their young (Fig. 3). A female completing a clutch of six eggs on 14 May would produce $0.781 \times 6 \text{ eggs} \times 8.5\% \text{ local recruitment (Fig. 6)} = 0.40 \text{ local recruits}$. If the same female produced nine eggs, fledging date would be delayed by a minimum of five days (Fig. 1), which reduces the rate of local recruitment to 7.6%, so that she would produce 0.46 local recruits. If we exclude 1993 from this analysis, the predicted number of local recruits is 0.35 for controls and 0.38 for the add manipulations. Although these figures still represent a 10–16% improvement in fitness, it is much less than the 50% assumed by our manipulations. This significantly weakens the strength of the conclusion that a natural clutch size of nine would be better. An additional consideration is whether adult survival is affected by delays in completing breeding; however, return rates were not related to completion date of nests (logistic regression, Wald $\chi^2 = 1.5$, $P = 0.22$). The rest of the reason that parents do not raise larger clutches may involve costs that we are unable to detect, which we discuss in the next paragraph. Costs of egg production are not measured by clutch manipulations, and although we recognize that these may account for some of the reasons that birds do not lay larger clutches (e.g., because of calcium constraints; Bidwell and Dawson 2005), we note that many birds are capable of laying far more eggs than they actually do (e.g., Kremenetz and Ankney 1986, Monaghan and Nager 1997), including Tree Swallows (Mitchell and Robertson 1993). Thus, it seems likely that our experiments increased the bulk of parental effort necessary to produce costs and trade-offs that theory predicts should exist.

Gustafsson et al. (1994) stated: "The occurrence of trade-offs is not mysterious, but actually rather trivial. ... The important issue is not whether any [trade-offs] exist, as some are inevitable, but rather, which of the possible [trade-offs] occur and are strongest." Thus,

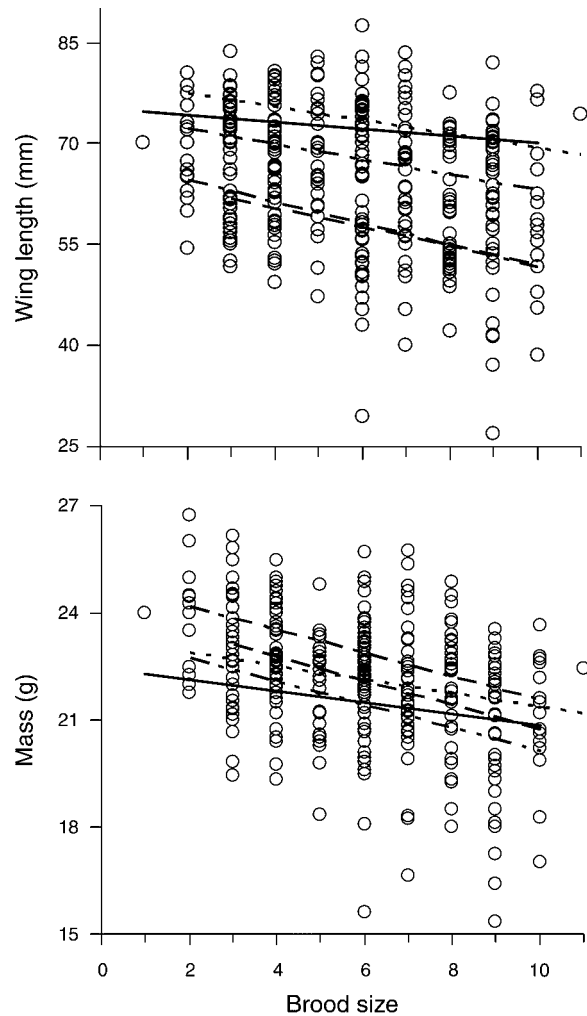


FIG. 5. Growth rate and brood size. Growth rates were slower in larger broods (each point is the mean for a nest in clutch size manipulations). Separate regression lines are shown for each year (starting from top left and descending to bottom left for wing length, regressions are for 1994, 1991, 1992, 1996, and 1998; for mass, regressions are for 1996, 1998, 1994, 1992, and 1991).

failure to detect trade-offs can arise because costs are partitioned among several possible outlets, resulting in low-effect sizes (*sensu* Cohen 1988). Hence, a series of small responses by parents in feeding rate, dispersal, survival, subsequent reproduction, and offspring recruitment, each of which was statistically insignificant by itself, could cumulatively conceal any consequences of manipulation. For example, local recruitment was 4% higher from control than from add nests, which is in the predicted direction, but is not statistically significant. There are also potential costs of enlarged clutches that we were unable to assess. For instance, females that lay more eggs may be exposed to more partners and more sexually transmitted diseases, while males rearing large broods may have less time to seek extra-pair fertilizations or in subsequent years are more often cuckolded.

TABLE 2. Consequences of clutch manipulation for Tree Swallows (control vs. egg addition or reduction).

Parameter	Error df	Clutch size treatment						Test statistic	P
		Reduce		Control		Add			
		Mean	N	Mean	N	Mean	N		
Recruits									
Apparent return (%)		5.4	354	4.9	651	4.3	831	0.7†	0.72
Subsequent breeding years/individual		3.3	19	2.9	32	2.9	36	2.3‡	0.32
Subsequent relative initiation date (d)	79	-0.1	18	0.3	30	0.7	34	0.5§	0.64
Mean clutch size at recruitment	78	6.1	18	6.4	30	6.3	33	0.7§	0.48
Lifetime fledgling production	11	6.0	1	5.0	6	5.3	7	0.2§	0.85
Adult female									
Apparent return (%)		61.4	88	52.7	93	47.3	74	3.3†	0.19
Subsequent breeding years/individual		2.2	88	1.9	93	2.0	74	2.6‡	0.27
Subsequent relative initiation date (d)	126	-0.4	52	-0.8	45	-1.5	32	2.1§	0.13
Mean subsequent clutch size	126	6.1	52	6.4	45	6.1	32	1.8§	0.17
Lifetime fledgling production	252	7.7	88	8.9	93	12.6	74	4.8§	0.004
Adult male									
Apparent return (%)		42.4	59	62.2	74	55.0	60	5.2†	0.07
Subsequent breeding years/individual		1.8	59	2.1	74	1.9	60	5.0‡	0.08
Subsequent relative initiation date (d)	95	-0.5	24	-0.2	42	-0.3	32	0.1§	0.92
Mean subsequent clutch size	95	6.3	24	6.5	42	6.2	32	0.7§	0.48
Lifetime fledgling production	190	7.8	59	11.1	74	12.7	60	12.6§	<0.0001

Notes: Each individual is represented only once in analyses (using reproductive parameters closest to the year of manipulation, or in the case of lifetime fledgling production, summed over their lifetimes). For recruits, sample sizes for all but the analysis on percentage of apparent return include only recaptured individuals (because such a small percentage recruit). For adults, sample sizes for initiation date and clutch size are for recaptured individuals only; other sample sizes include all manipulated individuals. Clutch manipulation did not significantly affect apparent subsequent survival or subsequent reproduction of recruits or adults (analyses for adults exclude individuals born on the grid).

† Likelihood ratio χ^2 with 2 df.

‡ Kruskal-Wallis χ^2 with 2 df.

§ General linear model F with numerator df = 2.

Aside from low-effect sizes in each of the variables we could measure, statistical power to detect trade-offs will also be low when the variables exhibit high variability. One source of variation is individual quality (Reznick 1985, McNamara and Houston 1996) and a second is weather (parents may pass on more of costs of reproduction to offspring in years in which food is limiting than in good years; Boyce and Perrins 1987, Nur 1988b, Festa-Bianchet and Jorgenson 1998). Accordingly, we observed high mortality of nestlings, but not of adults, in a year with low food resources.

We recognize that our nest box grid is not completely representative of conditions under which life histories evolved. For example, if predation were higher on natural nests, this could select for shorter nest cycles and smaller clutches. However, predation rates and other aspects of Tree Swallow breeding biology in natural cavities are broadly similar to those in nest boxes (Erskine and McLaren 1976, Robertson and Rendell 1990, Barber et al. 1996). Thus, although we cannot entirely dismiss the influence of nest boxes on our results, we suggest that the patterns emerging from our data are largely representative of what would occur in natural cavities.

In summary, our inability to find evidence of costs of reproduction is consistent with previous research on Tree Swallows (De Steven 1980, Wiggins 1990, Wheelwright et al. 1991, Burness et al. 2000, Murphy et al.

2000). We failed to detect costs despite requiring parents to bear costs of incubation as well as of provisioning nestlings, and despite large sample sizes. This body of evidence suggests that the costs of producing and raising additional young are of only minor significance for Tree Swallows. Instead, it appears that the more important reason Tree Swallows do not produce larger clutches is that they are constrained in finding sufficient food to

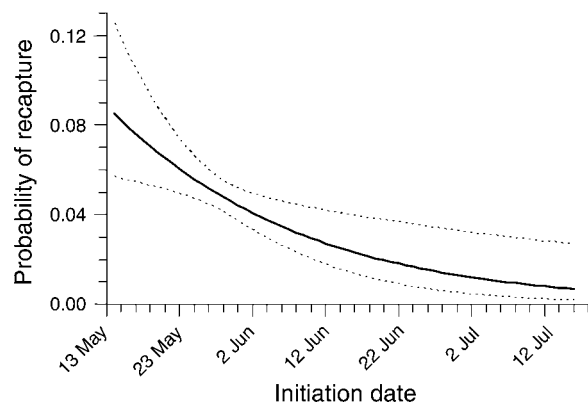


FIG. 6. The probability of recapture (likelihood of local recruitment; $N = 4689$) decreased by 2.6% per day as the season progressed. Shown are results of a logistic regression (response = 1 for individuals recaptured, 0 for those not) bounded by 95% confidence limits.

initiate breeding early, and once food is available, constraints in time dictate that they terminate laying so that their offspring recruit successfully.

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