The Role of Cavity Size in the Evolution of Clutch Size in Tree Swallows

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The individual-optimization hypothesis states that parents lay a clutch size that maximizes their own individual recruitment (Pettifor et al. 1988). Pettifor et al. (1988) found that when Great Tit (*Parus major*) nests were manipulated to an equal brood size, tits that began with a larger clutch size had higher recruitment than those that began with smaller clutches. They concluded that females lay the size of clutch that is optimal for their ability or quality as parents and that this clutch size varies as a result of intrinsic and extrinsic differences among individuals. In hole-nesting species, optimal clutch size may be selected to correspond to the maximum number of nestlings that can fit in a cavity at the least cost to reproduction. In this case, the intrinsic difference is parental quality, and the extrinsic difference is cavity size. This hypothesis has been supported by studies showing that clutch size is positively correlated with cavity size in hole-nesting passerines (Karlsson and Nilsson 1977; Rendell and Robertson 1989, 1993; Robertson and Rendell 1990; Rendell and Verbeek 1995).

Rendell and Robertson (1993) examined the cavity / clutch size relationship in Tree Swallows (*Tachycineta bicolor*) via two experiments. The first determined that when given the choice between large (standard size) versus small (less than 50% of standard size) nest boxes, Tree Swallows preferred to nest in large boxes. Rendell and Robertson (1993) hypothesized that in small nest boxes, a reduced clutch size translates into reduced reproductive success. However, no significant differences in success (percent or number of young fledged) were found between large and small boxes, even when controlling for clutch size (experiment 2). Thus, the possibility that females were using box size as a predictor of future nestling conditions was rejected. However, the lack of a difference in reproductive success between large and small nest boxes may be explained by the fact that females in both large and small box types had the opportunity to optimize their clutch size to their environment. In this way, females may have selected the clutch size that was most appropriate to their environment (cavity size) and capabilities (parental quality), resulting in all females having approximately equal success, regardless of cavity size. Any reduction in reproductive success would indi-

cate the female's proximate reaction to reduced box size, but would not ultimately reveal the cause of her behavior.

Rendell and Robertson's (1993) second experiment controlled for quality of parents by altering nest-box size after pairs had chosen a site. After controlling for clutch size, they found no differences in reproductive success between large and small boxes. However, by limiting comparisons to nests of equal clutch size for statistical analysis, the initial random spread of parental quality was no longer present. That is, comparing equal-sized broods between nest-box sizes does not control for the possibility that females are adjusting clutch size according to individual abilities.

In this study, we examined the constraints of nest-box size on nestling growth and survival while controlling for variation in clutch size and parental quality. By manipulating brood size, females were prevented from optimizing their brood size to their environment (via clutch-size adjustments). Our study is therefore based on the following argument: if females from small nest boxes suffer reduced nestling growth or decreased fledging success when attempting to raise experimentally enlarged broods, these females may be using nest-box size as a predictor of future reproductive success.

To test this hypothesis, we manipulated all nests to a common brood size of six (the modal brood size in large boxes), thereby forcing females in small boxes to raise, on average, a brood size that is larger than normal. This approach eliminated the need for comparisons within clutch sizes during analyses, thus maintaining the random spread of parental quality between box sizes throughout the experiment.

Study area and methods.—We studied Tree Swallows from May to early July 1992 at the Queen's University Biological Station near Chaffeys Locks, Ontario (44°34'N, 76°19'W). All data were obtained from the Northeast Sanctuary study grid, which is a shallow, weedy bay of Lake Opinicon that contains 50 nest boxes (see Rendell and Robertson 1989).

Data were obtained from (1) standard-sized nest boxes (floor area = 178 cm^2, volume = 3,897 cm^3) that constituted the control treatment, and (2) boxes fitted with inserts that constituted the experimental treatment (floor area = 84 cm^2, volume = 1,733 cm^3; Rendell and Robertson 1993). Experimental boxes were not modified until pairs had settled at a nest site. As an indication of settlement, a nearly complete nest of 2 to 4 cm in depth was required at experi-

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mental boxes before inserts were added. Allocation of the first box as either control or experimental was determined with a coin toss, with subsequent boxes given the other designation until each group had a total of 15 boxes.

To assess reproductive performance we measured (1) first-egg date, (2) clutch size, (3) length of the incubation period, (4) length of the nestling period, (5) length of the hatching period, (6) percent of eggs hatched, (7) fledging date, (8) percent of young fledged, and (9) number of blowfly (*Protocalliphora sialia*) larvae in the nest. Initially, we examined nests every three days. First-egg dates were estimated by backdating, assuming one egg was laid per day. Tree Swallows occasionally skip one or more days between eggs (Robertson et al. 1992), so first-egg dates were correct to ± 1 day. Final clutch size was recorded when the number of eggs in the nest had remained unchanged for three days. The sudden appearance of an egg may indicate nest usurpation because replacement females occasionally lay a new clutch on top of existing eggs. Nests from such cases were excluded from the sample. Two nests from the control boxes and four nests from the experimental boxes were excluded due to usurpation. One additional nest was eliminated from the control boxes because two females were nesting in the same box. Thus, our study included data from 12 control nests and 11 experimental nests.

Daily nest checks began near the estimated time of hatching. The day that the first nestling hatched was assigned day 0 for all young in the nest. Nestlings were transported between nests until, by day 4, all boxes contained six nestlings with at least one foreign nestling per box, including controls. Foreign nestlings were no more than two days younger than their first-hatched brood mates, similar to the variation in age found in natural broods (Quinney et al. 1986). To evaluate the effects of brood manipulations, we counted the number of foreign nestlings per nest and the average age of nestlings within each brood upon completion of the brood manipulations.

The incubation period began at day 0 when the last egg was laid and continued to the first day of hatching. Similarly, the nestling period ranged from the day the first nesting hatched (day 0) to the day the last one fledged. Fledging date was determined by daily nest checks beginning on day 15 and represented the first date when no live nestlings remained in the box.

The number of blowfly larvae was determined by examining nests for pupal cases and remaining larvae. When adult blowflies emerge, the pupal cases are shed and remain in the nest (Rogers et al. 1991). Nests were removed one week postfledging to allow any remaining larvae time to pupate.

Nestling growth was evaluated by measuring body mass (±0.1 g using a Pesola scale), tarsus length (±0.01 mm using digital calipers), and length of the
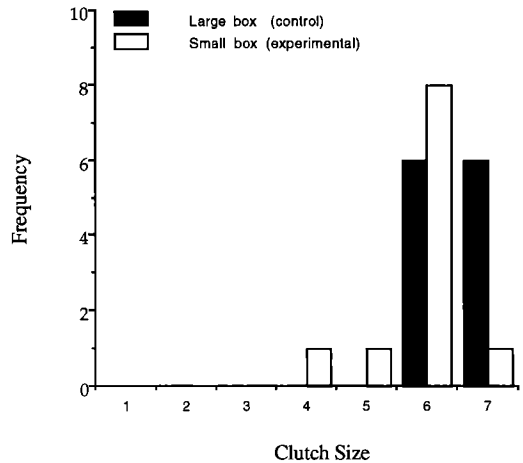

FIG. 1. Distribution of Tree Swallow clutch sizes in large ($n = 12$) and small ($n = 11$) nest boxes. Clutch size was recorded when the number of eggs in the nest had remained unchanged for three days.

ninth primary (±1 mm using a ruler) of the right wing. Body mass and ninth primary length were found to be the most suitable indicators of stressful environmental conditions in Tree Swallows (Zach and Mayoh 1982). Body mass was recorded on days 4, 8, 12, and 15; tarsus length on days 8, 12, and 15; and ninth primary length on days 12 and 15. Mean nestling growth for each variable was determined for each nest for all days that measurements were recorded.

While visiting nest boxes during the egg stage, we accidentally broke two eggs from an experimental nest. This nest was excluded when comparing length of the incubation period, percent of eggs hatched, and length of the hatching period. In addition, the last day of fledging was not observed at two nests (one experimental and one control), and these nests were not included when analyzing length of the nestling period and last fledging date.

Results.—Clutch size in small boxes ($\bar{x} = 5.82 \pm$ SE of 0.23, $n = 11$) was significantly smaller than in large boxes ($\bar{x} = 6.50 \pm 0.15$, $n = 12$; Mann-Whitney test, $U = 30$, $P = 0.02$; Fig. 1), but first-egg date, length of the incubation period, length of the nestling period, length of the hatching period, percent of eggs hatched, fledging date, and percent of young fledged did not differ between the standardized broods in large and small boxes (Table 1). The percent of eggs hatched, although not significantly different between treatments, was appreciably lower in small nest boxes (Table 1). Only 5 of the 23 nests examined contained signs of blowfly larvae, and no more than three pupal cases were found per nest in these cases. After the brood manipulations, small boxes contained significantly more foreign nestlings

TABLE 1. Reproductive parameters of Tree Swallows nesting in large (control) and small (experimental) nest boxes. Values are $\bar{x} \pm$ SE, with n in parentheses.

Variable	Large boxes	Small boxes	P[a]
First-egg date (1 = 1 May)	15.2 ± 0.5 (12)	14.9 ± 1.1 (11)	0.42
Incubation period (days)	14.7 ± 0.2 (12)	14.9 ± 0.3 (10)	0.75
Nestling period (days)	20.3 ± 0.4 (11)	20.7 ± 0.5 (10)	0.66
Clutch size	6.5 ± 0.1 (12)	5.8 ± 0.2 (11)	0.02
Percent of eggs hatched	83.5 ± 4.4 (12)	71.5 ± 5.7 (10)	0.07
Hatching period (days)	1.9 ± 0.2 (12)	2.3 ± 0.3 (10)	0.28
No. of foreign nestlings	1.2 ± 0.1 (12)	2.2 ± 0.3 (11)	0.02
Fledging date (1 = 1 May)	56.0 ± 0.6 (11)	56.1 ± 1.4 (10)	0.57
Percent of young fledged	97.2 ± 1.9 (12)	90.9 ± 4.7 (11)	0.20
Age at day 4[b]	3.8 ± 0.1 (12)	3.7 ± 0.1 (11)	0.57

[a] Mann-Whitney U-test.

[b] Foreign and natural nestlings combined.

than did large boxes, and the average brood age in large and small nest boxes differed by only 0.1 days (Table 1).

Comparisons of mean nestling mass on days 4, 8, 12, and 15 revealed no effect of box size (Table 2). Similarly, tarsus length on days 8, 12, and 15 was independent of box size (Table 2). Ninth primary length did not differ significantly between treatments on day 12 but was significantly shorter in nestlings in small boxes on day 15 (t = 2.29, df = 21, P = 0.04; Table 2).

Discussion.—Our study showed that female Tree Swallows adjusted their clutch size based on box size. The difference in clutch size cannot be attributed to differences in timing of breeding, because the mean date of clutch initiation was 15 May in both large and small boxes.

The number of foreign nestlings was larger in small boxes than in control boxes. This resulted because brood size in small boxes was smaller such that

TABLE 2. Body mass, tarsus length, and length of ninth primary of Tree Swallow nestlings from large (control) and small (experimental) nest boxes. Values are $\bar{x} \pm$ SE.

	Large boxes (n = 12)	Small boxes (n = 11)	P[a]
Body mass (g)			
Day 4	8.4 ± 0.3	7.8 ± 0.4	0.27
Day 8	19.8 ± 0.3	19.0 ± 0.5	0.20
Day 12	23.4 ± 0.3	23.1 ± 0.4	0.50
Day 15	22.4 ± 0.3	22.4 ± 0.5	0.96
Tarsus length (mm)			
Day 8	15.2 ± 0.1	15.1 ± 0.2	0.57
Day 12	15.7 ± 0.1	15.7 ± 0.1	0.90
Day 15	15.8 ± 0.1	15.8 ± 0.1	0.61
Length of ninth primary (mm)			
Day 12	29.9 ± 0.9	27.2 ± 1.1	0.07
Day 15	46.9 ± 0.9	42.5 ± 1.3	0.04

[a] Two-tailed group t-test.

more nestlings had to be added in order to achieve a brood size of six. In addition, two nestlings were added to an experimental nest to replace broken eggs. However, Quinney et al. (1986) found no difference in growth between natural and foreign nestlings, so this difference should not have affected our results.

Before brood manipulations, the modal brood size was five in experimental boxes and six in control boxes. Therefore, manipulating brood size to six at all nests forced experimental pairs to raise a larger-than-average brood. The lower nestling quality associated with this manipulation may reveal why hole-nesting species adjust their clutch size to cavity size.

Prior to the completion of brood manipulations on nestling day 4, experimental and control nests did not differ for parameters measured during the incubation period, such as first-egg date, length of the incubation period, length of the hatching period, and percent of eggs hatched. Slagsvold and Amundson (1992), however, found that the hatching period in Great Tits was significantly longer in small cavities early in the breeding season compared with large cavities. They also noted a gradual increase in hatching spread over the course of the breeding season. Both of these findings suggest an effect of ambient temperature. Although not significant, our data showed a slight trend toward larger hatching spreads in small boxes (Table 1). This suggests that the conditions within small boxes affected incubation, which may have caused the substantially lower (albeit nonsignificant) percent of young hatched in small boxes (Table 1).

Differences in parameters measured during the nestling period (after brood manipulations), such as nestling growth, length of the nestling period, percent of young fledged, fledging date, and number of blowfly larvae, can be attributed to increased nestling density in the experimental boxes. Any differ-

ences in these parameters could indicate why females reduced clutch size to fit cavity size.

Nestling growth was affected by box size. Although mass and tarsus length showed no difference between large and small boxes, ninth primary lengths of experimental nestlings were significantly shorter than the controls on day 15. Shorter ninth primaries are unlikely to be attributed to a younger mean age of nestlings in the experimental boxes, because the mean age difference was only 0.1 days and was not significant.

A number of factors can influence nestling growth, including brood size, parental quality, parasite load, and overcrowding. However, because we controlled for brood size and parental quality, these factors should not have caused any of the observed differences in growth between box sizes. Parasite load was also well below that which would cause an effect on nestling growth. Thus, only the effects of overcrowding would seem to explain the growth differences between large and small boxes.

The shorter length of the ninth primary on day 15 in small boxes was not compensated for by a proportional increase in fledging date (Table 1). Therefore, experimental nestlings fledged with shorter ninth primaries. Ninth primary growth of Tree Swallows is 66% complete at fledging (Zach and Mayoh 1982), as opposed to mass and tarsus length, which are nearly 100% complete. In Tree Swallows, ninth primary growth is most rapid during the first few days of appearance, after which growth is slow. Hence, the start of the growth period may be the most important time for establishing primary length. Because Tree Swallows are aerial feeders, wing length is undoubtedly important in determining postfledging survival. Nestlings that fledge with shorter wings could have a reduced ability to feed, especially during the postfledging period. Although this difference in wing length would decrease with time, shortened wings at fledging time could affect the long-term survival of young Tree Swallows.

Based on the above, we have hypothesized that the slow development of the ninth primary in Tree Swallows represents a selective disadvantage of a large brood in a small box because it may result in offspring of lower quality. From these results, we hypothesize that clutch size, cavity size, and parental quality may interact to determine reproductive success. Because cavity size and parental quality are fixed, Tree Swallows have evolved to alter their clutch size with respect to differences in these two parameters.

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