

THE ROLE OF DEVELOPMENT, PARENTAL BEHAVIOR, AND NESTMATE COMPETITION IN FLEDGING OF NESTLING TREE SWALLOWS

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ABSTRACT.—Fledging (i.e. leaving the nest) in altricial birds is a major step toward independence. The timing of this important event may be influenced by nestling development, parental behavior, and sibling interactions. In this study, we examine the effect of these factors on fledging in Tree Swallows (*Tachycineta bicolor*). Wing length explained a significant proportion of the variance in fledging age across broods. Similarly, within broods, longer-winged nestlings fledged before shorter-winged nestlings. Feeding rate per nestling did not decrease in the period leading up to fledging, as might be expected if parents stimulated fledging by decreasing their feeding rate. Parental activity near the nest varied in that the frequency of parental passes and hovers within 1 m of the nest opening increased in the period before fledging. Brood size also explained a significant proportion of the variance in fledging age independent of wing length, although the direction of the relationship was not consistent across years. Finally, longer-winged nestlings spent more time in the nest opening and initiated fledging of the brood more often than did shorter-winged nestlings. Overall, our study suggests that nestling development is the most important determinant of fledging age in this species. Once a critical wing length has been reached, sibling interactions, and possibly parental behavior, may influence the timing of fledging. *Received 23 July 1999, accepted 21 May 2000.*

PARENTAL CARE provides obvious benefits to parents through increased growth and survival of young (Clutton-Brock 1991). However, feeding offspring is energetically costly (Drent and Daan 1980, Bryant and Tatner 1991), and protecting them from predators increases the risk of injury or death to the parents (e.g. Randall and Matocq 1997). Therefore, parents are expected to care for offspring until the costs of care outweigh the benefits. Because offspring may benefit from care that extends beyond the parental optimum (Trivers 1974), the length of the dependent period may be a source of conflict for parents and young (Trivers 1974).

In altricial birds, conflict also could occur over the timing of leaving the nest, or fledging (Trivers 1974). Parents may benefit by decreasing the length of the nestling period and conserving energy for future reproductive attempts and/or migration (Burger 1981, Bustamanté and Hiraldo 1990), whereas offspring may benefit by extending the nestling period and decreasing their thermoregulatory and activity costs (McCarty 1995). The timing of fledging may not necessarily be a source of

conflict, however. For instance, parents and young may benefit from earlier fledging when the risk of nest predation is high.

Before determining whether conflict over the timing of fledging occurs, it is necessary to understand the factors that influence fledging. At least three factors are potentially relevant (1) nestling development, (2) parental behavior, and (3) nestmate interactions. Despite the potential importance of the timing of fledging to survival of nestling birds, few studies have focused exclusively on the process, and none has examined the three factors simultaneously. In addition, the influence of parental behavior has received little systematic attention.

The condition of nestlings at the time of fledging influences postfledging survival (Greig-Smith 1985, Lindén et al. 1992) and predicts a relationship between nestling development and fledging. Earlier studies have found a relationship between features such as wing length (Nilsson and Svensson 1993, Ottosson 1997) or body mass (Lemel 1989, Nilsson and Svensson 1993) and fledging age.

Parents also could influence the timing of fledging. Indeed, parental behaviors that stimulate fledging might be adaptive if the optimum fledging time for parents is before that of

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their young. For instance, a decrease in feeding rate in the period leading up to fledging could encourage nestlings to leave the nest and approach parents for food (Bustamanté and Hiraldo 1990). Similarly, parents might lure young from the nest by perching nearby with food (Bustamanté and Hiraldo 1990) or by calling to nestlings (Woods 1993). Although we do not directly examine the role of conflict during fledging, an understanding of how parental behavior influences fledging could provide insight into the dynamics between parents and young during this time.

Finally, competition among nestmates could play a role in the fledging process. In several species, large broods fledge before small broods, apparently because of an increase in competition for food and space in larger broods (Zach and Mayoh 1982, Husby and Slagsvold 1992). Nestmate interactions also could affect individual nestlings differently and thus influence fledging order within broods. For instance, in Marsh Tits (*Parus palustris*), smaller nestlings initiate fledging under low food conditions, presumably to reduce competition from larger nestmates (Lemel 1989).

The purpose of our study was to examine factors that influence fledging in altricial birds, particularly passerines, using Tree Swallows (*Tachycineta bicolor*) as a model. Specifically, we considered the role of nestling development by examining how wing length, tarsus length, and body mass were related to fledging age across broods and to fledging order within broods. We also examined the influence of parental behavior by determining whether parents decreased feeding rates before their young fledged, or increased behaviors that potentially could stimulate fledging. Finally, we investigated the role of nestmate interactions by determining the relationship between brood size and fledging age and by determining which nestlings within broods initiated fledging. We expanded on previous work by conducting this study over several years and by examining the influence of the three factors simultaneously.

METHODS

General methods.—We conducted this study at two sites in Kings County, Nova Scotia, Canada (45°05'N, 64°22'W), between May and July from 1996 to 1998. Tree Swallows in our population bred in nest boxes

that were spaced approximately 10 m apart at each site. We used 83 broods (23 broods in 1996, 27 in 1997, and 33 in 1998) that ranged in size from two to seven nestlings (two, $n = 3$; three, $n = 12$; four, $n = 12$; five, $n = 31$; six, $n = 21$; and seven, $n = 4$). Sample sizes varied across analyses because we did not have complete information for each nest in all years.

Before eggs were laid, we trapped adults in their nest boxes and banded them with aluminum Canadian Wildlife Service bands and colored plastic leg bands. Nestlings were given the same bands at 13 days posthatching (hatching day = day 1). In 1997 and 1998, nestlings were also individually marked on the forehead with a small dot of nontoxic paint. We determined first egg dates and clutch size by checking nest boxes every one to two days until clutches were complete. Nests were not disturbed again until the predicted hatching date, at which time they were checked daily until all eggs had hatched.

We considered the fledging age of a brood to be the number of days between hatching of the first egg and fledging (i.e. leaving the nest) of the first nestling in that brood. We determined the fledging day of the first nestlings and, where possible, the fledging order within broods through a series of nest checks and observations (see below). In 1996, nests were checked every other day beginning at 16 days posthatching. In 1997 and 1998, checks also began at 16 days posthatching but were conducted twice daily. If a nestling was missing at a particular check, we considered it to have fledged between the current and previous checks. Fledgling Tree Swallows do not return to the nest once they have left. To avoid disturbing nestlings and potentially causing premature fledging, we approached nest boxes only when the nest opening was vacant. In 1997 and 1998, we observed each box for 5 min following nest checks. In 3 of the 60 broods that we observed, the first nestling fledged during or within 1 min of our visit to the nest. We excluded these broods from our analyses.

Nestling measurements.—To determine the relationship between nestling development and fledging age, we measured nestling body mass (± 0.1 g), right tarsus length (± 0.05 mm; in 1996 and 1997 only), and flattened right wing chord (± 0.5 mm) at 13 days posthatching. We measured nestlings on day 13 rather than at later ages to prevent disturbance and premature fledging. Measurements at day 13 should adequately represent nestling development at fledging because mass in Tree Swallows reaches an asymptote by day 13, and asymptotic mass is correlated with fledging mass (Zach and Mayoh 1982). Tarsus length also reaches its asymptote by day 13 (Zach and Mayoh 1982) and thus should be equivalent to tarsus length at fledging. Although wing length does not reach its asymptote until after fledging (Zach and Mayoh 1982), relative differences in wing length among and within broods should persist through the

prefledging period (e.g. Bryant 1978). We therefore make the assumption that relative differences in wing length at day 13 represent differences at fledging. All nestlings measured at day 13 fledged successfully.

Observations.—In 1996 and 1997, we conducted 30-min watches on 29 broods of five and six nestlings to determine if feeding rate varied in the period before fledging. Our watches initially were 1.5 h long. However, feeding rates based on 30-min watches were highly correlated with those based on 1.5-h watches ($r = 0.87$, $n = 13$, $P < 0.01$), so we decreased the length of the observation period to 30 min to increase the number of broods sampled.

We conducted watches between 0700 and 2000 AST on the same broods every other day in 1996 and daily in 1997 beginning at 13 days posthatching and continuing until fledging. Watches on individual broods were conducted at the same time each day. During watches, we recorded the number of times parents entered the nest box, placed their head through the nest box opening, or fed a nestling that occupied the nest opening. We assumed that a feeding occurred each time a parent visited the nest. This is a reasonable assumption because video tapes of nestlings show that 98% of visits to 15-day-old broods ($n = 17$) and 19-day-old broods ($n = 5$) include a feeding (T. Michaud unpubl. data). During watches, we also recorded the amount of time individual nestlings spent perched in the nest-box opening and the identity of each nestling that fledged during the observation period.

In 1998, we also conducted 30-min watches daily on 19 broods and to increase sample size, we video taped an additional 14 broods for 2 h per day beginning at day 16. Video tapes were made with a Panasonic PV-900-K VHS video camera (with 12 \times zoom) that was placed on a tripod approximately 7 m from the box. We used both sets of observations to determine time spent by individual nestlings in the nest opening, fledging time, and fledging order. We did not examine parental feeding rates in 1998.

Information on parental behavior was recorded during watches (1997, 1998) and video tapes (1998) from 16 days posthatching to fledging. In particular, we recorded the number of times parents passed or hovered within 1 m of the nest opening when a nestling was in the opening. We also recorded the amount of time a parent was present within 5 m of the nest box. This included time spent perched on wires or branches within 5 m, time perched on the nest box, and time spent inside the nest box. We could not distinguish between male and female parents.

Analyses.—All analyses were performed using SYSTAT, and all means are presented ± 1 SE. We used parametric tests throughout because data met the assumptions of these tests. We also conducted power tests for medium effect sizes (Cohen 1977) when 0.05

$< P < 0.20$. Initially, we examined years separately, and when patterns were consistent across years we pooled data to increase sample sizes and statistical power. We report results for the combined years, unless otherwise stated. Tree Swallow occasionally remate in consecutive years (Robertson et al. 1992), but we considered broods from the same parents in different years to be statistically independent.

We used multiple regression to examine the influence of average brood mass, tarsus length, and wing length on fledging age across broods while controlling for brood size (see below). Because we were unable to determine fledging order for each nestling in many nests, we assigned nestlings within broods to an early fledging or a late-fledging group based on breaks in the fledging order. For example, if two of six nestlings fledged before a nest check and the remaining four fledged by the next check, the first two were considered early fledging nestlings and the latter four were considered late-fledging nestlings. In all cases, at least two nestlings occurred in the early and late-fledging groups. When we knew the complete fledging order, we divided the brood in half in even-numbered broods. In odd-numbered broods, we placed the middle nestling in the group that fledged closest to that individual. Measurements for early and late-fledging groups within broods were compared using paired t -tests, with significance levels adjusted to $P = 0.016$ using a Bonferroni correction.

We used a repeated-measures ANOVA to determine if feeding rate varied across days 6, 4, 2, and 0 before fledging (0 = day of fledging). We also examined whether the time spent by parents within 5 m of the nest and the frequency of parental passes and hovers per time that the nest opening was occupied varied across days 2, 1, and 0 using repeated-measures ANOVA. We used multiple regression to examine the relationship between fledging age and brood size while controlling for wing length.

Finally, we examined the wing length of nestlings that initiated fledging. We considered the two nestlings with the longest wings in a brood to be "long-winged" and the two with the shortest wings in a brood to be "short-winged." We also compared the mean amount of time long-winged and short-winged nestlings occupied the nest-box opening using a paired t -test. Nestlings that did not fall into either category were considered "middle-winged" nestlings. These analyses were conducted only on broods of five and six nestlings.

RESULTS

General description.—The mean fledging age for broods across all years was 20.0 ± 0.14 days (range 18 to 23 days, $n = 74$). The mean time from departure of the first nestling to fledging

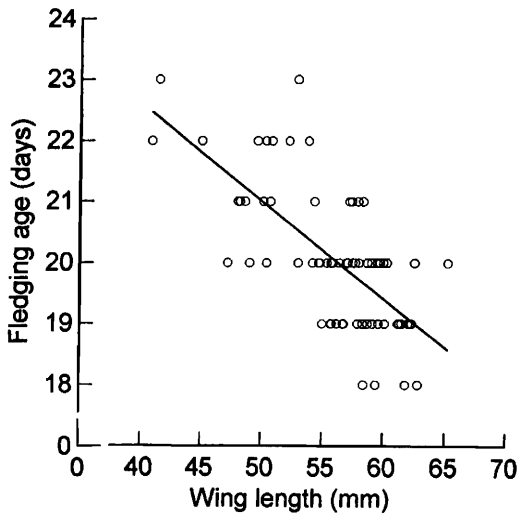


FIG. 1. Relationship between mean wing length of Tree Swallow broods at 13 days posthatching and fledging age of nestlings in 1996, 1997, and 1998 ($y = -0.16x + 29.1$).

of the entire brood was 12.0 ± 1.6 h (range 30 s to 48 h).

Nestling development.—Wing length explained 47% of the variance in fledging age across broods ($F = 62.5$, $df = 2$ and 68 , $P < 0.001$; Fig. 1), with longer-winged broods fledging before shorter-winged broods. Neither body mass nor tarsus length had a significant effect on fledging age (mass, $F = 0.00$, $df = 1$ and 72 , $P = 0.97$; tarsus length, $F = 1.79$, $df = 1$ and 41 , $P = 0.19$, power = 0.67).

Within broods, early fledging nestlings had significantly longer wings than late-fledging nestlings (early fledging, $\bar{x} = 58.9 \pm 0.50$ mm; late fledging, $\bar{x} = 56.4 \pm 0.60$ mm; paired $t = 6.51$, $df = 38$, $P < 0.0001$). Early fledging nestlings also weighed more than late-fledging nestlings (early, $\bar{x} = 23.3 \pm 0.20$ g; late, $\bar{x} = 23.0 \pm 0.20$ g; $t = 2.24$, $df = 38$, $P = 0.03$), but the difference was not significant after Bonferroni correction. Tarsus length did not differ significantly between the two groups (early, $\bar{x} = 14.8 \pm 0.08$; late, $\bar{x} = 14.9 \pm 0.06$; $t = -0.75$, $df = 16$, $P = 0.47$).

Parental behavior.—Feeding rate per nestling did not differ significantly in the period preceding fledging ($F = 1.57$, $df = 3$ and 26 , $P = 0.22$). Similarly, time spent by parents within 5 m of the nest did not differ before fledging ($F = 1.02$, $df = 2$ and 29 , $P = 0.37$). Parents did,

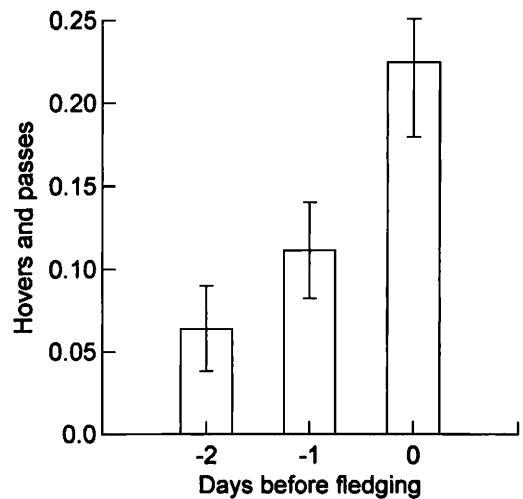


FIG. 2. Mean (\pm SE) number of hovers and passes by Tree Swallow parents within 1 m of the nest opening per time in which the opening was occupied by a nestling on days 2 and 1 before fledging and on the day of fledging (fledging day = 0; $n = 33$ broods).

however, increase the frequency of passes and hovers in front of the nest opening in the period leading up to fledging ($F = 4.00$, $df = 2$ and 31 , $P = 0.02$; Fig. 2).

On the day of fledging, parents were present at the nest for 20.6% (i.e. 6.18 ± 0.96 min) of the watch period. However, they were present during 81% of observed fledging events (17 of 21 fledgings from separate broods). In 16 of these 17 fledging events, parents were within 1 m of the nest and vocalized in the 20 s preceding the departure of a nestling.

Nestmate interactions.—Brood size explained a significant proportion of the variance in fledging age independent of wing length in each year of the study (1996, $F = 4.66$, $df = 1$ and 21 , $P = 0.04$, 11% of variance explained; 1997, $F = 9.86$, $df = 1$ and 19 , $P = 0.01$, 35% of variance explained; 1998, $F = 4.82$, $df = 1$ and 30 , $P = 0.04$, 7% of variance explained). However, the direction of these relationships varied across years. In 1996 and 1998, the relationship between fledging age and brood size was positive, whereas in 1997 the relationship was negative.

Long-winged nestlings spent significantly more time in the nest-box opening than short-winged nestlings (long, $\bar{x} = 10.56 \pm 1.28$ min; short, $\bar{x} = 5.27 \pm 0.74$ min; $t = 3.29$, $df = 27$, $P = 0.003$). Long-winged nestlings also initiated

fledging in 15 of the 21 broods (71%) in which the identity of the first nestling to leave the nest was known. A middle-winged nestling fledged first in one brood, and short-winged nestlings fledged first in the remaining five broods.

DISCUSSION

Nestling development.—Wing length appears to be the most important morphological variable associated with fledging in Tree Swallows. Broods of longer-winged nestlings fledged before broods of shorter-winged nestlings, and within broods, longer-winged individuals fledged before shorter-winged individuals.

Factors influencing fledging in Tree Swallows have not been systematically studied. However, two earlier studies (De Steven 1980, Zach and Mayoh 1982) on general breeding biology of different populations of this species found a negative relationship between wing length and fledging age. This pattern also has been observed in other passerines (Nilsson and Svensson 1993, Ottosson 1997), suggesting that development plays a common role in the fledging process.

The requirements of nestlings in the post-fledging period may explain relationships between development and fledging. For example, Tree Swallows have a relatively short post-fledging period during which they receive progressively less food from their parents (M. Leonard and A. Horn unpubl. data). Fledgling Tree Swallows must be capable of capturing insect prey on the wing shortly after they leave the nest, thus requiring relatively well-developed wings at fledging. Similarly, nestling Common Swifts (*Apus apus*), which have no postfledging care and are on the wing continuously after fledging, leave the nest only after they attain a critical ratio of body mass to wing length (Martins 1997).

Parental behavior.—Tree Swallow parents did not vary their feeding rates in the period before their young fledged. These results are consistent with a study of two passerine species that found little or no change in feeding rates at this time (Nilsson and Svensson 1993). A decline in feeding rate before fledging also has been observed (Grundel 1987, Ottosson 1997). However, in these studies, declining feeding rates did not appear to hasten fledging. Taken together, these results suggest that parents do

not induce nestlings to leave by decreasing feeding rates before fledging.

Parent Tree Swallows made progressively more passes and hovers in front of nestlings as fledging approached and were within 1 m of the nest during 81% of observed fledging events. These results suggest a relationship between fledging and the behavior and presence of parents, but they do not provide conclusive evidence that parents induce fledging. Previous observations on parental "luring" behavior are limited. However, anecdotal reports exist of parents perching near the nest with food late in the nestling period (Rowan 1955, Walker 1972) or calling by the nest immediately before fledging (Woods 1993). Clearly, systematic studies and experiments need to be conducted to determine the role of parental behavior in the timing of fledging.

Our study was not designed to examine parent-offspring conflict. However, it is worth noting that we did not observe any form of overt behavioral conflict. That is, parents did not reduce feeding rates or apparently "force" their young from the nest. These behaviors might be expected if parents benefited from a shorter nestling period than was optimum for the nestlings (but see Mock and Forbes 1992).

Nestmate interactions.—We found a significant relationship between brood size and fledging age independent of wing length; however, the direction of the relationship was not consistent across years. Larger broods fledged later than smaller broods in 1996 and 1998, whereas the reverse was true in 1997. One explanation for the positive relationship is that space is limited in large broods such that nestlings cannot stretch their wings and exercise their flight muscles as effectively as those in small broods. The inability to fully prepare for flight could delay fledging (Skutch 1976) and thus could explain why larger broods fledged later than smaller broods.

A negative relationship between fledging age and brood size, however, appears to be the common pattern in passerines (Husby and Slagsvold 1992), including Tree Swallows (Zach and Mayoh 1982). Increased competition for food in large broods could select for earlier fledging, especially in species where parents feed fledglings more than nestlings (Lemel 1989, Bustamanté and Hiraldo 1990, Kopechena and Falls 1993). We have no information

on postfledging feeding rates in Tree Swallows, which makes it difficult to assess this hypothesis. In summary, it is not clear why the relationship between brood size and fledging age varied across years. Factors such as food supply and weather conditions could influence brood sizes and/or nestmate competition between years and explain the observed interannual variation. Whatever the case, our results suggest that brood size influences the fledging process.

Finally, long-winged nestlings spent more time in the nest opening than did short-winged nestlings. More than 90% of parental feedings are delivered to the nestling that occupies the opening (T. Michaud unpubl. data), which suggests that longer-winged nestlings received more food. Fledging also was initiated by long-winged nestlings. These results are consistent with the hypothesis that the nestling that is most prepared in terms of development will initiate fledging, presumably to approach parents for food (Nilsson 1990). The exception to this may occur when feeding rates are low and smaller nestlings may reduce competition from larger nestmates by leaving the nest (Lemel 1989).

In summary, fledging represents a major transitional step toward independence that includes changes in behavior, lifestyle, and mode of nutrition (Ydenberg et al. 1995). Thus, fledging represents an important stage in the life history of altricial species. In Tree Swallows, attaining a critical wing length before fledging may be necessary for survival in the postfledging period. Once this threshold is achieved, the exact timing of fledging could be influenced by interactions among siblings and possibly by parental behavior. Future work should focus on the effect of these latter two factors in the fledging process.

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