

USE AND IMPORTANCE OF FEATHERS AS NEST LINING IN TREE SWALLOWS (*TACHYGINETA BICOLOR*)

DAVID W. WINKLER

Section of Ecology and Systematics, Division of Biological Sciences, Cornell University, Ithaca, New York 14853, USA

ABSTRACT.—Tree Swallows (*Tachycineta bicolor*) commonly line their grass nests with feathers of other species. In one of three years studied, there was a significant negative correlation between numbers of feathers in the nest and chick nestling periods (i.e. broods surrounded by more feathers fledged earlier). In the third year of the study, the population was divided into two groups, balanced for all measurable aspects of parental quality. In the "removal" group, all feathers were removed daily and in the "control" group all feathers were allowed to remain. All nests and their contents were disturbed equally. Chicks in removal nests had lower growth rates (in mass, wing chord and tarsus) and higher infestations of mites and lice. I suggest that feathers aid chicks directly by preventing hypothermia and indirectly through higher growth rates by allowing earlier fledging when necessary. Protection from ectoparasites may be an important advantage in natural nests where nest cavities are not cleaned out annually. Inadvertent removal of feathers from nest boxes may be an important cause of posthatching declines in feather numbers. Received 19 July 1991, accepted 14 August 1992.

TREE SWALLOWS (*Tachycineta bicolor*) usually line their nests with feathers, and one of the most conspicuous and distinctive behaviors during this swallow's breeding season is the frequent contests over feathers. These contests involve high-speed aerial chases accompanied by considerable aerial jostling and bodily contact, often involving several birds (e.g. Weydemeyer 1934, Kuerzi 1941; for an illustration see Audubon [Peterson and Peterson 1981:plate 276]). Having been intrigued by these aerial contests and the apparent worth of the resource being contested, I began a study of the feathers used in Tree Swallow nests in 1987. I present here a brief description of the natural history of the use of feathers as nest lining, some correlative evidence of the feathers' importance, and the results of an experimental study documenting the effect of feathers in the nest on chick growth and ectoparasite infestations. The nest linings of birds generally have been thought to provide insulation for the developing offspring (e.g. Haftorn 1978, Capreol 1983, Møller 1984) or protection against ectoparasites (e.g. Wimberger 1984), and my experiment tested the two predictions that feather removal would lead to: (1) decreased chick growth and/or survival; and (2) increased numbers of ectoparasites.

METHODS

This study is based on a Tree Swallow population established in 1985 in a grid of 105 nest boxes. The

nest boxes are situated around a series of 41 0.1-ha experimental ponds and a 5.25-ha lake located 10 km north of the campus of Cornell University, Ithaca, New York. Each box was mounted with the opening facing east on a metal fencing post approximately 1.5 m above the ground, with a conical metal "predator guard" attached to the post beneath. Each box was within 2 m of open water, and the nearest neighboring box was 20 m away. Fifty pairs of swallows bred on the plot in 1987, 67 pairs in 1988, and 58 pairs in 1989. In 1987 and 1988, 27 and 47 of the nests, respectively, were part of an experiment (Winkler 1991) that involved manipulations of clutch or brood size. Other than these manipulations, all nests were subjected to the same degree of researcher disturbance: checks of the nests every day during the laying period to count feathers and mark and measure eggs; and checks every second or third day during the nestling period to count feathers and mark, measure and weigh chicks. After the 12th day of nestling age, the nests were checked by looking into a dental mirror held in the nest hole and illuminated with a flashlight. Following this procedure prevented me from taking any further measurements of the chicks, but avoided the danger of premature fledging (fledging typically occurs on nestling day 20 or later).

In 1989, the nests on the plot were divided into two groups: a "removal" group had all the feathers removed from nests each day from the day after the last egg was laid to the 12th nestling day. A parallel "control" group was checked every day for the same period, but instead of removing the feathers, the feathers were counted and the eggs or nestlings and nest were disturbed to approximate the disturbance associated with feather removal. When feathers were removed from the nest, eggs or nestlings were jostled

and the dried grass of the nest was teased up out of the nest cup; I approximated this disturbance in control nests by scraping at the nest cup with a finger to leave it approximately as disheveled as a removal nest would be immediately after feather removal. The removal and control groups were balanced as closely as possible for other aspects of parental quality (female age, date of clutch initiation, clutch size, egg size). In 1989, 82 of the adults attending nests were captured at the nest for identification and marking and, at 8 nests, one of the parents was seldom seen at the nest and could not be captured. Such situations are not uncommon (Winkler unpubl. observ.), but because these "trap-shy" birds may have been subnormal in some aspect of parental quality, these "single-parent" nests were not included in the comparisons. With all balancing of parental qualities and deletion of single-parent nests, the control group was left with 15 pairs and the removal group with 19 pairs. Because the nests were being disturbed so much as a result of feather checking and removal, all chicks in 1989 were weighed and measured only once, on day 12 of their development. Chicks were weighed to the nearest 0.1 g with a Pesola spring balance, their flattened and straightened wing chords were measured to the nearest millimeter, and their tarso-metatarsal (henceforth "tarsal") lengths were measured to the nearest 0.1 mm with dial calipers. Each chick also was scrutinized for ectoparasites (on day 12 their feather coat is still quite sparse), and numbers of mites, lice, and larvae of parasitic flies (*Protocalliphora* sp.) were recorded.

Statistical methods.—In presenting data graphically, I use two methods available in SYGRAPH (Wilkinson 1988a). In two of the figures, it is informative to discern trends in scatter plots of data. Rather than assuming *a priori* that such trends are linear, I used a locally weighted smoothing algorithm (in this case LOWESS; Cleveland 1981) that bases trends on a restricted window of sampling within the data. Thus, if the "real" trend is a curve, LOWESS will draw a curve that conforms more to the data rather than forcing a straight line through the data.

The other graphic method used involved Tukey box plots (Velleman and Hoaglin 1981) to represent distributions of data. A traditional way to represent the distributions of data is to construct a box-and-whisker plot in which the mean (represented by a horizontal line) is surrounded by a symmetric rectangle that is bordered above and below by the upper and lower limits of the 95% confidence limit about the mean. Vertical lines extend above and below the rectangle to the upper and lower extreme data points. Unfortunately, if the data's distribution is markedly non-normal, especially if it is strongly asymmetric, using this method can give a misleading impression of the data's distribution since one of the confidence limits calculated may actually lie outside the range of the data. Tukey box plots avoid this problem, since they

use the median to center the plot and use quartiles of the data to define the borders of the surrounding box. Thus, if a distribution is asymmetric, the portions of the box above and below the median will vary in size accordingly; they need not be symmetric.

The distributions of morphological measurements taken on the chicks were generally quite symmetrically distributed. Because they showed significant differences from a normal distribution by Lilliefors' test (SYSTAT NPAR module; Wilkinson 1988b), however, I tested differences between them with the Mann-Whitney *U*-test. The distributions of parasites were markedly asymmetric, with most individual chicks having zero parasites, and the variances of control and removal groups appeared quite different. For these measures, I reduced the scores to zeros (no parasites) and ones (some parasites) for each chick and each of the three parasites counted. Differences between control and removal groups were then tested with Fisher's exact test using StatXact software (Cytel Software 1991).

For all comparisons between control and removal groups, I used a critical α -level of 0.05. Because of the directional nature of my hypotheses (i.e. reduced feathers would decrease growth and increase ectoparasites), I used one-tailed probabilities for interpreting the tests.

Chicks within a nest are clearly not entirely independent of each other in their growth and parasite infestations, although they are more independent than repeated measures on a single chick in a nest would be. As a guide to the lack of independence among chicks within a nest, I estimated the within-nest chick correlations by first computing the variance components for nests and chicks. In an analysis of variance (ANOVA) with nest as the predictor variable, the residual mean square represents the component of variance due to chick variation that is independent of variation between nests (e.g. Snedecor and Cochran 1980:243). The mean square for nests is equal to the chick variance plus n_0 times the nest variance, where n_0 can be computed from the formula in Snedecor and Cochran (1980:246) to be 4.73 for this analysis. Because the chick variance is known, the nest variance can then be calculated directly. Once the nest variance is obtained, the within-nest correlation of chick measures is simply the nest variance divided by the sum of the nest and chick variance (Snedecor and Cochran 1980:243). The *P*-value for this correlation is the same as for the nest effect in the ANOVA. I tested for differences between experimental groups using both individual chick values and mean values for the chicks in each brood, and the within-nest chick correlations guide the choice of which of these analyses are most appropriate for each variable. In plotting the data from the chick measures, I use the individual chick data, rather than the brood means, since the chick data preserve the maximum variability in the data set.

RESULTS

Natural history of feathers as nest lining.—The nests of Tree Swallows are generally constructed of dry grass formed into a cup (e.g. Sheppard 1977). I use "nest" to refer to the dried-grass nest structure, distinct from its feather lining. The numbers of feathers in nest linings that I counted are similar to those listed in Sheppard (1977:27–28, 48–52), with the maximum number of feathers per control nest ranging from 0 to 114 and averaging approximately 45 (Fig. 1). As noted by Sheppard (1977) and Cohen (1985), the great majority of feathers were gathered by males. Like Sheppard (1977:48), I occasionally (<10% of nests) found nonfeather material in the nest lining, including scraps of cellophane, old cigarette filters, and hair of rodents and horses. While 90% of the linings of nests reported by Sheppard (1977:51) consisted exclusively of white feathers, the linings in this study contained many gray-brown feathers from Canada Geese (*Branta canadensis*), as well as the barred feathers of female Wood Ducks (*Aix sponsa*). Although Sheppard (1977:27) reported that feathers are not added to the nest until after the clutch is complete, birds at Ithaca usually began adding feathers before the eggs were laid, and at times even before the nest was complete. For example, only 3 of 56 pairs in 1989 waited until the clutch had been initiated to begin lining their nests, and 10 started lining their nests before I conducted the first nest check on 1 May, at least 17 days in advance of laying. By the time of clutch initiation, the Ithaca swallows average about five feathers in the nest (Fig. 1). Feathers accumulated rapidly throughout incubation and at a sharply reduced rate after chicks hatched (i.e. nest ages of about 20 days; Fig. 1).

Correlative evidence for importance of feathers as nest lining.—To investigate the possible benefits of feathers, I tested for correlations of the numbers of feathers in the nest at clutch completion and at chick hatching with the following measures of breeding success: mean chick growth rate, maximum nestling period, percent fledging success, and percent hatching success. In 1987 and for the control nests (see below) in 1989, there were negative correlations between the numbers of feathers in the nest and chick nestling period, but none of these correlations was significant. In 1988, the negative correlations between chick nestling period and the

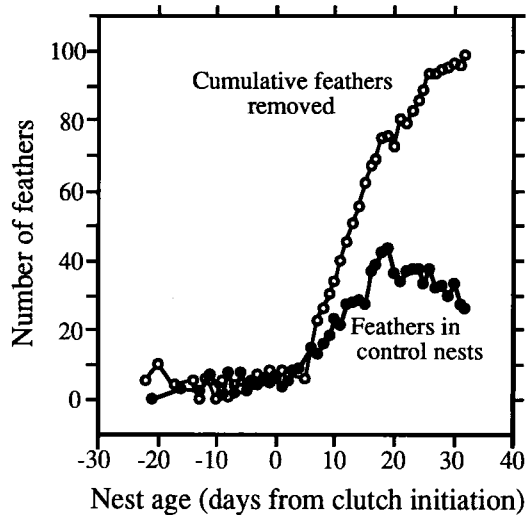


Fig. 1. Mean numbers of feathers vs. nest age in nests of Tree Swallows on Ithaca study area in 1989. Numbers plotted for control nests (filled circles) are mean numbers counted, whereas numbers plotted for removal nests (open circles) are mean cumulative numbers removed from nests (i.e. mean number that would have been in nests if all feathers brought to nest had been allowed to remain). Day 0 is the day of clutch initiation, and most birds laid either five or six eggs. One egg is laid per day, and incubation takes approximately 14 days; thus a nest age of 20 corresponds approximately to chick hatching. Feather removals began on day after last egg laid (i.e. nest age of 6 or 7) and terminated by day 32, at which stage the risk of premature fledging in older chicks dictated a cessation of direct nest checks.

number of feathers in the nest, both at clutch completion ($r = -0.500$) and at chick hatching (Fig. 2; $r = -0.586$) were highly significant (Bonferroni-adjusted $P < 0.02$). Chicks reared in nests with more feathers fledged at a younger age.

Experimental evidence for importance of feathers as nest lining.—The correlations between numbers of feathers in the nest and chick nestling periods observed in 1988 prompted me to conduct an experimental removal of feathers in 1989. This experiment seemed necessary, since the correlations observed in 1988 might have been due to a joint correlation of both numbers of feathers in the nest and reproductive success with some unmeasured aspect of parental quality. Balancing measurable aspects of parental quality in both removal and control groups allowed me to isolate the effects of feathers per se on chick growth and ectoparasites.

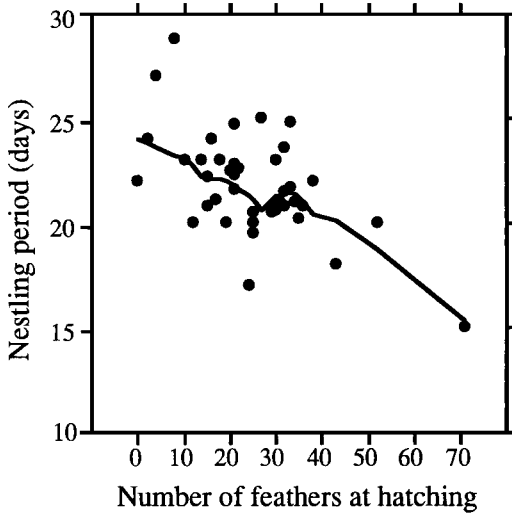


Fig. 2. Relation between number of feathers in nest at chick hatching and nestling period in days ($r = -0.586$, Bonferroni-adjusted $P = 0.017$). Range in fledging periods is 14 days. Curve plotted through points is a LOWESS (locally weighted scatterplot smoothing; Cleveland 1981) fitted to the points with the F -parameter set at 0.5. This smoothing algorithm has advantage of making no *a priori* assumptions about shape of overall function relating fledging period to number of feathers in nest.

The removal treatment clearly created a large difference between the control and removal groups. If one compares the cumulative number of feathers removed by experimenters from the nests of birds in the removal group with those present in the control group (Fig. 1), there is a highly significant effect of experimental treatment (ANOVA, $P = 0.001$), as well as nest age ($P < 0.001$), and a highly significant interaction between these two factors ($P < 0.001$) in their effects on total feathers. The cumulative feathers for the removal group are the total numbers of feathers added to nests by parents in this group. By the end of the experiment, this total averaged 99 feathers (range 2 to 180).

The within-nest correlations of chick measures (Table 1) reveal interesting patterns. The morphological measures most highly correlated among chicks within nests are tarsal length and flattened wing length. Given these high correlations, I gave greater weight to the brood-level analyses for these measures. The correlation for chick weight is considerably lower, and the individual chick analysis should be given greater weight for this measure. In ectoparasite

TABLE 1. Within-nest correlations of measures of chicks taken on nestling day 12.

Variable	r	P
Mass	0.42	0.04
Tarsus	0.85	<0.01
Wing chord	0.94	<0.01
Fly larvae	0.27	0.10
Lice	0.68	<0.01
Mites	0.26	0.11

levels, chicks tend to be less highly correlated with their brood mates, although lice should probably still be interpreted at the brood level. Given their low between-chick correlations, comparisons of levels of fly larvae and mites seem best done at the individual chick level (I indicate analyses that I think are most appropriate for each measure by highlighting their P -values in bold in Table 2).

As predicted, removal of feathers had a significant negative effect on the growth rates of chicks. Chicks from the removal group on day 12 of their development averaged significantly smaller masses, and shorter wings and tarsi (Fig. 3, Table 2) than did control chicks. Thus, as suggested by the correlations observed in 1988, chicks reared in nests with feather lining had faster growth rates, not only in terms of mass, but also in other indicators of body size. The advantage of feathers rises rapidly with feather number, and variation in number of feathers among nests with relatively large numbers did not seem to influence chick growth, at least in 1989 (Fig. 4).

Also, as predicted, removal of feathers had a detectable, albeit much weaker, effect on the levels of ectoparasites. Chicks in the feather-removal group had significantly higher numbers of mites and lice than did control chicks (Table 2, Fig. 3), but there were no significant differences in numbers of fly (*Protophthora* sp.) larvae (Table 2).

Overall, despite the clear effect of the experiment on chick growth, feather removal had no significant effect on chick survival.

DISCUSSION

The results of this study support the prediction that the presence of feathers in the nest promotes growth of nestlings. Just how this effect is brought about is unclear, but it seems likely that the principal mechanism is in pro-

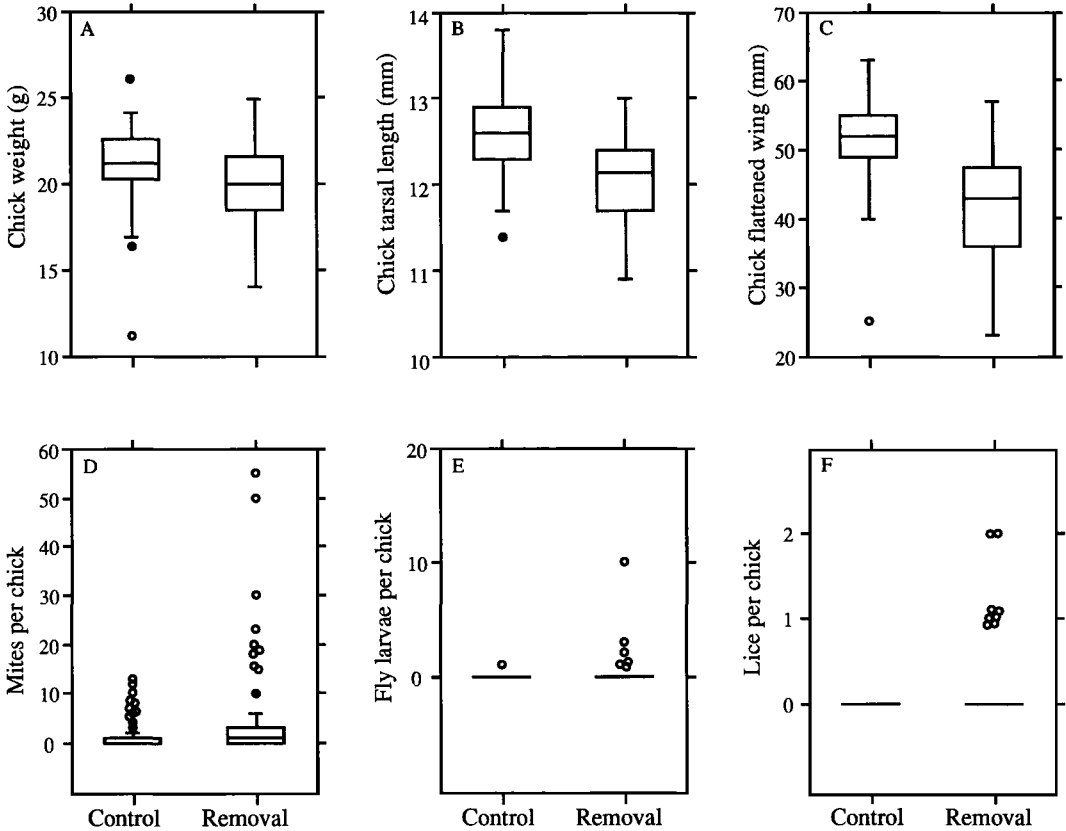


Fig. 3. Effect of feather removal on individual (A) chick masses (i.e. weights), (B) tarsal lengths, (C) flattened, straightened wing chords, and (D) infestations per chick of mites, (E) fly (*Protocalliphora* sp.) larvae, and (F) lice. All measured on day 12 of nestling development. Figures plotted are Tukey box plots (see Velleman and Hoaglin, 1981). Horizontal line bisecting each box is median, and upper and lower edges of each box are midpoints of those data above and below the overall median (i.e. box encompasses central half of data, or the interquartile range). "Whiskers" extending above and below boxes extend to the most extreme data value that still is within 1.5 times the interquartile range of either side of median. Values more than 1.5 times the interquartile range above or below the median plotted as a filled circle, and those more than 2.5 times the interquartile range above or below plotted as empty circles. Data points with tied values outside interquartile range displaced slightly to allow all data to be seen. The great majority of chicks had no detectable parasites. Chicks in removal group had parasites most frequently and at higher levels of infestation.

TABLE 2. Results of statistical tests for effect of experimental treatment on aspects of chick growth and ectoparasite numbers. Results presented both for analyses based on all individual chicks ($n = 161$) and on brood means ($n = 34$) for each measure. Morphological variables analyzed using Mann-Whitney U -tests. Asymmetrically distributed variables compared with a Fisher's exact test, which directly calculates probability of observed and more extreme results and, thus, has no test statistic. P -values at what I consider to be the most appropriate level of analysis for each variable are in bold.

Dependent variable	By individual chicks		By broods	
	Test statistic (U)	P	Test statistic (U)	P
Chick mass	4,221.5	<0.001	192.5	0.042
Chick tarsus	5,158.0	<0.001	260.5	<0.001
Chick chord	5,142.0	<0.001	241.0	<0.001
Mites per chick		0.001		0.116
Fly larvae per chick		0.094		0.397
Lice per chick		0.007		0.020

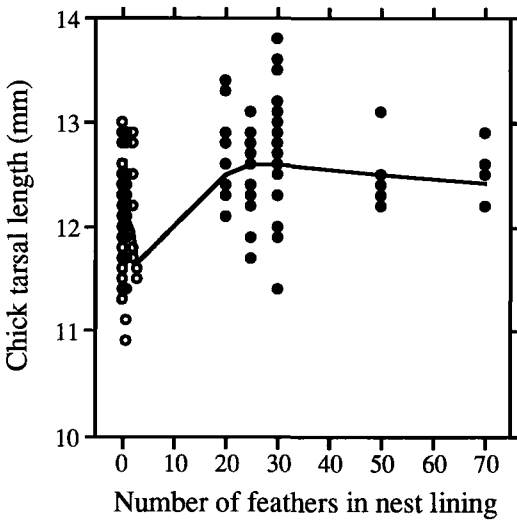


Fig. 4. Relation between chick tarsal length on day 12 and number of feathers in nest at same time. Curve running through points is a LOWESS smoothing as in Figure 2. The principal effect of feathers is between those that have relatively large numbers of feathers (i.e. control birds represented by filled circles) and those that have few or none (i.e. removal birds, open circles). Same pattern is found in comparisons of chick wing lengths and masses.

viding young chicks with supplemental insulation before they become homeothermic at about four to five days after hatching (Dunn 1979, Marsh 1980). Capreol (1983) showed in a nonmanipulative study that feathers decreased the rate of heat loss from Tree Swallow nests, and a similar advantage was suggested by Haforn (1978) in his studies of incubation energetics in Goldcrests (*Regulus regulus*). Another possibility to explain the observed results is that parents in the feather-removal group may have been spending so much time searching for feathers that they failed to keep up with their broods' feeding requirements and, consequently, chick growth may have been retarded. Given that parents in the removal group were only adding an average of five feathers per day to their nests (Fig. 1), it seems unlikely that this effort could dramatically depress feeding rates, which average about 300 visits per day (Winkler unpubl. data). Furthermore, preliminary results from experiments presenting feathers to nesting Tree Swallows (Winkler unpubl. data) indicate that swallows with their nest linings removed show very little interest in feathers during the chick-feeding phase of the breeding cycle.

The data from my study suggest that the advantage of feathers may extend to an anti-ectoparasite function as well. Because the nest boxes were cleaned out every fall or early spring, the numbers of ectoparasites in our boxes were kept artificially low. The numbers of ectoparasites during the 1989 experiment were low relative to even this low standard. Nevertheless, the lower incidence of ectoparasites in feathered nests in 1989 suggests that feathers may act to reduce ectoparasite infestations, and this effect may be especially important in natural areas where parasites are not controlled and where ectoparasites can have substantial deleterious effects on reproductive success (e.g. Burgerjon 1964, Camin and Moss 1970, Stahura 1982). Alternatively, higher parasite densities in removal nests may arise because more feathers were imported to removal nests (Fig. 1), bringing with them more ectoparasites. Although it is unlikely that lice imported in this way could establish successfully on swallows, it is quite possible that some mites could (D. H. Clayton pers. comm.), and further study of this possibility is needed.

Given that chicks in nests with feather linings can grow faster than those in nests without, it is important to ask whether such accelerated growth is likely to lead to higher chick survival and postfledging success. Even though feather removal had no effect on nestling survival in this study, it seems likely that in many years it would. Like most passerines, Tree Swallow chicks in their first week or so of nestling life exhibit little thermoregulation (Dunn 1979, Marsh 1980), and periods of low insect availability and low temperatures during this period can force the parents to stop brooding so they can search for food. The chicks often succumb to hypothermia in such situations (e.g. Chapman 1935, Rustad 1972), and it seems likely that the insulation provided by feathers in the nest lining would increase the brood's resistance to hypothermia. In addition, higher chick growth rates would decrease the period of chick vulnerability to this source of mortality. The range of nestling periods observed (Fig. 2) is on the order of two-thirds of the mean nestling period, and faster growth rates can have a significant effect on the length of time in the nest. Faster growth rates also could reduce the length of time the nestling is at risk to other threatening factors, such as ectoparasite infestation, predation, and hyperthermia. Shorter nestling periods also could conceivably lead to advantages

in allowing offspring greater time to forage before molting and migrating south. In any event, the advantage of faster growth rates need not always be expressed in shorter nestling periods, as chicks are likely to respond quite flexibly to the current environment when deciding when to fledge. Thus, it is no surprise that there was a significant correlation observed between numbers of feathers and chick nestling period in only one of the three seasons studied. The advantage of accelerated growth rates appears to be that they allow earlier fledging, not that they require it. Even if chicks raised in a nest with more feathers may fledge at the same age as chicks with fewer feathers in their nest, the former seem likely to fledge in better condition and with greater chances of success in their subsequent independence.

My results present several interesting contrasts with the work of Møller (1984, 1987a, b), who has concentrated to a greater extent on the disadvantage that greater numbers of feathers can have in increasing the risk of hyperthermia in the nests of European Barn Swallows (*Hirundo rustica*). The balance of these potential advantages and disadvantages of feathers in my study area seems to fall in favor of the potential advantages, since large numbers of young have appeared to die of hypothermia (on the basis of body and ambient temperatures at death) in the six years I have studied the birds, while very few, if any, have succumbed to hyperthermia (Winkler unpubl. data). Møller (1987b) observed a posthatching decline in the number of feathers in swallow nests, and he reported swallows removing feathers from their nests after the young hatched, apparently as a response to the risk of hyperthermia for older chicks. In my studies, involving many hundreds of hours of observation at hundreds of nests, Tree Swallows have been seen to willingly remove feathers very rarely, if ever. Feathers occasionally (<5% of visits) come out of the nest with an exiting parent after a feeding visit inside the box, but it has always appeared that these feathers were lost inadvertently, either because they were clinging to some part of the parent's body (other than its bill), or were stuck to a fecal sac being removed from the nest. I cannot preclude the possibility that the gradual posthatching decline in the numbers of feathers in the nests of the control group in 1989 (Fig. 1) was due to willful removal of feathers. If, however, the risk of hyperthermia were a strong force selecting for behaviors to reduce feather number later in

the nestling growth cycle, it is difficult to understand why the parents in the removal group were still trying to add feathers to their nests (Fig. 1) at the same time that the control parents were expected to be removing them. The current study cannot distinguish between these possibilities of willful versus inadvertent removal of feathers, but it does suggest that the latter possibility is a realistic alternative.

The rate of inadvertent removal of feathers from the nest might even help explain differences between species in the numbers of feathers in nests. Tree Swallows in my study averaged a little over 40 feathers in their nests at around chick hatching, whereas European Swallows average only about 20 at the same stage (Møller 1987b). Because inadvertent loss of feathers would be more likely from the more open nest of *H. rustica*, all else being equal, the "equilibrium" number set by the rate of addition and inadvertent removal would be lower in that species. There are, of course, other adaptive possibilities to explain such interspecific differences. Møller (1987a) has shown that feathers in nests comprise an important source of elevated predation risk in open- and cup-nesting species compared to hole-nesting species, and it may be that the relatively more exposed nest of European Barn Swallows has selected for reduced numbers of feathers in the nest. Another possibility is that the relative risks of hyper- and hypothermia differ and that the thermal advantages of feathers in the nests of *H. rustica*, thus, are reduced relative to Tree Swallow nests, perhaps because the former species breeds later than does the Tree Swallow where they breed sympatrically in North America (e.g. Bull 1985). Such questions and their potential answers will no doubt proliferate as more quantitative data become available on variation in the nest linings of birds, both between and within habitats and species.

For the Tree Swallow, variation in the number of feathers in the nest lining can have significant effects on reproduction, and this variation is almost certainly associated with variation in costs associated with procuring feathers and defending them against neighboring birds. Thus, feathers can be viewed as a measure of parental effort (cf. Winkler and Wilkinson 1988) just as can more traditional measures such as the feeding behavior of parent birds or egg size and number. Unlike some of these more traditional measures, this feature of the breeding biology of swallows is easily manipulated and

interfaces directly and intriguingly with the social behavior of these birds.

ACKNOWLEDGMENTS

The 1987 and 1988 field work on this project was supported by a grant from the Whitehall Foundation and by an NSF Postdoctoral Fellowship in Environmental Biology. The 1989 field work was supported by the U.S. Department of Agriculture (Hatch Project No. 428). Mike Clark, Peter Kleinman, Shai Mitra, Randy Moore, Ray Moranz, David O'Neill, Evan Siemann, and Cynthia Schiefflin provided valuable field assistance, and John McCarty, Ray Moranz and David O'Neill were particularly helpful in the execution and analysis of the 1989 experiment. Bob Johnson made the Cornell Ponds an enjoyable and productive place to work, and support for the 1989 use of the pond area was provided by the Cornell Experimental Ponds Management Committee. I thank Greg English-Loeb, John McCarty, Shai Mitra, Jamie Smith, and David Ward for stimulating discussions about feathers and bird nests. C. Ray Chandler, Steve Emlen, Svein Haftorn, John McCarty, Ernest J. Willoughby, Peter Wrege, and an anonymous reviewer provided valuable comments on various drafts of this paper. Chuck McCulloch provided invaluable statistical advice and help with StatXact, and Raleigh Robertson kindly sent me a copy of an unpublished thesis during manuscript preparation.

LITERATURE CITED

- BULL, J. 1985. Birds of New York state. Cornell Univ. Press, Ithaca, New York.
- BURGERJON, J. J. 1964. Some census notes on a colony of South African Cliff Swallows *Petrochelidon spilodera* (Sundevall). Ostrich 35:77-85.
- CAMIN, J. H., AND W. W. MOSS. 1970. Nest parasitism, productivity, and clutch size in Purple Martins. Science 168:1000-1002.
- CAPREOL, M. J. 1983. The adaptive significance of the feather lining in Tree Swallow (*Tachycineta bicolor*) nests and its effect on reproductive success. B.S. thesis, Queen's Univ., Kingston, Ontario.
- CHAPMAN, L. B. 1935. Studies of a Tree Swallow colony. Bird-Banding 6:45-57.
- CLEVELAND, W. S. 1981. LOWESS: A program for smoothing scatterplots by robust locally weighted regression. Am. Statistician 35:54.
- COHEN, R. R. 1985. Capturing breeding male Tree Swallows with feathers. N. Am. Bird Bander 10: 18-21.
- CYTEL SOFTWARE. 1991. StatXact, version 2.0. Cambridge, Massachusetts.
- DUNN, E. H. 1979. Age of effective homeothermy in nestling Tree Swallows according to brood size. Wilson Bull. 91:455-457.
- HAFTORN, S. 1978. Energetics of incubation by the Goldcrest *Regulus regulus* in relation to ambient air temperature and the geographic distribution of the species. Ornis Scand. 9:22-30.
- KUERZI, R. G. 1941. Life history studies of the Tree Swallow. Proc. Linn. Soc. N.Y. 52-53:1-52.
- MARSH, R. L. 1980. Development of temperature regulation in nestling Tree Swallows. Condor 82: 461-463.
- MØLLER, A. P. 1984. On the use of feathers in birds' nests: Predictions and tests. Ornis Scand. 15:38-42.
- MØLLER, A. P. 1987a. Egg predation as a selective factor for nest design: An experiment. Oikos 50: 91-94.
- MØLLER, A. P. 1987b. Nest lining in relation to the nesting cycle in the Swallow *Hirundo rustica*. Ornis Scand. 18:148-149.
- PETERSON, R. T., AND V. M. PETERSON. 1981. Audubon's birds of America. Cross River Press, New York.
- RUSTAD, O. A. 1972. Tree Swallow nesting study on a bluebird trail in south central Minnesota. Loon 44:100-105.
- SHEPPARD, C. D. 1977. Breeding in the Tree Swallow, *Iridoprocne bicolor*, and its implications for the evolution of coloniality. Ph.D. dissertation, Cornell Univ., Ithaca, New York.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods, 7th ed. Iowa State Univ. Press, Ames.
- STAHURA, J. J. 1982. Breeding biology of a Pennsylvania Tree Swallow colony: Effects of the parasitic blowfly on growth rates. N. Am. Bird Bander 7:140-145.
- VELLEMAN, P. F., AND D. C. HOAGLIN. 1981. Applications, basics and computing of exploratory data analysis. Duxbury Press, Boston.
- WEYDEMEYER, W. 1934. Tree Swallows at home in Montana. Bird-Lore 36:100-105.
- WILKINSON, L. 1988a. SYGRAPH. SYSTAT, Inc., Evanston, Illinois.
- WILKINSON, L. 1988b. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.
- WIMBERGER, P. H. 1984. The use of green plant material in bird nests to avoid ectoparasites. Auk 101:615-618.
- WINKLER, D. W. 1991. Parental investment decision rules in Tree Swallows: Parental defense, abandonment and the so-called Concorde fallacy. Behav. Ecol. 2:133-142.
- WINKLER, D. W., AND G. S. WILKINSON. 1988. Parental effort in birds and mammals: Theory and measurement. Ox. Surv. Evol. Biol. 5:185-214.