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

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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 nesting 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. Weidemeyer 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, Caprella 1983, Möller 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 con-
trol 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 re-
moval and control groups were balanced as closely as
possible for other aspects of parental quality (fe-
male 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 sub-
normal in some aspect of parental quality, these "sin-
gle-parent" nests were not included in the compar-
isons. 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 15 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 flat-
tened 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 (Protocellaphora 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 dis-
cern trends in scatter plots of data. Rather than as-
suming 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 re-
stricted 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 for-
cing a straight line through the data.

The other graphic method involved involved Tukey box
plots (Velleman and Hoaglin 1981) to represent dis-
tributions 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 symmetric, 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 symmetri-
cally distributed. Because they showed significant
differences from a normal distribution by Lilliefor's
 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 con-
trol and removal groups were then tested with Fis-
cher's exact test using StatXact software (Cytel Soft-

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

Chicks within a nest are clearly not entirely inde-
dependent of each other in their growth and parasite
infections, 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 com-
ponents for nests and chicks. In an analysis of variance
(ANOVA) with nest as the predictor variable, the re-
sidual mean square represents the component of vari-
ance 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_s times the nest variance, where
n_s can be computed from the formula in Snedecor and
Cochran (1980:246) to be 4.73 for this analysis. Be-
cause 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 mea-
sures 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 dif-
fferences between experimental groups using both indi-
vidual 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 broad 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 number of feathers in the nest, both at clutch completion \((r = -0.500)\) and at chick hatching \((r = -0.586)\) 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 at 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. 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.
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 (Protocalliphora 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-

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<td>Wing chord</td>
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<td>Fly larvae</td>
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<td>Lice</td>
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<td>Mites</td>
<td>0.26</td>
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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.

<table>
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<th>Dependent variable</th>
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<td>Test statistic (U)</td>
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<td>Chick mass</td>
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<td>Chick tarsus</td>
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<td>Chick chord</td>
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<tr>
<td>Mites per chick</td>
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<tr>
<td>Fly larvae per chick</td>
<td>0.094</td>
<td></td>
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<tr>
<td>Lice per chick</td>
<td>0.007</td>
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</table>
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., Bergeron 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 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 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 prolif rate 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 Siermann, 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 Em- len, Svein Hafstrøm, 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
