

THE FUNCTION OF FEATHERS IN TREE SWALLOW NESTS: INSULATION OR ECTOPARASITE BARRIER?

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Abstract. Altricial young face two significant energetic challenges in the nest: thermoregulation and stress caused by ectoparasites. Ectoparasites feed on blood of nestlings and serve as vectors for bacterial and viral infections. Many bird species line their nests with feathers, which insulate the nest and reduce heat loss from chicks. Feathers may also affect ectoparasite numbers by serving as a parasite barrier. We tested the possible roles of nest feathers and the effects of nest parasites on the growth and survival of Tree Swallow (*Tachycineta bicolor*) nestlings by comparing young in control nests with those in nests from which we removed feathers and removed feathers plus used an insecticide in an attempt to reduce ectoparasites. On the day chicks fledged, control nests had seven times more feathers in them than both categories of nests from which we removed feathers. Nestlings in control nests were larger than those in nests from which feathers were removed, and chick growth was positively related to number of feathers in the nest. Among the three categories, however, time between hatching and fledging and number of chicks fledged did not differ. Time between hatching and fledging may have been influenced by amount of rain just prior to fledging. The abundance and composition of arthropods in the nest did not differ among the categories either, suggesting that our treatments did not significantly reduce parasite numbers. Therefore, the effect of parasites on chick growth and survival remains equivocal. We concluded that feathers did not serve as an ectoparasite barrier, though they affected nestlings' growth rates positively.

Key words: ectoparasites, feather removal, growth, nest feathers, survival, *Tachycineta bicolor*, Tree Swallow.

Función de las Plumas en Nidos de *Tachycineta bicolor*: ¿Aislamiento o Barrera a los Ectoparásitos?

Resumen. Los jóvenes altriciales enfrentan dos desafíos energéticos significativos en el nido: termorregulación y estrés causado por ectoparásitos. Los ectoparásitos se alimentan de sangre de los pichones y sirven como vectores para infecciones bacterianas y virósicas. Muchas especies de aves forran sus nidos con plumas, lo cual aísla el nido y reduce la pérdida de calor de los pichones. Las plumas también pueden afectar los números de ectoparásitos al representarles una barrera. Evaluamos los posibles roles de las plumas de los nidos y los efectos de los parásitos de nidos en el crecimiento y la supervivencia de los pichones de *Tachycineta bicolor*. Comparamos jóvenes en nidos control con aquellos nidos en los cuales removimos las plumas, y en los cuales removimos las plumas y usamos un insecticida para tratar de reducir la cantidad de ectoparásitos. El día en que los pichones dejaron el nido, los nidos control presentaron siete veces más plumas que aquellos nidos en los cuales removimos las plumas (en ambas categorías). Los pichones en los nidos control fueron más grandes que aquellos en nidos de los cuales fueron removidas las plumas, y el crecimiento de los pichones se relacionó positivamente al número de plumas en el nido. Entre las tres categorías, sin embargo, el tiempo entre eclosión y emplumamiento y el número de pichones que dejaron el nido no difirió. El tiempo entre eclosión y emplumamiento puede haber estado influenciado por la cantidad de lluvia justo antes del emplumamiento. La abundancia y composición de artrópodos en el nido tampoco difirió entre las categorías, sugiriendo que nuestros tratamientos no redujeron significativamente el número de parásitos. Por lo tanto, el efecto de los parásitos en el crecimiento y la supervivencia de los pichones permanece incierto. Concluimos que las plumas no sirven como una barrera a los ectoparásitos, aunque afectan de modo positivo las tasas de crecimiento de los pichones.

INTRODUCTION

For altricial young, the nestling period is one of the most energetically expensive of their lives, and birds must trade off energy expended among growth, maintenance, and thermoregulation (Lombardo 1994). In cool climates, thermoregulation

uses over 30% of all energy acquired by altricial young (Weathers and Sullivan 1991). Another stress that reduces nestlings' growth and survival is loss of blood to hematophagous ectoparasites, such as fleas (*Ceratophyllus*), parasitic mites (Acari), and blow-fly larvae (*Protophthora*), which live in the nest and feed on the blood of nestlings (Heeb et al.

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2000, Shutler et al. 2004, Dawson et al. 2005a, O'Brien and Dawson 2005). Some birds line their nests with feathers, which could reduce the amount of energy chicks expend in thermoregulation (Lombardo et al. 1995, Chaplin et al. 2002). In addition, feathers lining the nest could reduce the number or effectiveness of ectoparasites by acting as a barrier between the young and the arthropods in the nest (Winkler 1993).

The Tree Swallow (*Tachycineta bicolor*) nests in cavities and lines its nests with feathers. The effect of nest microclimate on Tree Swallow nestlings' growth and survival has been experimentally tested with removing feathers from the nest (Winkler 1993, Lombardo 1994, Lombardo et al. 1995) or heating the nest (Dawson et al. 2005b). Nestlings in cooler nests and those with fewer feathers had lower growth and survival rates than those in insulated or warmer nests. However, Winkler (1993) found higher ectoparasite loads in nests from which feathers had been removed and postulated that feathers may also function as a parasite barrier. However, the separate effects of nest feathers in lowering parasite load and/or creating a warmer microclimate on the growth and survival of nestlings have not been tested.

We designed an experiment to test whether nest feathers reduce parasite loads or increase insulation of the nest and to examine the effect of parasite loads on chick growth and survival. The experiment comprised three treatments: removal of nest feathers, removal of nest feathers and application of an insecticide, and controls. We predicted that if nest feathers are important for insulation, nestlings would grow more rapidly in control nests and the reproductive success would be better in control nests than in nests from which feathers were removed. We predicted that if nest feathers also act as a parasite barrier, then removing feathers from nests should increase the parasite load in the nest. Removing feathers and adding an insecticide allowed us to separate the effects of feathers on parasitism and insulation: any reductions in growth or survival of juveniles should be due to the effects of reduced insulation alone. In addition to reporting our experimental results, we describe the community of invertebrates found in Tree Swallow nests.

METHODS

STUDY AREA AND FIELD TECHNIQUES

We conducted the study from June through July 2007 near the Meanook Biological Station in north-central Alberta (54° 37' N, 113° 20' W). The study region is primarily agricultural, consisting of mostly cropland (alfalfa, canola, and barley) and cattle pastures (Hannon and Cotterill 1998). During the Tree Swallow's nestling period (12 June through 12 July), average daily maximum temperature was 20.6 °C, average minimum temperature was 9.6 °C, and average daily precipitation was 2.8 mm. Weather data were taken from the closest Environment Canada weather station at Slave Lake, Alberta, 115 km northwest of Athabasca. We did not have access to data closer to our study site, but patterns of precipitation at Slave Lake were similar to those we observed.

We used 55 nest boxes, originally erected as part of a Mountain Bluebird (*Sialia currucoides*) trail, located on fence posts along rural roads; boxes were at least 100 m apart and 1–1.5 m off the ground. Each box was 26.5 cm high and 14 cm wide with floors 196 cm², including a small triangle of 1.6 cm² removed from each of the four bottom corners to allow water to drain. All boxes were cleaned before the breeding season to remove all old nest material.

Before starting our experiment, at each box we recorded clutch size, number of feathers in the nest, and age of the female (second year [SY] or after second year [ASY], Robertson et al. 1992). We also recorded the orientation of the box since south-facing cavities may be preferred over north-facing ones and could have a more favorable thermal environment (Robertson et al. 1992). We assigned our three treatments by stratifying them among the boxes according to clutch size, age of female, number of feathers in the nest cup at clutch completion, and orientation of the boxes. Nest boxes were checked daily to determine hatch date. In this area, the Tree Swallow's incubation lasts 12–15 days, chicks hatch in mid-June, and young fledge after 18–22 days, at the beginning of July (Hannon, unpublished data from a control area ~5 km from the study area).

TREATMENTS

Once eggs hatched, we began our three treatments: control ($n = 19$), feather removal ($n = 18$), and feather removal plus insecticide ($n = 18$). For the latter two, we removed and counted the feathers lining the nests on nestling day 1 (i.e., day of hatch), day 4, and day 8, and we also counted the feathers in the nest cup after nestlings had fledged. For the third treatment we applied insecticide by spraying a 10% malathion solution through the triangular spaces at the bottom of the nest boxes on each of the 3 days. Malathion is an insecticide with low toxicity to birds and humans and was used by Pacejka et al. (1998) to remove nest mites of House Wrens (*Troglodytes aedon*). We removed chicks from the box, measured them while the box was fumigated, and replaced them after approximately 5 min. For all treatments we measured nestlings on days 1, 4, and 8. Flattened wing length was measured to the nearest 0.1 cm, mass to the nearest 0.1 g. Control nestlings were measured and handled the same amount, but nest feathers were left in place and no insecticide was applied. To prevent premature fledging, boxes were not opened after day 15 and date of fledging was determined by looking into the nest daily with a dental mirror and light. Date of fledging was the date that the last young left the nest.

COUNTING AND IDENTIFYING ECTOPARASITES

Within 24 hr of the nestlings' fledging, we removed the bottom of the nest box, emptied the nest material into a plastic bag, and scraped the inside walls of the box into the bag. The

nest contents consisted of grass, feathers, fecal matter, and other particulate matter. The nest material was frozen for at least one week and then placed in a drying oven at 50–60 °C until the nest material was dry to touch (at least 24 hr). The dry material was weighed to the nearest 0.01 g. We enumerated ectoparasites in 34 randomly selected nests: 12 control, 11 feather removal, and 11 feather removal/insecticide. Because of the large amount of nest material and invertebrates, we subsampled one quarter of the mixed nest contents.

We rehydrated the nest material (added water to twice the volume of nest contents) to sort parasites, then added a drop of dish detergent to combat surface tension and 50 ml of 95% alcohol to preserve contents. The rehydrated nest material was refrigerated for up to 2 days and then passed through four sieves: 4 mm, 1 mm, 250 µm and 150 µm. Because of the large amount of material captured on the 250 µm and 150 µm sieves, we further subdivided it into quarters (1/16th of total). The representative material was then sorted under a microscope and invertebrates were removed, counted, and preserved in 70% alcohol. We used Moss (1968, 1978) to identify parasitic mites, Holland (1985) to identify fleas, and Sabrosky et al. (1989) to identify blow flies (*Protocalliphora*). We deposited voucher specimens of the invertebrates at the E. H. Stickland Entomological Museum, University of Alberta.

STATISTICAL ANALYSES

We used MANOVA for most comparisons of dependent variables across treatments, presenting univariate *F*-statistics for comparisons that were statistically significant at $P < 0.05$. We used nestlings' weight and wing length, fledging dates, and nest success (at least one nestling successfully fledged) as indices of reproductive success. For each nest, nestlings' weight and wing length were averaged. Difference in nest success was analyzed with a *G*-test. In the comparison of abundance of major arthropod taxa against treatments we again used a MANOVA with the nest's dry weight as a covariate. These analyses were done with SPSS (version 16.0). Values reported in the Results are means \pm SD.

To test whether the feather lining and/or insecticide affected the nests' overall characteristics or the assemblage of arthropods in the nests, we compared the three treatments by using the multivariate software program PATN (version 3.03) (Blatant Fabrications Pty., Ltd. 2001). We used the Gower metric to construct distance matrices and the semi-strong hybrid multidimensional scaling algorithm (SSH) with 1000 random starts to create 3-dimensional ordinations (Belbin 1991). We used 3-dimensional rather than 2-dimensional ordinations to reduce stress to below 0.15 (high stress is a reflection of poor fit between the distance matrix and the ordination).

Two ordinations were developed. In the first, arthropod data (numbers of individuals per arthropod group: flea larvae, adult fleas, blow-fly larvae, parasitic mites, and predatory mites) were used as intrinsic variables (analogous to

independent variables). Extrinsic variables were total number of deaths of nestlings, number of nestlings fledged, days taken to fledge, number of feathers in nest (at fledging and total number collected), nestlings' wing and weight measurements, and the nest's dry weight. Intrinsic variables were rescaled to range from 0 to 1, and nest variables were left raw. To test whether any of the treatments significantly altered the arthropod assemblage from the control nests we used analysis of similarity (ANOSIM, analogous to ANOVA) with 1000 randomizations and $P < 0.05$ as the cutoff for significance. Principal-axis correlation (PCC) and Monte Carlo attributes in ordination (MCAO) were employed to determine which intrinsic and extrinsic variables were most strongly correlated with the ordinations. Significant ($P < 0.05$) correlations for intrinsic variables indicate that those variables were important in creating the pattern shown in the ordination. Significant correlations for extrinsic variables imply that the extrinsics "agree" with the pattern created by the intrinsics.

In the second ordination, the nest data (as above) were used as intrinsic variables. To reduce the overwhelming influence of variables that had large ranges, feather numbers and the nest's dry weight were rescaled to range from 0 to 1. Other intrinsic variables were left as raw values. Extrinsic variables were the numbers of individuals per arthropod group (flea larvae, adult fleas, blow-fly larvae, parasitic mites, and predatory mites) and these were left in raw form. Ordination figures were created in SigmaPlot 10 (Systat Software 2006) with coordinates exported from PATN.

RESULTS

A PRIORI DIFFERENCES AMONG TREATMENTS

There were no differences between treated and control nests for hatch date, brood size at hatching, wing length, weight of chicks or number of feathers in the nest prior to treatment (MANOVA, Pillai's trace = 0.12, $F_{2,54} = 0.6$, $P = 0.81$, Table 1). Only four of the 55 females were SY (three from control nests and one from the feather-removal-plus-insecticide group). Fifty-one of 55 boxes had entrances oriented to the south, west or east, all orientations in which one of the box's sides faced south (as opposed to the back of the box, which was affixed to a wooden fence post). Only four boxes, all inhabited by ASY females, faced north, a position with a possible thermal disadvantage, since the sun would have to heat up the fence post before its benefits would be felt inside the box.

TREATMENT EFFECTS ON NUMBER OF FEATHERS

For the two feather-removal treatments we removed an average of seven feathers (range 3–15 feathers) on the second day we removed feathers (day 4) and an average of two feathers (range 0–39 feathers) on the third and last day we removed feathers (day 8). Failed nests excluded, by the time chicks fledged, control nests had seven times more feathers than nests

TABLE 1. Mean (\pm SD) hatch date, brood size at hatching, mass, and wing length of nestling Tree Swallows on day 1 and number of feathers lining the nest prior to experimental treatments.

	Control	Feather removal	Feather removal and insecticide
Nests	19	18	18
Julian hatch date ^a	165.7 \pm 2.0	166.5 \pm 2.3	166.5 \pm 1.5
Brood size at hatching	6.1 \pm 0.9	6.4 \pm 1.1	6.7 \pm 0.8
Mass (g)	2.3 \pm 0.5	2.2 \pm 0.6	2.2 \pm 0.4
Wing length (mm)	12.1 \pm 0.9	12.0 \pm 1.1	12.1 \pm 1.1
Feathers pre-treatment (<i>n</i>)	32.4 \pm 10.7	33.2 \pm 7.5	33.3 \pm 8.1

^aDay 166 = 15 June.

in either of the feather-removal treatments ($F_{2,46} = 37.4$, $P < 0.001$; Table 2). To compensate, between hatching and fledging, Tree Swallows brought twice as many feathers to experimental nests as to control nests ($F_{2,46} = 8.4$, $P = 0.001$; Table 2). Post-hoc least-significant-difference tests indicated that number of feathers in the nest and total feathers brought to the nest in the two feather-removal experiments did not differ.

TREATMENT EFFECTS ON NEST-DWELLING ARTHROPODS

Most of the nest-dwelling arthropods belonged to three major groups: larval and pupal blow flies (Diptera: Calliphoridae; *Protocalliphora*), larval and adult fleas (Siphonaptera), and mites (Acari: Mesostigmata). A small number of swallow bugs (Heteroptera: Cimicidae) were also found. Several mounted voucher specimens of adult fleas were identified as *Ceratophyllus idius* Jordan and Rothschild. This is the flea most commonly associated with the Tree Swallow (Holland

1985) and is probably the only species collected. However, because three species of *Ceratophyllus* have been recorded from the Tree Swallow (Holland 1985), without having examined all of them, we cannot be certain of their identity. All specimens of parasitic mites were *Dermanyssus hirundinus* (Hermann), which feeds on several species of hosts of the Hirundinidae and other bird families (Moss 1978). Predatory mites of the taxa Macrochelidae, Parasitidae, Ascidae, Laelapidae, and Uropodoidea were widespread among nests but were found in small numbers (less than 4 individuals per nest on average). Neither the removal of feathers nor the application of pesticide significantly altered the arthropod load in nests (MANOVA Pillai's trace = 0.18, $F_{2,30} = 0.6$, $P = 0.76$; Table 3).

Results of multivariate analysis were similar to those of univariate analyses: when arthropod groups were used as intrinsic variables, there were no significant differences among treatments (ANOSIM $P > 0.30$). All of the intrinsic arthropod variables were significantly correlated with the ordination,

TABLE 2. Mean (\pm SD) number of feathers lining the nest at fledging for successful nests, total numbers of feathers brought to nest by parents between hatching and fledging of young at successful nests, number of chicks fledged for all nests and successful nests, increase in mass and wing length from day 1 to day 8, and number of days between hatching and fledging for nestling Tree Swallows in successful nests under three treatments.

	Control	Feather removal	Feather removal and insecticide
All nests ^a	18	18	17
Chicks fledged	5.5 \pm 1.7	4.8 \pm 2.3	4.9 \pm 2.6
Successful nests ^b	17	16	15
Number of feathers in nest at fledging	68.3 \pm 35.8	10.4 \pm 12.3	7.1 \pm 5.3
Total feathers	36.4 \pm 33.1	73.4 \pm 25.0	82.7 \pm 40.9
Chicks fledged	5.8 \pm 1.1	5.4 \pm 1.5	5.5 \pm 1.9
Wing growth (mm)	32.9 \pm 0.8	27.5 \pm 4.1	26.7 \pm 5.0
Mass growth (g)	17.5 \pm 1.1	16.2 \pm 1.6	16.1 \pm 1.1
Days between hatching and fledging	20.4 \pm 1.5	20.8 \pm 2.2	20.6 \pm 1.8

^aExcludes two nests that were depredated.

^bSuccessful nests are those from which at least one young fledged.

TABLE 3. Mean (\pm SD) number of adult and larval fleas, parasitic mites, and blow-fly larvae in nests under three treatments.

	Control	Feather removal	Feather removal and insecticide
Nests	11	10	10
Adult fleas	12.1 \pm 10.3	11.0 \pm 7.6	12.1 \pm 9.3
Larval fleas	179.6 \pm 187.4	129.4 \pm 38.5	133.7 \pm 38.5
Parasitic mites	10.9 \pm 21.7	16.4 \pm 32.0	19.7 \pm 26.3
Larval blow flies	21.6 \pm 12.5	19.1 \pm 8.7	32.5 \pm 22.4

as was one extrinsic variable (dry weight of nest). Plotted vectors for these variables do not reveal any clear patterns by treatment, although vectors for dry weight of nest and numbers of adult fleas share a similar direction and the vector for predatory mites appears opposed to that of parasitic mites (Fig. 1). These patterns suggest that larger volumes of nest material provide a more suitable environment for pupal and/

or adult fleas and that predatory mites suppress densities of hematophagous mites.

In the second ordination, we found significant differences among treatments when nest data were used as intrinsic variables. Nests in the control group were significantly different from those treated with feather removal and feather removal plus pesticide ($P < 0.005$ in both cases), whereas the latter two

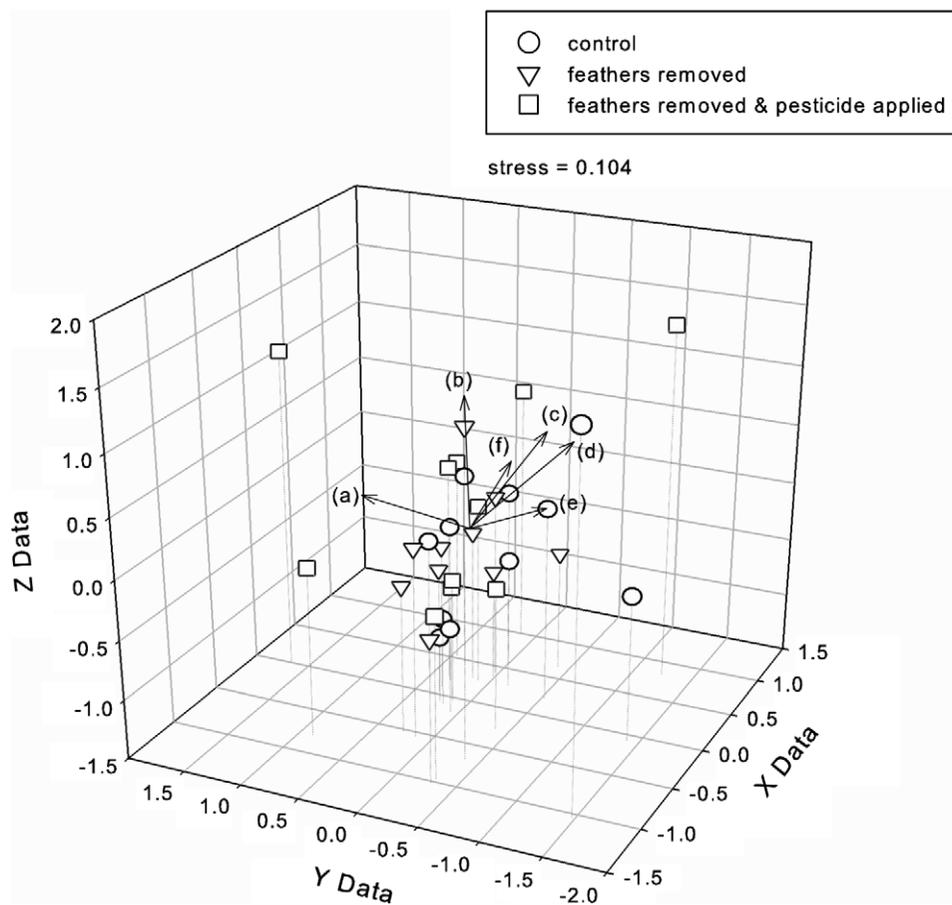


FIGURE 1. Three-dimensional ordination with arthropod data as the intrinsic variables and nest data as extrinsic variables (see Methods for details). Stress = 0.104. Significantly correlated variables ($P < 0.05$) are plotted: a = predatory mites; b = blow-fly larvae; c = nest dry weight; d = adult fleas; e = parasitic mites; f = flea larvae.

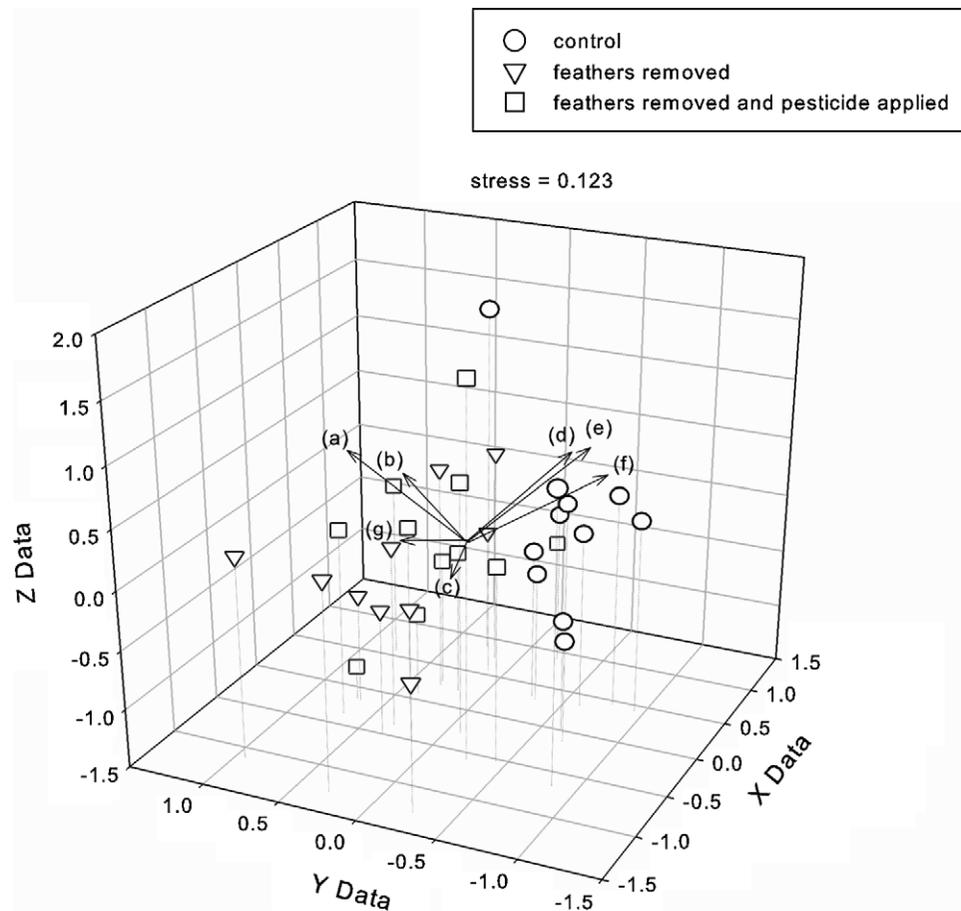


FIGURE 2. Three-dimensional ordination with nest data as the intrinsic variables and arthropod data as extrinsic variables (see Methods for details). Stress = 0.123. Significantly correlated variables ($P < 0.05$) are plotted: a = total feathers in nest; b = number of dead chicks; c = number of chicks fledged; d = mean wing length; e = feathers in nest at fledging; f = mean weight of chicks; g = dry weight of nest.

categories did not differ from each other ($P > 0.4$) (Fig. 2). All intrinsic nest variables were significantly correlated with the ordination except for days taken to fledge; no extrinsic arthropod variables were significantly correlated. Plotted vectors for the significant variables indicate, as expected, that number of feathers in the nest at fledging is directed toward the control group. Other vectors positively associated with the control nests are mean wing length and mean weight of chicks. Therefore, irrespective of whether nest data or arthropod data were used as intrinsic variables, we found no evidence of a differential effect of the pesticide treatment.

NEST FATES, CHICK GROWTH, AND DAYS TO FLEDGE

Of the 55 nests, 48 were successful (at least one young fledged), in five all the chicks died, probably from hypothermia (one control, two feather removal, and two feather removal and insecticide), and two nests were depredated before the end of the experiment (one control and one feather removal and insecticide). We used ANCOVA to compare effects of the treatments

on numbers of chicks fledged, including clutch size and hatch dates as covariates and omitting nests that were depredated. Overall, treatment had no effect on numbers of chicks fledged from all nests ($F_{2,52} = 0.4$, $P = 0.70$) or from successful nests only ($F_{2,50} = 0.2$, $P = 0.82$) (Table 2).

Next we compared the effect of treatment on chick growth in successful nests by comparing the increase in wing length and mass of chicks from day 1 to 8 across treatments. As in the ordination analysis, nestlings in control nests grew longer wings and amassed more weight than chicks in nests receiving either of the feather-removal treatments ($F_{2,47} = 11.1$, $P < 0.001$, $F_{2,47} = 5.6$, $P = 0.007$; respectively) and post hoc least-significant difference tests indicated that the two feather-removal treatments did not differ (Table 2). We then used a stepwise regression to determine the influence of number of feathers in the nest at time of fledging, hatch date, number of chicks hatched, the female's age, and box orientation on wing and mass increase between days 1 and 8. In both analyses, the only significant factor was number of feathers in the nest at fledging (wing: $F_{1,48} = 21.8$, $P < 0.001$, $\beta = 0.09$, $R^2 = 0.32$;

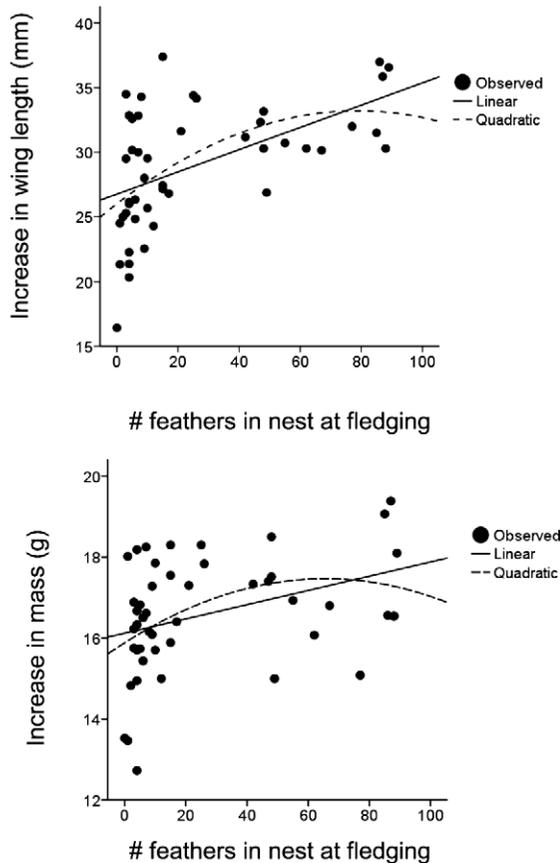


FIGURE 3. Relationship of growth in wing and mass of nestling Tree Swallows between days 1 and 8 and the number of feathers in the nest at the time of fledging. One outlier with double the number of feathers was removed. Linear and quadratic curves are plotted.

mass: $F_{1,48} = 5.9, P = 0.02, \beta = 0.02, R^2 = 0.11$). Both linear and quadratic curves were significant, but quadratic curves explained more variance, suggesting that growth rates may flatten in nests with more than 15–20 feathers (Fig. 3). Above this threshold further additions of feathers may not increase growth rates.

Despite the effect of feathers in the nest on chicks' growth rates, the time from hatching to fledging was similar for chicks from all three treatments ($F_{2,47} = 0.2, P = 0.81$; Table 2), suggesting that factors other than nest feathering or growth rates affect time in the nest. One possibility is that more advanced chicks might have delayed fledging if weather just prior to

fledging was poor, resulting in slowed growth rates at the end of the nestling period. To test this, we evaluated three weather variables: mean minimum temperature, mean maximum temperature, and total precipitation in the 5 days prior to fledging from each nest. Precipitation and maximum temperature were highly negatively correlated, but neither was correlated with minimum temperature, so we only used precipitation and minimum temperature. We predicted that chicks would stay in the nest longer after periods with higher rainfall and colder temperatures. We regressed (stepwise) chick size at hatching (to control for possible effects of size at hatching) and weather variables against days in the nest between hatching and fledging. Only one variable entered the model: total precipitation in the 5 days prior to fledging ($F_{1,47} = 19.4, P < 0.001, \beta = -0.55, R^2 = 0.30$). Interestingly, the relationship was opposite to what we predicted: chicks spent less time in the nest the more it rained in the previous 5 days.

DISCUSSION

Many species of birds line their nests with feathers, presumably to conserve heat and improve the energy budget of the nestlings (Winkler 1993, Lombardo et al. 1995). We predicted that if feathers are important for thermoregulation, nestlings' growth rates should be higher and reproductive success should be better in control nests than in both groups of nests from which feathers were removed. Consistent with our predictions, chicks were larger in control nests and the number of feathers in the nest was positively correlated with chick growth. Surprisingly, even though nestlings were larger in control nests, the number of chicks fledged and the interval between hatching and fledging did not differ by treatment. This result suggests that there is some plasticity in the timing of fledging that could be related to weather (Winkler 1993) or food supply. Interestingly, we found that temperature in the 5 days before fledging did not affect time to fledge, but rainfall did. Higher rainfall actually shortened the time to fledge, a result that at first seemed counterintuitive. However, the summer of 2007 was warmer and drier than the 30-year average (Table 4). Thus the rain may have stimulated insect production and increased food supply for chicks. We did not measure chicks close to their predicted date of fledging, to avoid provoking premature fledging. Therefore, we cannot determine whether growth rates of chicks in nests from which feathers were removed accelerated in the last few days prior to fledging

TABLE 4. Average daily weather conditions for the study period in 2007 and long-term averages from 1971 to 2000 for Slave Lake, Alberta. Data from Environment Canada Weather Service.

	June 2007	July 2007	June (1971–2000)	July (1971–2000)
Daily maximum temp (°C)	19.3	24.6	19.3	21.2
Daily minimum temp (°C)	8.3	12.6	7.9	10.0
Total rainfall (mm)	84.5	60.0	88.2	95.6

and perhaps erased earlier effects of slow growth due to lack of feathers in the nest.

A second goal of our study was to determine whether nest feathers also acted as a parasite barrier. If they had, then nests from which feathers were removed should have had a higher parasite load than controls. They did not: parasite numbers and community composition in control and feather-removal nests were similar. This is consistent with results of Lombardo et al. (1995), who did not find a significant difference in ectoparasite loads in Tree Swallow nests with and without feathers. Therefore, feathers apparently do not act as a parasite barrier. However, since we did not measure actual parasite loads on the chicks, only numbers of parasites in the nest, we cannot definitively conclude that feathers did or did not act as a barrier to the movement of parasites.

If parasites reduce chick growth and survival, as other studies have found (Winkler 1993, Lombardo 1995, Brown et al. 1995), we expected chicks in the feather-removal-plus-insecticide treatment to have higher growth and survival than those in the feather-removal group only. This, however, was not the case, as growth and survival of nestlings in the two feather-removal treatments were similar. One possible explanation is that the pesticide treatment did not reduce the parasite load. We applied 10% malathion as per Pajcika et al. (1998), who successfully reduced numbers of mites (*D. hirundinis* and *Androlaelaps casalis* [Berlese]) in nests of House Wrens. However, we used a different method for enumerating arthropods. Pajcika et al. (1998) used Tullgren funnels that extracted living animals, whereas we examined nesting material after it was preserved and hence could not differentiate between living and dead arthropods. We used this method because of logistical constraints at the field site. The number of parasites in the nest is the sum of those introduced by the parents on feeding visits and during brooding, plus reproduction of the parasites in the nest, plus those introduced by the parasites themselves (e.g., blow flies). Our pesticide treatment may have killed some invertebrates in the nest material whose bodies remained in the nests, but the parents and blow flies could have reintroduced more between treatments. Thus our measurement of parasites in the nest may not have been an accurate measure of actual parasite load on the chicks.

A second possible explanation of the lack of an effect of parasites on chick growth (assuming that our treatment did kill some parasites) is that the parasite loads were low in all nests and hence had little effect on the energetics of the chicks (Thomas and Shutler 2001). Our nests contained a mean of 26 blow flies, half the number reported by Dawson et al. (2005a) (mean of 50) in Tree Swallow nests in northern British Columbia but higher than the mean of 2.5 reported by Shutler and Campbell (2007) from Nova Scotia and New Brunswick. The flea load in our nests was much lower (mean of 12 for adults and 151 for larvae) than the mean of 773 fleas reported by Shutler and Campbell (2007). In addition, the loads of

parasitic mites in our nests were much lower than those reported by Burt et al. (1991) in Ohio (mean 9745 versus 15 in our nests). Thus, overall, the numbers of parasites in our nests were lower than at most other sites in North America and hence, even if the insecticide had worked, we may have seen little difference in growth rates between treatments.

Overall, our study found that feathers added to nests increased growth rates of chicks primarily through their effects on improving insulation of the nest and probably not by serving as a barrier to parasites. However, since our results are equivocal on whether the insecticide actually reduced parasite loads on the chicks and because parasite loads in the nests appeared to be low compared to those in other areas, this experiment should be repeated in areas with higher parasite loads and actual loads on chicks should be measured. In addition, since differences in growth rates did not translate into differences in numbers of chicks fledged (which may be related to weather in the days prior to fledging), multi-year studies should be done to test for interactions with weather. Finally, further studies should include a treatment where feathers are left intact but the nest is fumigated in order to isolate the effects of parasites on growth independent of feather insulation.

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