

# Tree swallow reproductive investment, stress, and parasites

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**Abstract:** We reduced or increased tree swallow, *Tachycineta bicolor* (Vieillot, 1808), clutch sizes by three eggs (50% of modal clutch size) to test experimentally for relationships between stress and parasite loads. In the first year of the study (1996), we enumerated two measures of stress (granulocyte to non-granulocyte ratios and heterophil to lymphocyte ratios), blood parasites, and ectoparasites living on birds (and not in nesting material). Stress indices increased for parents, but not for nestlings, associated with larger broods. Only one blood parasite (a trypanosome) was detected in blood smears from 221 different individuals. On individual birds, we found a median of 0 fleas, 0 lice, and 7 feather mites. In the second study (1998), we focused on parasites living in nesting material. Here, we found a median of 106 fleas and, of the parasites we observed, these probably had the greatest potential impact on the birds. Per capita flea loads were higher in nests that contained more young. However, despite higher stress to parents and higher per capita flea loads in enlarged broods, flea numbers were not associated with smaller nestlings or with reduced fledging success.

**Résumé :** Nous avons réduit ou augmenté la taille des couvées de l'hirondelle bicolor, *Tachycineta bicolor* (Vieillot, 1808), de trois oeufs (50 % du nombre modal d'oeufs dans une couvée) afin de vérifier expérimentalement s'il y a une relation entre le stress et la charge parasitaire. Durant la première année de l'étude (1996), nous avons mesuré le stress de deux façons, par le rapport des granulocytes sur les non-granulocytes et par le rapport des hétérophiles sur les lymphocytes, ainsi que dénombré les parasites sanguins et les ectoparasites trouvés sur les oiseaux, mais non sur les matériaux des nids. Dans les plus grandes couvées, les indices de stress sont plus élevés chez les parents, mais pas chez les oisillons. Un seul parasite sanguin, un trypanosome, a été observé dans les frottis sanguins provenant de 221 individus différents. Le nombre médian de parasites par oiseau est de 0 puce, 0 pou et de 7 acariens des plumes. Dans une seconde étude (1998), nous nous sommes intéressés aux parasites présents dans les matériaux du nid. Le nombre médian de puces est alors de 106 et, de tous les parasites observés, ce sont elles qui risquent d'avoir le plus grand impact sur les oiseaux. La charge individuelle de puces est plus grande dans les nids qui contiennent plus d'oisillons. Cependant, malgré le stress accru pour les parents et la charge de puces plus importante chez les oisillons dans les couvées plus grandes, le nombre de puces ne semble pas entraîner une réduction de la taille des oisillons, ni une baisse du succès de l'envol.

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## Introduction

The apparent restraint which birds and other organisms exhibit in the number of young that they produce has led to the suggestion that there are costs to reproduction, a hypothesis modified from Lack (1947) by Williams (1966), Charnov and Krebs (1974), and Perrins and Moss (1975). Several mechanisms could produce costs from excessive investment in reproduction, including physical exhaustion and susceptibility to predation (Lima 1987), parental starvation or inability to sufficiently provision young (Martins and Wright 1992), or susceptibility to parasites (Gustafsson et al. 1994). A broad definition of costs of reproduction could include those passed on to offspring (Hochachka 1992). Costs

to nestlings could arise because of lower per capita investment by parents in provisioning, which may reduce nestling growth rates, increase competition among nestlings, lower fledging mass, lower investment in immunity, and therefore increase susceptibility to parasitism or death (Martins and Wright 1992; Hörak et al. 1999).

Birds host a diversity of parasites (Clayton and Moore 1997), and avian immune systems are designed to limit their proliferation (Wakelin and Apanius 1997). One arm of the immune system includes white blood cells that can be involved in phagocytosis and inflammatory responses (Glick 1986). This arm of the immune system responds to stress from parasitism or other causes, and two commonly used indices of a stress response include higher granulocyte to non-

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granulocyte ratios and heterophil to lymphocyte ratios. Changes in white blood cell ratios may be mediated by hormones and other chemical messengers, but the important point here is that there is ample evidence that these indices reliably reveal stress, and do so within hours following exposure to a variety of different stressors (Gross and Siegel 1983; Ots and Hōrak 1996; Vleck et al. 2000; Ruiz et al. 2002).

One of the most demanding stressors that organisms face is reproduction. Reproductive stress can in turn be associated with parasite proliferation in hosts. For example, when clutch sizes of great tits (*Parus major* Linnaeus, 1758) were experimentally increased, fathers were more likely to have detectable levels of blood parasites (Norris et al. 1994; Richner et al. 1995; Allander 1997). The general interpretation of these results is that there is a trade-off between investments in reproduction versus immune function (Folstad and Karter 1992; Gustafsson et al. 1994; Deerenberg et al. 1997; Nordling et al. 1998); this trade-off may be mediated by stress. Links between stress and immune response and between immune response and parasitism are well-established (e.g., Apanius 1998; Hōrak et al. 1999; Ilmonen et al. 2000). Links between stress and parasitism may be less direct but have also been demonstrated (e.g., Saino et al. 2003a). We manipulated tree swallow, *Tachycineta bicolor* (Vieillot, 1808), clutch sizes to alter reproductive stress and tested whether changes in clutch size were associated with changes in parasite loads of young or adults.

Tree swallows are passerines that breed over a wide geographic area in North America. They are secondary cavity nesters that readily use nest boxes, so the species has been well studied (Robertson et al. 1992). Modal clutch size is usually 5 or 6, but previous experiments have shown that parents are able to fledge as many as 11 young (D. Shutler, R.G. Clark, C. Fehr, and A.W. Diamond, unpublished data). We predicted that swallows associated with enlarged clutches would have higher granulocyte to non-granulocyte and heterophil to lymphocyte ratios, and as a consequence of this stress, they would also have higher parasite loads. We also tested whether higher parasite loads in nests would reduce either nestling size or fledging success.

## Methods

### General methods

All methods were approved by the University of Saskatoon Animal Care Committee. Our study site was the St. Denis National Wildlife Area, 40 km east of Saskatoon, Saskatchewan, Canada. The tree swallow population in the area has been studied since 1990 (for additional details see Shutler and Clark 2003); the grid has had 115 nest boxes since 1993. Because some ectoparasites overwinter in old nesting material, this was removed at the end of each breeding season; however, an undetermined number of ectoparasites hid in spaces and cracks of boxes (D. Shutler, personal observation).

From early May, all boxes were monitored daily until clutches were complete (when no new eggs appeared for 3 consecutive days). Additional visits were timed to record date of hatch (14–16 days after clutch completion), take measurements of birds (mass, wing length, tarsus length,

ninth primary length), band adults and chicks, determine the number of young fledging (nest contents were checked for dead nestlings or unhatched eggs the day after fledging was expected, 20 days after hatch), and collect other data (see below).

Adults were captured opportunistically in boxes at any time or trapped when the oldest nestlings were approximately 4 days old. If two adults of the same sex were captured in a nest box, we called the first individual a floater (defined as a bird assumed not to have a territory; see Shutler and Weatherhead 1991) if they were caught before the nest initiation date. However, we called the second individual a floater if they were caught after the nest initiation date (Shutler and Clark 2003).

### Experimental methods

We report on two separate data sets from 1996 and 1998. In both years, clutch sizes were manipulated 3 days after the last egg was laid so that reproductive stress to parents included both incubation and feeding of young. We randomly assigned 58 trios of nests (27 in 1996 and 31 in 1998) with the same initiation date (defined as when the first egg was laid) to reduce (three eggs removed), control (eggs picked up and replaced), or add (three eggs added) treatments. This stratified treatments among initiation dates; initiation day was not significantly associated with any of the variables we considered, so we did not discuss it further. Sample sizes indicate the number of nests that survived until data collection (additional details provided in Shutler and Clark 2003). Number of young fledging was correlated with manipulated clutch size ( $r = 0.66$ ,  $P < 0.001$ ).

In 1996, a blood smear was made from a drop of blood extracted from the brachial vein (Bennett 1970) of adults and two randomly chosen nestlings from 90 different nests. Adult blood was sampled when their oldest nestlings were 4 days old (and not following opportunistic captures) and nestling blood was sampled when the oldest chick was 12 days old. Also in 1996, to assess ectoparasite loads on a subset of 52 individuals (18 females, 10 males, and 24 nestlings), flea powder was rubbed into plumage covering the entire body of the birds for 5 min (dust-ruffling; Walther and Clayton 1997) while they were held over the top of a rectangular container. Because of time constraints, most of the birds that were dust-ruffled were captured late in the breeding season and were not part of clutch manipulations. After birds were released, dust-ruffled parasites were transferred to a labelled vial.

Blood smears were stained with DiffQuik® and scanned by A. Mullie with a compound microscope for blood parasites; 100 fields were observed at 400 power for leucocytozooids and 100 fields at 1000 power for haemoproteids and leukocytes (Bennett 1970). Counts were made of heterophils, eosinophils, basophils, lymphocytes, and monocytes. Differential leukocyte counts were based on roughly 100 cells (mean  $\pm$  SD = 105.3  $\pm$  14.8). Floaters invest less in reproduction (they occasionally feed; Lombardo 1987) than box occupants, so we compared their stress indices with those of parents. Nestlings were considered separately.

Dust from dust-ruffled birds was emptied into a petri dish containing a few millimetres of 30% alcohol. Ectoparasites in petri dishes were systematically enumerated by D. Shutler

**Table 1.** Descriptive statistics for principal variables from the 1996 experiments on tree swallows, *Tachycineta bicolor* (Vieillot, 1808).

Variable	Minimum	Maximum	Mean	SD
Reproductive investment ( $N = 90$ nests)				
Initial clutch size	3	8	6.3	0.9
Number of young fledging	0	10	5.2	2.3
Leukocytes ( $N = 220$ individuals)				
Heterophils (%)	0.0	52.4	15.8	9.9
Eosinophils (%)	1.9	41.7	17.8	8.5
Basophils (%)	0.0	48.5	18.2	8.0
Lymphocytes (%)	10.7	90.7	43.9	14.2
Monocytes (%)	0.0	17.6	4.2	2.9
Granulocyte to non-granulocyte ratio	0.0	52.4	15.8	9.9
Heterophil to lymphocyte ratio	1.9	41.7	17.8	8.6
Dust-ruffled ectoparasites ( $N = 52$ individuals)				
Fleas	0	3	0.3	0.6
Lice	0	21	2.3	4.1
Feather mites	0	193	36.1	52.7

using a dissecting microscope. Representative specimens of lice, fleas, and feather mites were sent to Terry Galloway (University of Manitoba, Winnipeg, Man.), Glen Chilton (then at the University of Calgary, Calgary, Alta.), and Warren Ayteo (Museum of Natural History, University of Georgia, Athens, Ga.), respectively, for identification. Because of small samples for each age–sex category of birds and because of light parasite loads (see below), we pooled all individuals for these analyses.

In 1998, we manipulated clutches as above, but blood smears and dust-ruffling were not performed. Although we fumigated with a commercial bird flea spray each of the odd-numbered boxes 2 days before the first eggs were laid on our grid, this had no significant effect on flea populations at the end of the experiment (D. Shutler, A. Mullie, and R.G. Clark, unpublished data), probably because rates of colonization were high (Heeb et al. 1996). After fledging had occurred, nest boxes were shaken vigorously and scraped to empty contents into plastic bags. Bags were sealed and frozen and later thawed, dried, and emptied into shallow dishes. Fleas and blow fly (species of *Protocalliphora* Hough, 1899) pupae for each nest were systematically enumerated by A. Mullie.

### Analyses

Statistical analyses were performed in SAS (SAS Institute Inc. 2000). There is substantial evidence that adult females and males respond differently to reproductive stress in terms of parasitism (Poulin 1996; Schalk and Forbes 1997; McCurdy et al. 1998); this may be mediated by interactions among hormones, reproductive effort, and immunity (Folstad and Karter 1992). Thus, we included sex as a variable in analyses of stress levels of adults. For adults, we used general linear models with white blood cell ratios as response variables and initial clutch size, sex, treatment (reduce, control, or add), and the interaction between sex and treatment as explanatory variables. Nestling immunity is not mature, so we considered their stress responses separately. Because nestlings could not be sexed based on morphology, explanatory variables in the former models were initial clutch size

and treatment; we pooled data from nestlings sampled within broods.

Because dust-ruffling yielded few lice or fleas from most birds (see below) and because many of these birds were not part of clutch manipulations, we assessed whether the number of young fledging (rather than treatment) was associated with parasitism (presence–absence) by lice and fleas, and we tested whether feather mite loads were correlated with the number of young fledging.

For the 1998 data, nests were our experimental unit. We used logistic regression to test whether parasitism (presence–absence) by blow fly larvae was associated with initial clutch size and treatment, and we used general linear models to test whether initial clutch size and treatment were associated with flea numbers, which were  $\log_{10}(x + 1)$  transformed.

To produce minimum sufficient general linear models, variables with the largest  $P$  values were sequentially dropped from multiple regressions until only significant associations remained (Sorci et al. 1996).

## Results

### Stress, blood parasites, and ectoparasites on birds (1996 data)

Simple statistics for variables analysed in 1996 are summarized in Table 1. Initial clutch size was not associated with stress indices (white blood cell ratios) for either adults or nestlings (Table 2). Adults in the reduce treatments had lower indices of stress than did adults in the control treatments and in turn lower than did adults in the add treatments (Table 2, Fig. 1). Females had higher stress indices than did males, but there was no significant interaction between sex and treatment. In contrast, there were no significant effects of clutch manipulation on nestling stress responses (Table 2, Fig. 1). Stress indices were not significantly lower for 23 floaters than they were for 126 breeding adults (granulocyte to non-granulocyte ratio:  $F_{[1,147]} = 0.9$ ,  $P = 0.35$ ; heterophil to lymphocyte ratio:  $F_{[1,147]} = 0.3$ ,  $P = 0.57$ ).

In blood smears from 184 adults captured in 1996, only one *Trypanosoma* Gruby, 1841 sp. was found (in a male

**Table 2.** Stress responses (indexed by differential white blood cell counts) of tree swallows in 1996.

Explanatory variable	df	Granulocyte to non-granulocyte ratios		Heterophil to lymphocyte ratios	
		F	P	F	P
<b>Adults</b>					
Initial clutch	1	0.8	0.38	1.6	0.21
Sex	1	3.5	0.06 <sup>†</sup>	9.1	0.003**
Treatment	2	2.7	0.07*	3.9	0.02**
Sex × treatment	2	0.7	0.48	1.3	0.28
Model	6	2.0	0.07	3.9	0.002
<b>Nestlings</b>					
Initial clutch	1	0.1	0.82	0.3	0.60
Treatment	2	1.5	0.24	1.9	0.15
Model	3	1.1	0.36	1.6	0.20

**Note:** Treatment was experimental manipulation of brood size (reduce, control, or add). Shown are results of general linear models. For the adult models,  $N = 126$  individuals (excluding 23 floaters) and  $R^2 = 0.09$  for granulocyte to non-granulocyte ratios and 0.16 for heterophil to leucocyte ratios. For nestling models,  $N = 71$  nests and  $R^2 = 0.05$  for granulocyte to non-granulocyte ratios and 0.07 for heterophil to leucocyte ratios. Adults appeared to be more stressed when in add treatments than when in reduce or control treatments, whereas nestlings were unaffected (Fig. 1). The treatments differ significantly as follows after the sequential removal of terms from the model with  $P > 0.10$ : <sup>†</sup>,  $P < 0.10$ ; \*,  $P < 0.05$ ; and \*\*,  $P < 0.01$ .

parent), and no other blood parasites were detected. A subsample of 71 nestling blood smears contained no blood parasites.

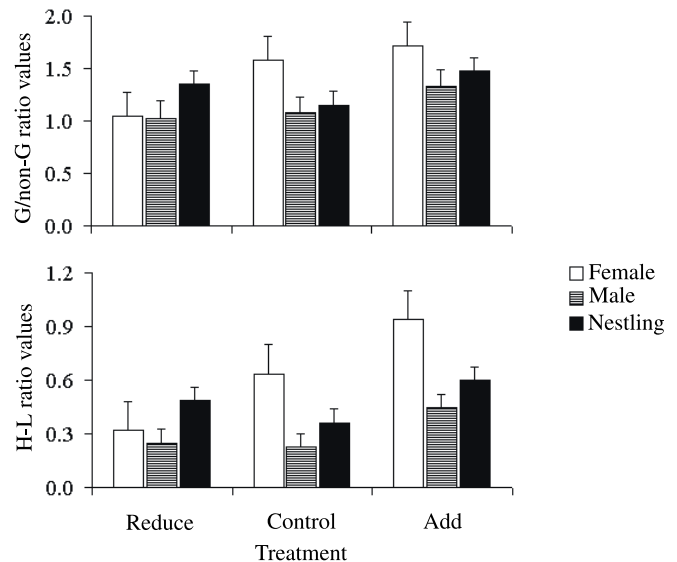
The taxonomy for some of the ectoparasites that we obtained from dust-ruffling is unresolved (T. Galloway, personal communication; W. Ayteo, personal communication). We obtained two species of lice identified tentatively as belonging to the genera *Brueelia* Kéler, 1936 and *Myrsidea* Waterston, 1915; one species of flea identified as *Ceratomyllus idius* Jordan and Rothschild, 1920; and three species of feather mites identified as *Pteronyssoides tyrrelli* Canestrini, 1882, a new species of *Trouessartia* Canestrini, 1881, and tentatively, a species of *Hemialges* Trouessart, 1888. Dust-ruffling yielded few parasites per individual (Table 1). Of 52 tree swallows dust-ruffled, 24 had lice and 11 had fleas, and mean loads of infested individuals were less than 2 fleas and 5 lice. All but four individuals had feather mites. Parasitism by lice (Wald's  $\chi^2_1 = 0.01$ ,  $P = 0.92$ ), fleas (Wald's  $\chi^2_1 = 2.2$ ,  $P = 0.12$ ), and feather mites ( $r_s = -0.10$ ,  $P = 0.47$ ) was not associated with the number of young fledging.

### Nest sampling (1998)

Blow flies were found in 39 nests, with a median of 3 per infested nest (maximum 81) and 0.5 per nestling (maximum 2.6). Neither initial clutch size (Wald's  $\chi^2_1 = 1.2$ ,  $P = 0.27$ ) nor treatment (Wald's  $\chi^2_2 = 4.0$ ,  $P = 0.13$ ) was related to blow fly parasitism (model, Wald's  $\chi^2_2 = 4.6$ ,  $P = 0.20$ ). Number of blow flies was independent of the number of fleas in 61 nests ( $r_s = -0.14$ ,  $P = 0.28$ ).

Fleas were found in all nests, with a median of 106 per nest (range 1–1682) and a median of 18.1 per nestling (range 0.6–210.3). Larger clutches ( $F_{[1,55]} = 3.3$ ,  $P = 0.07$ )

**Fig. 1.** Least square means ( $\pm$ SE) of stress responses (after controlling for other variables in Table 2), indexed by white blood cell ratios (G, granulocytes; non-G, non-granulocytes; H, heterophils; L, lymphocytes), of tree swallows, *Tachycineta bicolor* (Vieillot, 1808), relative to clutch manipulation in 1996. Adult tree swallows raising enlarged broods were more stressed; nestling stress indices were not related to treatment (statistical analyses are presented in Table 2).



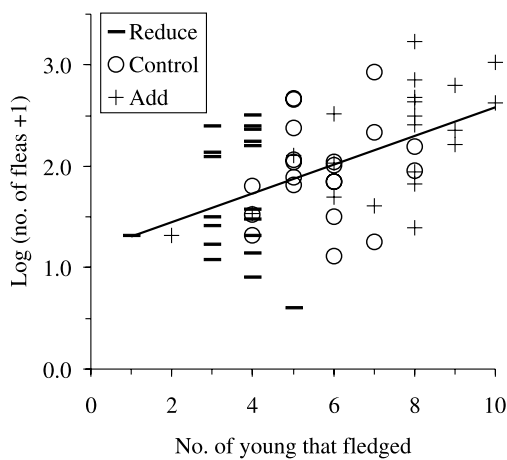
and treatment ( $F_{[2,55]} = 4.6$ ,  $P = 0.01$ ) were both associated with variation in the number of fleas (model  $R^2 = 0.19$ ,  $F_{[3,55]} = 4.3$ ,  $P = 0.009$ ). Least square mean  $\pm$  SE numbers of fleas from reduce, control, and add treatments were  $105 \pm 62$ ,  $143 \pm 62$ , and  $343 \pm 59$ , respectively. In general, nests that fledged more young had more fleas per capita; linear regression of log-transformed data predicted that nests fledging 1 young would have had ~22 fleas per nestling, whereas nests fledging 10 young would have had ~39 fleas (Fig. 2).

Elsewhere (D. Shutler, R.G. Clark, C. Fehr, and A.W. Diamond, unpublished data), with data from 12 years, we showed that nestling tree swallows in larger broods grew more slowly. Using data from 1998 alone, we again found here that broods containing more nestlings tended to be smaller, but that fleas had no additional effect on nestling size (Table 3). Moreover, the proportion of young fledging from a nest was not associated with flea load ( $r_s = 0.15$ ,  $P = 0.26$ ).

## Discussion

Our results showed that reproductive stress from larger broods affected white blood cell proportions of adults, as reported for other species (Gustafsson et al. 1994; Deerenberg et al. 1997; Ilmonen et al. 2000), particularly for female tree swallows that alone bore the costs of incubation. Ideally, we would have wanted to capture parents after they had paid the costs of feeding young for more than 4 days, but parents become increasingly difficult to capture as chicks age. We also found higher flea loads in nests with larger broods. Each of these results suggests a cost to reproduction (in which we include costs passed on to offspring; Hochachka 1992).

**Fig. 2.** In 1998, tree swallow nests fledging more young had more fleas and more fleas per capita (linear regression combining all nests,  $F_{[1,59]} = 20.8$ ,  $P < 0.0001$ ,  $N = 61$  nests).



However, larger brood sizes have not been associated with lower return rates (assumed to be related to survival) of adults or nestlings in our tree swallow population or other populations (De Steven 1980; Wiggins 1990; Wheelwright et al. 1991; Murphy et al. 2000). Although we did not measure stress levels and flea loads within nests in the same year, it is reasonable to assume that similar qualitative changes in both variables occurred in each instance that tree swallow clutch size was manipulated; an assumption reinforced by the results of clutch manipulations on other species (Norris et al. 1994; Richner et al. 1995; Ots and Hörak 1996; Deerenberg et al. 1997), even though some variation among years was expected (e.g., Sanz et al. 2002). This suggests that neither reproductive stress for adults nor higher flea loads in nests are associated with lower survival in tree swallows. Although we did not measure immune function, other studies (e.g., Saino et al. 2003a, 2003b) have shown that nestlings in enlarged broods have lower immunocompetence than those in reduced broods, so these birds may have been susceptible to parasites that we did not measure. Again, despite this possibility, there is no evidence that enlarged broods affect tree swallow return rates, although the data are only compelling for adults because most nestlings disperse too far to be recaptured (Shutler and Clark 2003).

Recent work (Heeb et al. 2000) has provided evidence that fleas influence nest microclimates in ways that improve their own survival and reproduction; possibly larger avian broods also contribute to an improved microclimate, leading to higher per capita flea loads. Immune systems can affect ectoparasite populations (e.g., Preston and Jongejan 1999), and higher per capita flea loads could also arise because immune systems of nestlings in larger broods may be compromised (Saino et al. 2003a, 2003b), although we did not find that nestlings in larger broods were more stressed. Higher per capita flea loads could also arise because parents are less active in performing behaviours that retard parasite population growth (e.g., Pacejka et al. 1996).

Despite large flea populations in our tree swallow nests, we found no deleterious consequences for nestling size or

**Table 3.** Tests of combined effects of the number of young fledging and fleas on tree swallow nestling size in 1998.

Response variable (based on mean of all nestlings within brood)	Explanatory variable			
	Number of young fledging		Fleas	
	$F_{[1,58]}$	$P$	$F_{[1,58]}$	$P$
Tarsus	-0.0	0.97	-1.6	0.21
Wing	-6.5	0.01*	-2.3	0.14
Ninth primary	-6.8	0.01*	-1.7	0.20
Mass	-9.0	0.004**	0.0	0.99

**Note:** Although broods containing more nestlings tended to be smaller and lighter at 12 days old, broods with more fleas were not significantly smaller. Negative  $F$  statistics (from general linear models) indicate that larger values of the explanatory variable were associated with nests containing smaller nestlings. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ . Nests are the unit of analysis.

fledging success. Moreover, although more fleas per nestling in larger broods suggests a constraint on optimal clutch size (Møller 1991; Poiani 1993; Richner and Heeb 1995), we have not found evidence of this trade-off. Several other studies have also failed to find effects of ectoparasites on nestling tree swallows (Burt et al. 1991; Rogers et al. 1991; review in Thomas and Shutler 2001), despite a significant literature on negative impacts of ectoparasites on the reproductive ecology of other species (Møller et al. 1990; Lehmann 1993; Brown and Brown 1996). Because they are constrained to the nest, nestlings have limited options for responding to parasitism. They could reduce metabolic rate to compensate for nutrients lost to parasites, which would also be associated with slower growth rates; but marsh tit (*Parus palustris* Linnaeus, 1758) nestlings increase it (Nilsson 2003). Thus, it has been suggested that where nestlings show no ill effects, parents must be compensating for nestlings' metabolic loss to parasites (Moss and Camin 1970; Johnson and Albrecht 1993); supporting data have been obtained for some species (Christe et al. 1996; Hurtrez-Boussès et al. 1997; Tripet and Richner 1997). Our results suggest that not only would parents have to increase feeding rates to compensate for enlarged broods, higher per capita ectoparasite loads in enlarged broods would add a further burden. However, Thomas and Shutler (2001) found that tree swallow parents did not adjust feeding rates to nests with more fleas or blow flies, although parasite populations were low (median blow fly larvae = 0, median fleas = 6.5) in the year that they did the study. Manipulations of ectoparasite loads will be necessary to properly test whether parents compensate for higher ectoparasite loads in nests, but such manipulations will not be straightforward because some ectoparasites move readily among nests (Heeb et al. 1996) and because other mechanisms, such as competition among parasites, may result in parasite populations that are unaffected by manipulations (e.g., Rogers et al. 1991). Finally, fleas may provide some benefit to tree swallows, perhaps by direct competition or perhaps by stimulating immune systems so that other parasites are less able to become established.

Blood parasites were rare in our tree swallow population; they are also rare in an Ontario population (C. Barber, personal communication) and in a few locales in the Maritimes (A. Campbell, M. Smith, and D. Shutler, unpublished data). Greiner et al. (1975) suggested that birds which are largely aerial foragers, such as tree swallows, tend to have low levels of blood parasites, possibly because it is more difficult for vectors to attack them than species in other foraging guilds. There were also few large ectoparasites extracted by dust-ruffling tree swallows (also see Brown and Brown 1995). Lice cannot survive off their hosts for very long (Roberts and Janovy 1996), so dust-ruffling is useful for measuring their numbers (Clayton and Drown 2001). In contrast, fleas are intermittent blood feeders and are far more numerous in the nesting material than on the bird. Feather mites are also obligate passengers on hosts, are much smaller than lice or fleas, and were comparatively numerous on our tree swallows as they are on most birds (Behnke et al. 1995; Figuerola 2000), but feather mites are usually described as commensals because they have not been consistently associated with significant detriments to hosts. Thus, for tree swallows, nesting material was more useful than blood or the birds themselves as the place to search for parasites (also see Rothschild and Clay 1952, p. 61) that are likely to impact reproductive ecology. Nonetheless, we were unable to find impacts of any parasites on tree swallows.

In summary, although we found evidence that enlarged broods stressed parent tree swallows and that enlarged broods had higher per capita flea loads, we did not find evidence that fleas were associated with smaller nestlings or reduced fledging success. Evidence from several sources (De Steven 1980; Wiggins 1990; Wheelwright et al. 1991; Murphy et al. 2000) also suggests that long-term return rates of tree swallows is not compromised by reproductive stress or high flea loads. Thus, the conundrum of optimal clutch size for tree swallows remains unresolved.

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