Ectoparasites, nestling growth, parental feeding rates, and begging intensity of tree swallows

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Abstract: Many studies fail to show relationships between ectoparasite loads and nestling growth rates. One explanation is that parent birds increase feeding rates to compensate for nestling energetic losses to ectoparasites. Nestling begging behaviours could signal need to parents. Accordingly, we tested whether higher flea and blow fly loads in tree swallow (*Tachycineta bicolor*) nests were associated with smaller nestlings, higher parental feeding rates, and increased nestling begging intensity. The study area was the Gaspereau Valley of Nova Scotia, Canada. When nestlings were 10 days old, parental feeding rates and nestling begging intensity were measured with tape recorders. At 13 days of age, nestlings were weighed and measured. Within 2 days of fledging, nest material was removed from nest boxes and enumerated for adult fleas and blow fly pupae. After including brood size and date of first egg as covariates in general linear models, no significant relationships were found between ectoparasite loads and nestling size, parental feeding rate, or nestling begging intensity. Our results suggest that nestling tree swallows were able to buffer the effects of naturally occurring ectoparasite loads without significant help from their parents. Low levels of virulence may have resulted from relatively benign weather during the study, low numbers of ectoparasites, selection on ectoparasites to avoid killing their hosts, and host defences.

Résumé : Beaucoup d'études n'ont pas réussi à établir de relation entre le fardeau d'ectoparasites et les taux de croissance des oisillons au nid. Parmi les explications possibles, on peut penser que les parents sont en mesure d'augmenter l'apport de nourriture au nid de façon à compenser la perte énergétique due aux ectoparasites. Par leurs sollicitations, les oisillons au nid peuvent communiquer leurs besoins à leurs parents. Nous avons tenté de voir si les fardeaux plus importants de puces et de mouches de la viande dans les nids de l'Hirondelle bicolore (*Tachycineta bicolor*) sont associés à des oisillons plus petits, à des taux d'apport de nourriture plus élevés et à des comportements de sollicitation plus intenses. La vallée de Gaspereau, Nouvelle-Écosse, Canada, a servi de site d'étude. Des magnétophones ont permis d'enregistrer l'intensité des sollicitations des oisillons âgés de 10 jours et les taux d'approvisionnement par les parents. À l'âge de 13 jours, les oisillons ont été pesés et mesurés. Moins de 2 jours après l'envol des oisillons, les boîtes à nids ont été vidées afin de permettre l'inventaire des puces adultes et des pupes de mouches de la viande. L'intégration de la taille de la couvée et de la date de la première ponte comme covariables dans des modèles linéaires généraux n'a pas mis en lumière de relation particulière significative entre le fardeau d'ectoparasites et la taille des oisillons au nid, l'intensité de leurs comportements de sollicitation, ou le taux d'approvisionnement par leurs parents. Nos résultats laissent croire que les Hirondelles bicolores au nid sont capables de neutraliser les effets des fardeaux naturels de parasites sans recevoir d'aide importante de leurs parents. La faible virulence de ces infections peut être attribuable au conditions climatiques modérées durant l'étude, au nombre faible de parasites, au système de défense des hôtes ou à la pression sélective exercée sur les ectoparasites pour éviter de tuer leurs hôtes.

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Introduction

Avian ectoparasites not only take blood from their hosts, they can also serve as vectors for viral, bacterial, and other diseases. Consequently, ectoparasites elicit significant immune and behavioural responses (Marshall 1981; Hart 1997; Janovy 1997; Wakelin and Apanius 1997). Because of these and related costs, higher ectoparasite loads can be associated with slower nestling growth (Møller et al. 1990; Lehmann 1993; Merino and Potti 1995; Richner and Heeb 1995; Heeb

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et al. 1999) and, in rare cases, death (Arendt 1985). However, negative effects on nestlings have not been detected in several studies, even when substantial numbers of ectoparasites were present (Gold and Dahlsten 1983; Eastman et al. 1989; Johnson and Albrecht 1993; Mappes et al. 1994; Rendell and Verbeek 1996a; Dawson and Bortolotti 1997). To explain these insignificant relationships, it has been suggested (Moss and Camin 1970; Johnson and Albrecht 1993) that parents may increase feeding rates to nestlings to compensate for energy losses to parasites. Parents would need to assess these energy losses; one cue could be nestling begging behaviour. In this study, associations among ectoparasite loads in nests, indices of nestling growth, parental feeding rate, and nestling begging intensity were examined in the tree swallow (*Tachycineta bicolor*).

Tree swallows nest in cavities and incubate their clutches (usually 5 or 6 eggs) for 12 to 14 days; both parents feed young for 18 to 20 days in the nest (Robertson et al. 1992).

Tree swallow nests are frequently home to fleas (Siphonaptera) and blow flies (Diptera: Calliphoridae) (Bennett and Whitworth 1991, 1992; Rogers et al. 1991; Whitworth and Bennett 1992; Rendell and Verbeek 1996a, 1996b). Fleas that parasitise temperate bird populations overwinter as adults in nesting material. In spring, females copulate and then search for blood meals from hosts before beginning to lay eggs. Larvae hatch after a few days and are initially detritivores on nest material. They soon pupate and emerge as sanguivorous adults. Prior to host fledging, 5000 or more adult fleas may occupy a single nest, although 100 or fewer is more typical, depending on ecological conditions (Harper et al. 1992; Dufva 1996; Dufva and Allander 1996; Heeb et al. 1996). Blow flies also overwinter as adults, usually under the bark of trees, but occasionally in nest material. In spring, females lay eggs in host nests (Bennett and Whitworth 1991; Dahlem 1991; Wittmann and Beason 1992). Once hatched, larvae of the common blow fly parasite of tree swallows, *Protocalliphora sialia*, feed through the skin on blood, primarily of nestlings, and primarily at night. Prior to host fledging, up to 1200 sanguivorous larvae may occupy a single passerine nest, although 50 is more typical (Eastman et al. 1989; Bennett and Whitworth 1991; Johnson et al. 1991; Rogers et al. 1991; Whitworth and Bennett 1992; Wittmann and Beason 1992; Johnson and Albrecht 1993; Johnson 1996). Although most blow flies are attached to hosts only intermittently, *Protocalliphora braueri*, which lives under the skin of its host, has also not been associated with significant detriments to hosts (Eastman et al. 1989).

Nestlings beg to communicate their hunger to parents, and acoustic components of begging are one set of cues to which parents respond (Henderson 1975; Bengtsson and Ryden 1983; Hussell 1988; Price et al. 1996; Cotton et al. 1996; Leonard et al. 1997, 2000; Granadeiro et al. 2000; Leonard and Horn 2001). Thus, begging vocalisations could provide signals to parents of decreased nutritional condition and increased hunger resulting from parasites. Accordingly, we tested whether higher numbers of fleas and blow flies in tree swallow nests were associated with slowed nestling growth, increased parental feeding rate, and increased intensity of nestling begging vocalisations.

Study areas and methods

In 1999, data were collected from four locations in the Gaspereau Valley, King's County, Nova Scotia (45°5′N, 64°20′W). All locations were within 5 km of each other and had been in use since 1988 (Garron 1989).[2] The location called River (30 nest boxes) is adjacent to hay fields, whereas Coldwell's (17), Pam's (30), and Hynes (20) are adjacent to apple orchards. At each location, nest boxes were attached to metal poles approximately 1.5 m above the ground. Poles were greased to prevent predation by raccoons and squirrels. Nest boxes were placed at least 15 m apart and faced in random directions. Nest boxes in this population are cleaned each year, usually in the spring before tree swallows have returned. Beginning in early May, tree swallow nest boxes were monitored for signs of fresh nesting material, date of first egg, clutch size, brood size, and fledging.

The intensity of begging vocalisations increases with nestling age (McCarty 1996; Price et al. 1996), so in all cases we measured

vocalisation intensity when nestlings were 10 days old. Recordings of vocalisations were usually taken in the morning between 08:00 and 11:00 (latest 12:00). Lapel microphones were hidden inside the nest box and portable tape recorders were hidden in ground vegetation, to minimise the disturbance to adults. Audiotaping continued for 30- or 45-min intervals, depending on cassette length. Christe et al. (1996) detected significant associations with shorter intervals than this. Recordings were scored on a subjective scale by KT (before ectoparasite assays were done) for each instance of nestling begging. Begging intensity was the average of all scores for a taping session. Begging was scored on a scale from 1 to 5, where 1 was no begging, 2 was multiple nestlings uttering one or two notes or a single individual persisting for some time with low-volume notes, 3 was either many nestlings uttering 2–5 notes or a few nestlings persisting with medium-volume notes, 4 was all nestlings begging at high volume, and 5 was intense prolonged begging that persisted after the adult was heard leaving (Leonard et al. 1997; M.L. Leonard, personal communication). A subsample of 10 tapes was chosen randomly and scored a second time under blind conditions; in all cases the scores assigned were the same. Begging occurred only when parents entered boxes, so feeding rate was the same as the number of begging events recorded. It was verified on two broods that visual counts of parental entrances corresponded exactly to the number of entrances detected on the tapes. It was assumed that each time a parent was heard entering that it had come to feed the nestlings (also see Rogers et al. 1991).

When nestlings were 13 days old, mass was measured to the nearest 0.1 g, using a 30-g Pesola spring scale. Right-wing length was measured to the nearest 0.1 cm, using a wing ruler, and right-tarsus length was measured to the nearest 0.01 mm, using calipers. Because nestlings and nest boxes were not statistically independent, we averaged morphological measurements for all nestlings within a nest box.

Nests were collected in June and July, 1 or 2 days after the last nestling had fledged. Nest-box contents were emptied into plastic bags and fleas that remained in the nest boxes were dislodged with a probe or screwdriver and added to the bags. Nests were frozen for at least 1 week, and then the slightly open bags were placed in a drying oven at 38°C for at least 24 h, or until the nests were dry to the touch (up to 1 week). After drying, bags were sealed and returned to the freezer until they were examined for ectoparasites.

To enumerate parasites, nest material was placed over a 2.00 mm gauge upper sieve and a 0.71 mm gauge lower sieve, both of which sat in a tray. Large pieces of grass and feathers were retained in the upper sieve. The number of feathers was recorded and all items in this sieve were teased apart to dislodge attached fleas. Remaining material from the lower sieve and the tray were sorted for adult fleas and blow fly pupae under a magnification light and using a fine paintbrush.

Statistical analyses were performed in SAS (SAS Institute Inc. 1990); tests are described and explained below.
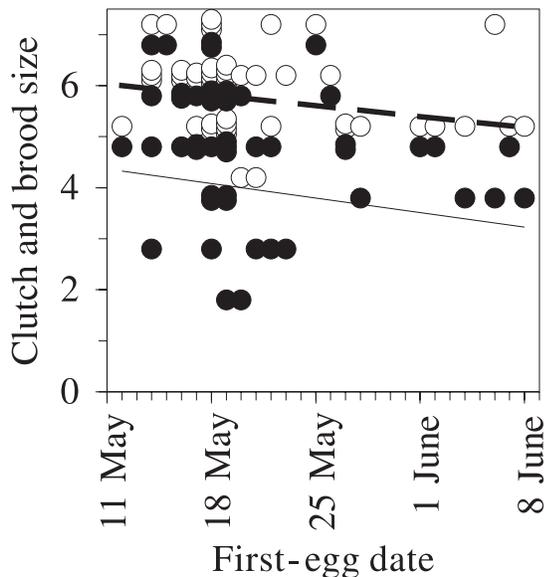
Results

General observations

At the River location, 22 of 30 nest boxes were occupied by tree swallows in 1999; corresponding numbers were 3 of 17 for Coldwell's, 14 of 30 for Pam's, and 9 of 20 for Hynes. First-egg dates ranged from 12 May to 8 June (Fig. 1), and there were 2, 17, 21, and 8 clutches of 4, 5, 6, and 7 eggs, respectively. Although clutch size was smaller in nests initiated later (Fig. 1; Pearson's $r = -0.38$, $P = 0.01$), brood size was not (Fig. 1; $r = -0.18$, $P = 0.22$). One nest

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[2]C.A. Garron. 1989. Influence of timing of breeding and female age on the breeding success of the tree swallow, *Tachycineta bicolor*. B.Sc. (Hons.) thesis, Acadia University, Wolfville, Nova Scotia, Canada.

Fig. 1. Tree swallow clutch (○ and dashed line) and brood (●
and solid line) sizes over the course of the year. Clutch and
brood data and overlapping points are offset for clarity. Regres-
sion lines are based on actual data and not on the offset points.

Table 1. Summary statistics for variables considered in the analyses.

Variable	N	Mean	SD	Low	High
Mass at day 13 (g)	48	23.2	1.7	15.6	25.6
Right-wing length (mm)	48	58.7	3.9	46.7	71.4
Right-tarsus length (mm)	48	15.0	0.3	14.3	16.5
No. of fleas per nestling	48	3.2	6.2	0	40.8
No. of blow flies per nestling	48	0.8	1.7	0	8.1
No. of feeds (per hour)	39	18.7	6.4	5.3	30.7
Begging intensity[a]	38	3.5	0.9	1.3	5.0

[a]See the Study areas and methods section for description of scoring.

did not produce any fledglings and, because this may have
prevented ectoparasites from developing to the same extent
as in nests that did fledge, it was removed from the analyses
involving ectoparasites. For various logistic reasons, beg-
ging intensity and parental feeding rates were not measured
at all nests (Table 1).

Fleas were identified as *Ceratophyllus idius* (Holland
1951; Benton and Shatrau 1965) by Dr. Glen Chilton. All
blow fly pupae and adults (a total of 10 specimens) that have
been found in tree swallow nests so far have been identified
as *P. sialia* (Bennett and Whitworth 1992) by Dr. Terry
Whitworth, although other blow fly species may also be
present. No larvae or prepupae were found, possibly because
freezing made their bodies undetectable among nest con-
tents.

Previous research has suggested that there is a negative re-
lationship between feathers and fleas in tree swallow nests
(Winkler 1993; both variables were log(x + 1)-transformed
in all analyses to improve their fit to normality, as assessed
with Shapiro–Wilk tests); the number of fleas was not signif-
icantly lower in nests with more feathers (r = –0.15, P =
0.31) and was also not related to dry nest mass (r = 0.13,
P = 0.37). Moreover, the number of feathers in nests with
blow flies (mean ± SD = 79.1 ± 34.0) did not differ from the
number in nests without blow flies (mean ± SD = 76.9 ±
93.5; *t* test: t = 0.2, P = 0.15). A significant positive relation-
ship was found between number of feathers and date of initi-
ation (r = 0.30, P = 0.04).

Ectoparasites as explanatory variables

Summary statistics for principal variables appear in
Table 1. Mean nestling mass was lower in larger broods (r =
–0.32, P = 0.03). When a lightweight outlier brood was re-
moved (mass = 15.6 g; none of this brood fledged), the rela-
tionship was still significant (r = 0.37, P = 0.01). Neither

tarsus length (r = 0.14, P = 0.35) nor wing length (r = –0.14,
P = 0.33) were related to brood size. Hence, brood size was
included as a covariate in general linear models involving
mass but not in models involving tarsus or wing length.
The first principal component (PC) from a PC analysis on
the correlation matrix of tarsus and wing lengths (first
eigenvalue = 1.26, 63% of the variation) explained less vari-
ation than expected by chance (according to the broken-stick
criterion described in Frontier 1976; Jackson 1993), so tar-
sus and wing lengths were treated as independent variables.
Nests initiated late had fewer fleas (Fig. 2; r = –0.36, P =
0.01) but were more likely to have blow flies (mean initia-
tion date ± SD for 34 nests without blow flies = 19.6 May ±
5.3 days and for 13 nests with blow flies = 23.5 May ±
7.8 days; general linear model F = 3.9, P = 0.06). Hence, to
control for initiation date in analyses involving ectoparasites
and to avoid multicollinearity, residuals from separate re-
gressions of fleas against first-egg date and blow flies
against first-egg date were used as explanatory variables.

Nestling mass, wing length, and tarsus length were not
significantly associated with flea number (Table 2). The lat-
ter relationship was essentially unaffected if an outlier brood
with unusually long tarsi (16.5 mm; Table 2) was excluded.
Mass, wing length, and tarsus length were not significantly
associated with blow flies (Table 2), and the latter result was
unchanged if the outlier for tarsus length was excluded. Be-
cause separate species of ectoparasites could have cumula-
tive or synergistic effects, analyses were repeated with both
residual fleas and residual blow flies as explanatory vari-
ables but, in no case, were significant associations with ecto-
parasites observed; associations with brood size remained
significant.

Larger broods begged more intensely (r = 0.38, P = 0.02).
Thus, brood size was included as a covariate in general lin-
ear models involving begging. Begging intensity was not
significantly related to fleas (Table 2) or blow flies (Table 2).
Analyses of begging intensity were repeated with both resid-
ual fleas and residual blow flies as explanatory variables and
brood size as a covariate, but combined ectoparasite loads
were not related to begging intensity.

Larger broods were fed more frequently by their parents
(r = 0.38, P = 0.02). Thus, brood size was included as a
covariate in general linear models involving parental feed-
ing. Feeding rate was not significantly related to fleas (Ta-
ble 2). Feeding rate was slightly higher at nests with blow
flies present (Table 2). Analyses of feeding rate with both
residual fleas and residual blow flies as explanatory vari-
ables and brood size as a covariate produced similar results.

Fig. 2. Change in flea numbers collected from nests relative to date of first egg.
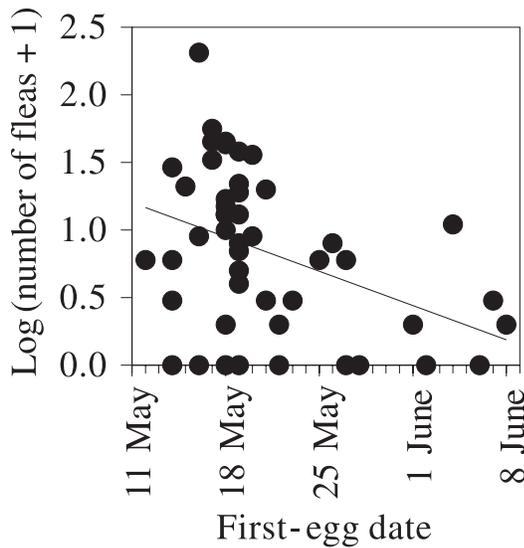

Fig. 3. Relationship between average mass of all nestlings from a nest and residual begging intensity (derived from a regression against brood size).
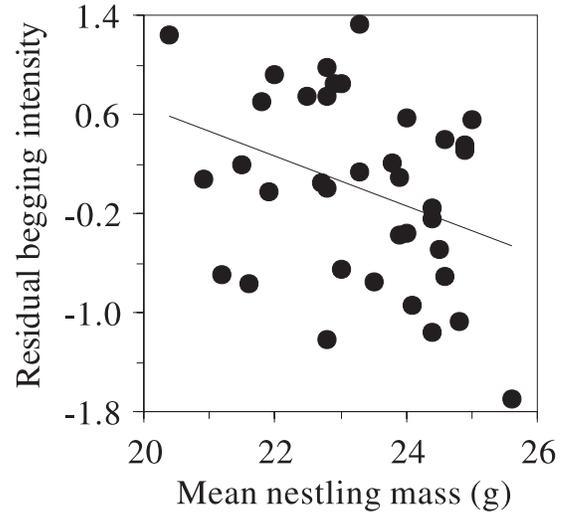

Table 2. Results of general linear models testing for relationships with ectoparasite numbers.

Response variable	Overall model		Brood-size covariate		Explanatory variable		
	R^2	P	F	P		F	P
Mass	0.13	0.05	6.1	0.02	Fleas	0.1	0.71
			6.2	0.02	Blow flies	0.0	0.84
Right-wing length	0.00				Fleas	0.0	0.96
	0.01				Blow flies	0.6	0.46
Right-tarsus length	0.01				Fleas	0.2	0.63
	0.00				Blow flies	0.0	0.85
Begging intensity	0.25	0.007	9.4	0.004	Fleas	1.0	0.32
	0.26	0.005	11.0	0.002	Blow flies	1.5	0.23
Feeding rate	0.14	0.07	5.8	0.02	Fleas	0.0	0.88
	0.23	0.01	5.9	0.02	Blow flies	3.9	0.06

Note: Explanatory variables are based on residuals; see text. P values for the overall model are the same as for the explanatory variable when there is no covariate.

Interactions among focal variables

In this study, the primary interest was in whether the negative effects of ectoparasites on growth were compensated for by increased parental feeding. Such compensation was tested for with general linear models that had a growth index as a response, brood size as a covariate, and residual fleas, residual blow flies, nestling begging intensity, and parental feeding rate as explanatory variables. First, multicollinearity was tested for among explanatory variables. Broods that begged more intensely were fed more often by their parents ($r = 0.52$, $P = 0.001$). Because of collinearity between these variables, residuals from a regression of parental feeding rate against begging intensity were used in subsequent analyses.

Variables with the lowest F values were iteratively dropped from general linear models until only significant associations remained (Alisauskas and Ankney 1994; Sorci et al. 1996). With mass as the dependent variable, only residual begging intensity was retained in final models (Fig. 3; $r = -0.34$, $P =$

0.04, $N = 37$); heavier nestlings begged less. Parasite variables and covariates were not retained in models analysing for effects on wing or tarsus length.

Discussion

No substantive evidence that ectoparasites affected tree swallow nestling growth or begging intensity was found. Moreover, we were unable to detect parental compensation in the form of increased feeding rate to nestlings with higher flea loads. Parents tended to feed nestlings more frequently if they had higher blow fly loads, but we highlight this with caution because of the number of tests conducted (Rice 1989) and because more thorough analyses failed to detect this relationship. Previous studies of other host species have found that parents increased feeding rates to nestlings with higher flea (Christe et al. 1996) and blow fly (Hurtrez-Boussès et al. 1997) loads; however, slowed nestling growth was also observed in these studies. In contrast, but consistent with the

overall results presented here, previous studies on tree swallows failed to show effects of ectoparasites on nestling growth or parental feeding rate (Rogers et al. 1991; Rendell and Verbeek 1996*a*), even though parasite loads higher than those seen in this study were observed.

One explanation for the insignificant effects is that the ectoparasite loads observed in this and in other studies (blow flies reviewed in Johnson and Albrecht 1993) are often inconsequential to nestling energy budgets. Low ectoparasite numbers could result from cleaning out nest boxes each year (Møller 1989), although empirical evidence of this is equivocal. For example, Mappes et al. 1994 found *more* fleas in cleaned nest boxes. Moreover, even if nest boxes had not been cleaned out, there are several studies that failed to detect effects of naturally occurring ectoparasite loads on avian reproductive ecology (e.g., Whitworth and Bennett 1992; Lee and Clayton 1995). This low level of virulence (the degree of harm caused) could arise for a number of reasons. First, parasites may distribute themselves in an ideal free manner (Fretwell and Lucas 1970), so that they avoid the danger of killing their host, which could compromise their transmission success (also see Dufva 1996). An ideal free strategy may be especially applicable to particularly mobile ectoparasites (Heeb et al. 1996; Rendell and Verbeek 1996*a*). Second, parasite populations are probably limited by density-dependent factors, including diseases, starvation, cannibalism, predation, etc., so that collectively they are seldom virulent. Third, hosts may influence ectoparasite density by choosing nest sites that are relatively free of ectoparasites (e.g., Brown and Brown 1996), by adding green plants that affect ectoparasite populations (Wimberger 1984; Clark 1991; but see Gwinner et al. 2000), or by other behaviours (Pacejka et al. 1996) or immune responses.

A second explanation for not observing significant effects of ectoparasitism is that weather and other conditions were benign during the year of the study, so that all nestlings were relatively free of other kinds of stress (Howe 1992; de Lope et al. 1993; Dufva and Allander 1996; Allander 1998; Ilmonen et al. 1999). During our study, from May to the end of July, precipitation totalled 74.0 mm, compared with a 38-year average of 219.4 mm for the same period. Moreover, for the same 3 months, mean daily temperatures were 3.6, 2.9, and 1.9°C warmer than the 38-year average. It is possible that these represent benign conditions, so that parents had no trouble providing more food than nestlings could assimilate (Lepczyk and Karasov 2000); in fact, several studies have found that tree swallows are capable of raising extra nestlings without apparent survival or reproductive costs (De Steven 1980; Wheelwright et al. 1991; R. Shutler and G. Clark, unpublished data). On the other hand, parents produce larger clutches when food is abundant (Hussell and Quinney 1987), and dry weather may have reduced insect numbers.

A third explanation for not detecting effects of ectoparasitism could be more efficient use of nutrients by parasitised nestlings, so that less food was lost to egesta or as heat. A related possibility is that nestlings respond to ectoparasitism by allocating more energy to growth of tissues, such as feathers, that will allow them to leave the nest (and the parasites) sooner, rather than investing in tissues associated with other functions, such as immunity (Hurtrez-Boussès

et al. 1997; Saino et al. 1998). In any case, if reallocation to specific kinds of growth occurs when nestlings are parasitised, effects on growth opposite to those predicted may occur.

Because blow fly larvae feed primarily at night (Bennett and Whitworth 1991), nestlings may be hungriest at dawn, which preceded the measurement of begging intensity in this study. Thus differences in begging intensity between nests with and without blow flies might more profitably be compared earlier in the day or by experimentally preventing feeding until such time as measurements could be taken. However, blow flies were found in only 13 of 47 nests, whereas fleas were found in 38 nests. Because of their higher prevalence, fleas may be a more important ectoparasite in the study area. Another methodological issue is that only the acoustic components of begging behaviour were measured; it is possible that visual components of the behaviour could provide more precise information about parasites, which in turn, would affect parental feeding.

If low virulence is characteristic of ectoparasite communities, demonstrating their effects may require manipulation experiments that increase their numbers (e.g., Richner et al. 1993; Christe et al. 1996). However, manipulations do not always result in higher parasite loads (Rogers et al. 1991; Merino and Potti 1998), possibly because of density-dependent ectoparasite survival and emigration. For these reasons, manipulation experiments will not be straightforward in the effects they generate. Moreover, manipulations to increase one parasite may lower the numbers of another, potentially unmeasured, parasite species. These may be some of the reasons why manipulation experiments have been no more able to detect effects of parasites than observational studies (Møller 1997).

There are some alternative hypotheses to the ones expressly tested. First, it was assumed that higher ectoparasite loads would cause more begging; however, some parasites decrease hunger (e.g., Crompton 1991) and, by association, could presumably reduce begging intensity. However, the data do not reveal a relationship between begging intensity and ectoparasite load. It is possible that increasing ectoparasite loads reduce begging intensity (via anemia and consequent weakness) at the same rate as actual nutritional needs increase, so that no relationship is detected. However, the growth indices detected no greater nutritional needs (but see above). In any case, in situations where there is an association between ectoparasite load and parental feeding rate (Christe et al. 1996; Hurtrez-Boussès et al. 1997), parents may be relying on cues other than begging intensity to decide how often to feed their young. This hypothesis requires further investigation. Second, parents may not increase feeding rates to nestlings if they themselves may become parasitised in the process; a similar hypothesis has been invoked in mate choice (Borgia 1986; Borgia and Collis 1989). However, feeding rates were not affected by parasite loads. Third, if ectoparasites increase the amount of food nestlings require to reach fledging, this would reduce fitness value of these young to parents (e.g., Forbes 1993). Because no effect of parasites on nestling growth or feeding rate was seen, the data do not permit an evaluation of this hypothesis. However, because tree swallows may only survive long enough to

breed once in their lives (Robertson et al. 1992), they might be expected to maximise their efforts regardless.

Brood size was positively related to nestling begging intensity (also see Henderson 1975; Leonard et al. 2000); this pattern could arise simply because more nestlings make more noise or because nestlings in larger broods weigh less (Cronmiller and Thompson 1980; Nur 1984; this study; R. Shutler and G. Clark, unpublished data). Both brood size and begging intensity were positively associated with parental feeding rate. Heavier nestlings might be expected to have become so from more intense begging, but we found that they begged less. Although causality cannot be ascribed, this suggests that heavier nestlings had enough nutrients for growth and thus signalled their lesser needs and hunger to the parents (Bengtsson and Ryden 1983; Godfray 1991; Granadeiro et al. 2000). However, Leonard et al. (2000; M.L. Leonard, personal communication) found that begging was still more intense in larger broods after controlling for brood size and feeding rate, suggesting that something else (e.g., the competitive social environment) also contributes to this relationship.

This study illustrates the complexity of ecological relationships between hosts and parasites. Carefully controlled manipulations are needed to evaluate these relationships, although we caution that field conditions will make it difficult to perform manipulations that provide easily interpretable results.

Acknowledgements

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