

## RESEARCH LETTERS

**Research letters** are short papers (preferably  $\leq 5$  printed pages, about 4000 words), ideally presenting new and exciting results. Letters will be given priority, whenever possible, in the publication queue. Contributions should be as concise as possible. An abstract is required.

---

JOURNAL OF AVIAN BIOLOGY 36: 269–275, 2005

# Perceived risk of ectoparasitism reduces primary reproductive investment in tree swallows *Tachycineta bicolor*

Erin L. O'Brien and Russell D. Dawson

O'Brien, E. L. and Dawson, R. D. 2005. Perceived risk of ectoparasitism reduces primary reproductive investment in tree swallows *Tachycineta bicolor*. – J. Avian Biol. 36: 269–275.

Many birds have been shown to reduce their reproductive investment in response to infestation of nest sites by ectoparasites. Nest-dwelling parasite populations increase throughout the breeding season, and can reduce the condition and future survival of both breeding adults and their offspring. Thus, avian hosts should be capable of assessing early cues that predict future ectoparasitism risk, and should be able to facultatively adjust their primary reproductive investment in response to anticipated future costs of parasites. We tested this hypothesis in the tree swallow *Tachycineta bicolor*, a cavity nesting passerine, by presenting a visual cue of avian fleas on the outer surface of nest boxes. This treatment manipulated perceived ectoparasitism risk without exposing birds to parasites, thereby allowing us to examine facultative responses in the absence of early physiological effects of parasites on female reproductive investment. During one of the study years, birds preferentially occupied control boxes, however, across both years, birds nesting in treatment boxes produced significantly smaller clutches, resulting in smaller broods at hatching, relative to those in control boxes. This difference in clutch size could not be explained by differences in phenotypic quality of breeding birds, indicating that for cavity nesting birds such as tree swallows, the perception of future ectoparasitism risk may be sufficient to induce a facultative reduction in reproductive investment early in the breeding season, before nest-dwelling parasite populations have grown very large.

*E. L. O'Brien (correspondence) and R. D. Dawson, Ecosystem Science and Management Program, University of Northern British Columbia, 3333 University Way, Prince George BC, V2N 4Z9 Canada. E-mail: obriene@unbc.ca*

Nest-dwelling haematophagous ectoparasites have been shown to reduce both reproductive success and condition of breeding birds (Brown et al. 1995, Saino et al. 2002, Nilsson 2003), particularly cavity nesting species (e.g. Oppliger et al. 1994, Fitze et al. 2004). Consequently, many birds exhibit parasite-induced behavioural responses, adjusting timing of breeding (Oppliger et al. 1994), clutch size (Moss and Camin 1970, Heeb et al. 1998), or nestling provisioning rates

(Tripet and Richner 1997) in response to infestation of nest sites by ectoparasites. However, many of these responses require reproductive decisions to be made early in the breeding season, before ectoparasite populations have grown very large. Avian hosts are therefore expected to exhibit such responses when, at the onset of breeding, the parasite load of the nest after hatching can be predicted (Johnson and Albrecht 1993, Richner and Heeb 1995).

The most reliable predictor of future ectoparasite load is the presence of parasites in the nest at the beginning of the breeding season. Many female birds respond to early parasite exposure by producing smaller clutches (Fitze et al. 2004), or smaller broods at hatching (Oppliger et al. 1994) relative to unexposed females. This reduction in reproductive investment may be a strategic response by females to expected costs of ectoparasitism later in the nesting period, and the associated reduction in perceived reproductive value of offspring produced in infested nest sites (Johnson and Albrecht 1993). Alternatively, this response may be a direct consequence of early physiological effects of parasites on females, such as reduced body condition or activation of immune defenses (Tschirren et al. 2004). However, previous studies have been unable to distinguish between these mechanisms, since experimental manipulations have typically involved physical exposure of birds to live parasites and the physiological effects thereof. Consequently, the extent to which cavity nesting birds are able to strategically adjust their primary reproductive investment in response to perceived risk of ectoparasitism is not known.

In this study, we investigated whether tree swallows *Tachycineta bicolor*, a cavity nesting passerine, facultatively reduce their primary reproductive investment in response to a high perceived probability of ectoparasitism by avian fleas *Ceratophyllus idius* during the incubation and nestling periods. Fleas are common nest-dwelling parasites of tree swallows (Robertson et al. 1992). Studies of other avian hosts have shown that fleas may affect nestling characteristics (Richner et al. 1993, Nilsson 2003), as well as adult female condition or survival (Brown et al. 1995, Christe et al. 1996, Richner and Tripet 1999), although the effects of fleas on tree swallows remain unclear (Thomas and Shutler 2001, Shutler et al. 2004). We used a visual cue to manipulate perceived ectoparasite risk in nest boxes, without simultaneously exposing females to live parasites; this approach allowed us to examine facultative responses independent from physiological effects of parasites on female reproductive output. We discuss our results in the context of host-parasite co-evolution and the adaptive significance of clutch size variation in cavity nesting passerines.

## Materials and methods

### Study area and species

We studied two populations of tree swallows located near Prince George (53°N, 122°W), B.C., Canada, during the 2003 and 2004 breeding seasons. Each population was studied during one of the two study years. The study sites are characterized by pasture and wetlands surrounded by second-growth forest of

various ages. Birds nest in artificial boxes that are mounted 1.5 m above the ground on fence posts. Nesting material is removed from boxes at the conclusion of each breeding season. Tree swallows have been intensively studied at both sites since 2001. The sites are separated by at least 40 km, and we assume the populations are independent since birds from one site have never been recaptured at the other site in subsequent breeding seasons.

### Experimental procedure

As a dispersal mechanism, newly emerged avian fleas *Ceratophyllus* spp. aggregate on the outside of nest cavities to seek out hosts (Humphries 1968). This may serve as a visual indicator of both current and future ectoparasite load of potential nest sites, since it may signal the presence of additional adult fleas in the nest cavity (Harper et al. 1992) as well as developing eggs or larvae. Thus, to manipulate perceived ectoparasite load we mimicked this dispersal behaviour by affixing 20 dead fleas to the outside of experimental nest boxes, beside the entrance hole. This visual display approximated natural flea aggregations previously observed on boxes at both study sites. The fleas used in this manipulation had been removed from heat-treated nests collected in the previous breeding season, from the same study areas. The use of dead fleas ensured that experimental boxes exhibited an appropriate visual cue without simultaneously influencing the parasite load, and thus condition, of resident birds. We attached fleas to a 6 × 10 cm piece of white, waterproof paper using spray-on adhesive; this ensured visual detection of fleas by birds inspecting experimental nest boxes. Control boxes had paper coated with adhesive attached in the same position beside the nest box entrance. Papers were affixed to nest boxes at the beginning of the breeding season, and left for the duration of the nesting period. Experimental and control conditions were alternately assigned to groups of four nest boxes, distributed throughout each study area. In the 2003 population, this included 24 treatment and 25 control boxes. The 2004 population consisted of 40 treatment and 43 control boxes. Nest boxes were not treated to eliminate living parasites.

We monitored nest boxes throughout the breeding season to determine occupancy, date of clutch initiation, clutch size, brood size at hatching and number of chicks fledged. Once clutches were completed, eggs were individually weighed to the nearest 0.01 g with an electronic scale (Ohaus Scout II, Model 2020, Pine Brook NJ) to determine average and total egg mass. Adult birds were captured in nest boxes using a swing-door trap once hatching was complete. We measured body mass (nearest 0.25 g) with a spring balance. Linear measures of body size, including lengths of the right

wing, right ninth primary feather, and tail, were determined to the nearest 0.5 mm using a ruler. To obtain a single measure of body size, we then entered these measurements into a principal component analysis; the first principle component (PC1) was used in all subsequent analyses of adult body size. Female birds were aged as either second year (SY), or after second year (ASY), based on plumage characteristics (Hussell 1983).

To estimate nestling growth rates, we measured chick mass (nearest 0.125 g using a spring balance) and length of ninth primary (nearest 0.5 mm) every two days, from post-hatching day four until day 16. We selected appropriate growth models for body mass and ninth primary using the methods reported by Dawson and Bidwell (2005). We applied the logistic model to describe growth rates of mass, and a linear model for growth of ninth primary. Individual curves were estimated for each nestling within a brood, and the averages of these growth rates were used in subsequent comparisons among broods. To determine growth rates of mass, we used all measurements taken from ages four to 16 days. Since ninth primary feathers of most nestlings do not begin to grow until after six days of age, we determined ninth primary growth rates from day eight to day 16. Structural size (length of ninth primary) and body mass at day 16 were used as estimates of fledging size and mass of chicks.

## Statistical analysis

If our nest site treatment increased perceived risk of ectoparasitism, tree swallows may be expected to preferentially settle in control boxes in addition to reducing reproductive investment in treatment boxes. To test this hypothesis, we used the likelihood ratio test to compare proportions of control and experimental boxes that were occupied by breeding birds. To assess primary reproductive investment, we tested the effect of nest site treatment on clutch size, brood size at hatching, and average egg mass of control and experimental nests using analysis of covariance (ANCOVA). Since female age and clutch initiation date are known to influence clutch size in tree swallows (Robertson et al. 1992), and to account for possible year or site effects between 2003 and 2004, we included in the analysis female age and year (site) as fixed factors, and clutch initiation date as a covariate, in addition to the nest site treatment.

To examine possible differences in female or male quality that may have accounted for differences in reproductive investment, we used ANCOVA to assess differences in clutch initiation date, body mass and size of resident females, mass and size of their social mates, average nestling growth rates, fledging success (number of chicks fledged), and body mass and size of chicks at

fledging. We included nest site treatment and year (site) as fixed factors in all initial models. In the analyses of female phenotype, we also included female age as a fixed factor, and included initial brood size as a covariate in addition to female age in the analyses of nestling characteristics and number fledged. Effects of factors, covariates and all first-order interactions were initially tested in all ANCOVA models. Variables that did not approach significance ( $P > 0.10$ ) were then removed by a stepwise backward procedure. Fledging success was only determined for nests from which at least one young fledged. We also used contingency tables to test whether sub-adult (SY) females were more likely to settle in treatment boxes than older (ASY) females, and whether birds occupying treatment boxes were less likely to fledge at least one young than those nesting in control boxes.

In the 2003 population, three nest sites (all treatment boxes) were reoccupied by the same female as in a previous breeding season. Since in these cases females may have made investment decisions according to prior knowledge of the nest site, and less in response to our manipulation during the current breeding season, we conducted all analyses both including and excluding these data. Statistical analyses were performed using SPSS (Norusis 1993), with a significance level of 0.05. Means are presented  $\pm 1$  SE.

## Results

In the 2003 population, the visual cue of parasites on the outside of nest boxes reduced the probability of settlement, with eight out of 22 treatment boxes occupied by breeding pairs, compared to 16 out of 24 control boxes ( $G = 4.21$ ,  $df = 1$ ,  $P = 0.04$ ). However, no settlement bias was detected when the three reoccupied boxes were included in the analysis ( $G = 2.57$ ,  $df = 1$ ,  $P = 0.11$ ). No settlement bias was observed in the 2004 population: 21 out of 40 treatment boxes were occupied, compared to 16 of 43 control boxes ( $G = 1.97$ ,  $df = 1$ ,  $P = 0.20$ ).

Table 1. Comparison of primary reproductive investment of female tree swallows nesting in treatment boxes (displaying fleas), and in control boxes.

Variable	Nest site manipulation	
	Control	Treatment
Average egg mass (g)		
2003	1.79 $\pm$ 0.03 (n = 13)	1.79 $\pm$ 0.03 (n = 8)
2004	1.67 $\pm$ 0.03 (n = 16)	1.74 $\pm$ 0.03 (n = 21)
Clutch size**	6.2 $\pm$ 0.1 (n = 32)	5.7 $\pm$ 0.2 (n = 29)
Brood size at hatching*	5.7 $\pm$ 0.2 (n = 27)	5.1 $\pm$ 0.2 (n = 24)

Note: Means ( $\pm 1$  SE) are presented. \*  $P < 0.05$ , \*\* $P < 0.01$ .

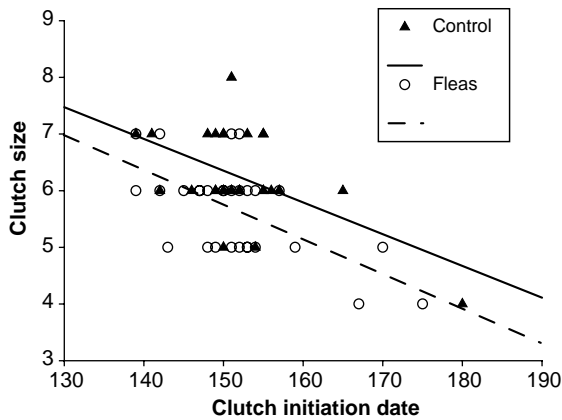


Fig. 1. Effect of clutch initiation date (1 = 1 January) and nest site treatment (visual presentation of fleas on nest boxes) on clutch size in tree swallows. Regression lines describe the decline in clutch size with initiation date for treatment ("fleas") and control nests. Each data point represents one nest. Data from the 2003 and 2004 populations are combined since site (year) was not a significant factor in the ANCOVA model. Some data points have identical values.

In all subsequent analyses, results using data from the three reoccupied boxes (see Materials and methods) did not differ from those where these data were excluded; we therefore present results only from those tests where these nests are excluded from the data set. Average egg mass differed between study years ( $F_{1,55} = 7.40$ ,  $P < 0.01$ ), but was not influenced by the nest site treatment ( $F_{1,55} = 1.90$ ,  $P = 0.17$ ; Table 1). However, both the nest site treatment and clutch initiation date were significant predictors of clutch size (treatment:  $F_{1,56} = 4.34$ ,  $P < 0.01$ ; Table 1; initiation date:  $F_{1,56} = 12.52$ ,  $P < 0.001$ ; Fig. 1), explaining 40% of the variation in clutch size across both study sites. Thus, although females initiating clutches later in the breeding season laid fewer eggs, birds nesting in treatment boxes produced smaller clutches than those in control boxes across all initiation dates (Fig. 1). No additional variation in clutch size was explained by female age or year (site). As with clutch size, brood size at hatching was smaller in treatment boxes (treatment:  $F_{1,46} = 6.36$ ,

Table 2. Comparison of clutch initiation date (1 = 1 January) and phenotypic characteristics of adult tree swallows nesting in treatment boxes (displaying fleas), and in control boxes.

Variable	Nest site manipulation	
	Control	Treatment
Clutch initiation date	152.1 ± 1.3 (n = 30)	151.5 ± 1.5 (n = 29)
Female mass (g)	19.8 ± 0.3 (n = 30)	19.3 ± 0.3 (n = 27)
Male mass (g)	19.6 ± 0.2 (n = 27)	19.9 ± 0.2 (n = 27)
Female PC1 size	0.098 ± 0.2 (n = 29)	-0.13 ± 0.2 (n = 26)
Male PC1 size	0.060 ± 0.19 (n = 28)	0.051 ± 0.16 (n = 26)

Note: Means (±1 SE) are presented. Differences between treatments did not approach significance (all P values > 0.05).

$P = 0.02$ ; Table 1), as well as in nests that were initiated later in the breeding season (initiation date:  $F_{1,46} = 6.67$ ,  $P = 0.01$ ).

Age distribution of females in treatment and control boxes did not differ (control: 18/31 ASY, treatment: 16/30 ASY;  $\chi^2 = 0.14$ ,  $df = 1$ ,  $P = 0.71$ ). Thus, although older (ASY) females initiated clutches earlier than sub-adult (SY) females ( $F_{1,53} = 13.93$ ,  $P < 0.001$ ), clutch initiation date did not differ between nest site treatments ( $F_{1,53} = 0.43$ ,  $P = 0.51$ ; Table 2). In addition, ASY females were significantly larger than SY females ( $F_{1,51} = 11.35$ ,  $P < 0.01$ ), however there was no difference in size of females occupying treatment and control boxes ( $F_{1,51} = 0.16$ ,  $P = 0.69$ ; Table 2). Similarly, female body mass did not differ between nest site treatment groups ( $F_{1,55} = 1.96$ ,  $P = 0.17$ ; Table 2), nor did we detect differences in male phenotype with nest site treatment (male size:  $F_{1,52} = 0.001$ ,  $P = 0.97$ ; male mass:  $F_{1,52} = 1.11$ ,  $P = 0.30$ ; Table 2).

Nestling growth rates did not differ between treatment and control groups (growth of mass:  $F_{1,43} = 0.002$ ,  $P = 0.97$ ; growth of ninth:  $F_{1,51} = 0.04$ ,  $P = 0.83$ ; Table 3). Results for length of the ninth primary at 16 days similarly showed no effect of nest site treatment ( $F_{1,43} = 0.01$ ,  $P = 0.92$ ; Table 3). However, length of ninth primaries differed between study years ( $F_{1,43} = 52.11$ ,  $P < 0.001$ ), and nestlings produced by ASY females had significantly longer ninth primaries than those of SY females ( $F_{1,43} = 4.84$ ,  $P = 0.03$ ). Brood size at hatching predicted nestling mass at 16 days ( $F_{1,39} = 4.63$ ,  $P = 0.04$ ), but nest site treatment was not significant ( $F_{1,39} = 0.04$ ,  $P = 0.85$ ; Table 3). Among nests that fledged at least one young, the number fledged increased with brood size at hatching ( $F_{1,34} = 9.52$ ,  $P < 0.01$ ) and female age ( $F_{1,34} = 4.89$ ,  $P = 0.03$ ), but did not differ between treatment and control boxes ( $F_{1,34} = 1.64$ ,  $P = 0.21$ ; Table 3). There was no difference between treatment and control groups in the probability that

Table 3. Comparison of tree swallow nestling growth, size and fledging success in treatment boxes (displaying fleas), and in control boxes.

Variable	Nest site manipulation	
	Control	Treatment
Mass growth rate	0.58 ± 0.03 (n = 27)	0.58 ± 0.02 (n = 25)
Ninth primary feather growth rate	4.23 ± 0.09 (n = 28)	4.26 ± 0.13 (n = 25)
Length of ninth primary at 16 days		
2003 (mm)	36.2 ± 1.9 (n = 11)	32.8 ± 4.1 (n = 4)
2004 (mm)	46.2 ± 1.0 (n = 13)	47.9 ± 1.1 (n = 20)
Nestling mass at 16 days (g)	19.7 ± 0.4 (n = 24)	20.2 ± 0.4 (n = 24)
Number of chicks fledged	4.43 ± 0.23 (n = 23)	4.43 ± 0.33 (n = 21)

Note: Means (±1 SE) are presented. Differences between treatments did not approach significance (all P values > 0.05).

nests would fledge at least one young ( $\chi^2 = 0.02$ ,  $df = 1$ ,  $P = 0.89$ ).

## Discussion

The presence of avian fleas on nest boxes reduced female reproductive investment, with birds in treatment boxes producing smaller clutches than those in control boxes across all clutch initiation dates. Cavity nesting birds have been shown to reduce clutch size when physically exposed to ectoparasites (Moss and Camin 1970, Heeb et al. 1998). However, in the present study a similar response was observed in birds that had only been exposed to a visual cue indicating a high probability of future ectoparasitism. This supports the hypothesis that the detection of parasites at a nest site is sufficient to induce cavity nesting birds to facultatively reduce their primary reproductive investment, even in the absence of physical exposure to parasites.

The feeding activities of ectoparasites tend to increase resting metabolic rate of nestlings (Nilsson 2003), thereby reducing the size or condition of chicks at fledging (e.g. Richner et al. 1993, Nilsson 2003). Since nestling size commonly predicts survival to the next breeding season (Tinbergen and Boerlijst 1990), chicks produced in nests that have a high probability of current or future ectoparasite infestation would be less likely to survive to breeding age and, thus, would be of lower reproductive value relative to chicks produced in uninfested nests. In addition, nest-dwelling parasites may have direct impacts on female health (Christe et al. 1996) and long-term survival (Brown et al. 1995, Richner and Tripet 1999), and these effects would also reduce the reproductive value of offspring produced in infested nests, since investment in such offspring may reduce future reproductive output of females. Birds occupying infested nest sites may therefore be predicted to reduce their current reproductive effort in favour of future breeding opportunities. Our finding that female tree swallows produce smaller clutches (and therefore smaller broods at hatching) when the probability of future ectoparasitism is high supports this prediction.

By adjusting initial brood size, birds may be capable of indirectly influencing future parasite load of their nests. Larger broods are commonly associated with higher per capita parasite loads (Saino et al. 2002, Shutler et al. 2004, but see Richner et al. 1993). This may be a consequence of reduced cellular immunity of nestlings in large broods (Saino et al. 2002), mediated by nutritional stress and the associated production of glucocorticosteroids (Saino et al. 2003, Franchimont 2004). Parasite population growth under these conditions would be enhanced due to the relative inability of nestlings to express anti-parasite immune defenses. In addition,

developmental rate of ectoparasites such as fleas is influenced by microclimate conditions in the nest, particularly temperature and humidity (Cotton 1970), and crowding of nestlings in large broods has been suggested to create a microhabitat that may be more favourable for parasite growth and reproduction (Saino et al. 2002). Thus, reduced reproductive investment (i.e. reduced brood size) of cavity nesting birds in response to a high perceived risk of ectoparasitism, as demonstrated in this study, may have the additional consequence of minimizing the potential growth of parasite populations in the nest.

At the beginning of the breeding season, both male and female tree swallows compete aggressively for access to nest sites (Leffelaar and Robertson 1985, Rendell and Robertson 1989), and this competition may ensure that higher-quality birds are able to occupy the best sites. Our nest site treatment was intended to influence the perception of future parasitism risk, and hence perceived quality of potential nest sites. It could therefore be argued that higher-quality birds would disproportionately occupy control boxes, and that the observed difference in clutch size in our study was the result of differences in quality of birds nesting in treatment and control boxes. In tree swallows, older females or those in better condition tend to initiate clutches earlier than either second-year females or those in poorer condition (Stutchbury and Robertson 1988, Robertson and Rendell 2001). In this study, neither female age nor clutch initiation date (Table 2) differed between treatment and control nests. Comparisons of body size and mass of breeding birds similarly showed that quality or condition of birds nesting in treatment boxes did not differ from those in control boxes (Table 2). In addition to these comparisons of parental phenotype, analysis of nestling growth rates, as well as size and mass at fledging, indicated no difference in offspring quality (Table 3). Finally, despite the initial difference in brood size at hatching, birds nesting in treatment boxes were able to fledge as many young as those in control boxes (Table 3). Tree swallows may also adjust clutch size according to phenotypic characteristics other than those we measured, such as individual foraging efficiency (Burness et al. 2001), and it is therefore possible that the observed difference in clutch size in this study reflected phenotypic differences that we were unable to detect. However, any such phenotypic difference underlying variation in clutch size should also be manifested in differential reproductive success; since birds in control boxes did not produce more offspring, nor were their offspring larger or heavier than those of birds occupying treatment boxes, it is unlikely the observed difference in clutch size was due to differences in quality of breeding birds. Moreover, the lack of a treatment effect on number of fledglings produced, despite the initial difference in brood size, suggests that birds in treatment

boxes may have been capable of subsequently increasing their investment in nestlings when they did not experience the high flea loads anticipated in treatment nest boxes.

In addition to altering their investment in clutch size, birds in the 2003 population were more likely to settle in control boxes, suggesting they avoided nest sites with a high perceived risk of ectoparasitism. However, no settlement bias was observed in the 2004 population. Reasons for this discrepancy are not clear, and require additional investigation. Further, control boxes were not consistently occupied earlier than treatment boxes at either site, suggesting other factors may have also influenced nest site selection. In tree swallows, nest site choice is strongly limited by intraspecific competition (Leffelaar and Robertson 1985, Rendell and Robertson 1989, Rendell 1993), and in returning adults or recruiting juveniles, may be influenced by previous knowledge of the breeding area (Shutler and Clark 2003). Thus, the influence of our nest site manipulation on settlement patterns at both sites was probably minimal, and appeared to be a more important determinant of primary reproductive investment by birds once they had established a nesting territory.

Whereas many studies have examined the effects of ectoparasites on their avian hosts and the responses of birds to experimental infestation, the mechanisms by which parasites influence host reproductive investment have received less attention. Physical exposure to parasites has direct impacts on breeding birds, and these effects may in turn influence reproductive investment. For example, stimulation of maternal antibody production by parasite exposure enhances the transfer of maternal immunoglobulins to chicks via the egg (Buechler et al. 2002). Strategic adjustments to initial reproductive investment such as reductions in clutch size, however, may be a response to anticipated effects of parasites over the nesting period (Johnson and Albrecht 1993), and may therefore be less dependent on immediate physiological effects of parasite exposure. While continued physical exposure to parasites throughout the nesting period is arguably necessary to influence parental behaviours expressed after clutch formation, such as incubation behaviour and nestling feeding rates, results of this study suggest that in cavity nesting birds, the perception of future ectoparasitism risk may be sufficient to induce a facultative reduction in reproductive investment early in the breeding season, before nest-dwelling parasite populations have grown very large.

*Acknowledgements* – We thank D. Baxter, P.-P. Bitton and B. Schonewille for assistance in the field, and A. and P. Castle, G. and G. Sanders and D. and K. Steward for allowing us access to their properties. Comments by J. Williams and two anonymous referees greatly improved the manuscript. Funding for this research was provided by the Natural Sciences and Engineering Research Council of Canada through a Discovery

Grant to R.D.D. Additional support was provided by the Canada Foundation for Innovation and the British Columbia Knowledge Development Fund.

## References

- Brown, C. R., Brown, M. B. and Rannala, B. 1995. Ectoparasites reduce long-term survival of their avian host. – *Proc. R. Soc. Lond B* 262: 313–319.
- Buechler, K., Fitze, P. S., Gottstein, B., Jacot, A. and Richner, H. 2002. Parasite-induced maternal response in a natural bird population. – *J. Anim. Ecol.* 71: 247–252.
- Burness, G. P., Ydenberg, R. C. and Hochachka, P. W. 2001. Physiological and biochemical correlates of brood size and energy expenditure in tree swallows. – *J. Exp. Biol.* 204: 1491–1501.
- Christe, P., Richner, H. and Oppliger, A. 1996. Of great tits and fleas: sleep baby sleep . . . – *Anim. Behav.* 52: 1087–1092.
- Cotton, M. J. 1970. The life history of the hen flea, *Ceratophyllus gallinae* (Schrank) (Siphonaptera, Ceratophyllidae). – *Entomologist* 103: 45–48.
- Dawson, R. D. and Bidwell, M. 2005. Dietary calcium limits size and growth of nestling tree swallows *Tachycineta bicolor* in a non-acidified landscape. – *J. Avian Biol.* 36: 127–134.
- Fitze, P. S., Tschirren, B. and Richner, H. 2004. Life history and fitness consequences of ectoparasites. – *J. Anim. Ecol.* 73: 216–226.
- Franchimont, D. 2004. Overview of the actions of glucocorticoids on the immune response: a good model to characterize new pathways of immunosuppression for new treatment strategies. – *Ann. N.Y. Acad. Sci.* 1024: 124–137.
- Harper, G. H., Marchant, A. and Boddington, D. G. 1992. The ecology of the hen flea *Ceratophyllus gallinae* and the moorhen flea *Dasypsyllus gallinulae* in nestboxes. – *J. Anim. Ecol.* 61: 317–327.
- Heeb, P., Werner, I., Kölliker, M. and Richner, H. 1998. Benefits of induced host responses against an ectoparasite. – *Proc. R. Soc. Lond B* 265: 51–56.
- Humphries, D. A. 1968. The host-finding behaviour of the hen flea, *Ceratophyllus gallinae* (Schrank) (Siphonaptera). – *Parasitology* 58: 403–414.
- Hussell, D. J. T. 1983. Age and plumage colour in female tree swallows. – *J. Field Ornithol.* 54: 312–318.
- Johnson, L. S. and Albrecht, D. J. 1993. Effects of haematophagous ectoparasites on nestling house wrens, *Troglodytes aedon*: who pays the cost of parasitism? – *Oikos* 66: 255–262.
- Leffelaar, D. and Robertson, R. J. 1985. Nest usurpation and female competition for breeding opportunities by tree swallows. – *Wilson Bull.* 97: 221–224.
- Moss, W. W. and Camin, J. H. 1970. Nest parasitism, productivity, and clutch size in purple martins. – *Science* 168: 1000–1003.
- Nilsson, J.-Å. 2003. Ectoparasitism in marsh tits: costs and functional explanations. – *Behav. Ecol.* 14: 175–181.
- Norusis, M. J. 1993. SPSS for Windows advanced statistics release 6.0. – SPSS, Inc., Chicago, IL.
- Oppliger, A., Richner, H. and Christe, P. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the great tit. – *Behav. Ecol.* 5: 130–134.
- Rendell, W. B. 1993. Intraspecific killing observed in tree swallows, *Tachycineta bicolor*. – *Can. Field Nat.* 107: 227–228.
- Rendell, W. B. and Robertson, R. J. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. – *Condor* 91: 875–885.

- Richner, H. and Heeb, P. 1995. Are clutch and brood size patterns in birds shaped by ectoparasites? – *Oikos* 73: 435–441.
- Richner, H. and Tripet, F. 1999. Ectoparasitism and the trade-off between current and future reproduction. – *Oikos* 86: 535–538.
- Richner, H., Oppliger, A. and Christe, P. 1993. Effect of an ectoparasite on reproduction in great tits. – *J. Anim. Ecol.* 62: 703–710.
- Robertson, R. J. and Rendell, W. B. 2001. A long-term study of reproductive performance in tree swallows: the influence of age and senescence on output. – *J. Anim. Ecol.* 70: 1014–1031.
- Robertson, R. J., Stutchbury, B. J. and Cohen, R. R. 1992. Tree swallow. – In: Poole, A., Stettenheim, P. and Gill, F. (eds). *Birds of North America*, no. 11. American Ornithologists' Union, Washington, D.C. and Academy of Natural Sciences, Philadelphia.
- Saino, N., Ferrari, R. P., Romano, M., Ambrosini, R. and Møller, A. P. 2002. Ectoparasites and reproductive trade-offs in the barn swallow (*Hirundo rustica*). – *Oecologia* 133: 139–145.
- Saino, N., Suffritti, C., Martinelli, R., Rubolini, D. and Møller, A. P. 2003. Immune response covaries with corticosterone plasma levels under experimentally stressful conditions in nestling barn swallows (*Hirundo rustica*). – *Behav. Ecol.* 14: 318–325.
- Shutler, D. and Clark, R. G. 2003. Causes and consequences of tree swallow (*Tachycineta bicolor*) dispersal in Saskatchewan. – *Auk* 120: 619–631.
- Shutler, D., Mullie, A. and Clark, R. G. 2004. Tree swallow reproductive investment, stress, and parasites. – *Can. J. Zool.* 82: 442–448.
- Stutchbury, B. J. and Robertson, R. J. 1988. Within-season and age-related patterns of reproductive performance in female tree swallows (*Tachycineta bicolor*). – *Can. J. Zool.* 66: 827–834.
- Thomas, K. and Shutler, D. 2001. Ectoparasites, nestling growth, parental feeding rates, and begging intensity of tree swallows. – *Can. J. Zool.* 79: 346–353.
- Tinbergen, J. M. and Boerlijst, M. C. 1990. Nestling weight and survival in individual great tits (*Parus major*). – *J. Anim. Ecol.* 59: 1113–1127.
- Tripet, F. and Richner, H. 1997. Host responses to ectoparasites: food compensation by parent blue tits. – *Oikos* 78: 557–561.
- Tschirren, B., Richner, H. and Schwabl, H. 2004. Ectoparasite-modulated deposition of maternal androgens in great tit eggs. – *Proc. R. Soc. Lond B* 271: 1371–1375.

(Received 25 October 2004, revised 2 February 2005, accepted 12 March 2005.)