

Chick parasitism by blowflies affects feeding rates in a Mediterranean population of blue tits

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Abstract

Offspring fitness depends on interactions between parental care and environmental constraints. It has been suggested that in altricial birds parents are able to compensate for the detrimental effects of ectoparasites by improving food provisioning. We tested this prediction in a population of blue tits highly parasitized by blowfly larvae. The frequency of parental feeding visits was significantly higher in parasitized broods than in broods experimentally deparasitized. Despite a strong increase in parental care, chicks of parasitized broods were lighter, smaller, and more anaemic than chicks in deparasitized broods. Parents invest more in feeding parasitized young but cannot fully compensate for the negative effects of parasites, hence young are in poor condition at fledging.

Keywords

Blowfly, blue tit, Corsica, feeding rate, parasitism.

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INTRODUCTION

In altricial birds, parents often expend a considerable amount of time and energy in feeding young. The quantity and quality of food provisioning influence the condition at fledging (e.g. van Balen 1973), which governs post fledging survival and recruitment rates in the population (e.g. Tinbergen & Boerlijst 1990). The nestlings condition depends not only on food provisioning, but also on its interactions with other environmental constraints such as parasitism (e.g. Møller 1997). As suggested by Christe *et al.* (1996), the detrimental effects of parasitism may be enhanced if parasitized chicks beg less for food or if parents do not invest in rearing young already doomed by parasitism, and detrimental effects of parasitism may be lowered if parents of parasitized chicks increase food provisioning.

For parasites that attack both chicks and parents (e.g. fleas, mites), direct effects of parasites on parents may affect their ability to rear young. Parasites that attack only chicks allow the study of changes in parental investment in food provisioning, without the confounding factor of parasite load on adults. The free-living blowflies of the genus *Protocalliphora* have haematophagous larvae that are ectoparasites of nestling birds (Bennett 1957). The three larval stages feed intermittently on chicks and do not attack the adults (S. Hurtrez-Boussès, personal observation). Although most of the studies on these parasites are non experimental, it seems that they have little or no effect

on chick condition and survival (reviewed in Johnson & Albrecht 1993; Hurtrez-Boussès 1996). Johnson & Albrecht (1993) suggested that, by increasing their feeding rate, parents of parasitized chicks compensate (at least partially) for the negative effects of blowfly larvae, but this hypothesis has never been tested experimentally.

A Corsican population of blue tits (*Parus caeruleus*) suffers the highest infestation rates by blowflies so far recorded in Europe: prevalences are higher than 90% and mean intensity is about 10 larvae per chick (Hurtrez-Boussès 1996; Hurtrez-Boussès *et al.* 1997a). Blondel (1985) suggested that, in this population, parasitic constraints due to blowflies might have influenced the differentiation of life history traits: as compared with those in populations on the nearby mainland, clutch size is reduced by $\approx 30\%$ and laying date is delayed by ≈ 3 weeks.

The aim of this study was to assess whether blue tit parents could compensate for the effects of blowflies. We tested the effects of parasitism on feeding frequency and on the condition of young at fledging by comparing control broods (naturally parasitized by blowfly larvae) and treated broods (deparasitized). The following predictions were made: (i) if parents do not compensate for the effects of blowfly larvae, feeding rates would not differ between treated and control broods and nestling condition would be higher in treated broods; (ii) if parents fully compensate, feeding rates would be higher in parasitized broods and nestling condition would not be affected by parasitism; (iii) if parents partially compensate, we would

expected higher feeding rates but lower nestlings condition in the control broods than in the treated broods.

MATERIALS AND METHODS

Study site and study species

The study was carried out in 1996, in a site located in Corsica (near Calvi, France), in a forest of holm oak (*Quercus ilex*) (Blondel *et al.* 1987), in which 145 nest-boxes are available for breeding tits.

The hatching of blue tits occurs at the end of May and the nestling stage lasts ≈ 20 days. Both males and females feed young. The diet mainly consists of caterpillars, spiders, and grasshoppers (Banbura *et al.* 1994). The main ectoparasites of nestlings are blowfly larvae (*Protocalliphora* spp.). The presence of other ectoparasites (fleas, lice, mites) is extremely scarce (prevalences $< 3\%$). Therefore, we only took into account the effects of blowflies.

Breeding parameters, feeding rates, and condition of chicks

From the beginning of the breeding season, each nest-box was visited at least once a week.

When chicks were 9 days old, we equipped the hole entrance of the nest-box with a photoelectric cell, connected to a counter, for 3 days. The reliability of this system for measuring feeding rates was confirmed by comparing the records with those obtained with direct observations and with a video camera (Perret, unpublished data). Each evening (after 9 h PM), we recorded the total number of visits and reinitialized the recorder. Feeding rates were thus recorded during two complete days (ages 10 and 11).

For each 15-day-old chick, we measured the body mass (to the nearest 0.1 g), the tarsus length (to the nearest 0.01 mm), and the haematocrit (proportion of the volume of red blood cells in the blood total sample; see Richner *et al.* 1993 for the method).

Experimental procedure and determination of the blowfly load

In order to test the effects of blowfly larvae on feeding rates and on nestling condition, we randomly chose 12 of the 26 broods and treated them as follows (method modified after Richner *et al.* 1993): when chicks were 2, 5, 7, 9, 12, and 15 days old, we replaced the nest by another nest of the same size, in which blowfly larvae were previously killed with microwave treatment (1 min at 850 W). The other broods were kept as controls, i.e. they were naturally parasitized. Chicks of both treated and control

broods were systematically weighed, for another study, at 2, 5, 7, 9, 12, and 15 days (during the removal of the nest for treated broods), so that the duration of manipulation did not differ between the groups. The two groups did not differ in hatching date ($F_{1,24} = 0.06$, not significant), in brood size at hatching ($F_{1,24} = 0.15$, not significant), or in brood size at 11 days ($F_{1,24} = 0.02$, not significant). After fledging, the nest was collected and stored into a plastic bag. In the laboratory, each nest was checked in order to assess the presence of ectoparasites and to record the total blowfly load (number of larvae, pupae, and pupal cases, hereafter called parasite load).

Statistical analyses

Feeding frequencies were highly repeatable between day 10 and day 11 (repeatability calculated according to Lessells & Boag 1987: $r = 0.88$, $F_{25,26} = 15.09$, $P < 0.0005$). We used the average of data from day 10 and day 11 in our analyses. To avoid pseudoreplication, we considered the brood as the statistical unit. We tested the effects of status (treated vs. control) on mean feeding rate (number of visits/h/chick), mean body mass, mean tarsus length, and mean haematocrit value as dependent variables, using a MANOVA (Scheiner 1993). We controlled for the effects of brood size and for the interaction between status and brood size. Mean feeding rate values were log-transformed. This analysis was performed with the SAS computer program.

The other analyses were performed with the GLIM computer program (NAG 1986), using a Poisson model, which is more appropriated than linear regression for "count data" (number of parasites, number of feeding visits) (see Crawley 1993 for further details).

RESULTS

Infestation rates

None of the 14 control broods was free of parasites (prevalence 100%). The mean parasite load was significantly different between the two groups (treated, 0.08 ± 0.17 SD; control, 14.5 ± 3.7 SD; $\chi^2_1 = 30.0$, $P < 0.001$).

Effects of treatment

All the dependent variables were affected by the treatment (MANOVA Pillai's Trace $F_{4,12} = 20.35$, $P < 0.0001$). The number of visits per chick and per hour was significantly higher in the control group (7.4 ± 2.7 SD) than in the treated one (4.5 ± 1.5 SD; $F_{1,15} = 14.11$, $P < 0.002$). As compared with those of control broods, at 15 days, chicks of treated broods had significantly higher

body mass (control, $9.0 \text{ g} \pm 0.80 \text{ SD}$; treated, $9.7 \text{ g} \pm 0.79 \text{ SD}$; $F_{1,15} = 5.95$, $P < 0.03$), tarsus length (control: $15.93 \text{ mm} \pm 0.35 \text{ SD}$; treated, $16.32 \text{ mm} \pm 0.39 \text{ SD}$; $F_{1,15} = 7.66$, $P < 0.02$), and haematocrit value (control, $40.9\% \pm 6.1 \text{ SD}$; treated, $51.4\% \pm 4.8 \text{ SD}$; $F_{1,15} = 37.39$, $P < 0.0001$). None of the dependent variables was affected by brood size (MANOVA Pillai's Trace $F_{34,76} = 1.46$, not significant) or by the interaction between treatment and brood size (MANOVA Pillai's Trace $F_{9,25} = 0.99$, not significant).

DISCUSSION

Our results experimentally demonstrated that parents decreased their feeding frequencies when blowfly larvae were eliminated, which is consistent with the hypothesis of Johnson & Albrecht (1993). Feeding visits per hour of both parents were 65% higher in infested broods than in treated ones (treated, $21.9 \pm 7.6 \text{ SD}$; control, $36.1 \pm 15.0 \text{ SD}$). Because the mean feeding frequency was 4.5 visits per chick per hour, the increase of 14.2 visits per hour in control broods as compared with treated ones is roughly equivalent to the addition of 3.2 chicks in a deparasitized brood. In our experimental design, the nest was removed only in the treated group, which could account for a reduction in parental visits only in the treated group. However, the test was conservative and nestling condition remained better in the manipulated (treated) group.

Analysing our data set with logistic regression (GLIM Poisson model), we obtained a model on the effects of brood size ($\chi^2_1 = 10.9$, $P < 0.005$) and mean parasite load ($\chi^2_1 = 21.3$, $P < 0.001$) on the number of feeding visits per hour (Fig. 1). For example, in five chick broods, the total feeding rate would be 20 visits per hour in a brood without parasites, 30 visits per hour in a brood with 10 blowfly larvae per chick, and 43 visits per hour with 20 blowfly larvae per chick. Our results were consistent with

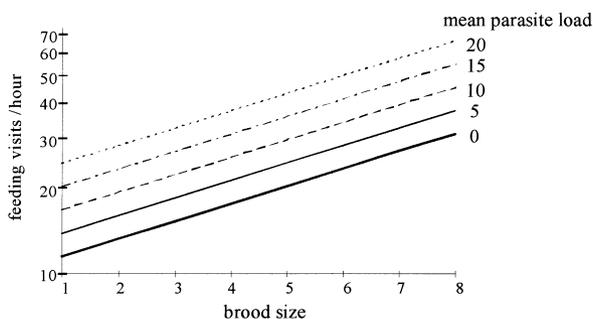


Figure 1 Effects of brood size and mean parasite load on the total feeding rate of parents (number of visits per hour, log-transformed). Lines are fitted for different mean parasite loads (per chick). Model fitted to 26 data points, with logistic regressions (GLIM computer program).

those of Christe *et al.* (1996) in great tits (*Parus major*) and those of Tripet & Richner (1997) in blue tits, who found, respectively, a 24% and a 29% increase in rates of food provisioning when broods were infested by hen fleas. One possible proximate mechanism for such a response may be an increase in begging calls of parasitized chicks, as experimentally found by Christe *et al.* (1996).

Although parents increased the total feeding visits in infested broods, they did not fully compensate for the effects of parasitism: chicks of infested broods had lower body mass, tarsus length, and haematocrit levels at fledging, as compared with those of treated broods. At least two non exclusive hypotheses may account for this pattern: (i) parents may compensate for the effects of parasitism only at the beginning of the nestling stage, i.e. when the chicks demand and the blood uptake by blowfly larvae are still relatively low, which is consistent with the fact that we did not find any effects of blowflies on body condition of chicks from 2 to 9 days (Hurtrez-Boussès *et al.* 1997b); (ii) there may be a trade-off between the quantity and the quality of food delivered (van Balen 1973). In the study population, when total feeding rates exceed 30 visits per hour, parents tend to bring small size and low quality prey (e.g. ants) (Perret, unpublished data).

The increase in feeding rates as a response to parasites suggests that blowflies may incur a cost not only to chicks, but also to their parents. If this is the case, both current and future reproductive success might be affected by blowflies.

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REFERENCES

- van Balen, J.H. (1973). A comparative study of the breeding ecology of the great tit *Parus major* in different habitats. *Ardea*, 61, 1–93.
- Banbura, J., Blondel, J., de Wilde-Lambrechts, H., Galan, M.J. & Maistre, M. (1994). Nestling diet variation in an insular Mediterranean population of blue tits *Parus caeruleus*: effects of years, territories and individuals. *Oecologia*, 100, 413–420.
- Bennett, G.F. (1957). Studies on the genus *Protocalliphora* (Diptera: Calliphoridae). Ph.D. Thesis, University of Toronto.

- Blondel, J. (1985). Breeding strategies of the Blue tit and Coal tit (*Parus*) in mainland and Island Mediterranean habitats: a comparison. *J. Anim. Ecol.*, 54, 531–556.
- Blondel, J., Clamens, A., Cramm, P., Gaubert, H. & Isenmann, P. (1987). Population studies of tits in the Mediterranean region. *Ardea*, 75, 21–34.
- Christe, P., Richner, H. & Oppliger, A. (1996). Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. *Behav. Ecol.*, 7, 127–131.
- Crawley, M.J. (1993). *GLIM for Ecologists*. Oxford: Blackwell Scientific.
- Hurtrez-Boussès, S. (1996). Interactions hôte-parasite: le système mésange bleue-*Protocalliphora* en région méditerranéenne. Ph.D. Thesis, University of Montpellier II.
- Hurtrez-Boussès, S., Perret, P., Blondel, J. & Renaud, F. (1997b). Relationship between intensity of blowfly infestation and reproductive success in a Corsican population of Blue Tits. *J. Avian Biol.*, 28, 267–270.
- Hurtrez-Boussès, S., Perret, P., Renaud, F. & Blondel, J. (1997a). High blowfly parasitic loads affect breeding success in a Mediterranean population of blue tits. *Oecologia*, 112, 514–517.
- Johnson, L.S. & Albrecht, D.J. (1993). Effects of haematophagous ectoparasites on nestling house wrens: who pays the costs of parasitism? *Oikos*, 66, 255–262.
- Lessells, C.M. & Boag, P.T. (1987). Unrepeatable repeatabilities: a common mistake. *Auk*, 104, 116–121.
- Møller, A.P. (1997). Parasitism and the evolution of host life history. In *Host-parasite Evolution: General Principles and Avian Models*, ed. Clayton D.H., Moore J. Oxford: Oxford University Press, pp. 105–127.
- NAG (1986). *The Generalised Linear Interactive System. Release 3.77*. London: The Royal Statistical Society.
- Richner, H., Oppliger, A. & Christe, P. (1993). Effect of an ectoparasite on reproduction in great tits. *J. Anim. Ecol.*, 62, 703–710.
- Scheiner, S.M. (1993). MANOVA: Multiple response variables and multispecies interactions. In *Design and Analysis of Ecological Experiments*, ed. Scheiner S.M., Gurevitch J. London: Chapman and Hall, pp. 96–112.
- Tinbergen, J.M. & Boerlijst, M.C. (1990). Nestling weight and survival in individual great tits (*Parus major*). *J. Anim. Ecol.*, 59, 1113–1127.
- Tripet, F. & Richner, H. (1997). Host responses to ectoparasites: food compensation by parent blue tits. *Oikos*, 78, 557–561.

BIOSKETCH

Sylvie Hurtrez-Boussès works on host-parasite interactions. She is involved in studies on blue tit-ectoparasites system and in a program on population genetics of *Fasciola hepatica*.