*Ibis* (2002), **144** (on-line), E73–E78

# The effect of nest ectoparasites on parental provisioning in a north-African population of the Blue Tit *Parus caeruleus*

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Bird nests are often heavily infested with several haematophagous ectoparasite species that drain energy and other essential resources needed for the development of the rapidly growing chicks. The nutritional requirements of altricial chicks can only be satisfied by the parents frequently bringing prey to the nest. In a 3-year study, we tested experimentally whether a parasite-induced change in the nutritional budgets of the chicks in an Algerian population of the Blue Tit, could be compensated by a response in parental food provisioning behaviour. We found that nestling body mass and size did not differ between heat-treated 'parasite-free' nests and heavily infested control nests. However, after controlling for potential confounding variables (laydate, clutch size, chick age, year), we found that broods of heavily infested control nests were more frequently visited and fed than broods that received antiparasite treatment. The results are discussed in the framework of theory related to behavioural responses of hosts to parasites.

To a large extent, resource constraints determine how life-history traits will develop and evolve (Roff 1992, Stearns 1992). Parasites exploiting hosts drain energy and other resources, and therefore may influence host life-history features related to reproduction, survival and growth (Loye & Zuk 1991, Forbes 1993, Clayton & Moore 1997). A classical view is that parasites generally have a minor impact on host fitness because of long-term coevolutionary processes between parasites and hosts (e.g. Alexander 1981). However, recent studies suggest that parasite virulence, as defined through the deleterious effects on hosts, can sometimes be high in the case of haematophagous ectoparasite species attacking the rapidly growing chicks of altricial birds (Lehmann 1993, Møller 1997, Merino & Møller 1999). Bird nest ectoparasites drain energy and essential nutrients, which can reduce the development of fitness-related traits in hosts, such as body size or sexually selected traits (e.g. Møller *et al.* 1990, Lozano 1994). Furthermore, nest ectoparasites can act as vectors of diseases (Loye & Zuk 1991, Clayton & Moore 1997) and influence host reproductive effort, possibly increasing a cost of reproduction (Forbes 1993, Ilmonen *et al.* 2000, Råberg *et al.* 2000). Hence parents have evolved a series of response mechanisms that reduce the impact of parasites on chicks (e.g. Loye & Zuk 1991, Clayton & Moore 1997).

Parasites have more detrimental effects when hosts are exposed to severe environmental conditions, such as food constraints (de Lope *et al.* 1993, Dufva & Allander 1996). Because food may contain essential nutritional elements that stimulate cell-mediated immunity, nutritional constraints may reduce resistance against parasites (e.g. Lochmiller *et al.* 1993, Saino *et al.* 1997, Brinkhof *et al.* 1999). Lower resource availability may force parents to invest more in food searching and less in nest sanitation perhaps increasing the parasite susceptibility of the chicks. The nutritional requirements of altricial bird chicks, either invested in growth or parasite resistance, can only be satisfied by the parents frequently delivering prey to the nest. Any parasite-induced change in the nutritional budgets of the chicks could therefore be compensated for by a change in parental feeding rates (e.g. Forbes 1993, Johnson & Albrecht 1993). In several wild bird

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populations, high infestation intensities of haematophagous ectoparasites do not reduce chick growth or body size. One explanation is that parents have been able to provide the essential resources that compensate somehow for potential costs induced by the ectoparasites, for instance by increasing the number of prey delivered to the chicks (Johnson & Albrecht 1993, Tripet & Richner 1997). Here we examine this possibility with a 3-year study of an Algerian population of Blue Tits *Parus caeruleus ultramarinus* living at the southern edge of the distribution range of the species. In this study population, infestation rates and parasite intensities exceed those of most European study populations (Bouslama *et al.* 2001). We predicted that parents should reduce their provisioning rates in response to an experimental reduction of ectoparasite pressures on the chicks. Because provisioning rates can be influenced by factors other than parasites, such as the timing of reproduction, clutch size, brood size at fledging, chick age and year, we controlled for these variables in our analyses (cf. Råberg *et al.* 2000).

## METHODS

The Blue Tits bred in nestboxes erected at a density of 2 boxes/ha, and were studied during the years 1998–2000; further details of the study site are given in Chabi and Isenmann (1997) and Bouslama *et al.* (2001).

Nestboxes with Blue Tit nests for which parental provisioning was quantified were randomly classified into controls without experimental manipulation of the parasite intensities and experimental boxes with heat-treated nests (1998: three controls and two treated; 1999: four controls and five treated; 2000: four controls and three treated). Nests were treated using a microwave oven (3 min at 830 W) (cf. Richner *et al.* 1993, Hurtrez-Boussès *et al.* 1997b). In the experimental nestboxes, nests were replaced with a heat-treated nest every 2–3 days from 2 days post-hatching until the end of body mass and tarsus length development of the chicks at 13 days after hatching (cf. Hurtrez-Boussès *et al.* 1998).

After the chicks fledged, each nest was stored in a plastic bag and transported to the laboratory for the nest ectoparasites (ticks *Ixodes ricinus*, adult hen fleas *Ceratophyllus gallinae* and blow fly *Protocalliphora* sp. pupae) to be counted. Following Hurtrez-Boussès *et al.* (1997a, 1997b) and Heeb *et al.* (2000), we used the total number of pupae counted as a measure of blow fly parasite intensity ignoring *Protocalliphora* species identity. Mites (*Dermanyssus gallinae*) were also observed (see Bouslama *et al.* 2001), but were not considered in this study. The life-histories of these nest parasites have been described in more detail elsewhere (e.g. Loye & Zuk 1991, Harper *et al.* 1992, Bauchau 1998).

The total number of nestbox visits by parents delivering prey was determined with binoculars, for 1 h in the morning and 1 h in the afternoon. An observer was hidden in dense vegetation at less than 10 m from the nest. Parental feeding rates were estimated for chicks of 9 days post-hatching (21 nests), i.e. the age at which energy requirements peak (Perrins 1979, Gaubert 1985). Additional observations were carried out at the same nests at 15 days post-hatching (20 nests). The total number of nestbox visits without prey was also quantified and analysed separately. Feeding rates of males and females were not quantified separately.

For each of the Blue Tit pairs examined, data on the onset of egg laying, clutch size and the number of offspring fledged were available. Chicks were ringed at 5 days after hatching and body size measures were taken using protocols described in Hurtrez-Boussès *et al.* (1997a, 1997b) and Bouslama *et al.* (2001). We calculated the average mass gain per day between 2 and 9 days post-hatching, which was used as a measure of the growth rate of the chicks.

Data were analysed with SAS using General Linear Model procedures (type III, SAS Institute 1992). This procedure allowed us to test the effects of treatment (control vs. treated) on ectoparasite intensities, chick features and parental feeding frequencies, after controlling for potential confounding variables, such as the timing of reproduction, clutch size, brood size at fledging and year (see Tables 1 and 2). We used the brood averages for each variable tested. For technical reasons, not all parameters were available for all nests.

## RESULTS

In the 21 nests with known parental feeding rates, heat treatment reduced the ectoparasite intensities considerably, and significantly for ticks and blow flies, after controlling for the timing of reproduction (lay-date), clutch size, brood size at fledging, year, and the year–treatment interaction (Tables 1 and 2).

Parental feeding rates at 9 and 15 days post-hatching were very significantly lower in heat-treated nests with low parasite intensities than in control nests

**Table 1.** Averages and standard deviations of parent life-history traits, nest ectoparasite intensities, and chick features in unmanipulated and heat-treated Blue Tit nests for broods of which the parental rate of food provisioning was quantified.

| | Treatment | |
|---|---|---|
| | Control | Heat-treated |
| Parent life-history traits | | |
| Laydate | 18 April ± 23 (11) | 15 April ± 20 (10) |
| Clutch size | 7.09 ± 1.04 (11) | 7.10 ± 0.87 (10) |
| Number of fledglings | 4.64 ± 2.54 (11) | 6.00 ± 1.70 (10) |
| Parasites | | |
| Ticks | 20.5 ± 14.7 (9) | 8.8 ± 4.71 (10) |
| Blow flies | 54.9 ± 41.9 (10) | 2.0 ± 0.67 (10) |
| Fleas | 15.1 ± 12.7 (10) | 3.1 ± 4.0 (10) |
| Chick features | | |
| Mass gain | 1.03 ± 0.14 (10) | 0.89 ± 0.23 (10) |
| Body mass 15 days post-hatch | 10.50 ± 0.60 (9) | 10.50 ± 1.03 (10) |
| Tarsus 15 days post-hatch | 15.62 ± 0.70 (8) | 17.14 ± 1.23 (10) |
| Parental feeding frequency per chick per hour | | |
| 9 days post-hatch | 3.13 ± 0.17 (11) | 2.70 ± 0.20 (10) |
| 15 days post-hatch | 2.47 ± 0.30 (11) | 2.17 ± 0.10 (9) |
| Parental visiting frequency without prey per chick per hour | | |
| 9 days post-hatch | 1.28 + 0.30 (11) | 0.31 + 0.08 (10) |
| 15 days post-hatch | 0.91 + 0.24 (11) | 0.22 + 0.09 (9) |

Number of nests studied is given in parentheses.

**Table 2.** Effects of parent life-history traits (onset of egg laying, clutch size, brood size at fledging), year (1998–2000), treatment (heat-treated, control) and the year × treatment interaction on parasite intensities, chick features and parental feeding rates (total number of visits per chick per hour) using GLM procedures (SAS, type III).

| | *F* | | | | | |
|---|---|---|---|---|---|---|
| | Laydate | Clutch size | Brood size | Year | Treatment | Y × T |
| Parasites | | | | | | |
| Ticks | 2.06[1,10] | 0.69[1,10] | 1.96[1,10] | 4.07[2,10] | 9.08[1,10] | 0.85[2,10] |
| Blow flies | 3.72[1,11] | 1.18[1,11] | 0.98[1,11] | 3.07[2,11] | 18.02[1,11]** | 2.18[2,11] |
| Fleas | 0.00[1,11] | 0.68[1,11] | 0.26[1,11] | 0.12[2,11] | 5.37[1,11] | 0.57[2,11] |
| Chick features | | | | | | |
| Mass gain | 0.20[1,11] | 0.69[1,11] | 0.07[1,11] | 0.37[2,11] | 1.13[1,11] | 2.30[2,11] |
| Mass 15 days | 0.03 [1,10] | 0.16[1,10] | 0.14[1,10] | 0.34[2,10] | 0.02[1,10] | 0.41[2,10] |
| Tarsus 15 days | 0.04[1,9] | 0.08[1,9] | 3.55[1,9] | 0.64[2,9] | 9.00[1,9] | 0.61[2,9] |
| Parental feeding frequency per chick per hour | | | | | | |
| 9 days post-hatch | 1.15[1,12] | 0.15[1,12] | 1.71[1,12] | 1.88[2,12] | 25.26[1,12]** | 0.33[2,12] |
| 15 days post-hatch | 1.47[1,11] | 3.16[1,11] | 1.38[1,11] | 6.00[2,11] | 21.42[1,11]** | 4.61[2,12] |
| Parental visiting frequency without prey per chick per hour | | | | | | |
| 9 days post-hatch | 6.13[1,12] | 1.31[1,12] | 0.25[1,12] | 1.49[2,12] | 168.11[1,12]*** | 6.51[2,12] |
| 15 days post-hatch | 0.13[1,11] | 3.21[1,11] | 11.76[1,11] | 0.28[2,11] | 85.40[1,11]*** | 0.14[2,11] |

*F* refers to *F*-value of GLM. Probability *P* with Bonferroni correction: ***$P < 0.001$, **$P < 0.01$.

with high parasite intensities, even after controlling for effects of timing of reproduction, clutch size, brood size at fledging, year, and the year × treatment interaction (Tables 1 and 2). A similar result was obtained for the visiting rates without prey, which were very significantly lower in the heat-treated nests than in the control nests, after controlling for potential confounding variables (Tables 1 and 2). However, the average mass gain between 2 and 9 days post-hatching, the tarsus length and body mass at 15 days after hatching were not significantly affected by nest treatment (Tables 1 and 2).

The analyses also show that the timing of egg laying, clutch size, brood size at fledging, year and the year × treatment interaction did not have significant effects on parasite intensity, chick features, and parental food provisioning behaviour (Table 2). Similar results were obtained when parasite numbers were included as covariates.

## DISCUSSION

Nest ectoparasites and micro-organisms may have played a key role in the evolution of parental care (e.g. Hart 1997), as indicated by recent studies on the 'host–parasite–chick' system in natural populations of altricial birds. Avian parents seem to have evolved a series of behavioural tactics to protect the chicks against parasites (e.g. Hart 1997), which include delivery of fresh green plant material that repels or kills parasites (e.g. Clark & Mason 1995, Lambrechts & Dos Santos 2000, Lafuma *et al.* 2001) or stimulate immune function (Gwinner *et al.* 2000), avoidance of infested nest sites (Brown & Brown 1986, Merino & Potti 1995), avoidance of infested partners (Møller 1994, Møller *et al.* 1999), induced vaccination of the chicks (Heeb *et al.* 1998), nest sanitation behaviour (Hurtrez-Boussès *et al.* 2000, Bañbura *et al.* 2001, Tripet *et al.* 2002), and parental resource provisioning adjustment.

Experimental studies of the impact of parasites on parental feeding behaviour in free-living bird populations are rare (e.g. see Christe *et al.* 1996). Between-species or between-sex comparisons show that parasites can have different effects on the parental rate of food provisioning, with either an increase (Richner *et al.* 1995, Christe *et al.* 1996, Hurtrez-Boussès *et al.* 1998), a decrease (Møller *et al.* 1994), or no change (Rogers *et al.* 1991, Saino *et al.* 1998) in parental feeding frequencies in response to parasites (see also Tripet *et al.* 2002). This variation has been attributed partly to differences in the trade-offs between current and future reproduction, for instance with parents more willing to feed low-quality young when the probability of successful future reproduction is lower (e.g. see Christe *et al.* 1996, Møller 1997, Szép & Møller 1999).

Blue Tits are small, typically single-brooded, passerines with a short lifespan (Perrins 1979). Because future reproductive opportunities are relatively low in this species, life-history theory would predict (1) increased current parental investment in parasitized poorer-quality broods that require more food, and (2) a significant decrease in food provisioning in response to antiparasite treatment that diminishes the energy stress on the chicks. Consistent with these predictions, all four Blue Tit studies reported found a decrease in parental rate of food provisioning of the chicks in response to an experimental decrease in ectoparasite intensities of either common flea (Tripet & Richner 1997, Tripet *et al.* 2002), blow fly (Hurtrez-Boussès *et al.* 1998) or a combination of different ectoparasite species (this study). In our study, heat treatment of the nests decreased the nest intensities of blow flies and ticks significantly, but did not influence chick morphology and growth significantly (see also Bouslama *et al.* 2001). Parents therefore seem, somehow, to have been able to compensate for the deleterious effects of the parasites through a significant increase in their provisioning rates, as confirmed by our observations. However, the hypothesis that parasites might prejudice the development of other phenotypic traits in offspring, such as development of the immune system or sexual traits, was not examined, and requires studies of post-fledging survival. Furthermore, we cannot exclude the possibility that parents suffer from higher nest ectoparasite intensities if they have to invest more in immune defence (e.g. Råberg *et al.* 2000), either through the direct effect of parasites or the indirect effects of haematozoan parasites which are transmitted. Additional studies of adult survival are required to examine potential costs of increased food provisioning on the parents. Theory predicts that these survival costs should be relatively low (e.g. see Szép & Møller 1999).

Our study shows that the visiting rate without prey was lower in heat-treated nests than in heavily infested control nests. This supports the conclusions from an earlier Blue Tit study that parents invest more in nest sanitation behaviour when many parasites are present (Hurtrez-Boussès *et al.* 2000, but see Tripet *et al.* 2002). The hypothesis that our method of heat treatment (see Methods) would induce an increase in nest sanitation behaviour to restore the original nest microhabitat can therefore be rejected.

Although the experiments with Blue Tits demonstrate parental care adjustment in response to nest ectoparasites, responses of the parents and the chicks differed across the studies (Tripet & Richner 1997, Hurtrez-Boussès *et al.* 1998, Tripet *et al.* 2002, this study). Hurtrez-Boussès *et al.* (1998) showed a significant increase in parental rate of food provisioning in response to nest ectoparasites which did not completely compensate for the presence of parasites because the chicks of control broods with parasites were significantly smaller than the chicks receiving antiparasite treatment. By contrast, the other three Blue Tit studies did not show significant differences in chick body size measures between heavily infested control nests and 'parasite-free' nests, despite the fact that parental food provisioning effort was significantly higher in the infested nests (see also Bouslama *et al.* 2001). The observed between-study site variation in chick responses to parental food provisioning could have been caused by factors for which we did not control, such as between-population differences in prey quality, chick resistance, ectoparasite virulence, environmental constraints or the condition of the parents (e.g. de Lope *et al.* 1993, Lehmann 1993, Møller 1994, Dufva & Allander 1996, Merino & Møller 1999). Evidently, more detailed multifactor studies of the environment (e.g. prey types delivered to the chicks, environmental constraints), the host (e.g. immunocompetence, body condition, parental quality) and the parasites (e.g. virulence) will be required to elucidate the proximate and ultimate causes of intraspecific macrogeographical variation in this host–parasite system.

Sylvie Hurtrez-Boussès and two anonymous referees provided helpful comments on the manuscript.

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Received 4 July 2001, revision accepted 7 January 2002