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Effects of *Protocalliphora* parasites on nestling food composition in Corsican Blue Tits *Parus caeruleus*: consequences for nestling performance

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Abstract. The influence of a parasite (larvae of *Protocalliphora*, Diptera: Calliphoridae) on an avian host (Blue Tit) was studied in 1994–1997 as part of a long-term research project on a population of Blue Tits inhabiting nest boxes on the island of Corsica. The Blue Tit broods were heavily infested with *Protocalliphora* larvae. The abundance of caterpillars as a key food type for the tits was monitored. A random sample of 16 nests was experimentally subjected to an anti-parasite heat treatment, which resulted in a marked decline in the numbers of *Protocalliphora* larvae. Untreated nests, with high numbers of parasites, were regarded as control nests. Under the anti-parasite treatment, Blue Tit nestlings were fed less frequently than the control nestlings (8 v. 11 food items per hour per nestling). Significant changes in the diet composition occurred, with parasite-free nestlings being consistently fed with fewer caterpillars. An average parasitised nestling was supplied by its parents with 2.6 caterpillars more than an average parasite-free chick. This suggests that in the highly parasitised control nests, the parent tits made an effort to compensate for the detrimental effects caused by *Protocalliphora* larvae. Feeding rate and food composition were shown to influence chick condition and survival in the nest. In spite of these facts, the nestlings in parasitised nests developed less rapidly and had lower survival rates than in the anti-parasitically heat-treated nests. The parasitic *Protocalliphora* larvae have a double effect on their avian host: they adversely affect nestling performance, and they compel adult tits to work harder in order to at least partially compensate for that influence.

Key words: Blue Tit, *Parus caeruleus*, ectoparasite, *Protocalliphora*, food composition, diet, parental care, compensation, nestling performance

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INTRODUCTION

The multiple ways in which ectoparasites play an important role in generating direct and indirect pressures shaping life histories of hosts have received much attention lately (Loye & Zuk 1991, Clayton & Moore 1997, Richner 1998). Blood-taking ectoparasites can both directly affect the host physiology and, indirectly, vector microparasites. These effects will depend on the developmental stage and mobility of the stage at which they

exploit their hosts (Combes 2001). In the case of the direct effects on altricial nestlings, parasites drain blood and thus cause the developing host organisms to increase blood production on the basis of food delivered by parents.

Many ectoparasites can infest adult birds as well as nestlings, while blow flies *Protocalliphora* (Diptera: Calliphoridae) specialize in nestlings on which their larvae parasitise (Sabrosky et al. 1989, Whitworth & Bennett 1992). The amount of fresh blood taken from nestlings by one blow fly larva

can be as high as 0.2 g (usually less) (Whitworth & Bennett 1992). Gold & Dahlsten (1983) showed that as much as 55% of the blood volume of the nestling can be drained per day. Taking into account the fact that Corsican Blue Tit nests can harbour up to 100 larvae (Hurtrez-Boussès et al. 1997b), this means that the harm done to the nestlings may be heavy. Hurtrez-Boussès et al. (1997a, 1997b) proved that the larvae of *Protocalliphora* have negative effects on chick quality and survival before fledging in the Corsican population of Blue Tits. This is consistent with results of other studies (e.g. Merino & Potti 1995, O'Brien et al. 2001). Hence, the question arises, do parents try to reduce the effects by infestation-dependent feeding and other types of behaviour (Rothschild & Clay 1952, Johnson & Albrecht 1993, Morrison & Johnson 2002, Simon 2003)?

Under the ectoparasite pressure, Corsican Blue Tit parents were shown to intensify feeding of nestlings, spend more time on nest sanitation and even use aromatic plants as repellents (Hurtrez-Boussès et al. 1998, 2000, Lambrechts & Dos Santos 2000, Bañbura et al. 2001, Lafuma et al. 2001, Petit et al. 2002). All these responses of adult tits to parasites are time-consuming, which can potentially result in some changes in food preferences and selectivity. As far as we know, no papers have analysed the impact of parasitism on types and quantity of prey delivered to nestlings. The availability of food, or food constraints, may determine responses of parental tits to parasitism. Blondel (1985) suggested that poor abundance of food and a high level of *Protocalliphora* parasitism have far-reaching consequences for life-history strategies of Corsican Blue Tits. It was also shown that ectoparasites had much lower effects on nestlings during trophically rich seasons than in poor years (Simon 2003, Simon et al. 2004).

Some general predictions concerning the components of the bird-parasite system studied can be presented. In the case of food shortage (poor years) the proportion of caterpillars in the diet should decrease with increased load of parasites because parental birds would have less time to search for this optimal, preferred prey when the pressure of parasites is heavier. On the other hand, when food is abundant (rich years), the proportion of caterpillars should increase in response to heavier infestation to better compensate the negative effects of parasites. We assume here that providing a balanced diversified diet rather than only maximizing a proportion of caterpillars is an optimal strategy for Blue Tits (Perrins 1991,

Riddington & Gosler 1995, Bañbura et al. 1999) because, otherwise, even birds with parasite-free nests would have maximized the proportion of caterpillars.

Accordingly, major goals of this paper were:

- 1) to test if ectoparasitism of the larvae of *Protocalliphora* spp influences the composition of Blue Tit nestling diet and feeding rate,
- 2) to examine the extent to which parasitic pressure of *Protocalliphora* larvae influence chick performance at the nest, as measured by body mass and survival to fledging,
- 3) to investigate if food and feeding characteristics affect nestling performance in the context of parasitic exploitation?

Although different aspects of the Blue Tit – blowfly system in Corsica have already been analyzed by Hurtrez-Boussès et al. (1997–2001), the present paper is based on the video data, which have not been used so far.

MATERIAL AND METHODS

The data for this study were collected in PIRIO, Corsica (42°24'N, 08°44'E) as part of a long-term study of the population biology of Blue Tits in Mediterranean France (see Blondel et al. 1993, 1998, 1999, Tremblay et al. 2003). The study site was located in an evergreen forest dominated by the Holm Oak *Quercus ilex*. Parental feeding activity of individually-marked adult Tits was video-recorded in 6, 19, 15 and 9 nest-boxes in 1994–1997 breeding seasons, respectively. Using video surveillance micro-cameras (Panasonic WV-KS152) fixed to the nest-boxes, recordings were made on VHS video-tapes; time of recording particular broods ranged from 1.6 to 3.12 hours (mean 2.7 ± 0.6 SD). The nests studied were all at the same stage, 13 days after hatching on the day of recording. In 1994–1996, samples of 3, 7 and 6 nests, respectively, were randomly assigned to an anti-parasite treatment, the remaining nests being a non-manipulated control sample. The data collected in 1997 were non-experimental and were included to widen the pattern of inter-year changes in food composition. The experiments with blowfly parasitism were conducted randomly with respect to the time of breeding, so that the mean laying date did not differ between heat-treated and control nests ($t_{38} = 0.07$, $p = 0.94$). The experimentally treated nests were heated for 3 min using a microwave oven (850W), which killed most blow fly larvae (cf. Richner et al. 1993,

Hurtrez-Boussès et al. 1997a). The experimental nests were replaced with other heat-treated nests of the same size every 2–3 days until the nestlings were 15 days old. Larvae of two species of blow flies, *Protocalliphora azurea* and *P. falcozi*, parasitise Corsican Blue Tits. In this paper they were pooled because the larvae are difficult to distinguish (Hurtrez-Boussès 1997a, Draber-Mońko 2004). The experimental treatment was proved to be efficient, as the mean infestation rate per chick was 0.2 in heat-treated nests versus 15.0 in control nests ($G_1 = 126$, $p < 0.001$) (Hurtrez-Boussès et al. 2000).

In the laboratory, the tapes were played and all parental feeding activities of males and females were classified and quantified; in particular, the time when an adult bird arrived at the nest with a prey item, prey taxonomic category (caterpillars, grasshoppers, spiders, others), prey body-size category (3-step classification). To make analyses independent of brood sizes and time of video-recording, the number of feeding visits with a particular type of prey item per one hour per one nestling was calculated for each adult Blue Tit. Total feeding rate was also calculated as the number of all feeding visits of a particular individual parent per one hour per one chick.

The reason for considering the above prey taxa in this study is that caterpillars are the preferred prey, while spiders and grasshoppers are the main alternative prey in the study area with only a small proportion of other arthropods such as Coleoptera, Diptera, Dermaptera, and Hemiptera (Blondel et al. 1991, Bañbura et al. 1994, 1999). Caterpillar and spider items of prey were classified to three ordinal categories of body size by comparison with the beak and head size of adult birds: 1 = small (length < 1 cm for caterpillars, and abdomen diameter < 0.2 cm for spiders), 2 = middle (length 1–2 cm, and diameter 0.2–0.6 cm, respectively), 3 = large (length > 2 cm for caterpillars and diameter > 0.6 cm for spiders). The size categories were constructed in order to make individual prey volumes (masses) roughly comparable among the taxa (P. Perret, unpublished). Averages of these size categories were calculated for each individual parent; such averages constituted the basic data point in calculating indices of feeding.

Seven original variables, i.e. proportion of caterpillars, spider frequency, grasshopper frequency and proportion of other prey in nestling diet, caterpillar size index, spider size index, and per nestling feeding activity, were used to calculate indicators of different aspects of feeding nestlings.

Six principal components were extracted from

the original variables and applied as indicators of feeding. By applying this method we wanted to get mutually independent indices of feeding rather than to markedly reduce the number of variables as is usually the case in principal component analysis (James & McColloch 1990).

Breeding data were collected by visiting all nests once a week from the onset of the breeding season. Laying date, clutch size, hatching date, the number of hatchlings and the number of fledglings were determined. Measurements of nestling tarsus length to the nearest 0.1 mm were taken with calipers and body weight to the nearest 0.1 g were taken with a Pesola spring balance when the nestlings were 14 days old. Residuals from the regression of body weight on tarsus length was considered as indices of chick condition. Fledging success, being the ratio of the number of fledging to the number of hatchlings, was considered as a measure of chick performance at the nest.

Principal components were extracted applying varimax rotation using the SPSS 10 package. Contingency table analysis and different tests applying general and generalized linear models were performed using the SPSS 10, STATISTICA 6 and GLIM packages, following standard statistical procedures (Crawley 1993, Sokal & Rohlf 1996, StatSoft 1996).

The abundance of caterpillars was monitored by measuring their frass dropping from the canopy trees in four 0.25 m² collectors at each of five stations randomly distributed throughout the study area (Blondel et al. 1991, Bañbura et al. 1994).

RESULTS

Caterpillar abundance was relatively low during the years of the study, with the peak abundance being similar, as measured by frassfall of ca. 90 mg/m²/day, in 1994–1996 when the experiments were conducted (Fig. 1). Year 1997 was especially poor in terms of caterpillar abundance, with frassfall being ca. 50 mg/m²/day (Fig. 1). In 1994 and 1996 the timing of the within-season changes in caterpillar abundance was similar, whereas a period of the highest caterpillar abundance was ca. 2 weeks later in 1995 than in 1994 and 1996 (Fig. 1).

Total of 10213 parental trips were observed, with 7305 records of prey category. Over four years of this study, caterpillars were the most frequent prey category but some variation between years was observed; caterpillars constituted 25–53% of

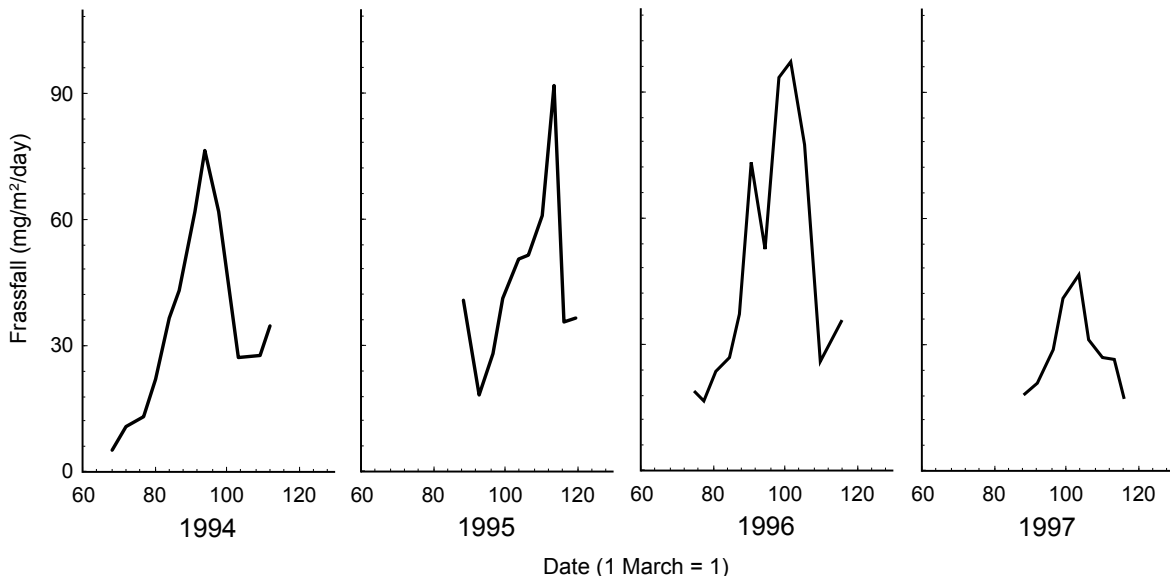


Fig. 1. Caterpillar abundance as measured by frassfall in the study area in 1994–1997.

prey items in particular years (Fig. 2). Spiders were the second most frequent prey category, 31–32%. Grasshoppers were present in nestling diet in two years with different frequency ca. 2% to 11%. The other prey category included different arthropods, mostly small body-sized ones. In general, nestling diet differed among years (Fig. 2) ($G_9 = 664.8, p < 0.0001$).

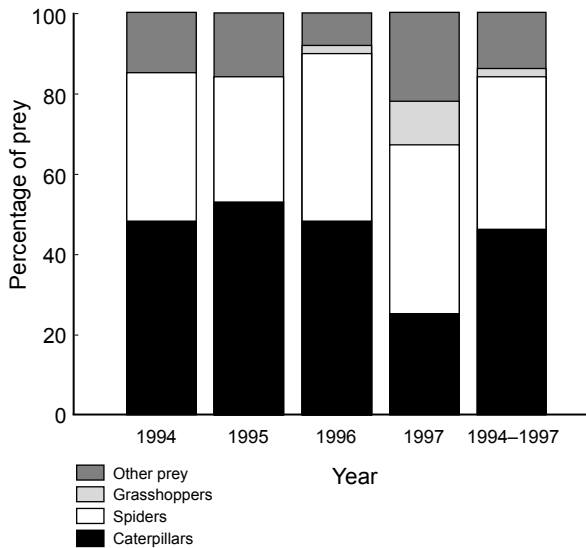


Fig. 2. Composition of the diet of Blue Tits nestling in Pirio in 1994–1997.

In response to the anti-parasite treatment, adult birds decreased the total number of prey items supplied to a nestling per hour (ANOVA $F_{1,66} = 4.71, p = 0.033$), resulting in an average treated nestling being provided by both the parents with 3 items fewer than a control nestling (Fig. 3). The difference between male and female parents was not significant (ANOVA $F_{1,66} = 0.038, p = 0.86$). Mean numbers of prey brought during one hour to an average nestling differed between years, with the respective averages ranging from 4.3 to 11.6 for nestlings in heat-treated nests and

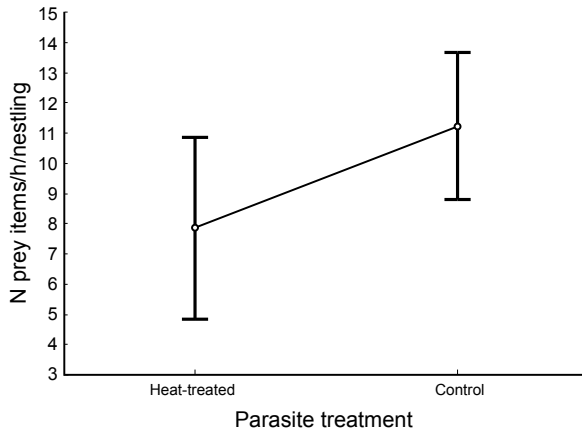


Fig. 3. Comparison of total feeding rate (number of items per hour per nestling) of Blue Tits nestlings between experimentally treated and control nests in Pirio in 1994–1996.

from 9.0 to 13.7 for control nestlings (ANOVA $F_{2,66} = 5.51$, $p = 0.006$).

Composition of food supplied to nestlings changed under the influence of the anti-parasite treatment as measured by a significant between-treatment difference in the multivariate parameter composed of caterpillar, spider and other prey item numbers supplied to a nestling during one hour (MANOVA Wilk's statistics = 0.87, $F_{3,64} = 3.23$, $p = 0.028$). A very clear pattern appeared in the case of the number of caterpillars supplied to an average nestling (Fig. 4): both parents brought more caterpillars to the control nests than to the experimentally heat-treated nests (ANOVA $F_{1,66} = 5.79$, $p = 0.019$), with no significant difference between years (ANOVA $F_{2,66} = 0.95$, $p = 0.39$) or between sexes (ANOVA $F_{1,66} = 0.79$, $p = 0.37$). Overall, an average parasitised nestling was supplied by its parents with 2.6 caterpillars more than an average parasite-free nestling. There was no

consistent pattern in feeding nestlings with spiders or other prey (Fig. 4). Multivariate analysis of variance showed significant effects of year (MANOVA Wilk's statistic = 0.68, $F_{6,128} = 4.61$, $p = 0.0003$) and sex (MANOVA Wilk's statistic = 0.88, $F_{1,64} = 3.04$, $p = 0.04$) factors on the numbers of the items of different categories of prey supplied to nestlings. This resulted from the fact that spiders were supplied in different numbers in different years (ANOVA $F_{2,66} = 12.66$, $p < 0.0001$) and by parents of different sex (ANOVA $F_{1,66} = 6.92$, $p = 0.011$), whereas the other prey category did not show any significant differentiation with respect to parasite-treatment, year or sex factors (ANOVA $p > 0.2$ in every case).

Principal components were calculated out of the original variables and applied as indices of food composition and per-nestling feeding frequency. We extracted six principal components which we treated as positive or negative indicators of food and feeding variables according to their

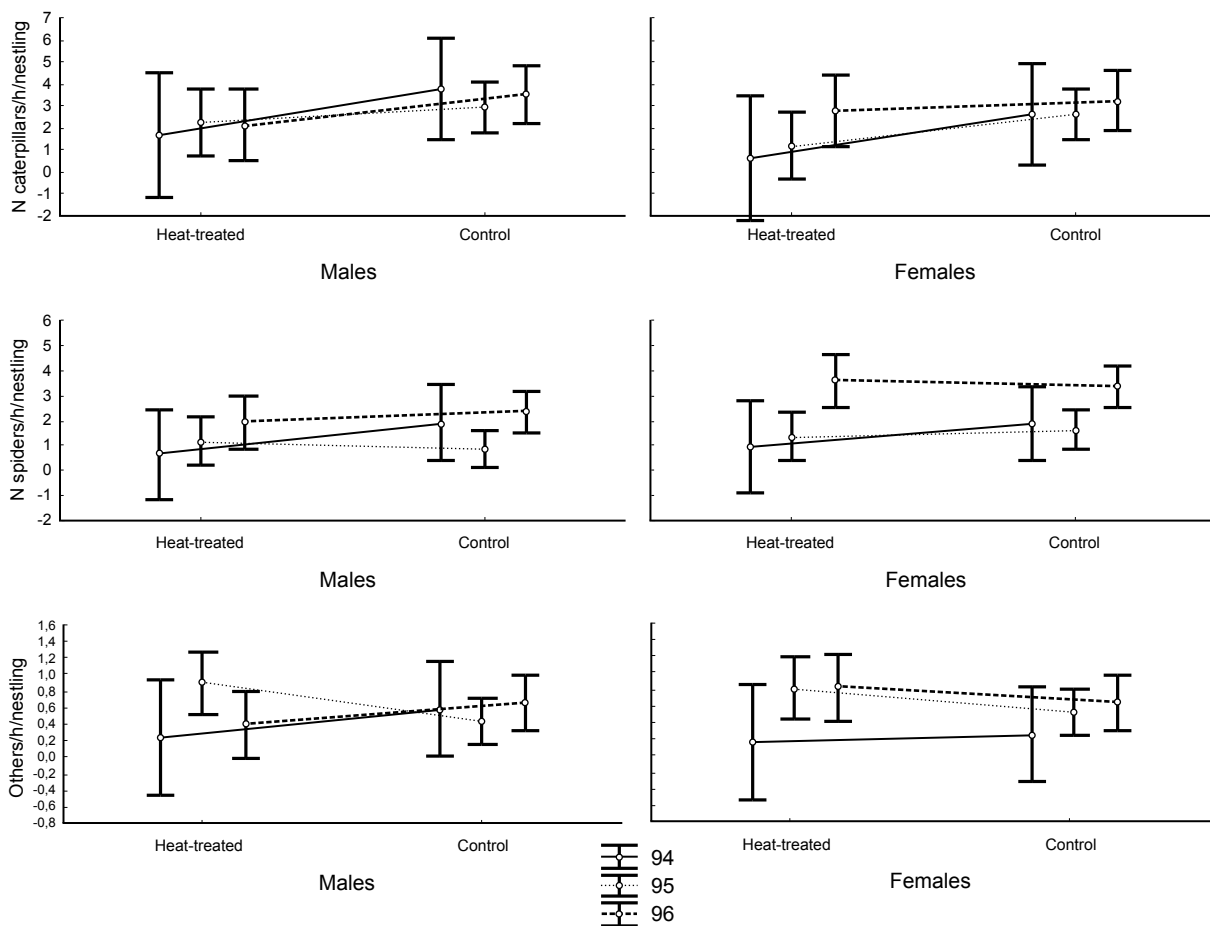


Fig. 4. Effects of the anti-parasite experiment on the number of caterpillar, spider and other prey items supplied to nestlings

Table 1. Principal components extracted from seven feeding variables as indicators of feeding traits. Loadings (positive or negative, as indicated) of particular variables in relation to principal components are given in parentheses.

| Principal component | Feeding variables | Indicator |
|---------------------|--|------------------------------|
| PC1: | + % caterpillars (0.891), - % spiders (-0.947) | Caterpillar/spider frequency |
| PC2: | + % others (0.977) | Other prey frequency |
| PC3: | + % grasshoppers (0.971) | Grasshopper frequency |
| PC4: | + feed/h/nestling (0.959) | Nestling feeding activity |
| PC5: | + spider body size (0.940) | Spider body size |
| PC6: | + caterpillar body size (0.928) | Caterpillar body size |

correlation (loadings) with the variables (Table 1). We analyzed effects of food and feeding indicators, parasite treatment and year factors on the per brood mean body mass of 14-day-old nestlings (Table 2). In food delivered by males, grasshopper frequency had a negative effect and body size index of spiders had a positive influence on the nestling body mass. Parasite treatment proved to have a significant effect in both males and females. Nestlings in nests with decreased parasitism (heat-treated) were heavier than those in control (non-treated) nests (mean mass $9.55 \text{ g} \pm 0.39$ and $9.25 \text{ g} \pm 0.30$, respectively). In analogous tests of the effects of feeding indicators, year and parasite treatment on the per-brood mean condition of nestlings (residuals from the regression of body mass on tarsus length) only a negative effect of grasshopper frequency in the nestling diet brought by males (PC3) appeared to be significant.

Finally, we tested the effects of different factors and variables on fledging success treated as a

direct indicator of nestling performance during the time between hatching and fledging. Year, laying date, parasite treatment and 14-day-old-nestling body mass appeared to influence fledging success (Table 3). The date of the onset of breeding negatively affected nestling performance whereas nestling body mass was affected positively. Mean fledging success for broods reared in nests with decreased parasitism (heat-treated) was 81.18%, whereas in control nests it was 68.26%. Some effects of food and feeding indicators were also recorded (Table 4). The effect of caterpillar/spider frequency indicator (PC1) was complex; the female indicator negatively influenced fledging success whereas the male indicator was positively related with fledging success. The former means that the higher proportion of caterpillars in connection with the lower proportion of spiders in the diet delivered by females, the lower was fledging success. In contrast, the latter suggests a positive effect when the male indicator is considered. A negative relationship between grasshopper frequency indicators of males and females and chick performance was apparent. Feeding activity indicators for both

Table 2. Results of testing the effects of feeding indicators, year and parasite treatment on the per-brood mean body mass of 14-days-old nestlings. Generalized linear modeling with log mean body mass as response variable and normal error distribution was applied.

| Variable | df | Males | | Females | |
|-------------------------------|----|-------|--------|---------|------|
| | | G | p | G | p |
| Caterpillar/spider freq (PC1) | 1 | 0.0 | 0.93 | 0.0 | 0.93 |
| Grasshopper freq (PC3) | 1 | 12.3 | 0.0005 | 0.4 | 0.50 |
| Other prey freq (PC2) | 1 | 0.0 | 0.92 | 0.6 | 0.44 |
| Caterpillar body size (PC6) | 1 | 0.0 | 0.88 | 3.2 | 0.08 |
| Spider body size (PC5) | 1 | 4.6 | 0.03 | 0.6 | 0.45 |
| Nestling feeding (PC4) | 1 | 0.2 | 0.62 | 0.1 | 0.76 |
| Year | 3 | 7.1 | 0.07 | 7.7 | 0.05 |
| Parasite treatment | 1 | 5.0 | 0.03 | 4.1 | 0.04 |
| Year x Parasite treatment | 2 | 2.0 | 0.37 | 3.5 | 0.18 |

Table 3. Effects of per brood mean nestling body mass (14 days old nestlings), parasite treatment, year and the date of clutch onset (laying date) on fledging success as a binomial response variable (number of fledglings in relation to the number of hatchlings). Generalized linear modeling was applied. Degrees of freedom for the year factor (2) result from including in the analysis only the three years when parasite treatment was applied.

| Variable | df | G | p |
|--------------------|----|------|----------|
| Year | 2 | 38.5 | 0.000000 |
| Laying date | 1 | 9.3 | 0.002 |
| Parasite treatment | 1 | 5.0 | 0.025 |
| Nestling body mass | 1 | 22.1 | 0.000003 |

Table 4. Results of testing the effects of feeding indicators and year on fledging success as a binomial response variable (number of fledglings in relation to the number of hatchlings). Generalized linear modelling was applied.

| Variable | df | Males | | Females | |
|-------------------------------|----|-------|--------|---------|----------|
| | | G | p | G | p |
| Caterpillar/spider freq (PC1) | 1 | 10.6 | 0.001 | 8.3 | 0.004 |
| Grasshopper freq (PC3) | 1 | 15.4 | 0.0001 | 13.4 | 0.0003 |
| Other prey freq (PC2) | 1 | 0.2 | 0.665 | 1.6 | 0.209 |
| Caterpillar body size (PC6) | 1 | 2.0 | 0.153 | 4.3 | 0.039 |
| Spider body size (PC5) | 1 | 0.0 | 0.992 | 0.5 | 0.482 |
| Nestling feeding (PC4) | 1 | 14.2 | 0.0002 | 20.2 | 0.000007 |
| Year | 3 | 97.0 | 0.0000 | 91.4 | 0.0000 |

males and females were negatively linked with fledging success. Female caterpillar size indicator slightly positively affected fledging success.

DISCUSSION

By definition, parasites exploit tissues and resources assimilated by a host, which may result in more or less severe consequences for the host performance (Combes 2001). Consequently, when supply of resources is constant, parasites should cause some deterioration of the host quality. Infestation of nestling birds creates a specific life-history investment situation in which parental birds may sometimes compensate parasite-induced damage to the nestlings at the cost of employing greater effort in parental care. Parents may or may not undertake the additional effort, depending on the influence of the parasite on the relation between reproductive effort and current and future reproductive success (Richner 1998, Richner & Tripet 1999). Capability of parents to compensate parasitic impact on nestlings may also depend on environmental constraints, especially food abundance (Simon et al. 2004). In the Corsican study area analyzed in this paper, the abundance of food is known to be rather poor and to show inter-year differences, causing a marked effect of year on nestling diet (Bañbura et al. 1994, this study). In general, all four years of this study, including one non-experimental research year (1997), are characterized by a relatively low abundance of caterpillars. In 1996, the peak value of the frassfall, ca. 97 mg/m²/day, was three or even more times lower than the peak value in 1992 and some other years (Bañbura et al. 1994, Blondel et al. 1999, Simon 2003, Simon et al. 2004).

As Blue Tits have on average a low year-to-year survival rate, for the study population estimated at

0.56 (Blondel et al. 1992), an increased investment in current reproduction should be expected under the pressure of parasites (Bousslama et al. 2002). The adult Blue Tits fed nestlings in heat-treated nests less frequently than they did control nestlings. Hurtrez-Boussès et al. (1998), applying a different method of monitoring nest visiting by adult tits, found a very clear positive direct effect of parasite load on nest visiting rate in the same population of Blue Tits. Enhanced parental feeding effort in response to parasitic pressure probably constitutes some compensation to the nestlings (Tripet & Richner 1997). A similar effect was reported for Marsh Tits *Parus palustris* infested by *Protocalliphora falcozi* (Wesołowski 2001), and for Algerian Blue Tits infested by several different ectoparasites, including *Protocalliphora* (Bousslama et al. 2002). Parasite load was also responsible for some anti-parasite behaviours of female Blue Tits on Corsica, especially nest sanitation (Hurtrez-Boussès 2000). All this suggests that parental Blue Tits undertake different time-consuming actions to limit consequences of ectoparasitism on chicks.

In the Blue Tit population studied in this paper, both the sexes decreased the intensity of feeding nestlings under the influence of the experimental anti-parasite treatment. Actually, one would expect a difference between the sexes on theoretical grounds (Richner 1998). Such a difference was reported in the Great Tit parasitised by fleas; in that study system males, but not females, intensified feeding the nestlings in response to experimental infestation of nests (Christie et al. 1996). The way in which the sexes respond to parasite pressure appears to depend on the general food conditions and on the balance between different parental activities performed during nesting (Tripet et al. 2002). In heavily food-limited systems both sexes may

respond in the same way, especially where the experimental treatment releases parasite pressure rather than intensifies it with respect to the control treatment.

The effect of the anti-parasite treatment on nestling food differed between years, but only the rate of supplying nestlings with caterpillars showed a consistent pattern. Both sexes fed parasitised nestlings with more caterpillars than parasite-free nestlings. Feeding nestlings with spiders and other alternative prey was highly variable between years and did not show any consistent pattern. Actually, an increase in feeding rate in parasite-infested nests as compared to parasite-free nests seems to result mostly from the increase in the number of caterpillars. This suggests that the parents of parasitised broods put a special effort into getting more caterpillars. Caterpillars are preferred prey of Blue Tits (Blondel et al. 1991, Perrins 1991, Bañbura et al. 1999) but the breeding tits need much effort to collect them in many poor habitats including the present study area (Blondel et al. 1991, Bañbura et al. 1994, Grieco 1999, 2002, Naef-Daenzer & Nager 2000). A lack of a consistent pattern in feeding on spiders and other prey suggests that they are collected more opportunistically than caterpillars. This is also supported by the fact that grasshoppers were present in food of nestlings only occasionally (see also Bañbura et al. 1994).

The increase in the number of caterpillars supplied to nestlings was observed in all years of the experimental study. Although the abundance of caterpillars was generally low during that time, there were also some inter-year differences in their peak abundance and timing of maximum availability. Breeding season 1995 may be considered as especially poor in caterpillars because a narrow peak of abundance occurred as late as in July. However, these inter-year differences did not influence the consistent pattern of feeding nestlings with caterpillars in response to experimental treatment. This is inconsistent with our initial predictions as it means that an increase in the effort to get additional caterpillars in response to increased parasitism is advantageous even under very poor trophic conditions. Other invertebrates, especially spiders, may be present in the diet of Corsican Blue Tit nestlings in ample proportions, so that their changes in food of both infested and parasite-free nestlings may just reflect their availability in breeding territories (cf. Bañbura et al. 1994). This would explain a lack of consistent patterns of feeding nestlings with non-caterpillar prey in response to the experiment. To our knowl-

edge, our results are the first to show an effect of parasites on diet composition in a bird species.

Different experimental bird-ectoparasite systems may differ in the efficiency of parental food compensation. In the case of our study population, less intensive feeding of parasite-free nestlings concurs with their higher body mass at the age of 14 days and better survival to fledging. An interpretation may be that in the studied system adult Blue Tits try to compensate parasitic exploitation to nestlings, which, however, is not completely successful. This is consistent with the reports of Hurtrez-Boussès et al. (1997a, 1997b, 1999) for the same Blue Tit population, that blowflies influence nestling body sizes, condition and fledging success.

Tripet & Richner (1997) suggested that the success of parents in compensating nestling damage caused by parasites depends on intensity of infestation, weather and food abundance. Consequently, the influence of infestation on nestling performance may widely differ (see Mazgajski & Kędra 1997 and Kędra et al. 1996 for review). Flea-infested Great Tit nestlings were lighter than parasite-free ones in trophically poor area, whereas no difference was shown in an oak forest rich in food (Christie et al. 1996, Tripet & Richner 1997). Dufva & Allander (1996) and Allander (1998) showed that the influence of fleas on Great Tit nestling body mass may depend on weather conditions, the influence being stronger in years with lower temperature and higher rainfall (see also Merino & Potti 1996, Mazgajski et al. 1997). Bouslama et al. (2001, 2002) found no difference in body mass between infested and parasite-free Blue Tit nestlings, suggesting that parental birds were successful in compensating for parasite damage. Conclusions concerning nestling performance and health under the influence of parasitism may depend on the kind of indicators taken into consideration. Johnson and collaborators suggested that nestling House Wrens *Troglodytes aedon* did not suffer from *Protocalliphora* parasitism when they analysed haematocrit levels but afterwards found a pronounced influence on haemoglobin concentration (Johnson & Albrecht 1993, O'Brian et al. 2001, Morrison & Johnson 2002).

Our results show that *Protocalliphora* parasitism negatively influences nestling performance at the nest as measured by body mass of 14-days-old nestlings and the fledging success, so that parasite-free nestlings are both heavier and better at surviving than infested nestlings. The direct relation between nestling body mass at

fledging and survival proved true in tits (e.g. Perrins 1965, Tinbergen & Boerlijst 1990, Perrins & McCleery 2001). It was also shown that the effect of *Protocalliphora* parasites on chick and juvenile survival may work by an interaction between blood physiology and body mass rather than directly by body mass (Simon 2003, Simon et al. 2003, 2004). Besides these influences of parasitism, we analyzed several other variables, including principal component food and feeding indicators, which also show some impact on nestling performance. In the case of nestling body mass, year effect was not a significant influence, nor were most of the principal component indicators. Only the grasshopper frequency indicator and spider body size indicator, both in male-delivered food, influenced nestling body mass, negatively and positively, respectively. Grasshoppers in nestling diet may indicate especially difficult trophic conditions for Blue Tits, so that their negative relationship with nestling weight would be expected (Bańbura et al. 1994, 1999).

Fledging success, as measured by the proportion of hatchlings that survived to fledging, depended on differences between years and was negatively influenced by laying date and parasite treatment and positively influenced by nestling body mass, which is all consistent with previous findings concerning tits (Perrins 1965, 1970, van Balen 1973, Blondel 1985, Hurtrez-Boussès 1997a, 1997b, 1999, Perrins & McCleery 2001). We also found some effects of multivariate food and feeding indicators on fledging success, including positive effects of the feeding indicator and caterpillar/spider frequency indicator as well as a negative effect of grasshopper frequency indicator. The positive effect of the caterpillar/spider frequency indicator (PC1), the indicator positively correlated with caterpillar frequency and negatively correlated with spider frequency in the nestling diet, suggests that there may be a mutually balanced proportion of caterpillars and grasshoppers which influences the performance of nestlings. It is also possible that the caterpillar/spider frequency indicator measures some favourable aspects of breeding conditions just as the grasshopper frequency indicator may index some detrimental aspects.

All these findings suggest that parental Blue Tits may try to compensate their nestlings for the harm done by the parasitic larvae of *Protocalliphora*, not only by intensifying feeding, but also by supplying the nestlings with a changed diet. More precise answers could be reached by experimental

treatment of both parasitism and food basis, which is unfortunately very difficult.

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STRESZCZENIE

[Wpływ pasożytniczych larw *Protocalliphora* na skład pokarmu korsykańskich sikor modrych: konsekwencje dla kondycji i przeżycia piskląt]

Przedmiotem pracy jest wpływ pasożytniczych larw plujek z rodzaju *Protocalliphora* (Insecta: Diptera, Calliphoridae) wywierany na sikory modre w warunkach korsykańskiego wiecznie-zielonego lasu liściastego. Badania były prowadzone w Pirio (Korsyka) w latach 1994–1997 jako część długoterminowego projektu dotyczącego populacji sikor w południowej części Francji. Badana populacja żyje w środowisku stosunkowo ubogim w pokarm, co wiadomo dzięki systematycznym badaniom obfitości gąsienic. Równocześnie pasożytnictwo larw *Protocalliphora* w stosunku do lęgów sikor osiąga tu rekordowe nasilenie; ekstensywność sięga niemal 100%, zaś intensywność – 100 larw przypadających na jedno gniazdo. W latach 1994–1996 przeprowadzono eksperyment, polegający na termicznym zabiciu pasożytów, któremu poddano 16 gniazd. Kolejne 24 gniazda, w stosunku do których nie dokonywa-

no manipulacji, traktowano jako próbę kontrolną. W roku 1997 nie prowadzono doświadczeń, a 9 gniazd włączono do analizy dla poszerzenia tła opisowego. Wszystkie wymienione gniazda były filmowane, a nagrania odtwarzane w warunkach laboratoryjnych były poddane analizie pozwalającej opisać częstość karmienia i skład pokarmu, a także różne zachowania rodzicielskie.

Pod wpływem zabiegu likwidującego pasożyty, pisklęta były karmione rzadziej niż pisklęta kontrolne (8 razy w stosunku do 11 razy na godzinę na pisklę, odpowiednio). Zaobserwowano także zmiany w składzie pokarmu piskląt. Najbardziej wyrazisty i stały wzorzec pojawił się w przypadku gąsienic jako kluczowego składnika diety. Lęgi pozbawione nacisku pasożytnictwa były karmione mniejszą liczbą gąsienic niż lęgi kontrolne. Przeciętne pisklę z zapasożyconego lęgu kontrolnego otrzymywało średnio 2.6 gąsienicy na godzinę więcej niż pisklę z lęgu eksperymentalnego. To wskazuje, że pod wpływem pasożytnictwa dorosłe sikory podejmowały specjalny wysiłek dla zrekompensowania pisklątom szkodliwego wpływu pasożytniczych larw plujek.

Mimo że zarówno intensywność karmienia, jak i skład pokarmu mają wpływ na kondycję i przeżycie piskląt w gnieździe, to jednak wysiłek rekompensacyjny rodziców nie jest w pełni skuteczny. Pisklęta zapasożycone i tak rozwijały się wolniej i przeżywały gorzej niż pisklęta wolne od pasożytów. Pasożytnicze larwy *Protocalliphora* mają zatem podwójny negatywny wpływ na sikory: oddziałują na pisklęta, ale także zmuszają dorosłe ptaki do większego wysiłku rodzicielskiego. O ile wiemy, jest to pierwsza praca dokumentująca wpływ pasożytnictwa na skład pokarmu dostarczanego pisklątom ptaków.