Variations in prevalence and intensity of blow fly infestations in an insular Mediterranean population of blue tits

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Abstract: A Corsican population of blue tits (*Parus caeruleus*) suffers extremely high levels of infestation by two species of blow flies (genus *Protocalliphora*) that have been suspected to influence the life-history traits of their hosts. By quantifying the abundance of the blow fly larvae infesting each brood of this population during 2 consecutive years, we showed that the distribution of these parasites did not differ from a Poisson distribution. The intensity of blow fly parasitism (mean parasite load per infested nest) was independent of the time of breeding and the available space in the nest of their bird hosts. Moreover, the total blow fly load per nest increased significantly with the number of chicks, whereas the parasite load per chick was not linearly related to brood size.

Résumé : Chez une population corse de Mésanges bleues (*Parus caeruleus*), les charges parasitaires des larves de deux espèces de *Protocalliphora*, se sont avérées exceptionnellement élevées et pourraient influencer les caracteristiques démographiques de l'hôte. Dans cette étude, nous avons quantifié l'abondance des larves de *Protocalliphora* dans chaque nichée de cette population durant 2 années consécutives et avons démontré que la distribution de parasites n'était pas significativement différente d'une distribution de Poisson. De plus, (l'intensité moyen de parasites par nid infesté) était indépendante de l'époque de reproduction et de l'espace disponible dans le nid hôte. Enfin, nombre totale de parasites par nid augmentait significativement en fonction du nombre d'oisillons dans la nichée, alors que la charge parasitaire par oisillon ne variait pas de façon linéaire en fonction du nombre d'oisillons dans la nichée.

Introduction

Since parasites can affect the fitness of their hosts (review in Toft et al. 1991; Combes 1995), they should play an important role as selective agents in the evolution of their hosts' behaviour (e.g., Clayton 1991; Keymer and Read 1991; Hart 1994), life-history traits (e.g., Minchella and Lo Verde 1981; Hudson and Dobson 1991; Hochberg et al. 1992; Lafferty 1993; Richner and Heeb 1995), sexual selection (e.g., Hamilton and Zuk 1982; Read 1988; Møller 1990), and habitat choice (e.g., Brown and Brown 1986; Loye and Carroll 1991; Christe et al. 1994). The relationship between the fitness consequences of parasitism and the evolution of host life-history traits would depend on the spatial distribution of parasites (e.g., May 1985; Minchella 1985; Jaenike 1996) and their life-history characteristics (e.g., Richner and Heeb 1995).

On the island of Corsica, one population of blue tits (*Parus caeruleus ogliastrae*) has the smallest clutch size and the latest breeding time so far recorded in Europe (Blondel

1985; Blondel et al. 1991, 1993). Moreover, in this population the variation in laying date is significantly smaller than in other Mediterranean mainland populations (Blondel et al. 1987) and individuals tend to build nests of smaller size than their mainland counterparts (P. Perret, unpublished data). Besides these differences in life-history traits, this Corsican population suffers the highest infestation rates by larvae of blow flies (*Protocalliphora*: Diptera: Calliphorideae) so far described in European birds (Hurtrez-Boussès 1996; for comparisons see Eeva et al. 1994 and Merino and Potti 1995).

Larval *Protocalliphora* spp. are intermittent blood-sucking parasites of chicks (Bennett 1957; Sabrosky et al. 1989; Rognes 1991). The free-living nectarivorous adults lay eggs in nests after the chicks hatch, and three larval stages develop on the nestlings before pupation occurs (Gold and Dahlsten 1989; Bennett and Whitworth 1991). Most of the studies on bird – blow fly systems have shown little or no effect of these parasites on nestling survival and growth patterns (see reviews in Johnson and Albrecht 1993; Møller 1997). In the population we studied, we found no effect of

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blow fly load on survival during the nestling stage (Hurtrez-Boussès et al. 1997*a*, 1997*b*). However, we showed that these parasites caused a severe decrease in body condition at fledging (Hurtrez-Boussès et al. 1997*a*, 1997*b*): infested chicks had significantly smaller body mass and tarsus length and lower haematocrit levels than chicks from experimentally deparasitized broods (Hurtrez-Boussès et al. 1997*b*). Additionally, parents of infested broods spent more time in sanitation and feeding activities than did parents of experimentally deparasitized broods (Hurtrez-Boussès 1996; Hurtrez-Boussès et al. 1998). Blow flies might therefore exert important pressure on the life-history characteristics of the host (Blondel 1985). Thus, determining the relationships between host life-history traits and infestation levels is crucial to any investigation of the susceptibility to parasitism of hosts with specific life-history traits. In this paper we address the following questions: (*i*) How are individual parasites distributed among nests of blue tit hosts, and what proportion of hosts suffers heavy parasite loads? When the parasite distribution is strongly clumped, only a small proportion of broods will suffer heavy parasite loads. (*ii*) Do infestation rates vary among years? As suggested by Richner and Heeb (1995) with respect to the evolution of clutch size, if parasite loads vary among years, we would expect selection for phenotypic plasticity in life-history traits that could be adjusted in response to parasite constraints. (*iii*) Do parasite loads fluctuate during the breeding season? It has been hypothesised that the extremely high abundances of individuals of *Protocalliphora* spp. in Corsica are related to the high ambient temperatures in this area, where blue tits start breeding very late in the season relative to mainland congeners (Blondel et al. 1987). Moreover, Rogers et al. (1991) suggested that infestation by blow flies increases over a breeding season because newly emerged flies can reinfest the nests. If so, earlier breeders should tend to escape heavy parasite loads compared with later breeders. (*iv*) Does nest volume affect blow fly load? The number of larvae of *Protocalliphora* spp. may depend on the space available in the nest because larvae would suffer from competition for space (Gold and Dahlsten 1983) and (or) nest sanitation would be more efficient in thin, flimsy nests (Eshuis-van der Voet and Houwink 1976). As parasite load may decrease with nest volume, blue tits that construct small nests should suffer fewer parasite constraints than their counterparts that construct larger nests. (*v*) Is there a relationship between parasite load and brood size? According to Richner and Heeb's (1995) model, since blow fly larvae are parasites with a long cycle relative to the duration of the nestling stage of their hosts, we would expect a "dilution effect," i.e., the parasite load per chick should decrease with increasing brood size.

Methods

Study area

The study was carried out during the 1995 and 1996 breeding seasons in an evergreen forest of holm oak (*Quercus ilex*) (for further details see Blondel 1985 and Blondel et al. 1987). In this 40-ha study site, 137 nest boxes are evenly distributed at a density of 2/ha. Almost all the blue tits in this population breed in the nest boxes. They usually start laying about May 10, and produce clutches of, on average, 6.4 eggs that are incubated for about 14 days. The young leave the nest when they are 20–21 days old.

Blow fly larvae usually pupate after the young birds have fledged (S. Hurtrez-Boussès, personal observation).

Daily ambient temperature and rainfall measurements were obtained from records of the meteorological station at Calvi, which is located 20 km from the study area and for which the range of altitude and vegetation parameters is similar to that of the study area.

Parasite load and traits of the host

From the beginning of the breeding season, each nest box was routinely visited at least once a week to record hatching date and brood size at hatching, and then at day 15 (hatching day = day 0) and at fledging. Just after fledging, nests were collected and stored in plastic bag. In the laboratory, nests were meticulously examined to determine the number of larvae and pupae of *Protocalliphora* spp. (parasite load). Because of possible bias due to decomposition of parasites after the chick's death, nests with complete failure (i.e., all the chicks of the brood died) were excluded from analyses.

Two species of blow flies were found (Dr. K. Rognes, personal communication): *Protocalliphora azurea* and *Protocalliphora falcozi*. However, since the current taxonomy of these parasites is based on adult characters, it was not possible to distinguish between the two larval forms. Thus, the two species were pooled and are referred to as *Protocalliphora* spp. The spatial distribution of other parasitic arthropods (fleas, mites, and lice) was minimal (prevalences <3%), so their impact on blue tits and their competition with blow fly larvae were considered to be negligible.

We measured the thickness of the nest material when chicks were 2 days old to estimate the volume of nest material (the dimensions of the nest boxes are constant). In the 1995 breeding season we manipulated the thickness of the nests as follows. At day 9 of incubation, the thickness of 14 nests was increased ("increased" group) to 8 cm by adding moss previously disinfected in a microwave oven (1 min at 850 W) to the nest material, and the thickness of 16 nests was decreased ("decreased" group) to 3 cm by removing nest material. During the manipulation, eggs were temporarily removed from the nest. The two groups did not differ in hatching date (Mann–Whitney U test, $U = 72.5$, ns) or in brood size at hatching ($U = 71.5$, ns), at day 15 ($U = 106.5$, ns), or at fledging ($U = 109$, ns).

Statistical analyses

The following ecological parameters of parasitism (Margolis et al. 1982) were examined: prevalence (percentage of nests infested by *Protocalliphora* spp.), mean abundance (mean parasite load per nest), and mean intensity (mean parasite load per infested nest). Since the blow fly larvae are attached to their hosts only intermittently, it was impossible to measure the parasite load per chick directly. Therefore, the statistical unit was the nest and the dependent variables were the total and mean (per chick) parasite load per infested nest. Statistical analyses were carried out using GLIM software (Numerical Algorithms Group 1986). Since the dependent variables were "count data," linear regressions were not appropriate (especially because they can lead to negative fitted values; Crawley 1993). Therefore, we used a Poisson error. Explanatory variables were year, hatching date, thickness of nest material (discrete variable for 1995 and continuous for 1996), and brood size at day 15. To test an eventual quadratic effect of brood size on total and mean parasite load per infested nest, we included the variable (brood size)^2 in the models. All the explanatory variables were introduced into the maximal model and those without significant effect were deleted in order to obtain the minimal model. With Poisson errors, the change in deviance due to a given variable follows a χ^2 distribution, therefore the significance of each explanatory variable was tested by comparing the change in deviance with the theoretical χ^2 value (Crawley 1993). Nonparametric tests were performed using Logitheq (Boy 1981) and NPSTAT 2.5 software (Praxème R&D, Montpellier, France).

Table 1. Parasitism of blue tit nests by *Protocalliphora* spp. in 1995 and 1996.

Year	n	Prevalence (%)	Intensity[a]	Abundance[a]	Intensity/ chick[a]	Abundance/ chick[a]
1995	30	93.3	39.1±20.3	36.5±21.9	9.7±4.4	9.0±4.9
1996	29	96.5	70.3±24.8	67.9±27.6	14.1±4.5	13.6±5.1

Note: n is the total number of nests; "prevalence" is the percentage of infested nests; "intensity" is the number of blow fly larvae per infested nest; "abundance" is the number of blow fly larvae per nest; "intensity/chick" is the number of blow fly larvae per chick in an infested nest; "abundance/chick" is the number of blow fly larvae per chick.

[a]Values are given as the mean ± SD.

Fig. 1. Total parasite load of blow fly larvae per infested nest (i.e., intensity) as a function of brood size at 15 days, and fitted curves. Parasite load values are ln-transformed. The open symbols and thin line denote data for 1995 (the fitted curve is linear); the solid symbols and thick line denote data for 1996 (the fitted curve is quadratic).
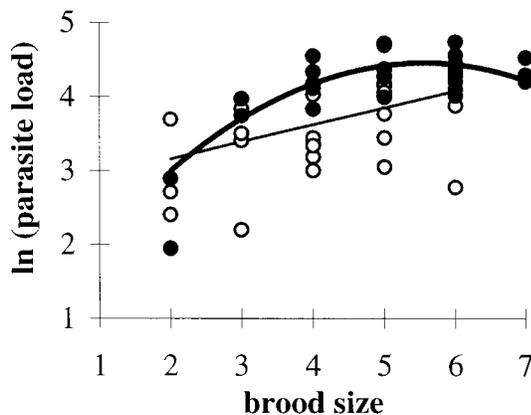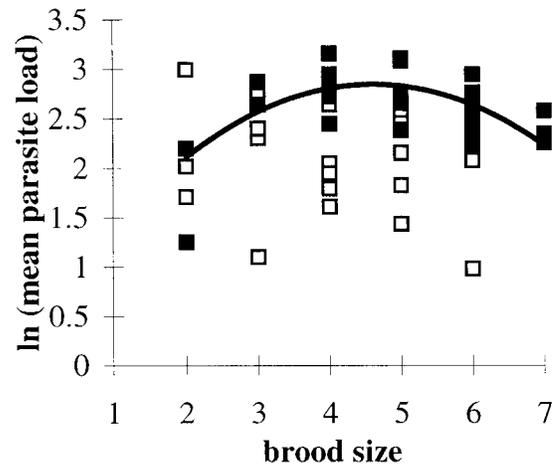

Fig. 2. Mean parasite load of blow fly larvae (number of larvae per chick in infested nests) as a function of brood size at 15 days, and the fitted curve for 1996. Mean parasite load values are ln-transformed. Open symbols denote data for 1995; the solid symbols and thick line denote data for 1996 (the fitted curve is quadratic).

Results

Ecological parameters for blow flies

Prevalences, mean abundances, and mean intensities of parasite loads are presented in Table 1.

For both years the frequency distributions of parasite load per nest (i.e., abundance) did not significantly differ from a Poisson distribution (Kolmogorov–Smirnov test, 1995: $K = 0.09$, ns; 1996: $K = 0.12$, ns). A similar result was found for the frequency distributions of mean parasite load per chick (i.e., intensity) (Kolmogorov–Smirnov test, 1995: $K = 0.09$, ns; 1996, $K = 0.07$, ns).

Year effect

Prevalences did not differ significantly between years (Fisher's exact test, $p = 0.51$, ns). Controlling for the other explanatory variables (brood size, date, thickness of the nest), both total and mean parasite load per infested nest differed significantly between years ($\chi^2_{[1]} = 14.0$, $p < 0.005$, and $\chi^2_{[1]} = 13.17$, $p < 0.005$, for 1995 and 1996, respectively).

Relation to host traits

Since parasite-load values and the procedure to test the nest-thickness effects differed between years, we analysed the effects of brood size, hatching date, and thickness of nest on parasite load separately for the 2 years. In both years nei-

ther hatching date (1995: $\chi^2_{[1]} = 0.11$, ns; 1996: $\chi^2_{[1]} = 0.006$, ns) nor thickness of nest material (1995: $\chi^2_{[1]} = 0.98$, ns; 1996: $\chi^2_{[1]} = 2.79$, ns) affected the parasite load per nest. In 1995, only brood size at day 15 had a statistically significant effect on parasite load per nest (brood size: $\chi^2_{[1]} = 8.71$, $p < 0.01$; (brood size)^2: $\chi^2_{[1]} = 2.07$, ns; Fig. 1); the number of blow fly larvae per infested nest increased significantly with brood size. In 1996 there was a significant quadratic relationship between brood size and parasite load (brood size: $\chi^2_{[1]} = 24.21$, $p < 0.001$; (brood size)^2: $\chi^2_{[1]} = 18.41$, $p < 0.001$; Fig. 1); the parasite load was greatest for broods of 5 chicks.

In 1995, none of the explanatory variables had a significant effect on mean parasite load per infested nest (brood size: $\chi^2_{[1]} = 0.20$, ns; (brood size)^2: $\chi^2_{[1]} = 0.132$, ns (Fig. 2); hatching date: $\chi^2_{[1]} = 0.10$, ns; thickness of the nest: $\chi^2_{[1]} = 1.36$, ns). In 1996 we found a significant quadratic relationship between mean parasite load and brood size (brood size: $\chi^2_{[1]} = 17.49$, $p < 0.001$; (brood size)^2: $\chi^2_{[1]} = 18.17$, $p < 0.001$ (Fig. 2)). Neither of the other two variables had a significant effect on mean parasite load in 1996 (hatching date: $\chi^2_{[1]} = 0.27$, ns; thickness of the nest: $\chi^2_{[1]} = 2.28$, ns).

Discussion

Distribution of blow fly larvae

In both years the distribution of *Protocalliphora* spp. larvae did not differ significantly from a Poisson model. These

findings differ from the usual frequency distribution of parasites, which is most often aggregated (May 1985; Dobson and Merenlender 1991; Combes 1995). More broods suffer heavy parasite loads in a Poisson distribution than in an aggregated distribution. Gold and Dahlsten (1983) estimated that a mean parasite load exceeding 8 blow fly larvae per chick would have a debilitating effect on birds with a body mass similar to that of blue tits. In this case study, the proportion of broods under this threshold was 50% in 1995 but only 7% in 1996.

Interannual variation in parasite load

Our results showed interannual variation in parasite load. Environmental factors that simultaneously affect the host and its parasites might be involved in this year effect. As shown by Perrins and McCleery (1989), one component of the between-year variation in clutch size of blue tits is the amount of food available. In our case study, resource availability for parasites (i.e., the number of chicks) was significantly higher in 1996 (5.03 ± 1.40 (mean $\pm$ SD)) than in 1995 (3.97 ± 1.27; $F_{[1,57]} = 9.40$, $p < 0.01$). However, this is insufficient to explain the significantly heavier parasite loads in 1996 than in 1995, since the year effect remains after brood size is controlled for. Environmental conditions during winter and at the beginning of spring (e.g., temperature, growth of vegetation) might affect the survival and (or) breeding patterns of both prey and parasites. During the breeding season (from the first hatching date to the last fledging date), the daily mean temperatures were significantly higher in 1996 ($21.1 \pm 2.7°C$ (mean $\pm$ SD), $n = 37$ days) than in 1995 ($19.9 \pm 2.5°C$, $n = 39$ days; $F_{[1,74]} = 4.28$, $p < 0.05$). Although the difference was not significant, daily rainfall was higher in 1995 (12.3 ± 45.7 mm (mean $\pm$ SD), $n = 39$ days) than in 1996 (9.6 ± 36.1 mm, $n = 37$ days; $F_{[1,74]} = 0.08$, ns). This is consistent with the results of Merino and Potti (1996), who found that blow fly infestations were lower during cold and wet years. Although parasite load varied among years, the levels were high enough in both years that the majority of the nests suffered detrimental effects of blow flies.

Parasite load and life-history traits of blue tits

Since we found no relationship between parasite load and hatching date, our results do not support the hypotheses of Blondel et al. (1987) and Rogers et al. (1991), who suggested an increase in blow fly load at the end of the breeding season. Therefore, later breeders did not suffer heavier parasite loads.

In contrast to the hypothesis of Gold and Dahlsten (1983), parasite load was independent of the thickness of nest material, even in 1995, when this parameter was manipulated. This result is similar to that obtained by Rogers et al. (1991) with *Protocalliphora sialia*, which parasitizes tree swallows (*Tachycineta bicolor*). Therefore, blue tits building thin nests would not suffer lower blow fly infestations than their counterparts with bulkier nests.

Finally, we found that the total number of blow fly larvae per nest was not independent of brood size; in 1995 the parasite load increased with brood size and in 1996 the parasite load was best described by a quadratic function of brood size, nests with 5 chicks (mean brood size) being the most heavily parasitized. Moreover, we found no significant linear relationship between the parasite load per chick and brood size (Fig. 2). In 1995 the mean parasite load was independent of brood size and in 1996 the mean parasite load was best described by a quadratic function of brood size, broods of intermediate size being the most heavily parasitized (Fig. 2). Richner and Heeb's (1995) model assumes that when ectoparasites have a long cycle relative to the duration of the host nestling stage, parasite load is independent of brood size and mean parasite load decreases linearly as brood size increases (i.e., a dilution of the number of parasites per chick). In this case, evolution should favour larger brood sizes. Surprisingly, although *Protocalliphora* spp. are long-cycled parasites relative to the blue tit nestling stage, we did not find a clear dilution effect (i.e., a decrease in mean parasite load with increasing brood size); mean parasite load was independent of brood size in 1995 and was minimal for both small and large broods in 1996 (Figs. 1 and 2). Therefore, contrary to the predictions of Richner and Heeb's (1995) model, we would not necessarily expect selection for larger brood size in the study population.

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