

# Ectoparasitism and the trade-off between current and future reproduction

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Ectoparasites are an ubiquitous element of the natural environment of most organisms, and by their effect on reproductive success of the host they are likely to affect the life-history trade-off between current and future reproduction. Since parents are in control of parental effort, they can compensate for the effect of ectoparasites on the current offspring by an increase in the rate of food provisioning to the nest. An increase in parental effort will enhance current reproductive success, but as predicted by the trade-off and tested here, the parents' future reproductive success will be impaired. Among passerine birds, the blue tit shows the highest prevalence and intensities of infection of the nest with ectoparasitic hen fleas. For blue tits (*Parus caeruleus*) we show experimentally that ectoparasitic hen fleas (*Ceratophyllus gallinae*) affect both the parents' likelihood to return as a breeder the year following ectoparasite exposure and their subsequent reproductive performance, suggesting that ectoparasites can modify this life-history trade-off. Our study suggests that parents pay the cost of ectoparasitism by a reduction in future reproductive success, which may be mediated by the increase in current parental effort, as predicted by life-history models.

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Life-history models predict a trade-off between current and future reproduction. Both current and future reproductive success are functions of reproductive effort: current reproductive success increases and future reproductive success decreases with current reproductive effort (Schaffer 1974, Roff 1992, Stearns 1992). Experimental studies have shown that hematophagous ectoparasites of birds can severely reduce current reproductive success through their effect on body condition and mortality of nestlings (Brown and Brown 1986, Møller 1990, Richner et al. 1993). For parasites which directly affect only current but not future reproduction, the expected host response is an increase in reproductive effort, as shown both theoretically (Perrin et al. 1996) and empirically in great tits (Christe et al. 1996) and blue tits (Tripet and Richner 1997a). The increase in parental effort partly compensates for the parasites' effect on the offspring. According to the trade-off,

however, an increased parental effort will indirectly reduce future reproductive success of the parents by its effect on parental survival ( $p_a$ ) and/or on the residual reproductive value ( $v_{t+1}$ ) of parents. Thus, the decrease in future reproductive success ( $p_a v_{t+1}$ ) of parents is mediated by their response to the ectoparasites.

Prevalence of fleas in hole-breeding passerines is naturally high, and the highest prevalence and intensity of infestation with the hen flea (*Ceratophyllus gallinae*) is found in the blue tit (*Parus caeruleus*) (Harper et al. 1992, Tripet and Richner 1997b). For blue tits, an experimental infestation of nests at hatching with hen fleas has shown no detectable effect of fleas on nestling body condition and nestling mortality (Tripet and Richner 1997a). Parents of infested nests, however, increased their rate of food provisioning to nestlings by 29% compared to nests kept free of fleas (Tripet and Richner 1997a). The fact that no measurable effect of

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fleas on nestlings could be detected may not be taken to suggest that hen fleas are benign parasites before the effect of parental food compensation on survival and reproductive value of parents has been assessed. Here we evaluate a main prediction of the reproductive trade-off hypothesis, which holds that an increase in current reproductive effort, due to the parasites, will lower one or both components of future reproductive success, survival  $p_a$  and/or residual reproductive value  $v_{t+1}$ .

## Methods

### Treatment in 1995

In a single-brooded population of blue tits (*Parus caeruleus*) near Basel, Switzerland, breeding in nest-boxes provided since 1994, we manipulated, in spring 1995, the load of ectoparasitic fleas (*Ceratophyllus gallinae*) after hatching of the birds. At hatching we first heat-treated the nest material of all nests in order to kill any naturally occurring nest parasites. On the second day after hatching, we then randomly infested 22 nests with 90 adult fleas and kept 21 nests free of fleas. The range of natural infestations at hatching is, to our knowledge, not known. Nevertheless, 90 fleas during the nestling period are within the range found naturally (Harper et al. 1992, Tripet and Richner in press). The experimental treatment with and without parasites at hatching was sequentially alternated (hatching date of infested nests: May  $5.3 \pm 1.9$  SD; parasite-free nests: May  $4.9 \pm 1.8$  SD;  $p = 0.61$ ). Five pairs deserted before fledging of the nestlings and are excluded from the present analysis, i.e. two nests of the parasite-free group and three of the infested group. Three infested broods with known polygamous fathers were also excluded. The resulting sample size in 1995 is then 19 parasite-free and 16 infested broods. Brood size at hatching in 1995 was  $10.8 (\pm 1.4$  SD) for parasite-free and  $10.2 (\pm 2.5$  SD) for infested nests ( $t$ -test,  $t = 0.895$ ,  $df = 33$ ,  $p = 0.38$ ). Nestlings were measured 14 d after hatching. The flea treatment had no significant effect on nestling mass, condition and tarsus length. Feather length was significantly reduced in nestlings of infested broods. Nestling survival in infested nests was 100% and 99.5% in parasite-free nests. Seven days after hatching, both parents were captured at the nest. There was no significant difference between the two experimental groups in adult body size: mean tarsus length was 19.3 mm ( $\pm 0.1$  SE) for females of parasite-free and 19.1 mm ( $\pm 0.1$  SE) for females of infested nests ( $t$ -test,  $t = 0.950$ ,  $df = 33$ ,  $p = 0.35$ ); mean tarsus length of males was 19.7 mm ( $\pm 0.1$  SE) in the parasite-free group and 19.8 mm ( $\pm 0.1$  SE) in the infested group ( $t$ -test,  $t = 0.652$ ,  $df = 33$ ,  $p = 0.52$ ). All adults and young birds were marked individually with numbered aluminium rings. More details may be found in Tripet and Richner (1997a, b).

### Treatment in 1996

In spring 1996 the parent blue tits of our study population were recaptured to assess return rates of breeders of 1995 as breeders in 1996. Twenty adult birds were recaptured within the study area of which 18 were breeding with a new partner. Breeding performance in 1996 is therefore evaluated for each partner separately and individual birds are taken as independent data points. Ten of the birds bred in another nestbox than in 1995. The change of breeding box was unrelated to parasite treatment in 1995 ( $p > 0.6$ ). In order not to influence the choice of breeding sites in 1996, the nest-boxes were in 1996 not infested before incubation. Reproductive success in 1996 was monitored as in 1995. Due to the small sample size of returning birds, sexes are not separated in the analysis of reproductive success. Since only local but not global survival of parents can be measured, we also evaluate the dispersal distances of infested and non-infested parents within the limits of the study population. No difference in dispersal distances supports the assumption that the ectoparasite treatment did not bias our measure of survival in favour of one of the treatment groups. In all analyses of data for 1996, birds only are included which completed breeding in 1995 up to fledging of young and thus supported the full cost of reproduction. These are in total 69 individuals.

## Results

### Return of breeders, $p_a$

Ectoparasites present in the nest of host parents in 1995 had a significant effect on the birds' likelihood to return as breeders in 1996: without fleas 15 of a total of 37 uninfested birds returned as breeders the following year (= 40.5%), whereas only 5 of 32 infested birds of the infested group returned (= 15.6%); females and males did not differ significantly in the likelihood to return (logistic regression: fleas: Wald  $\chi_1^2 = 4.93$ ,  $p = 0.026$ ; sex: Wald  $\chi_1^2 = 3.04$ ,  $p = 0.081$ ; interaction: Wald  $\chi_1^2 = 0.37$ ,  $p = 0.54$ ). Mean dispersing distances from 1995 to 1996 were not significantly different (Mann-Whitney  $U$  test,  $U = 34.5$ ,  $p = 0.78$ ) between birds uninfested ( $33.6$  m  $\pm 45.0$  SD) or infested ( $36.4$  m  $\pm 38.0$  SD) in 1995.

### Difference in residual reproductive value of parents $v_{t+1}$ in relation to parasitism

Among the parents of 1995 which returned to breed successfully in 1996, the ones which were infested in 1995 laid 1.8 ( $\pm 0.9$  SE) fewer eggs and raised 2.0 ( $\pm 1.1$  SE) fewer young in 1996 than in the previous year. Birds of the uninfested group laid 0.6 ( $\pm 0.4$  SE) eggs

more and raised 0.3 ( $\pm 0.5$  SE) young more in 1996 than in 1995. The difference between the two groups in the change of clutch size ( $t$ -test,  $t = 2.96$ ,  $df = 18$ ,  $p = 0.008$ ) and the number of young raised (Fig. 1) is significant ( $t = 2.24$ ,  $df = 18$ ,  $p = 0.038$ ).

### Future reproductive success, $p_{av_{t+1}}$ , in relation to parasitism

The effect of ectoparasites on future reproductive success can be calculated as the product of the probability of returning as a breeder and the offspring number after the return. For the uninfested parents this calculates as 4.31 young ( $\pm 0.19$  SE) but for the infested parents as 1.50 young ( $\pm 0.14$  SE) only ( $t$ -test,  $t = 7.99$ ,  $df = 18$ ,  $p < 0.001$ ).

### Discussion

This study illustrates that ectoparasites affect the trade-off between current and future reproduction. Nestlings are the main source of energy and nutrients required for the reproduction of the parasite, and this drain of resources will lower nestling growth and body condition, unless parents compensate by an additional investment. As shown previously parents of infested broods increased food provisioning rates to nestlings by 29%, and nestling body mass, condition, and survival were not significantly different ( $p > 0.25$ ) between infested and parasite-free broods (Tripet and Richner 1997a). Thus, we expect no significant difference in the number

of recruits from the two treatments. Four of the 19 uninfested broods of 1995 and two out of the 16 infested broods produced at least one recruit into the breeding population of 1996 (Fisher exact test,  $p = 0.67$ , but note the small sample size for recruits). This may suggest that the increase in parental effort compensates for the effect of ectoparasites on the nestlings. Male and female body condition, 7 d after hatching of the brood in 1995, was not different (Tripet and Richner 1997a) between parents of infested and parents of uninfested broods (females:  $p > 0.5$ ; males:  $p > 0.2$ ). Thus, even in the absence of direct effects of the parasites on parents, their future reproductive success is impaired, as predicted by the life-history model (Perrin et al. 1996) and shown by the present empirical example. We cannot entirely exclude, however, that effects on parental body condition occurred later in the period of parental care, i.e. between catching of the adults and fledging of their young. Observed return rates of breeders are probably not biased in favour of one or the other treatment group since there was no significant difference in local dispersal distances of uninfested and infested birds from 1995 to 1996.

How is a parasite-mediated increase in parental effort mediated to future reproductive success? One could argue that fleas may be vectors for other pathogens, and that the reduction in future reproductive success of infested parents may then not be due to the increase in parental effort but, although unlikely (Baker 1967), rather to such unknown flea-transmitted pathogens. In a study on great tits (*Parus major*) we have manipulated parental effort solely by changing brood size (Richner et al. 1995) and kept all broods free of ectoparasites. Males of enlarged broods increased feeding rates by 50%, and as a result the prevalence of bird malaria (*Plasmodium* spp.) in these males increased by nearly 40%. Return rates of infected males were significantly reduced (Richner et al. 1995). In a further study, reproductive effort of females was manipulated by increasing their rate of egg laying, which again had the effect of an increase in patent infections of females with *Plasmodium* (Oppliger et al. 1996). One physiological mechanism for the mediation of current reproductive effort into future reproductive success may therefore operate via a reduction in the immunocompetence (see also Gustafsson et al. 1994). Thus, if parent birds compensate for the effect of ectoparasites on nestlings by an increase in parental effort, a reduction in future reproductive success of flea-infested birds is predicted even without the transmission of other pathogens. Experimental evidence showing that ectoparasites affect the trade-off between current and future reproduction is still scarce: Møller (1993) has demonstrated that mites affect the intraseasonal trade-off between first and second clutches in barn swallows (*Hirundo rustica*), and Brown et al. (1995) have shown an effect of

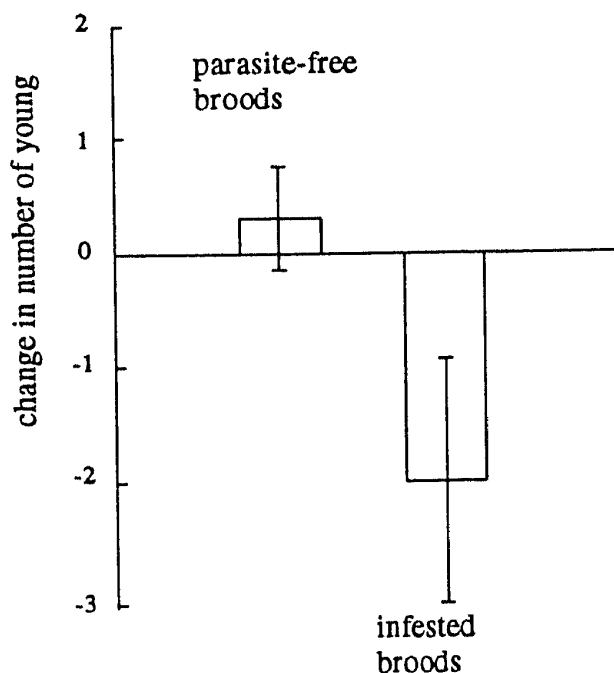


Fig. 1. Change in number of young ( $\pm 1$  SE) of individual adult blue tits from 1995 to 1996 in relation to experimental infestation status of their nest in 1995.

swallow bugs on long-term survival of adult cliff swallows (*Hirundo pyrrhonota*).

In summary, this study shows that ectoparasites affect the trade-off between current and future reproduction. It suggests that parents, by the increase in their rate of food provisioning to nestlings to compensate for the effect of a parasite, pay the cost of parasitism by a loss of future reproduction.

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