*Journal of Animal Ecology* 2004
**73**, 216–226

# Life history and fitness consequences of ectoparasites

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## Summary

**1.** For iteroparous organisms life-history theory predicts a trade-off between current and future reproduction, and therefore the evolution of host responses to current parasite infestation that will maximize lifetime reproductive success. The parasite-induced variation in reproductive success is thus not the net result of parasite infestation alone, but the parasite-mediated outcome of optimal resource allocation among current and future reproductive events. Understanding the importance of parasites for the evolution of host life history therefore requires an experimental investigation of the effects of parasites over the host's life span. Such studies are currently scant.

**2.** We manipulated the load of an ectoparasite, the hen flea (*Ceratophyllus gallinae*), in the nests of its most common host, the great tit (*Parus major*), over a period of 4 years and recorded, the components of current and future reproductive success including survival, divorce, breeding dispersal and various reproductive parameters. Finally we assessed, for females only as paternity of males was unknown, the lifetime reproductive success as a close correlate of Darwinian fitness.

**3.** For current reproduction, our experiment demonstrates that parasites reduce current reproductive success via an increase in the probability of nest failure during incubation and the nestling period. In the presence of fleas, clutch size and the number of fledglings were reduced while the incubation and the nestling period were prolonged. Thus parasitism led to an increase in parental effort but nevertheless reduced current reproductive success.

**4.** For future reproduction, the experiment shows that females breeding in infested nests dispersed over longer distances between breeding attempts. The divorce rate following infestation, the probability of breeding locally in the future and residual reproductive success were not affected significantly by ectoparasites. The study thus suggests that hen fleas play a minor role in shaping the trade-off between current and future reproduction.

**5.** Lifetime reproductive success of females, measured as the total number of locally recruiting offspring over the 4 experimental years, was reduced significantly by ectoparasites. The negative effect of parasites arose by a reduction of the number of fledglings per breeding attempt rather than by a reduction of the number of breeding attempts.

*Key-words*: *Ceratophyllus gallinae*, ectoparasite, great tit, hen flea, host–parasite interaction, life history, lifetime reproductive success, *Parus major*.

*Journal of Animal Ecology* (2004) **73**, 216–226

## Introduction

Life histories are often mediated by parasites, and are the outcome of a variety of adaptive behavioural responses to reduce the effects of costly parasitism (Clayton & Moore 1997). Parasite-induced adaptations usually occur during parasite exposure, as shown in a variety of experimental studies on bird–ectoparasite systems (e.g. alteration of the start of reproduction (Møller 1993; Oppliger, Richner & Christe 1994), of the clutch size (Richner & Heeb 1995; Møller 1997; Richner & Tripet 1999; Martin *et al.* 2001) or of parental investment (Møller 1993; Christe, Richner & Oppliger

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1996a; Tripet & Richner 1997). In iteroparous species parasite-induced behavioural changes may even occur after parasite infestation and several studies show that previous parasite exposure can lead to reduced parental survival or resource allocation to future reproduction (Perrin, Christe & Richner 1996; Clayton & Moore 1997; Richner & Tripet 1999). On the other hand, parental effort may be adjusted to the reproductive value of offspring (e.g. Schaffer 1974; Møller 1997) and thus reduced in ectoparasite presence. As a trade-off between current and future reproduction is predicted (Stearns 1992; Roff 1992), parents with reduced current investment should consequently invest more into future reproduction.

The parental decision to compensate for the effects of the parasites on current reproduction depends on the fitness function that links current and future reproductive success to current effort (e.g. Schaffer 1974; Perrin *et al.* 1996). These functions are not known for most host–parasite systems but current evidence suggests that hen flea-infested great tits should increase current reproductive effort (Perrin *et al.* 1996). Thus the estimation of parasite-induced fitness reduction requires an experimental assessment of the effects of parasites on both current and future reproductive success, and in particular the measuring of lifetime reproductive success as a close fitness correlate.

In an experiment over 4 subsequent years we studied short- and long-term effects of the nest-based haematophagous hen flea (*Ceratophyllus gallinae* Schrank) on its natural host, the great tit (*Parus major* L.), a small hole-nesting passerine (Gosler 1993). Finding an optimal design for the investigation of host–parasite interactions is not obvious (Møller 1989; Lehmann 1993). On one hand, results of non-manipulative studies cannot be interpreted properly; on the other hand, manipulating parasites in a natural way is difficult, as direct manipulation of parasites may interrupt the natural parasite dynamics, life cycles (Møller 1989) and the natural selection acting on the parasites. This can lead to over-estimation or under-estimation of the harmfulness of parasites depending on the timing (Lehmann 1993) and on the virulence of the parasites applied. We therefore estimated the effects of ectoparasitic hen fleas by using an experimental design that combines both approaches: natural immigration and experimental infestation.

## Materials and methods

### EXPERIMENTAL PROCEDURES

The effect of ectoparasites on adult great tits (*Parus major*) was investigated by an experimental 4-year study in the Forst, a forest near Bern (Switzerland 46°54′ N ,7°17′ E/46°57′ N, 7°21′ E). In December 1996 12 study plots, each consisting of a grid of 8 × 4 geometrically arranged nestboxes (referred hereafter to as the plot design) were installed. All nestboxes were cleaned and lined with 30 g of dry heat-treated moss. To create infested and uninfested study areas each plot was, in January 1997, split into two patches consisting of 4 × 4 nestboxes each, and patches were assigned randomly to one of two treatments. In the uninfested patches the nest material of each nest was heat-treated in a microwave oven in February to kill hen fleas (*Ceratophyllus galinae*) before nest construction. Occupied nestboxes were additionally heat-treated on the day when the birds laid their second egg, on the hatching day and after fledging to prevent immigrating fleas from reproduction. In the infested patches nestboxes were not heat-treated but were otherwise handled similarly.

To create homogeneous parasite levels among infested patches all boxes of the infested patches were, at the start of the experiment, infested with 40 (end of January 1997), 60 (beginning of March) and 30 (mid-March) hen fleas. During the following 4 experimental years fleas could reproduce, immigrate and emigrate naturally in the infested patches. At the end of the experiment (2000) we collected all intact nests ($N = 322$) and extracted all live and all visible dead arthropods. Infested nests contained significantly more adult hen fleas (Wilcoxon's signed rank test: $\chi^2 = 78{\cdot}56$, $P < 0{\cdot}0001$), but fewer *Protocalliphora azurea* larvae ($\chi^2 = 5{\cdot}88$, $P = 0{\cdot}015$) and fewer ticks ($\chi^2 = 5{\cdot}14$, $P = 0{\cdot}023$). Besides these haematophagous ectoparasites no other ectoparasites (e.g. feather lice or haematophagous mites) were found in the nests or on the great tits. Thus the observed effects cannot be attributed to other nest-based arthropods.

However, birds could prefer boxes containing the fewest parasites (Christe *et al.* 1994; Oppliger *et al.* 1994; Merilä & Allander 1995), leading potentially to a different phenotype distribution between infested and non-infested patches. To control for this we applied a second design (hereafter referred to as alternated design). An additional 88 boxes were installed within the same study area. In the alternated design we let birds first choose their nestbox. By the second egg all nests were heat-treated and 40 adult hen fleas *C. gallinae* were introduced randomly in half of the nests. Nestboxes of the uninfested nests were treated in the same way as the nestboxes of the unifested patches. Because the differences between the treatment groups of the fixed design are due exclusively to fleas, this experiment allows for the quantification of non-random effects (e.g. a non-random phenotype distribution) in the plot design by testing the interaction between design and treatment. A significant interaction would indicate that non-random effects occurred in the plot design. No significant interaction and no differences between alternated and plot design were found (see Results), showing that both designs had similar effects on adult behaviour and reproduction. It indicates that the experimental flea infestation in the alternated design was in the same range as the natural flea immigration in the plot design. This suggests strongly that the observed effects are due to hen fleas in both designs.

In contrast to the fixed plot design, the alternated design was applied in 1997 and 1998, while in 1999 and 2000 these nestboxes were used for other experiments. All broods initiated were part of the experiment, including late-, second- and replacement-broods (hereafter referred to as second broods).

The number of eggs laid, the start of incubation and the exact hatching date were determined. In 1997 and 1998 parental feeding rates were recorded 9 days post-hatching using an infrared-sensitive video camera as described in Christe, Richner & Oppliger 1996b). Infested and uninfested nests were filmed simultaneously (± 0·5 h). The first 30 min after installation of the camera were not analysed. Food provisioning rates (number of nest visits with feeding of nestlings) of male and female parents were counted during the following 60 min. Thirteen days after hatching the adults were captured, individually ringed, and sex and age were determined (Jenni & Winkler 1994). Dispersal distances were calculated by first determining the coordinates of each nestbox and then calculating the shortest distances between the two boxes occupied by the same bird in consecutive years. Altitudinal differences between nestboxes were small and therefore not considered in the analyses of dispersal distance (highest nestbox: 640 m above sea level, lowest nestbox: 570 m above sea level). Distances between two boxes were rounded to the nearest 10 m before analyses. The size of the study area was approximately 4 $km^2$.

### STATISTICS

Differences between treatments in nest desertion, brood failure and mortality from egg laying until fledging due to treatment were analysed using weighted logistic regression analysis with binomial errors and a logit link using GLM Stat (Beath 2000).

Statistical significance was estimated conservatively by applying $\chi^2$ tests if the estimated scale was $\leq 1$. *F*-tests were used if the scale was $> 1$.

To avoid pseudoreplication adults captured in more than one breeding season entered our analysis when trapped for the first time. Data of subsequent breeding events were used for analysing effects of ectoparasites on future reproduction. In the analysis of future reproduction we discuss only the effects of the treatment and design of the first recorded clutch, while the effects of the treatment and the design applied to the subsequent clutch are included into the analysis but not discussed here (see Table 1).

Sexes were analysed separately.

The feeding behaviour of 130 males and 134 females (in 1997 and 1998) was recorded and food provisioning rates analysed using analyses of variance (ANOVAS).

Reproductive parameters were analysed by starting with an ANOVA including the factors treatment (infested/uninfested), design (plot/alternated), brood (1st/2nd brood), year (1997, 1998, 1999, 2000) and all possible interactions. The final model was determined using backward elimination.

Estimates of the probability of local reproduction ($\phi$) of the adults were calculated using the program MARK (White & Burnham 1999; White 2000). We applied Cormack–Jolly–Seber models (e.g. Jolly 1965) to account for potential variation in capture probability among birds of different treatment groups. A total of 181 male and 174 female great tits, all captured for the first time in 1997–99 in our experimental nestboxes, were included in the analyses. Our estimates of the probability of reproducing a following year are based on the birds captured as breeders 13 days after hatching

**Table 1.** Effects of parasites on laying date, clutch size, and incubation period (*N* = 196 females). Given are the *F*-values, the degrees of freedom, the *P*-value and the percentage variance explained

| Variable measured | Factors | *F* | d.f. | *P* | % |
|---|---|---|---|---|---|
| Date 1st egg laid | Treatment | 0·11 | 1,182 | 0·74 | 0·03 |
| | Design | 2·67 | 1,183 | 0·10 | 0·60 |
| | Brood | **182·20** | **1,184** | **< 0·001** | **43·38** |
| | Year | **19·26** | **3,184** | **< 0·001** | **13·29** |
| | Treatment × design | 0·002 | 1,177 | 0·96 | |
| | Treatment × year | 0·99 | 3,179 | 0·40 | |
| | Treatment × brood | 0·02 | 1,178 | 0·89 | |
| Clutch size | Treatment | **4·86** | **1,190** | **0·03** | **2·13** |
| | Design | 0·71 | 1,189 | 0·40 | 0·31 |
| | Brood | **23·10** | **1,190** | **< 0·001** | **10·11** |
| | Year | **4·08** | **3,190** | **0·008** | **5·36** |
| | Treatment × design | 1·23 | 1,188 | 0·27 | |
| | Treatment × year | 0·39 | 3,185 | 0·76 | |
| | Treatment × brood | 0·08 | 1,184 | 0·78 | |
| Incubation period | Treatment | **6·12** | **1,182** | **0·01** | **2·95** |
| | Design | < 0·001 | 1,181 | 1·00 | < 0·001 |
| | Brood | **4·37** | **1,182** | **0·04** | **2·09** |
| | Year | **5·99** | **3,182** | **< 0·001** | **8·60** |
| | Treatment × design | 0·007 | 1,177 | 0·93 | |
| | Treatment × year | 0·29 | 3,178 | 0·83 | |

**Table 2.** Nest desertion and brood failures in relation to treatment (infested/uninfested) and design (fixed plot/alternated). To estimate the significance of the factors conservatively, Chi$^2$-tests were applied if the scale was ≤ 1 and *F*-tests were applied if the scale was > 1

| Parameter | Infested | Uninfested | Factor | Scale | Deviance | d.f. | $\chi^2/F$ | *P* |
|---|---|---|---|---|---|---|---|---|
| Nest desertion during egg laying (*N* nests deserted) | 8 | 7 | Treatment | 0·26 | 0·16 | 1,516 | 0·16 | 0·69 |
| | | | Design | | < 0·01 | 1,516 | < 0·01 | 0·96 |
| | | | Year | | 4·22 | 3,516 | 4·22 | 0·24 |
| | | | Treatment × design | | 1·22 | 1,512 | 1·22 | 0·27 |
| | | | Treatment × year | | 3·29 | 1,513 | 3·29 | 0·35 |
| Nest desertion during incubation (*N* nests deserted) | 15 | 4 | Treatment | 0·31 | 7·57 | 1,501 | 7·57 | 0·006 |
| | | | Design | | 1·84 | 1,501 | 1·84 | 0·18 |
| | | | Year | | 14·56 | 3,501 | 14·56 | 0·002 |
| | | | Treatment × design | | 0·25 | 1,498 | 0·25 | 0·62 |
| | | | Treatment × year | | 3·60 | 1,497 | 3·60 | 0·31 |
| Complete brood failures during the nestling period (*N* nests deserted) | 58 | 42 | Treatment | 1·00 | 6·53 | 1,482 | 6·58 | 0·01 |
| | | | Design | | 0·80 | 1,482 | 0·81 | 0·37 |
| | | | Year | | 9·66 | 3,482 | 3·25 | 0·02 |
| | | | Treatment × design | | 3·53 | 1,481 | 3·57 | 0·06 |
| | | | Treatment × year | | 3·94 | 3,478 | 1·33 | 0·26 |
| Nestling mortality till fledging (*N* nestlings died) | 1·91 ± 0·15 | 1·82 ± 0·13 | Treatment | 2·42 | 3·02 | 1,378 | 1·38 | 0·24 |
| | | | Design | | 0·33 | 1,378 | 0·15 | 0·70 |
| | | | Year | | 90·69 | 3,378 | 13·76 | < 0·001 |
| | | | Treatment × design | | 2·83 | 1,377 | 1·29 | 0·26 |
| | | | Treatment × year | | 4·29 | 3,374 | 0·65 | 0·58 |

of their nestlings. The processes leading to differences in the probability of reproducing a following year include survival, emigration and nest desertion until 12 days post-hatching. Survival analyses were started with the full model. For the model selection we used Aikake's information criterion (AIC). The model with the lowest AIC was selected as the best model using AIC-weight. Likelihood ratio tests were used to confirm the model selection. The significant parameters in the recapture probability model (Table 3a,c) remained in the model for the estimation of the probability of reproducing locally (Table 3b,d). Thus our estimates of the probability of local reproduction are independent of, e.g. hen flea-induced differences in the recapture probability and dispersal distance.

Dispersal distances of both males and females were not distributed normally. We therefore used a non-parametric rank-variance analysis with two factors (treatment: no parasites, parasites; age: 1, 2, 3 years old), using *H*-statistics (Bortz, Lienert & Boehnke 2000).

Divorce rates were analysed using logistic regression analyses with binomial errors and a logit link using the statistical package GLM Stat (Beath 2000).

For males, the frequency of extra-pair offspring was unknown; the effect of breeding in an infested nest on reproductive success was analysed for females only.

In the analysis on reproductive success over the 4 years the number of fledglings and recruits was standardized (standard normal deviates) for year and brood (1st or 2nd) (Sokal & Rohlf 1981) prior to the analyses. The standardized total number of fledglings per female was analysed using analysis of covariance (ANCOVA). To account for females captured for the first time in any of the 4 years of the experiment, the number of possible breeding attempts until the end of the experiment was included into the analyses. As several females bred twice in the annual breeding season but none three times, the number of possible broods per year was set to two. The number of recorded broods and the number of broods in infested nests were entered as covariates. The same analysis was conducted for the standardized number of recruits.

Power analyses were calculated according to Cohen (1988). Residuals of the models were tested for normality and unequal variances. If the model assumptions were not fulfilled non-parametric statistics were applied.

## Results

### EFFECTS OF PARASITES ON CURRENT REPRODUCTION

#### *Egg laying and incubation period*

Laying date of the first egg was not significantly different between infested and uninfested broods. It was significantly different between years and broods (1st vs. 2nd broods) (Table 1). All interactions with the treatment were not significant, suggesting that parasites did not affect laying date differently between designs, years and broods. Parasites reduced clutch size significantly (uninfested nests 9·3 ± 0·15; infested nests 8·9 ± 0·14; Table 1, Fig. 1). The interaction between treatment and design was not significant. Females of infested nests incubated their eggs significantly longer (12·8 ± 0·15 days) than those of uninfested nests (12·3 ± 0·13 days) (Table 1, Fig. 2). There were no significantly different effects of the treatment among designs, years, and broods.

**Table 3.** Probability of reproducing locally in a following year in relation to year, treatment and design. For each model the Aikaike information criterion (AIC), the AIC weight ($\mathrm{AIC_w}$), the number of parameters (np) and the deviance are given. All models include an intercept, both for survival ($\phi$) and recapture probability ($P$). Year (t) is entered into the model as a linear predictor. Each manipulated factor has two levels: Flea treatment (f): infested, uninfested; Design (d): plot-design, alternated design. Model algebra specification is conforming to MARK (White 2000). c∗t stands for c + t + c·t. Within each set of analyses, models are numbered according to decreasing complexity but ordered according to AIC. The selected model (the model with the lowest AIC) in each set of analyses and the key comparisons between models are shown in bold type

| Model | AIC | $\mathrm{AIC_w}$ | np | Deviance | Models compared, hypothesis tested, LRT test |
|---|---|---|---|---|---|
| (a) Modelling female recapture probability ($P$) | | | | | |
| **7. $\phi(f*d*t)P(\cdot)$** | **430·11** | **0·684** | **13** | **26·33** | **6–7, f, $P = 1$** |
| 6. $\phi(f*d*t)P(f)$ | 432·33 | 0·2257 | 14 | 26·33 | **5–6, d, $P = 0·78$** |
| 5. $\phi(f*d*t)P(f + d)$ | 434·48 | 0·0768 | 15 | 26·25 | 4–5, t, $P = 0·88$ |
| 4. $\phi(f*d*t)P(f + d + t)$ | 438·75 | 0·0091 | 17 | 26·00 | **3–4, f·d, $P = 1$** |
| 3. $\phi(f*d*t)P(f + d + t + f\cdot d)$ | 441·04 | 0·0029 | 18 | 26·00 | **2–3, f·t, $P = 0·54$** |
| 2. $\phi(f*d*t)P(f + d + t + f\cdot d + f\cdot t)$ | 444·44 | 0·0005 | 20 | 24·77 | 1–2, Interactions, $P = 0·59$ |
| 1. $\phi(f*d*t)P(f*d*t)$ | 451·10 | 0·00002 | 24 | 21·96 | |
| (b) Modelling female probability of reproducing locally a following year ($\phi$) | | | | | |
| **13. $\phi(\cdot)P(\cdot)$** | **413·58** | **0·6060** | **2** | **33·14** | **12–13, f, $P = 0·65$** |
| 12. $\phi(f)P(\cdot)$ | 415·41 | 0·2422 | 3 | 32·93 | **11–12, d, $P = 0·51$** |
| 11. $\phi(f + d)P(\cdot)$ | 417·03 | 0·1079 | 4 | 32·49 | 10–11, t, $P = 0·50$ |
| 10. $\phi(f + d + t)P(\cdot)$ | 419·81 | 0·0269 | 6 | 31·10 | **9–10, f·d, $P = 0·53$** |
| 9. $\phi(f + d + t + f\cdot d)P(\cdot)$ | 421·52 | 0·0114 | 7 | 30·70 | **8–9, f·t, $P = 0·49$** |
| 8. $\phi(f + d + t + f\cdot d + f\cdot t)P(\cdot)$ | 424·33 | 0·0028 | 9 | 9·26 | 7–8, Interactions, $P = 0·57$ |
| 7. $\phi(f*d*t)P(\cdot)$ | 430·11 | 0·0002 | 13 | 26·33 | |
| (c) Modelling male recapture probability ($P$) | | | | | |
| **5. $\phi(f*d*t)P(f + d + f\cdot d)$** | **440·67** | **0·8394** | **16** | **20·65** | **3–5, t, $P = 1$** |
| 3. $\phi(f*d*t)P(f + d + t + f\cdot d)$ | 445·22 | 0·0892 | 18 | 20·65 | **2–3, f·t, $P = 0·50$** |
| 4. $\phi(f*d*t)P(f + d + t)$ | 448·04 | 0·0218 | 17 | 25·76 | **3–4, f·d, $P = 0·024$** |
| 2. $\phi(f*d*t)P(f + d + t + f\cdot d + f\cdot t)$ | 448·45 | 0·0178 | 20 | 19·26 | 1–2, Interactions, $P = 1$ |
| 1. $\phi(f*d*t)P(f*d*t)$ | 457·92 | 0·0002 | 24 | 19·26 | |
| (d) Modelling male probability of reproducing locally a following year ($\phi$) | | | | | |
| **12. $\phi(\cdot)P(f*d)$** | **425·34** | **0·5888** | **5** | **29·18** | **11–12, f, $P = 0·72$** |
| 11. $\phi(f)P(f*d)$ | 427·29 | 0·2214 | 6 | 29·05 | **10–11, d, $P = 0·25$** |
| 10. $\phi(f + d)P(f*d)$ | 428·08 | 0·1495 | 7 | 27·73 | 9–10, t, $P = 0·83$ |
| 9. $\phi(f + d + t)P(f*d)$ | 431·96 | 0·0215 | 9 | 27·35 | **8–9, f·d, $P = 0·38$** |
| 8. $\phi(f + d + t + f\cdot d)P(f*d)$ | 433·34 | 0·0108 | 10 | 26·58 | 7–8, Interactions, $P = 0·43$ |
| 7. $\phi(f*d*t)P(f*d)$ | 440·67 | 0·0003 | 16 | 20·65 | |

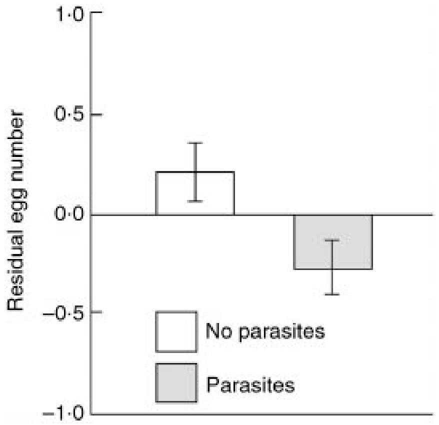

**Fig. 1.** Number of eggs laid in relation to the parasite treatment. Residual values of the final model (see Table 1) are presented. For statistics see Table 1.

### NEST DESERTION

During the 4 experimental years six of 216 infested and six of 231 uninfested nests of the fixed plot design, and two of 37 infested and one of 38 uninfested nest of the alternated design were deserted during egg laying. Nest desertion was not significantly different between treatments. During incubation 13 (6·2%) infested and three (1·3%) uninfested nests of the fixed plot design and two (5·7%) infested and one (2·7%) uninfested nests in the alternated design failed. Infested nests were abandoned more frequently (Table 2). The rate of nest desertion differed between years. All interactions were not significant.

During the nestling period 58 (25·2%) infested and 42 (16·9%) uninfested nests failed. The proportion of complete nest failures during the nestling period was significantly higher in infested nests (Table 4). Nestling mortality in successful nests was not significantly higher in infested nests (1·91 ± 0·15) than in uninfested nests (1·82 ± 0·13; Table 2).

### ADULT INVESTMENT DURING THE NESTLING PERIOD

In the presence of parasites parents provided their nestlings with food for a significantly longer time (uninfested: 19·5 ± 0·2 days; infested: 20·2 ± 0·2 days, $F_{1,165} = 8·01$, $P = 0·005$, 4·63% of total variance explained).

**Table 4.** Effects of parasites on future reproductive traits (for more details see Statistics)

| Variable measured | Factors | $F$ | d.f. | $P$ |
|---|---|---|---|---|
| Date 1st egg laid | Treatment | 0·11 | 1,82 | 0·75 |
| | Design | 3·06 | 1,87 | 0·08 |
| | Brood | 0·19 | 1,83 | 0·67 |
| | Year | **7·28** | **2,88** | **0·001** |
| | Treatment × design | 1·80 | 1,80 | 0·18 |
| | Treatment × year | 0·78 | 2,78 | 0·46 |
| | Treatment × subsequent treatment | 0·06 | 1,77 | 0·81 |
| Clutch size | Treatment | 0·58 | 1,88 | 0·45 |
| | Design | 0·68 | 1,89 | 0·41 |
| | Brood | 0·47 | 1,90 | 0·50 |
| | Year | **5·69** | **2,94** | **0·005** |
| | Treatment × design | 0·18 | 1,87 | 0·68 |
| | Treatment × year | 0·42 | 2,83 | 0·66 |
| | Treatment × subsequent treatment | 0·09 | 1,85 | 0·76 |
| Incubation period | Treatment | 0·24 | 1,85 | 0·63 |
| | Design | 1·12 | 1,88 | 0·29 |
| | Brood | 0·63 | 1,87 | 0·43 |
| | Year | 1·44 | 2,89 | 0·24 |
| | Treatment × design | 1·31 | 1,81 | 0·26 |
| | Treatment × year | 1·41 | 2,79 | 0·25 |
| | Treatment × subsequent treatment | 0·41 | 1,78 | 0·53 |
| Number fledglings | Treatment | 0·92 | 1,91 | 0·34 |
| | Design | 2·96 | 1,92 | 0·09 |
| | Brood | 0·27 | 1,90 | 0·60 |
| | Year | **8·54** | **2,95** | **< 0·001** |
| | Treatment × design | 0·01 | 1,84 | 0·92 |
| | Treatment × year | 0·12 | 2,85 | 0·89 |
| | Treatment × subsequent treatment | 0·40 | 1,88 | 0·53 |

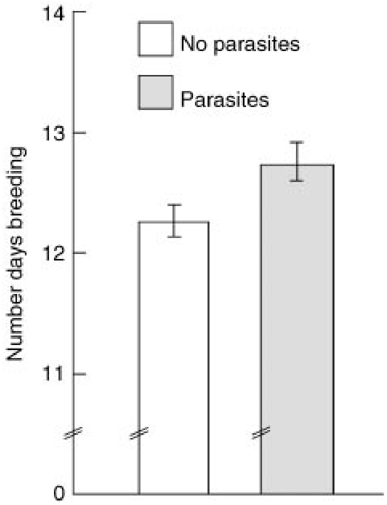

**Fig. 2.** Incubation period in relation to parasite treatment. For statistics see Table 1.

All interactions and the factors design, brood and year were not significant ($P > 0·1$).

Females of infested nests did not provide more food to offspring per hour than those of uninfested nests ($F_{1,121} < 0·01$, $P = 0·97$). Female food provisioning rate was slightly but not significantly different between years ($F_{1,122} = 3·45$, $P = 0·07$, 2·16% of total variance explained) and designs ($F_{1,122} = 3·90$, $P = 0·05$, 2·1%). Larger broods ($F_{1,122} = 16·76$, $P < 0·0001$, 10·17% of total variance explained) and broods early in the season ($F_{1,122} = 23·09$, $P < 0·0001$, 13·34%) were provided with significantly more food. The interactions were not significant ($P > 0·1$).

Similarly, males of infested nests did not provide more food to offspring than those of uninfested nests. Male food provisioning was not different between treatment groups ($F_{1,123} = 0·11$, $P = 0·74$) and designs ($F_{1,124} = 0·41$, $P = 0·52$, 0·28%), but between years ($F_{1,125} = 5·23$, $P = 0·02$, 3·51% of total variance explained). Larger broods ($F_{1,125} = 7·20$, $P = 0·008$, 4·84% of total variance explained) and broods early in the season ($F_{1,125} = 14·3$, $P < 0·001$, 9·64%) were provided with significantly more food. There were no significant interactions ($P > 0·1$).

### FLEDGLING NUMBER

The number of fledglings in the first recorded brood was significantly lower in females breeding in infested nests ($F_{1,192} = 5·19$, $P = 0·02$). There were both significant annual differences ($F_{3,192} = 9·20$, $P < 0·001$) and significant differences between first and second broods ($F_{1,191} = 9·08$, $P = 0·003$) in the number of fledglings and there was no significant difference between designs ($F_{1,190} < 0·001$, $P = 0·99$). All interactions were not significant ($P \leq 0·24$).

## EFFECTS OF PARASITES ON FUTURE REPRODUCTION

### *Egg laying and incubation period*

The laying date of the subsequent clutch was not significantly different between females that bred previously in infested and uninfested nests, between designs or between broods, but it was significantly different between years (Table 4). All interactions were not significant. This suggests that the parasite treatment did not affect future laying date differently among designs, years and broods. There was no significant interaction between the treatment of the first recorded brood and the treatment of the subsequent brood. The number of eggs of the subsequent brood was not influenced significantly by the treatment applied to the first recorded brood (Table 4). None of the interactions was significant and future incubation period was not affected significantly by any of the factors (see Table 4).

### *Adult investment during the nestling period*

The length of the subsequent nestling period was not influenced significantly by the treatment ($F_{1,79} = 0{\cdot}02$, $P = 0{\cdot}90$), the design ($F_{1,84} = 0{\cdot}85$, $P = 0{\cdot}36$) and the brood ($F_{1,81} = 0{\cdot}53$, $P = 0{\cdot}47$) of the first recorded brood. Future nestling period was significantly different between years ($F_{2,85} = 4{\cdot}18$, $P = 0{\cdot}02$). All interactions were not significant ($P > 0{\cdot}5$). Rates of food provisioning of 38 females and 33 males were recorded. The treatment applied to the first recorded brood did not cause significant differences in female and male food provisioning rates (females: $F_{1,34} = 2{\cdot}55$, $P = 0{\cdot}12$; males: $F_{1,27} \leq 0{\cdot}001$, $P = 0{\cdot}99$) in the subsequent brood. The design in which females were breeding during the first recorded brood significantly affected female provisioning rates ($F_{1,35} = 13{\cdot}93$, $P = 0{\cdot}001$), while male provisioning rates were not significantly different between designs ($F_{1,31} = 0{\cdot}11$, $P = 0{\cdot}74$). The number of nestlings had no significant effect on male and female provisioning rates (males: $F_{1,28} = 0{\cdot}06$, $P = 0{\cdot}82$; females: $F_{1,32} = 0{\cdot}28$, $P = 0{\cdot}60$) and the interactions were not significant ($P > 0{\cdot}1$).

### *Fledgling numbers*

The number of fledglings during the subsequent breeding attempt was not influenced significantly by the treatment applied to the first recorded brood (Table 4), and it was not different between designs and broods of the first recorded brood. It differed significantly between years (Table 4).

### *Probability of breeding and dispersal*

Ninety-one of 174 breeding females (56·3%) and 81 of 181 breeding males (44·8%) were recaptured as breeders in our study area a following year. The probability of reproducing locally a following year (ϕ) was in both sexes not affected significantly by parasites (Table 3b,d, model 12–13). Recapture probability and local reproduction were modelled together. Estimates of local reproduction are therefore not biased by different recapture probabilities or dispersal distances between treatments.

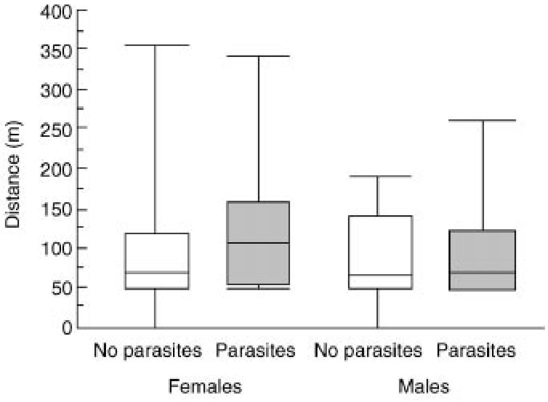

**Fig. 3.** Male and female dispersal distance (m) in relation to parasite treatment. Quantile boxes and 10% and 90% quantiles are shown. For statistics see Results.

In females the recapture probability ($P$) was not affected by any of the variables (Table 3a). In males recapture probability was differently affected by parasites in the two designs (Table 3c, models 3–4). While uninfested males in the plot design were recaptured with a higher probability than the infested males, in the alternated design, the infested males were recaptured with a higher probability.

Females dispersed 160 ± 30 m (median: 95 m, lower quartile: 50 m, upper quartile: 150 m) and males 140 ± 40 m (median: 70 m, lower quartile: 50 m, upper quartile: 160 m) between breeding attempts. While infested females dispersed longer distances ($N = 48$, median: 105 m, lower quartile: 55 m, upper quartile: 120 m) than uninfested females ($N = 50$, median: 70 m, lower quartile: 50 m, upper quartile: 120 m) ($N = 98$, $H = 17{\cdot}8$, $P < 0{\cdot}0005$, Fig. 3), parasites did not affect dispersal in males (infested: $N = 42$, median: 70 m, lower quartile: 50 m, upper quartile: 120 m; uninfested: $N = 39$, median 70 m, lower quartile: 50 m, upper quartile: 140 m; $H = 1{\cdot}45$, $P > 0{\cdot}2$, Fig. 3).

### *Divorce*

In 83 females the breeding partners of the first and second recorded breeding attempts were captured. Forty-four (53·0%) of the recaptured females were breeding with another male a following year. As breeding partners may die from one year to another, the change of partner may not be due exclusively to divorce. Thus we analysed confirmed divorces (where the males were recorded as being still alive but breeding with another female) and females breeding with another partner for unknown reasons separately. The estimate of confirmed divorce under-estimates the real divorce rate as emigrating and non-breeding partners, and partners breeding in natural cavities were not recorded.

Confirmed divorce was rare (five infested females, seven uninfested females) and not significantly different between treatments (scale = 1·38; $\Delta$D = 1·46, $F_{1,47}$ = 1·43, $P$ = 0·24), designs ($\Delta$D = 0·02, $F_{1,46}$ = 0·02, $P$ = 0·90), and years ($\Delta$D = 6·21, $F_{2,45}$ = 3·02, $P$ = 0·06). The interactions with the treatment were not significant ($P$ > 0·38). The number of females breeding with another partner for unknown reasons was not significantly different between treatments ($\Delta$D = 3·27, $F_{1,69}$ = 2·39, $P$ = 0·13), designs ($\Delta$D = 0·24, $F_{1,66}$ = 0·18, $P$ = 0·68) and years ($\Delta$D = 4·81, $F_{2,67}$ = 1·80, $P$ = 0·17). The interactions with the treatment were not significant ($P$ > 0·90).

Thirty-seven (48·1%) of the recaptured 77 males with known breeding partner were breeding with another female a following year. Confirmed divorce was rare (three infested males, seven uninfested males) and not significantly different between treatments (scale = 0·88; $\Delta$D = 2·94, $\chi^2_{1,48}$ = 2·94, $P$ = 0·09), designs ($\Delta$D = 0·57, $\chi^2_{1,45}$ = 0·57, $P$ = 0·45), and years ($\Delta$D = 3·47, $\chi^2_{1,46}$ = 3·47, $P$ = 0·18) and there were no significant effects (all $P$ > 0·4) of those on the frequency of divorce for unknown reason. This suggests that divorce was not affected by ectoparasites.

### EFFECTS OF PARASITES ON LIFETIME REPRODUCTIVE SUCCESS

The total number of fledglings per female decreased significantly with the number of breeding attempts in nests with fleas (Table 5a, Fig. 4). Similarly, the number of recruits per female was negatively correlated with the number of breeding attempts in nests containing fleas (Table 5b, Fig. 5). The number of breeding attempts influenced the number of fledglings significantly (Table 5a), and was positively but not significantly correlated with the number of recruits (Table 5b).

The number of breeding attempts was not correlated significantly with the percentage of broods raised in infested nests ($F_{1,196}$ = 1·03, $P$ = 0·31) when controlling for the number of possible breeding events ($F_{1,196}$ = 32·56, $P$ < 0·001) and there was no significant interaction between the percentage of broods raised in infested nests and the number of possible broods ($F_{1,195}$ = 0·23, $P$ = 0·63).

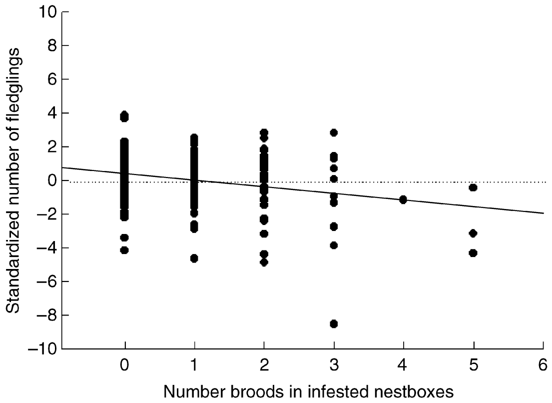

**Fig. 4.** Total number of fledglings produced by a female over the 4 experimental years in relation to the number of breeding attempts in the presence of fleas. Residual values of the model are shown (see Table 5a, $y = 0{\cdot}363 - 0{\cdot}388x$).

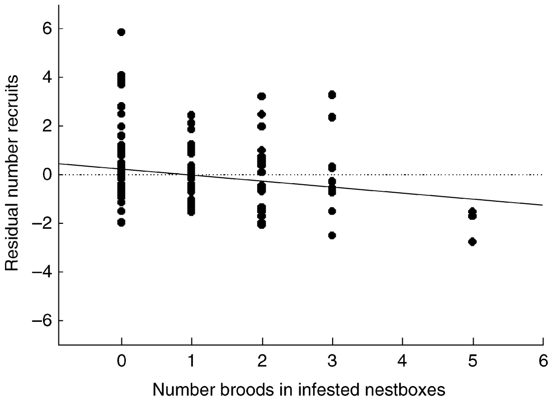

**Fig. 5.** Total number of recruits produced by a female over the 4 experimental years in relation to the number of breeding attempts in the presence of fleas. Residual values of the model are shown (see Table 5b, $y = 0{\cdot}215 - 0{\cdot}217x$).

## Discussion

### EFFECTS OF ECTOPARASITES ON CURRENT REPRODUCTION

Our study investigates experimentally ectoparasite-mediated costs at different stages of current and future reproduction. We show experimentally that hen fleas

**Table 5.** Total number of fledglings (a) and recruits (b) produced by a female over the 4 experimental years in relation to the number of breeding attempts in presence of fleas. The number of possible breeding attempts and the number of total recorded breeding attempts were included into the model as covariates (for details see Methods)

| | Factors | $F$ | d.f. | $P$ | % |
|---|---|---|---|---|---|
| (a) Total number fledglings | Number possible breeding attempts | 0·74 | 1,195 | 0·39 | 0·34 |
| | Number breeding attempts | 3·98 | 1,195 | 0·048 | 1·86 |
| | Number breeding attempts with fleas | 17·80 | 1,195 | < 0·001 | 8·34 |
| (b) Total number recruits | Number possible breeding attempts | 0·26 | 1,170 | 0·61 | 0·15 |
| | Number breeding attempts | 2·72 | 1,170 | 0·10 | 1·53 |
| | Number breeding attempts with fleas | 7·68 | 1,170 | 0·006 | 4·31 |

enhance nest desertion during incubation (see also Oppliger *et al.* 1994), raise the probability of a complete nest failure during the nestling period and enhance nestling mortality in successful nests slightly but not significantly. The negative effect of fleas on nestling mortality is explained mainly by complete nest failures rather than individual nestling mortality. This supports the idea that adults abandon their broods once a certain threshold of negative ectoparasite impact is reached (e.g. Brown & Brown 1986), due probably to a trade-off between investment into current and future reproduction.

Female great tits laid significantly fewer eggs and the nestling period was prolonged in the presence of long-cycled hen fleas (generation period around ≥ 15 days) (Richner & Heeb 1995; Tripet & Richner 1999). This result contrasts with theoretical models predicting an enlarged clutch size and prolonged nestling period in the presence of long-cycled parasites in order to reduce the parasite impact per nestling (Richner & Heeb 1995). The net gain in condition (condition gain per day – condition loss due to parasites) is suggested to be positive in the presence of long-cycled parasites as long as the subsequent parasite generation does not hatch. Thus a prolonged nestling period may result in relatively better offspring condition and thus higher survival to recruitment (e.g. Martin 1987).

The observed clutch size reduction in our study would, however, be predicted for short-cycled parasites (e.g. mites: generation period 5–7 days) because clutch size reduction is suggested to reduce the nestling period and thus the duration of exposure to parasites (Richner & Heeb 1995). The number of parasites per nestling increases faster over a given time unit in short-cycled parasites. Therefore, staying an additional day in a nest infested with short-cycled parasites might severely reduce nestling condition and thus survival to recruitment (Møller 1993). Here we show that great tits adjust their behaviour in the presence of hen fleas, on one hand, as predicted for a short-cycled parasite and on the other hand, as predicted for a long-cycled parasite, suggesting that a third optimal strategy for intermediate cycled parasites may exist.

In the presence of parasites females incubated their eggs significantly longer (see also Møller 1993), probably as a result of enhanced nest sanitation activities at the expense of incubation (Christe *et al.* 1996b). Parasites further increased the nestling period, suggesting that they increase reproductive cost. Parents may additionally have compensated for the parasite impact by increasing the rate of food provisioning (Christe *et al.* 1996a; Tripet & Richner 1997); this was, however, not the case in our study. In the study of Christe *et al.* (1996a) males but not females increased their food provisioning by 57·4% in the presence of fleas ($N = 30$ broods). The effect size ($d \approx 0{\cdot}95$) was approximately 26 times higher than the one found in our study ($d = 0{\cdot}036$) and the power of detecting a similar effect was 100% in our study, suggesting that the difference between the two studies might be due to different strategies or different constraints among different host populations.

Our results do not support the idea that due to environmental differences or similarly varying virulence of ectoparasites among years, the impact of fleas on their hosts differs between years (Allander 1998), as all interactions between year and treatment were not significant. This suggests that fleas are a relatively constant selective force in the evolution of their host's life history.

## EFFECTS OF ECTOPARASITES ON FUTURE REPRODUCTION

### *Reproductive parameters*

Future reproduction was not affected significantly by ectoparasites in adult great tits. Neither the number of eggs laid, the time spent incubating the eggs, the length of the nestling period, the parental feeding rates nor the number of fledglings were influenced by the ectoparasite treatment applied to the previous brood (Table 4).

Interestingly, effects of hen fleas on future reproduction were found in adult blue tits even with a small sample size ($N = 20$) (Richner & Tripet 1999), suggesting that hen fleas may act differently on future reproduction of different host species. Similarly, Møller (1993) found that high mite loads delayed future laying date, decreased future clutch and brood size and increased future incubation period in barn swallows (*Hirundo rustica*). In contrast to our findings, both studies demonstrate long-term effects of ectoparasites on adult birds, suggesting that the effects of ectoparasites cannot be generalized among different hosts.

### *Parasite-mediated investment into current and future reproduction*

In agreement with the hypothesis that parasites have direct negative effects, we show both that ectoparasitic hen fleas increased parental effort and thus the costs of current reproduction and that ectoparasite infestation reduces the host's lifetime reproductive success.

The second alternative hypothesis predicts that parents should adjust their reproductive effort to the reproductive value of their offspring (Schaffer 1974; Møller 1997). According to this hypothesis parents should reduce their investment in the presence of hen fleas and enhance future reproduction (Stearns 1992; Roff 1992).

These predictions are, however, not supported by our study, as current but not future reproductive investment was enhanced. Our study thus supports the idea that parasites have a direct negative effect and that parents adjust only current reproductive investment.

### *Probability of local reproduction, Dispersal and Divorce*

Brown, Brown & Rannala (1995) showed that fumigated and thus ectoparasite-free adult cliff swallows (*Hirundo pyrrhonota*) survived better to the following breeding season than non-fumigated birds. Cliff swallows were infested by several species of ectoparasites, all being removed by fumigation. Therefore it remains open whether the observed effect on adult survival was due to chewing lice, swallow bugs or fleas.

In contrast, in our study parasites did not affect the probability of reproducing locally a following year ($\phi$). On average infested females dispersed one nestbox further than uninfested ones (Fig. 3), probably as a result of active parasite avoidance, as proposed by Brown & Brown (1992) and Boulinier, McCoy & Sorci (2001). Occupying another nestbox the following year is advantageous as hen fleas pass the winter in nestboxes and start to disperse in February, thereby colonizing the surroundings. The chance of breeding again in an infested nest is therefore smaller (personal observations) when dispersing more than 50 m. Contrasting to natal dispersal where dispersal distances were reduced in hen flea presence (Heeb *et al.* 1999), the adult dispersal distances were much smaller and parasites did affect dispersal distances positively.

The probability of divorce in great tits is shown to be higher in pairs with low reproductive success (Linden 1991; Dhondt & Adriaensen 1994). Although infested females laid fewer eggs, parental effort was increased and less young were fledging, there was no significant effect of parasite treatment on divorce.

### EFFECTS OF ECTOPARASITES ON LIFETIME REPRODUCTIVE SUCCESS

Both the total number of fledglings and the number of local recruits per female decreased significantly with the number of breeding attempts in infested nests (Table 5a,b, Figs 4 and 5). Only 3·2% of the adults captured in 1997 survived until 2001, showing that measuring the impact of hen fleas among 4 consecutive years covers the entire life span of most adult great tits in the studied population. Therefore, the current study demonstrates experimentally that females were not able to compensate for the negative effects during a following breeding attempt and thus that hen fleas reduce the host's lifetime reproductive success. As there was no significant correlation between the percentage of broods raised in infested nests and the number of breeding events, the negative effects of hen fleas on lifetime reproductive success are due to a reduced breeding success in each event, rather than a reduced number of breeding events.

In conclusion, we demonstrate that flea infestation leads to higher nest failure during the incubation and nestling period, to a reduced clutch size, a prolonged incubation period and to a reduced number of fledglings. Furthermore, fleas raise parental reproductive costs by extending the nestling period, and influence female but not male dispersal. In contrast to findings in other species, fleas did not affect future reproduction significantly. Because fleas raise the probability of nest desertion and parents of deserted nests could not be identified, our study actually under-estimates the observed, significant negative effects of hen fleas on lifetime reproductive success. Nevertheless, our data show that parents could not compensate fully for the negative effects of fleas during subsequent breeding attempts and we did not find support that fleas impair hosts differently among years. This study suggests, therefore, that hen fleas are a relatively constant evolutionary force and underlines their importance for the evolution of the life history of its most common host.

## Acknowledgements

We thank K. Büchler, B. Holzer, A. Jacot, A. Klingenböck, V. Saladin and F. Tripet for their help in catching adult birds and J. Zbinden for analysing a part of the films. The work was supported financially by the Swiss National Science Foundation (grant nos 31–43570·95 and 31–53956·98 to H. Richner). The experiment was conducted under a licence provided by the Office of Agriculture of the Canton of Berne.

## References

Allander, K. (1998) The effects of an ectoparasite on reproductive success in the great tit: a 3-year experimental study. *Canadian Journal of Zoology*, **76**, 19–25.

Beath, K. (2000) *GLM Stat*, version 5·2·1. Sydney.

Bortz, J., Lienert, G.A. & Boehnke, K. (2000) *Verteilungsfreie Methoden in der Biostatistik*. Springer, Berlin, Heidelberg.

Boulinier, T., McCoy, K.D. & Sorci, G. (2001) *Dispersal and Parasitism in Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp. 169–179. Oxford University Press, Oxford.

Brown, C.R. & Brown, M.B. (1986) Ectoparasitism as a cost of coloniality in cliff swallows *Hirundo pyrrhonota*. *Ecology*, **67**, 1206–1218.

Brown, C.R. & Brown, M.B. (1992) Ectoparasitism as a cause of natal dispersal in cliff swallows. *Ecology*, **73**, 1718–1723.

Brown, C.R., Brown, M.B. & Rannala, B. (1995) Ectoparasites reduce long-term survival of their avian host. *Proceedings of the Royal Society London, Series B*, **262**, 313–319.

Christe, P., Oppliger, A. & Richner, H. (1994) Ectoparasite affects choice and roost sites in the great tit *Parus major*. *Animal Behaviour*, **47**, 895–898.

Christe, P., Richner, H. & Oppliger, A. (1996a) Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. *Behavioral Ecology*, **7**, 127–131.

Christe, P., Richner, H. & Oppliger, A. (1996b) of great tits and fleas: sleep baby sleep … *Animal Behavior*, **52**, 1087–7092.

Clayton, D.H. & Moore, H. (1997) *Host–Parasite Evolution*. Oxford University Press, Oxford.

Cohen, J. (1988) *Statistical Power Analysis for the Behavioral Sciences*, 2nd edn. Academic Press, New York.

Dhondt, A.A. & Adriaensen, F. (1994) Causes and effects of divorce in the blue tit *Parus caeruleus*. *Journal of Animal Ecology*, **63**, 979–987.

Gosler, A. (1993) *The Great Tit*. Hamlyn Limited, London.

Heeb, P., Werner, I., Mateman, A.C., Klliker, M., Brinkhof, M.W.G., Lessells, C.M. & Richner, H. (1999) Ectoparasite infestation and sex-biased local recruitment of hosts. *Nature*, **400**, 63–65.

Jenni, L. & Winkler, R. (1994) *Moult and Ageing of European Passerines*. Academic. Press, London.

Jolly, G.M. (1965) Explicit estimates for capture–recapture rates with both death and immigration-stochastic model. *Biometrika*, **52**, 225–247.

Lehmann, T. (1993) Ectoparasites – direct impact on host fitness. *Parasitology Today*, **9**, 8–13.

Linden, M. (1991) Divorce in great tits – chance or choice – an experimental approach. *American Naturalist*, **138**, 1039–1048.

Møller, A.P. (1989) Parasites, predators and nestboxes: facts and artefacts in nestbox studies of birds? *Oikos*, **56**, 421–423.

Møller, A.P. (1993) Ectoparasites increase the cost of reproduction in their hosts. *Journal of Animal Ecology*, **62**, 309–322.

Møller, A.P. (1997) Parasitism and the evolution of host life history. *Host–Parasite Evolution* (eds D.H. Clayton & J. Moore), pp. 105–127. Oxford University Press, Oxford.

Martin, T.E. (1987) Food as a limit on breeding birds: a life history perspective. *Annual Reviews in Ecology and Systematics*, **18**, 453–487.

Martin, T.E.M., Møller, A.P., Merino, S. & Clobert, J. (2001) Does clutch size evolve in response to parasites and immunocompetence? *Proceedings of the National Academy of Sciences USA*, **98**, 2071–2076.

Merilä, J. & Allander, K. (1995) Do great tits (*Parus major*) prefer ectoparasite-free roost sites? An experiment. *Ethology*, **99**, 53–60.

Oppliger, A., Richner, H. & Christe, P. (1994) Effect of an ectoparasite on lay date, nest-site choice, desertation, and hatching success in great tits (*Parus major*). *Behavioral Ecology*, **5**, 130–134.

Perrin, N., Christe, P. & Richner, H. (1996) On host life history response to parasitism. *Oikos*, **75**, 317–320.

Richner, H. & Heeb, P. (1995) Are clutch and brood size patterns in birds shaped by ectoparasites? *Oikos*, **73**, 435–441.

Richner, H. & Tripet, F. (1999) Ectoparasitism and the trade-off between current and future reproduction. *Oikos*, **86**, 535–538.

Roff, D.A. (1992) *The Evolution of Life Histories*. Chapman & Hall, New York.

Schaffer, W.M. (1974) Selection for optimal life histories: the effects of age structure. *Ecology*, **55**, 291–303.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*, 2nd edn. W.H. Freeman, New York.

Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, New York.

Tripet, F. & Richner, H. (1997) Host responses to ectoparasites: food compensation by parent blue tits. *Oikos*, **78**, 557–561.

Tripet, F. & Richner, H. (1999) Dynamics of hen flea *Ceratophyllus gallinae* subpopulations in blue tit nests. *Journal of Insect Behavior*, **12**, 159–174.

White, G.C. (2000) Program *MARK*. http://www.cnr.colostate.edu/~gwhite/mark/mark.htm.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–138.

*Received 23 April 2003; accepted 12 August 2003*