

Mites and blowflies decrease growth and survival in nestling pied flycatchers

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The effects of blood sucking mites (Acari) and blowfly larvae (Diptera) ectoparasites on the growth and survival of nestling pied flycatchers (*Ficedula hypoleuca*) breeding in nest boxes were studied. Mites significantly decreased mean within-brood tarsus length, a measure of skeletal size, and mass. High mite loads also increased within-brood variance in mass, although the effects varied depending on the quality of the nesting site. Significant interactions between the effects of mites and nest box quality and breeding phenology were detected, the lightest nestlings fledging from late, low quality nests with high mite loads. No effect of mite loads on nestling mortality was apparent. In contrast, blowfly larvae abundance contributed more to nestling mortality in one year, although this seemed to pave the way for brood survival in nests with high infestations. High abundances of both ectoparasite species were comparatively beneficial for pied flycatcher broods, suggesting a role for competition between ectoparasites that may ultimately increase host brood survival.

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Despite the important roles parasites may obviously play on the fitness of their hosts (Price 1980), the study of host-parasite interactions in bird populations has been a relatively neglected area until recently (Loye and Zuk 1991). The paper by Hamilton and Zuk (1982) spawned the field for a recent plethora of observational and experimental studies on the role of parasites in sexual selection, sexual dimorphism, and mate choice (reviews in Read 1988, Clayton 1991). In addition, a sizeable number of studies aimed to demonstrate detrimental effects of parasites on other components of fitness (e.g. growth, survival) have been conducted on wildlife populations in the last few years. Many studies have been conducted with birds and nest ectoparasites as model systems for attacking these problems. Nest ectoparasitism by bugs (Hemiptera), mites (Acari) and blood-sucking fly larval stages (Diptera) have received most attention, although except for Møller's work (1990a,b, 1993), most of the recent studies have been restricted to North American host-

parasite systems. These studies have demonstrated significant effects of ectoparasites on host dispersal (Brown and Brown 1992), temporal patterns of host colony occupation (Emlen 1986, Chapman and George 1991), hosts' costs of reproduction (Moss and Camin 1970, Møller 1993) and offspring growth and survival (Brown and Brown 1986, Shields and Crook 1987), in relation to variable degrees of naturally or experimentally controlled levels of nest parasitism. Despite the considerable insight already gained, the data are somewhat flawed by a taxonomic and life-style bias within birds towards colonial or semi-colonial species (Møller et al. 1990), namely hirundines (Brown and Brown 1986, 1992, Møller 1990a,b, 1993, de Lope et al. 1993), which may be exposed to atypical levels of nest ectoparasitism, at least when compared with other non-group living passerine species, whose territorial systems impose a more widely spaced nest dispersion pattern (see, e.g. Poulin 1991). Outside the hirundines, only a few detailed intraspecific studies

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on nest ectoparasites have been conducted (Gold and Dahlsten 1983, Burt et al. 1991, Johnson et al. 1991, Johnson and Albrecht 1993, Mappes et al. 1994), with variable, somewhat controversial conclusions regarding the effects of different nest ectoparasites. For example, while Moss and Camin (1970) and Møller (1990a), among others, found pronounced effects of mites on purple martins and swallows, respectively, Johnson and Albrecht (1993) disregarded the effects of mites on the growth and survival of nestling house wrens. Likewise, Johnson and Albrecht (1993) found little effects of blowfly larvae on nestling haematocrit values, nestling growth and survival, in rather contrast with the studies of Shields and Crook (1987) and Whitworth and Bennett (1992).

To date, few researchers have apparently exploited the potential of long-term studies of bird populations to gain insight on the effects of parasites on their hosts (Price 1991), although invaluable knowledge can be gained from the simultaneous study of marked individuals and their interactions with parasites. Before undertaking that task, however, any long-term study should control for potential biases that may present several pitfalls to correlational analyses of the parasite effects (Brown and Brown 1986, Shields and Crook 1987, Møller 1989, 1992). For example, due to adult site-tenacity (which depending of the type of parasite species may increase the likelihood of infestations in particular sites or patches), or to microclimate differences between nests groups (George 1959, Rogers et al. 1991) which may cause long-term interactions of site quality and ectoparasite abundance, the theoretical possibility at least exists that some nests and/or parents are more prone to have more parasites in their nests (Møller 1992). For similar reasons, non-experimental studies should also ideally control for other environmental and individual differences (e.g. Arnold and Lichtenstein 1993), as well as the parental influences on the traits examined for the effects of parasites, as some of these traits may have large heritabilities (Hailman 1986, Boag and van Noordwijk 1987), and genotypes and (or) phenotypes may distribute non-randomly in relation to parasite prevalence and abundance (Hamilton and Zuk 1982, Møller 1990a). Well-designed, randomized experiments have the potential to overcome these biases.

Here we analyze the effects on nestling growth and survival of ectoparasitic mites on a population of pied flycatchers (*Ficedula hypoleuca*) studied over a three-year period. In addition, data from one breeding season are analyzed for similar effects of another ectoparasite species, the larvae of the blowfly *Protocalliphora azurea*. Species of *Protocalliphora* blowflies are common hosts of passerine nests throughout most of their northern common ranges (Bennett and Whitworth 1991), although almost all published studies have dealt with North American species. All the data in this study were taken during a non-experimental, long-term study of pied flycatchers in an artificially increased population breeding in nest boxes in Central Spain (Potti and Montalvo 1990, 1991a,b). Specifically, the following questions are asked: 1) Do

mites and blowfly larvae affect nestling growth and survival independently of breeding phenology and parental trait variation and, if so, are their effects different (Johnson and Albrecht 1993)? 2) Does territory quality interact with breeding phenology and ectoparasite abundance in the expression of heritable traits in the brood? and 3) Are there any interactions between both types of nest ectoparasites that affect (i.e., either decreasing or benefiting) the host's brood growth and survival? To our knowledge, this is the first time this last question is examined in a field study on a wild bird population.

Methods

We studied nest ectoparasites in an intensively studied population of pied flycatchers in central Spain (Potti and Montalvo 1990, 1991a,b). Beginning in 1987, nearly all breeding birds were captured at their nests while incubating (females) or feeding nestlings (males), and their tarsus and mass were recorded. All nestlings were measured for the same variables and ringed on the 13th day of life, by which time the definitive, adult tarsus length has been already reached (Alatalo and Lundberg 1986, Potti and Merino 1994). Although mites were not quantified, from 1988 onwards we scored mite abundance of each nest on the date of ringing as with few or no mites and with many mites, roughly equivalent to a qualitative "presence/absence" index (see Results). No data on nestlings measurements or mite presence were taken in the 1990 breeding season, as almost all nests were depredated by weasels (*Mustela nivalis*) that year. In 1991, all nests were removed in labelled plastic bags after breeding, transported to the laboratory and placed in Berlese funnels for 48 h. The mites were then counted under a binocular microscope, and the nest material was subsequently dismantled in search of blowfly pupae.

Nest quality was approximated by means of an index assuming that, in the long term, the nest boxes most frequently used by the flycatchers have higher quality (see Askenmo 1984, Potti and Montalvo 1991a,b, Potti 1993). For the purposes of analysis, nest quality was treated as a categorical variable, i.e., nest boxes of high (above the mean) and low quality. All nest contents were removed after the breeding period in all years, as we aimed to standardize the initial conditions for the birds in all years (see Møller 1989). To ascertain the effects of ectoparasitism on nestling mortality in 1991, all nests that were neither abandoned nor depredated were divided into two classes, namely nests with nestling mortality and nests where all nestlings successfully fledged.

All statistical tests (Sokal and Rohlf 1981) are two-tailed. Means are given with one standard deviation, except where indicated.

Table 1. Results of analyses of covariance of mean within-brood tarsus-length (A) and mass (B). Nests were divided into two groups (early and late) according to hatching phenology. Numbers of broods were 141 in (A) and 128 in (B).

Source of variation	Mean Square	d.f.	F	P
(A) Tarsus length				
Covariates				
Male tarsus-length	0.65	1	4.08	0.0455
Female tarsus-length	3.84	1	23.99	0.0000
Factors				
Mite load	1.51	1	9.43	0.0026
Nest quality	0.45	1	2.84	0.0943
Nest phenology	1.45	1	9.09	0.0031
Interactions				
Mite load × Nest phenology	0.28	1	1.73	0.1910
Mite load × Nest quality	0.51	1	3.22	0.0751
Nest phenology × Nest quality	0.50	1	3.13	0.0793
Nest phenology × Nest quality × Mite load	1.41	1	8.83	0.0035
Residual	0.16	131		
(B) Mass				
Covariates				
Male mass	4.10	1	6.70	0.0109
Female mass	11.12	1	18.16	0.0000
Factors				
Mite load	4.54	1	7.42	0.0074
Nest quality	2.66	1	4.35	0.0391
Nest phenology	4.02	1	6.57	0.0117
Interactions				
Mite load × Nest phenology	0.04	1	0.06	0.8028
Mite load × Nest quality	2.71	1	4.43	0.0375
Nest phenology × Nest quality	0.11	1	0.18	0.6734
Nest phenology × Nest quality × Mite load	0.08	1	0.13	0.7273
Residual	0.61	118		

Parasite species

The mites infesting pied flycatcher nests in our population belong to the species *Dermanyssus gallinoides* Moss 1966. This species of fast-moving mite has a nonfeeding larval stage, which moults into haematophagous protonymphs that develop into nonfeeding deutonymphs and then into parasitic adults. In optimal conditions, eggs laid by these mites can reach the adult stage in 7 d, producing several generations while their host nestlings are growing. In most species of dermanyssid mites so far studied, most individuals emigrate from the nest soon after the host's nestlings fledge, although some may overwinter in the nest material (Philips 1990, Burt et al. 1991).

Blowfly pupae of the species *Protocalliphora azurea* Fall 1817, were the only parasitic diptera larvae found in the pied flycatcher nests. All species in this genus have obligate, nest-dwelling ectoparasitic larvae which attach to avian nestlings to intermittently feed before sinking into the nest material to pupate. The emerging adults apparently overwinter in diapause until spring, when the females lay eggs in bird nests where nestlings have hatched (Bennett and Whitworth 1991).

Results

Scoring ectoparasite abundance and prevalence

Our qualitative scores of mite abundance in the years 1988–1991 gave a rather good approximation to mite numbers on pied flycatcher nests, as shown by the highly significant difference in Berlese funnels mite counts between nests scored in 1991 as “with many mites” ($\bar{x} = 5280 \pm 4469$ mites, $n = 15$) and those “with few mites” ($\bar{x} = 2244 \pm 3579$, $n = 47$; Mann-Whitney U -test, $z = 3.21$, $p < 0.001$). Hence, assuming that mite numbers in the latter year are representative of conditions in previous years, nests scored as “with many mites” in the years 1988 and 1989 had probably more than twice the mites than those scored as “with few mites”. Throughout the remainder of this paper, the effects of nest ectoparasites on nestling growth and fledging success are analyzed on the basis of this low vs high scoring system. In addition to allow us the use of a 3-yr data set, this type of estimation is conservative in relation to the likelihood of finding significant results as, in our larger data set infested nests are, if anything, underestimated (see also Møller 1990, Brown and Brown 1992). On the basis of this scoring system, prevalences of mite-infested nests were 11.1 ($n = 54$), 17.9 ($n = 67$) and 26.2% ($n = 61$) in 1988, 1989 and

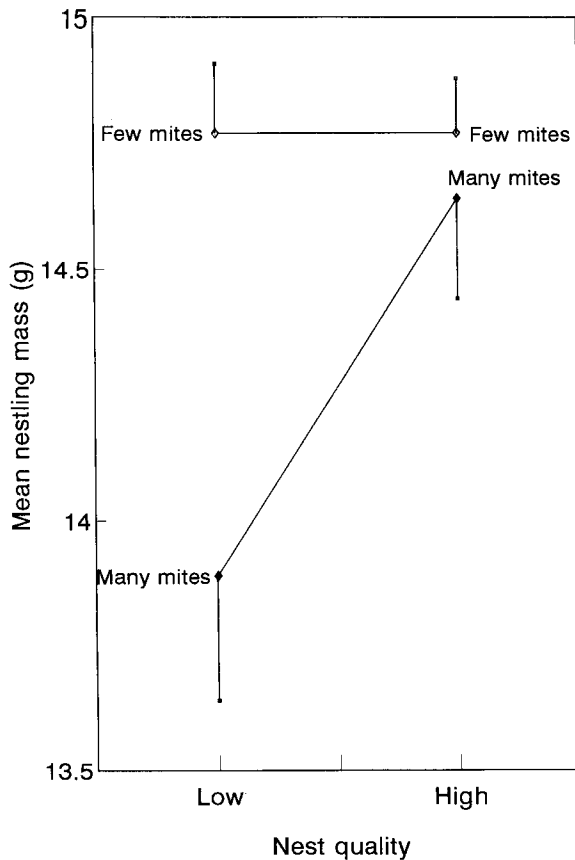


Fig. 1. The effect of mites on mean (SE) nestling mass varies depending on nest box quality.

1991, respectively. However, in practice, all nests in 1991 were infested by mites as shown by Berlese funnel counts (prevalence 100%, median 1175 mites, range 4–21454, $n = 70$). Prevalence of *P. azurea* pupae was also high that year (93.1%), with a median number of 16 pupae (range 0–60, $n = 68$).

Mite abundance and fledgling growth

Before analyzing the relationship between mite abundance and mean within-brood measurements, we statistically controlled some factors which are known to influence nestlings' development and survival, namely parental size (tarsus, mass) and date of hatching (Alatalo and Lundberg 1986, Potti and Merino 1994) and the quality of the territories (Potti and Montalvo 1991b). There was no effect of year on mean brood mass ($F_{2,179} = 0.62$, $p = 0.54$), while mean tarsus length varied across years ($F_{2,180} = 5.95$, $p = 0.003$) and was standardized before subsequent analyses. Nest box quality was unrelated to mite scores ($\chi^2_1 = 0.03$, n.s.). The number of nestlings in the brood was positively related to mean nestling tarsus

length and mass ($r = 0.16$, $n = 183$, $p = 0.03$, and $r = 0.18$, $n = 182$, $p = 0.01$, respectively). However, these relationships were due to the effect of hatching date on both nestling measurements and number of nestlings, as the effects disappeared when hatching date was controlled for. As shown in Table 1, mite presence had a negative effect on nestlings' tarsus length, after allowing for the genetic influence of parents' tarsi, and the environmental ones as reflected by the nest box quality and the decrease with hatching date. Moreover, there was a significant interaction between the three factors: mean within-brood tarsus length did not vary between nests of differing quality when there were few mites and the nestlings hatched early in the season. However, mean tarsus length in nests with both high mite loads and late hatching date was lower in nests of low quality. The same analysis was performed with mean nestlings' mass as the dependent variable. Results were similar to those with tarsus length, except that hatching phenology did not interact with the other factors (Table 1). There was, however, a significant interaction between the nest box quality and the mite load on mean nestling mass: mites had a greater effect on broods in low quality sites (Fig. 1).

To further search for influences of mites on brood development, we analyzed the relationships between the within-brood coefficients of variation in tarsus length and nestling mass with mite abundance. Nests with many mites had significantly greater variation in mass than nests with few mites, even after the positive effect of hatching date on within-brood variation ($r = 0.23$, $n = 182$, $p = 0.002$) was statistically controlled by using the residuals of a linear regression model (t -test, $t = 3.27$, $p = 0.001$). Furthermore, as was the case with nestling mass (Fig. 1), there was a significant interaction between nest box quality and mite abundance on within-brood variation in mass, with greater variation in the low quality nest boxes with many mites (interaction term: $F_{1,139} = 5.90$, $p = 0.016$). Within-brood variation in tarsus length was unrelated to mite abundance (t -test, $t = 1.49$, $p = 0.14$) and hatching phenology ($r = 0.09$, $n = 183$, $p = 0.24$).

Blowfly pupae, fledgling growth and nestling mortality

For the year 1991, we had also quantitative data on numbers of blowfly pupae in the nest material. Pied flycatcher nests were divided into two groups of blowfly pupae abundance, namely above or below the median, and mean nestling measurements were compared between groups. Apparently, blowfly larvae had negative effects on mean nestling tarsus length ($19.53 \text{ mm} \pm 0.15$ in nests with low pupae numbers ($n = 31$) vs 19.16 ± 0.33 in nests with high pupae abundance ($n = 29$; $F_{1,58} = 8.65$, $p = 0.005$) and mass (15.01 ± 0.82 vs 14.58 ± 0.84 , respectively; $F_{1,58} = 4.13$, $p = 0.047$). However, both trends were entirely due to an increase of pupae abundance with the advancing season ($r = 0.35$, $n = 68$, $p < 0.004$). When this

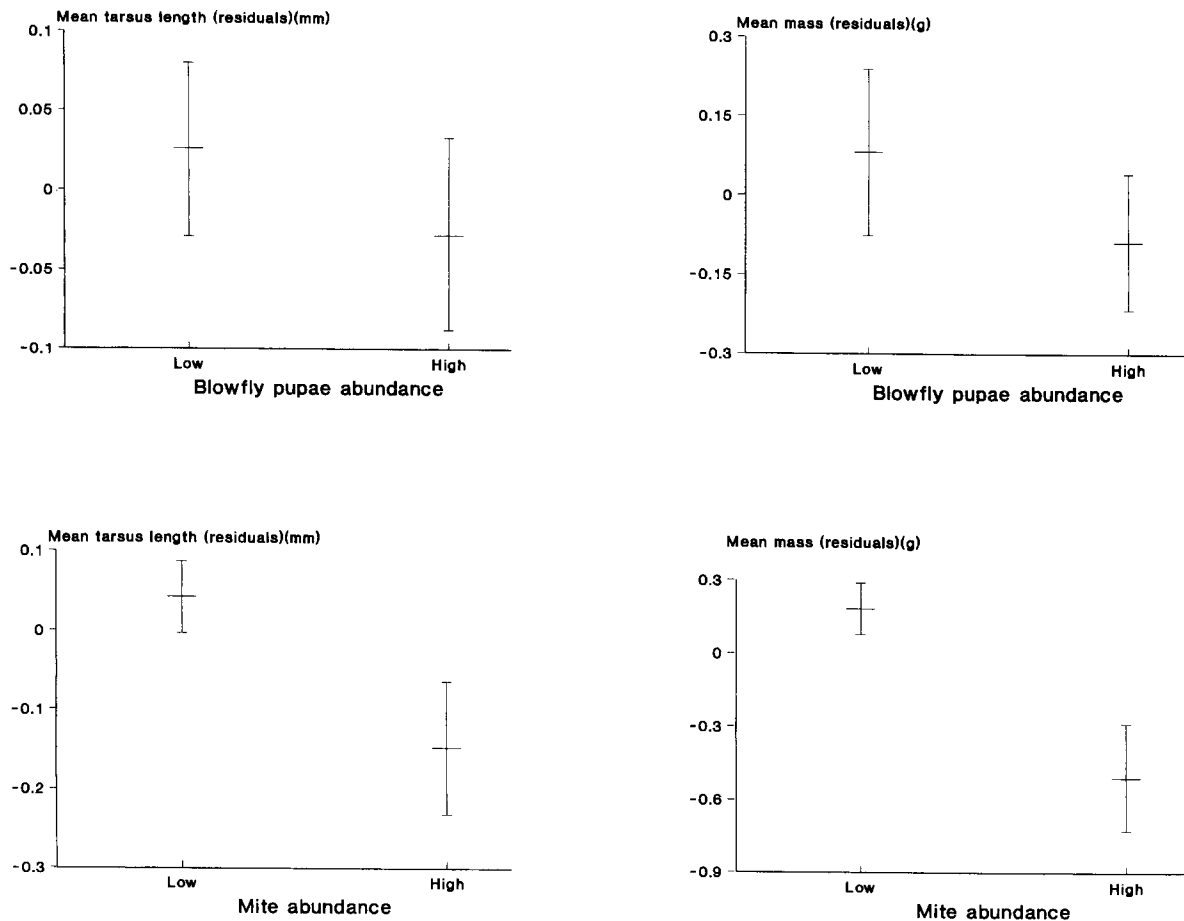


Fig. 2. Mean (± 1 SE) within-brood tarsus-length and mass of nestling pied flycatchers in relation to ectoparasite loads (below and above the median number of individuals in the nests) in 1991.

effect was statistically controlled by using the residuals of a linear regression analysis with hatching date as the independent variable, no significant effects of blowfly larvae abundance were detected on mean nestling tarsus or mass (Fig. 2) or variance in both traits (F -tests, in both $p > 0.60$). On the contrary, mite abundance had a negative influence on nestling growth measurements (Fig. 2).

Nestling mortality was affected by the presence of large numbers of blowfly pupae in the nest, as nests where some nestlings died had more pupae per nestling (9.57 ± 6.02 , $n = 8$) than those where all nestlings fledged (3.35 ± 2.48 , $n = 48$; t -test, $t = 5.13$, $p < 0.0001$). This relationship was still significant when the effect of the advancing season on both variables was statistically controlled (t -test, $t = 2.96$, $p = 0.005$). The presence of mites had no effect on fledging success (t -test, $t = 0.89$, $p = 0.38$).

There was no association between numbers of mites and blowfly pupae in the nests (Spearman rank correlation, $r_s = 0.07$, $n = 67$, $p = 0.57$). Neither was there an association when relative loads per nestling were used

($r_s = 0.21$, $n = 60$, $p = 0.10$), even after taking into account the effect of the advancing season on blowfly numbers ($r_s = -0.05$, $n = 60$, $p = 0.70$).

Combined effects of ectoparasites

To search for interactions between mites and blowfly larvae in 1991 we performed analyses of covariance on mean nestling mass and tarsus, with low (below the median) and high scores of both ectoparasite species as factors, and hatching date and parental traits as covariates. The ANCOVA on mean nestlings mass showed significant negative effects of mites ($F_{1,55} = 8.66$, $p = 0.005$), but not of blowfly pupae ($F_{1,55} = 0.15$, $p = 0.71$). However, there was a significant interaction term between both factors ($F_{1,55} = 4.48$, $p = 0.039$): mean nestling mass is always higher in nests with low infestations of mites, but the effects of mites are much reduced when there are high numbers of blowfly pupae in the nests (Fig. 3). Similar analyses on mean tarsus length only revealed

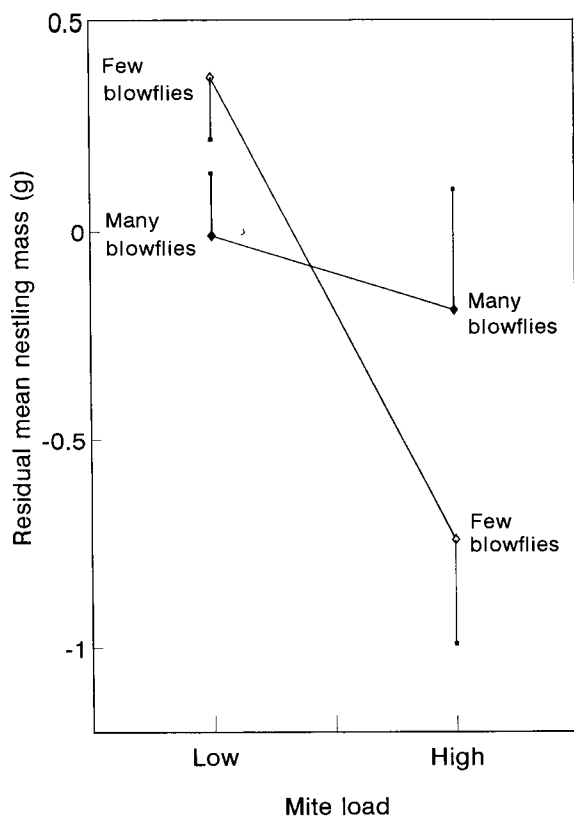


Fig. 3. Interaction between the effects of varying ectoparasite loads on mean (SE) nestling mass of pied flycatchers in 1991.

reduced growth in nests with high mite loads ($F_{1,54} = 3.87$, $p = 0.05$), and neither the effects of pupae nor the interaction term were significant.

Discussion

Any observational, long-term study as ours, on bird breeding biology may present some pitfalls to a correlational analysis of the effects of nest ectoparasites (e.g. Feare 1976, Brown and Brown 1986, Emlen 1986, Shields and Crook 1987, Møller 1989, 1992). In this study we have controlled for several potential biases when studying the effects of nest ectoparasites on pied flycatcher reproductive success. First, our nest boxes have been cleaned from the beginning of our study after the completion of the flycatchers' reproduction (and most years, again *before* breeding), thus minimizing the unknown, albeit plausible, long-term interaction of site quality and ectoparasite abundance. Our procedure of removing nests was successful in setting standardized initial conditions for the birds, as there were no significant between-year repeatabilities of either type of ectoparasite abundance scores within the same nest box

occupied in successive years, either within nest boxes, or individual males and females (Merino and Potti unpubl.). So, the nest boxes are probably recolonized each breeding season by gravid blowfly females (Bennett and Whitworth 1991), while mites may colonize our nest boxes by attaching to phoretic arthropods (Marshall 1981: 274) or to the adult parent birds. On the other hand, by controlling parental trait variation we have tried to avoid finding spurious correlations between parasite loads and nestling growth that may be partially or entirely due to the indirect effects of parental condition. For example, an adult bird in low condition may be more susceptible to ectoparasite infection, simply because it may have less time to deparasitize itself and may have to allocate more time to self-feeding at a cost of its brood, which thus grows slower.

In agreement with several previous studies that have found marked effects of mites on the body mass of their hosts (Moss and Camin 1970, Møller 1990a,b, 1993, Powlesland, cited in Lehman 1993), we found that mite abundance negatively affected mean nestling mass and tarsus length in our pied flycatcher population over a three-yr period. In addition, mite abundance also contributed to the increase in within-brood variance, thus potentially affecting sibling competition and survival. In the pied flycatcher, tarsus-length may be subject to directional selection, nestlings with short tarsi suffering from a high mortality after fledging (Alatalo and Lundberg 1986, Alatalo et al. 1990). On the other hand, fledglings with lower mass also have lower survival (Lundberg and Alatalo 1992). In surviving, recruiting pied flycatchers of both sexes, nestling mass is significantly related to adult breeding mass (Potti and Merino unpubl.); in female pied flycatchers, adult mass correlates positively with clutch size (Askenmo 1982, Potti and Merino unpubl.) and egg size (Potti 1993), while a low mass is usually related in at least the younger males to a late arrival from spring migration (Potti and Montalvo 1991a). This is important because an early arrival date is a strong determinant of pairing and reproductive success in the pied flycatcher (Alatalo et al. 1984, Slagsvold and Lifjeld 1988, Potti and Montalvo 1991a, Lundberg and Alatalo 1992). Thus, several important components of fitness in our pied flycatcher population were probably negatively affected by high mite loads in the nests, revealing the important role these nest ectoparasites may play on their hosts (Moss and Camin 1970, Møller 1990a,b, 1993).

Some authors have minimized the detrimental role mites may play on their host reproductive biology, by arguing that their small size (about 0.7–1.5 mm in our *Dermanyssus* species) makes them unlikely candidates to cause negative effects on their hosts through blood retrieval (Johnson and Albrecht 1993). Even if this were true, we think that other important effects are being overlooked with this argument. For example, mites could act as vectors of disease and/or Hematozoa, produce many small skin lesions, or irritate nestlings when hundreds of individuals scratch on their bodies (Moss 1978, Quiroz 1988, Soulsby 1988, Møller 1990a, 1991a, Philips

1990, 1993, Burt et al. 1991, Molyneux, cited in Apanius 1991, Durden et al. 1993). In addition, we observed some adult birds that were apparently reluctant to enter their nests to feed nestlings when there were great numbers of mites. When this occurs, nestlings may compete with each other for the best position near the nest box entrance (Potti and Merino pers. obs.), thereby increasing energy costs. The pronounced competition for the most suitable site near the nest box entrance may be reflected in the large within-brood mass variation encountered in this study. On the other hand, it is perhaps significant that in the heavily infested nest boxes we sometimes observed the adult birds bathing in nearby puddles immediately after feeding the nestlings, in an apparent attempt to try to deparasitize themselves. Hence, detrimental effects of mites on nestling growth may be enhanced by an effect of repulsion on the parents, or either by the adult birds allocating more effort to self-preening and maintenance; in both cases, we would predict a decrease of parental feeding rates in these nests (Møller 1990a; but see Møller 1991b). In a similar vein, Møller (1990b) found that heavy mite loads significantly increased the female incubation period in the swallow *Hirundo rustica*, maybe because those nests were more frequently left unattended. Evidence on the supposed repulsion effect of mites is the significant positive relationship in our flycatcher population between the mass of nestling faeces left in the nest and the number of mites counted in 1991 ($r=0.31$, $n=68$, $p=0.011$), suggesting that the parents somewhat neglect nest sanitation in the heavily mite-infested nest boxes.

The significant interaction between date of hatching, nest quality, and mite abundance on nestling development are interesting in the sense that they are reflecting a changing, dynamic relationship between nestling growth and the parasitic and other environmental influences. Nest quality and date of hatching possibly reflect the quality and/or quantity of insect food fed to young (Lundberg and Alatalo 1992), and when the food supply is scarce parasite detrimental effects seem to be much more marked (Shields and Crook 1987, de Lope et al. 1993).

As to the effects caused by blowfly larvae on nestling growth and survival, our results point to an apparent lack of effect on growth, but a significant effect on nestling mortality. There exists some controversy about the impact of these organisms on host fitness (Price 1991; cf. Johnson et al. (1991), Rogers et al. (1991), Whitworth and Bennett (1992)). Our study adds to the few demonstrating detrimental effects of blowfly larvae on nestling survival before fledging (see also Shields and Crook (1987), Møller et al. (1990), Lehman (1993), and references therein). The fact that we did not find any effect of these parasites on nestling growth parameters could be due to our sampling method, as nestlings were measured on the day 13 of life, and by then the nestlings had died in the most heavily parasitized nests. This idea can be refuted, however, because when the analysis was restricted

to those nests where no nestling mortality occurred results were the same. One alternative hypothesis may be that individual blowfly larvae may distribute less evenly throughout the individual nestlings of the brood than mites do. Because of their smaller size and different life cycle, the energy diverted by mites from each nestling for growth may cause less of a damage to individual nestlings than blowfly larvae. Blowfly suckling larvae may have a more contagious within-nestling distribution (i.e. activity feeding on the same nestling by different larvae). This might be mediated by within-brood competition and trampling, so that the smaller nestlings are more likely to be bled, and subsequently die, by the nest-dwelling larvae. Hence, as mites, blowfly larvae probably also have negative, detrimental effects on nestling growth, especially in the early life, ultimately causing nestling mortality although the cost of this type of ectoparasitism is probably low when infestations are mild. Once brood reduction has occurred, the parents might more easily compensate for the cost of parasitism and the effects of blowflies should not be readily noted in the growth measurements of the surviving nestlings (Johnson and Albrecht 1993). In contrast, mite feeding on the nestlings is not usually a cause of nestling mortality but of reduced nestling growth. An explanation for the differences in virulence between both ectoparasites may be that parasite virulence may depend on mode of transmission, so that the more virulent parasites (blowflies in our study) should not depend on survival of the host for transmission (Herre 1993). Mites have several generations in bird nests and, contrary to blowflies, their dispersal may be dependent on fledgling survival and dispersal.

There was a significant interaction between mite and blowfly abundance on mean brood mass of pied flycatchers. Mean nestling mass in nests with low loads, either of mites or blowflies, was unaffected, but decreased with high mite loads. However, the effect of high mite loads was less detrimental to the nestlings when there also were large numbers of blowfly larvae. This interaction between different ectoparasites may be due to the above mentioned effect of blowflies on nestling mortality, so that through blowfly-induced nestling mortality, parents can compensate for the effect of parasites on the growth of surviving nestlings. But other effects may be operating as well. One idea is that competition between ectoparasite species is only shown (i.e. measurable at our level of resolution) when both species reach high population densities. That sort of competition could work by reducing both the number of available foraging sites on the host surface, and/or habitat (host) quality. In addition, the possibility exists that some mites could forage on the blowfly larvae, as has been documented by Marshall (1981: 274) with other ectoparasite systems.

In conclusion, mites and blowflies have differential, detrimental effects on the reproductive success of pied flycatcher populations. Observational, correlative studies of the impact of ectoparasitism on bird breeding biology have the potential to detect these effects, although many

variables, parental and environmental, should be taken into account before undertaking this task.

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