Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*)

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SUMMARY

We report experimental data comparing the effects of Mesostigmatid mites and Ischnoceran lice on the reproductive performance of a single group of captive rock doves (*Columba livia*). Several components of host reproductive success were compared for the two groups, including number of eggs laid, hatching success, nestling growth rates, fledging success, post-fledging body mass and survival. Adult body mass and survival were also compared. There was a dramatic difference in the effects of the mites and lice. The former drove host reproductive success to zero, mainly by agitating adults and causing them to incubate eggs less faithfully. Nestling growth rates and post-fledging survival were also significantly reduced by mites. Lice showed no effect on reproductive success whatsoever, even though the feather damage they cause is known to have energetic consequences (Booth, Clayton & Block, 1993). Neither parasite had a significant effect on adult birds. Although Ischnocera are found on most species of birds, our results for lice constitute the first experimental test of the impact of Ischnocera on avian reproductive success (preliminary report by Clayton & Tompkins, 1994). We discuss reasons for the different effects of mites and lice, including the relationship of horizontal (mites) and vertical (lice) transmission to the evolution of virulence.

Key words: ectoparasites, reproduction, rock doves, mites, lice.

INTRODUCTION

Theory suggests that the evolution of parasite virulence is associated with the ease of transmission among hosts (Anderson & May, 1982; Ewald, 1983). Parasites transmitted to new hosts independently of host fitness (e.g. horizontally transmitted parasites) may not suffer a reduction in fitness by harming the host. However, parasites transmitted vertically from parents to offspring will suffer a severe reduction in fitness if they have too great an impact on host reproduction. In a recent paper, Lehmann (1991) compared the effects of dissimilar ectoparasites on a population of small mammals (*Gerbillus andersoni*). He showed that independently transmitted fleas reduce host fitness, whereas vertically transmitted lice have no detectable effect on components of fitness. Although the impact of fleas was tested via experimental manipulation of flea loads, the results for lice were correlational.

We have conducted a parallel study with rock doves (feral pigeons, *Columba livia*) in which we compared the effects of independently transmitted Mesostigmatid mites with the effects of vertically transmitted Ischnoceran lice. In a preliminary report (Clayton & Tompkins, 1994) we showed that mites are more virulent than lice, which accords with theory. A survey of the literature provided additional support for the hypothesis that ectoparasite virulence is linked to mode of transmission (Clayton & Tompkins, 1994). In the current paper we compare

the effects of mites and lice over a longer-term experiment, including data for a larger number of components of reproductive success, as well as data on adult body mass and survival. We then discuss probable constraints on the evolution of virulence in Ischnoceran lice.

Experimental tests of the effects of Ischnocera on avian reproduction had not been published prior to our preliminary report (Clayton & Tompkins, 1994) despite the fact that Ischnocera parasitize most species of birds (Marshall, 1981; Clayton, Gregory & Price, 1992). Derylo (1974*a*, *b*) reported a reduction in the egg production of Leghorn chickens parasitized by Ischnocera, but the subjects of study also had Amblyceran lice. In contrast to the feather-feeding Ischnocera, Amblycera feed on the skin and blood of the host as well as feathers and are known to promote dermatitis and scratching. They are responsible for up to a 46% reduction in the egg production of poultry (DeVaney, 1976). The pigeons in our study were host only to Ischnocera.

Background

Rock doves are a monogamous species with life-long pair bonds (Levi, 1957; Johnston, 1992). Two eggs are normally laid and both parents incubate until the eggs hatch after about 17 days in the nest. The nestlings spend about 1 month in the nest where they are fed by a regurgitated mixture of crop milk and grain by both parents. Feeding by the parents

continues for approximately 1 week after the young fledge. Thus, the period of parental care, from laying of eggs to independence of fledglings, ranges from 50 to 60 days. North American rock doves may attempt to breed year round (Johnston, 1992), but are normally successful only during March–November in Illinois, the site of this study (Clayton, 1989).

The species of mite we studied, *Dermanyssus gallinae*, is a member of the family Dermanyssidae (suborder Mesostigmata). It is a common parasite of both wild and domestic birds (Strandtmann & Wharton, 1958) and is frequently observed in the nests of pigeons (Levi, 1957; Johnston, 1992). *D. gallinae* spends most of its time in the nest material but emerges periodically to feed on the blood of its host (Sikes & Chamberlain, 1954). It usually feeds on nestlings, but will also attach to the lower belly of adults that are incubating eggs or brooding the young. The life-cycle is completed in just 8–9 days and consists of the following stages: egg, larva, 2 nymphal instars, and adult (Benbrook, 1965). Adults can survive for months without feeding.

The species of lice we studied, *Columbicola columbae* and *Campanulotes bidentatus*, are members of the suborder Ischnocera of the insect order Phthiraptera (formerly Mallophaga). They are common on feral pigeons and are the only Ischnocera found on this species of host. Ischnocera are obligate parasites that complete their entire life-cycle on the body of the host (Marshall, 1981). They do not leave the host's body except to pass among hosts during periods of direct contact, e.g. between parent birds and their offspring. The life-cycle, which requires 3–4 weeks, includes an egg, 3 nymphal instars, and the adult. Eggs are glued to the host's feathers with a glandular cement. *C. columbae* and *C. bidentatus* feed exclusively on the barbules of feathers (Nelson & Murray, 1971), which they metabolize with the aid of symbiotic bacteria (Eichler *et al.* 1972; Marshall, 1981). In this paper 'louse load' refers to the combined populations of the two species of lice. We have not distinguished between them as they were not manipulated independently and are known to have similar proximal effects on the host (D. H. Clayton, personal observation).

MATERIALS AND METHODS

Study population

All data were collected between March 1986 and March 1988 in an outdoor, free-flight enclosure near the University of Illinois, Urbana-Champaign. The enclosure (9·2 × 3·7 × 2·5 m) was constructed in 1982 in the loft of a barn and was stocked with 72 feral pigeons captured on rooftops and under bridges (Droge, 1986). During our study the flock contained 46 adult breeding pairs from the original stock or their descendants. The birds were continuously

exposed to fresh air and sunlight (ambient temperature and photoperiod), while being protected from direct wind and precipitation. They were fed on a commercial grain mixture (Kaytee Breeder and Conditioner Pigeon Feed #6®) and provided with grit, nesting material and water (heated during winter).

The pigeons nested year round in contiguous, open-face boxes mounted on the walls of the enclosure as illustrated in Levi (1957). Most pairs of adults defended two adjacent boxes, enabling them to overlap clutches with one adult incubating eggs while the other fed nestlings in the adjacent box. Eggs were incubated for a mean of 17·1 days (S.D. = 0·58, $N = 55$ nests) and the mean number of post-hatching days in the nest was 30·7 (S.D. = 1·73, $N = 55$) (data for April–September 1986). We periodically culled fledglings to prevent overcrowding in the enclosure. The flock contained from one dozen to several dozen fledglings on any given date.

In addition to the breeders the flock contained about a dozen non-breeding 'floaters', resulting in persistent competition for mates and nest boxes. Fighting over nest boxes was common, although residents were seldom usurped. Fighting over nest sites is common in free-ranging populations of rock doves (D. H. Clayton, personal observation).

Counting parasite loads

We use parasite 'load' as a generic phrase encompassing two explicit measures of parasite abundance: 'prevalence', the proportion of individual birds or nests parasitized; and 'intensity', the number of parasites harboured by an individual bird (Margolis *et al.* 1982).

Mites. It was not possible to count the total number of mites in nests non-destructively. Rather, mite intensity was estimated by counting the number of mites on nestlings during a careful examination of all body regions. This required less than 1 min for young nestlings but up to 3 min for pre-fledglings. Mite counts using this method are significantly correlated with the total number of mites in nests (Clayton & Tompkins, 1994). Data for nestmates were averaged to avoid pseudoreplication (Hurlbert, 1984). Nestlings were censused for mites about once a week between 11 April and 16 June 1987.

Lice. The louse loads of both adult and nestling birds were estimated. Nestling louse loads were estimated as described above for mites. This approach could not be used to estimate the louse loads of adult birds as their dense plumage made it difficult to see most of the lice. Adult loads were therefore estimated on the basis of timed counts of the number of lice on various body regions, as described by Clayton (1991). These counts were substituted into re-

gression models that accurately predict total louse load ($r^2 \geqslant 0.82$). During this procedure the treatment status of each bird was unknown to the person collecting the data. Adults were censused for lice in May and July 1987 and again from November 1987 to the end of the study in January 1988.

Manipulating parasite loads

Mites were not present in the enclosure in 1986. They were first detected on 9 April 1987. The source of mites is unknown but, as *D. gallinae* is a generalist occurring on many species other than pigeons, it is possible that they were transmitted to the captive flock by house sparrows (*Passer domesticus*) nesting in the barn.

Mites were first censused on 11 April and repeat censuses followed at about weekly intervals throughout the study. Mites were manipulated immediately after the second census (17 April) by fumigating 11 'low-load' nests, all of which were mite-free during the first two censuses. The fumigant was a 1.0% aqueous solution of pyrethrum. Eleven more 'high-load' nests, all of which contained mites during the first two censuses, were sham-fumigated with water. (Seven nests used in preliminary trials were excluded from the experiment.)

Boxes had to be refumigated periodically to prevent increases in mite intensity. Pyrethrum has no side-effects on birds (Jackson, 1985). To be sure of this, however, we fumigated 10 recently hatched nestlings and sham-fumigated another 10 with water. We then compared the growth rates, fledging success and post-fledging body mass and survival of the two groups.

It was possible to control the nest-based mite populations independently of lice, which were confined to birds' bodies. This was done by excluding birds from nests for 1–2 hours during fumigation and sham-fumigation. They were allowed to return to the nests after the fumigant was deactivated by drying nests with a hair-dryer.

By mid-June rapidly increasing populations of mites in the enclosure threatened the long-term stability of the breeding flock. On 20 June all nest boxes were fumigated, thus terminating the mite experiment. Boxes were refumigated as needed over the course of the month to eradicate mites from the enclosure.

Lice were manipulated using a two-step procedure. First, preening ability, which is the major defence of birds against ectoparasites (Marshall, 1981; Clayton, 1991), was impaired in order to convert the clumped distribution of lice among birds into a more continuous distribution. Preening was impaired with 'bits', small (< 0.8 g) C-shaped pieces of plated steel inserted between the mandibles of the bill and crimped slightly in the nostrils to prevent dislodging (but not enough to pierce the tissue). Bits create a 1.0–3.0 mm gap between the mandibles which prevents the full occlusion of the bill necessary for efficient preening.

Since pigeons feed their young by regurgitation, rather than by forceps-action of the bill, bits do not interfere with the feeding of offspring. Therefore, bits have no detectable side-effects on feeding ability (see below). However, bits might conceivably interfere with the ability of birds to defend nest sites since pigeons routinely bite opponents when fighting. To control for this possibility, *all* birds in the captive flock were bitted at the start of the louse experiment.

Unless fumigated, bitted birds experience a dramatic increase in louse load that mimics increases on birds with natural minor bill deformities (3 of 150 wild-caught birds censused for lice in spring 1988 (Clayton, 1989)). Bit-induced increases in louse load do not exceed the range of natural louse loads.

All adults in the flock were bitted on 4–6 July 1987. On 5–7 August, after ranking birds on the basis of 1986 reproductive success, 1 of every 2 pairs was randomly fumigated (low-load pairs) and the other pair was sham-fumigated with water (high-load pairs). In a few cases randomly assigned treatments were reversed to balance the distribution of treatments with regard to (1) previous mite infestation and (2) physical position of nest boxes. In total, there were 20 high-load pairs and 23 low-load pairs. Treatments were repeated on 10 September and 27 October. At the end of the experiment all birds had their bits removed.

Measuring host fitness

In 1986, data were collected to establish a baseline for reproductive success in the enclosure and to document seasonal trends. The mite and louse experiments were conducted in 1987. Main analyses for each experiment were limited to data collected over a period of 1 month, beginning 3 days after fumigation (20 April–20 May for mites; 10 August–10 September for lice). In the case of the louse experiment, additional analyses were performed using data collected from a smaller number of adult pairs during a follow-up period of 2 months (10 September–10 November). A smaller number of adults had to be used because half of the breeding pairs were removed from the enclosure in late October for use in a mate choice experiment (Clayton, 1990). All were returned to the enclosure in mid-January 1988 and the study was terminated in March 1988 (see below). The following components of host fitness were measured during the study.

Egg laying and hatching success. Nests and their contents were checked daily. Eggs that failed to hatch were discarded several days after the expected hatching date. The impact of parasites on hatching

was analysed independently by calculating hatching success contingent upon the number of eggs laid during the periods already indicated.

Nestling growth and fledging success. Since the mite experiment had to be terminated on 20 June, analysis of the impact of mites on growth and fledging success was for nestlings hatched during the month after fumigation. Fledging was analysed independently of pre-fledging components by calculating fledging success contingent upon the number of eggs hatched. Date of fledging was scored as the first day a bird was absent from its nest.

Nestlings were weighed every other day. Some were weighed on the day of hatching, and on odd days thereafter, whereas others were not weighed until the day after hatching, and on even days thereafter. To make data comparable a fifth-order polynomial regression was fitted to 'even-day' weights and used to estimate 'odd-day' weights. The regression did not give accurate estimates for Day 1 so analyses were restricted to Day 3–Day 25 weights. Birds sometimes fledged as early as Day 26; growth had reached an asymptote by this age in any case. All data for siblings were averaged to provide mean values per nest. Growth rates were compared using the general linear model procedure (GLM, controlled for repeated measures) of the Minitab 8.1 Accelerated statistics package (Minitab Inc.).

Post-fledging weight and survival. Fledglings were weighed every 2 weeks for 6 weeks after fledging. It was not possible to collect data for a longer post-fledging period because of the need to cull birds to prevent crowding. Analyses were restricted to birds fledged during the periods already indicated. This meant that all young in the mite experiment had either fledged or died in the nest by 20 June, when all nests were fumigated.

Adult weight and survival. Adults were weighed within 24 h of laying of the second egg of each clutch. A record of deaths was also kept. In late January the window coverings along one side of the enclosure were removed, enabling birds to come and go at will. Although still provided with an unlimited supply of heated water, the food supply was reduced by approximately 50%, thus encouraging birds to forage at other sites such as nearby grain silos. The survival and body mass of birds still roosting in the enclosure were monitored through March 1988 when the study was terminated.

RESULTS

Parasite loads and transmission

Mite loads. Mite prevalence increased rapidly from mid-April through to the end of May (Fig. 1A).
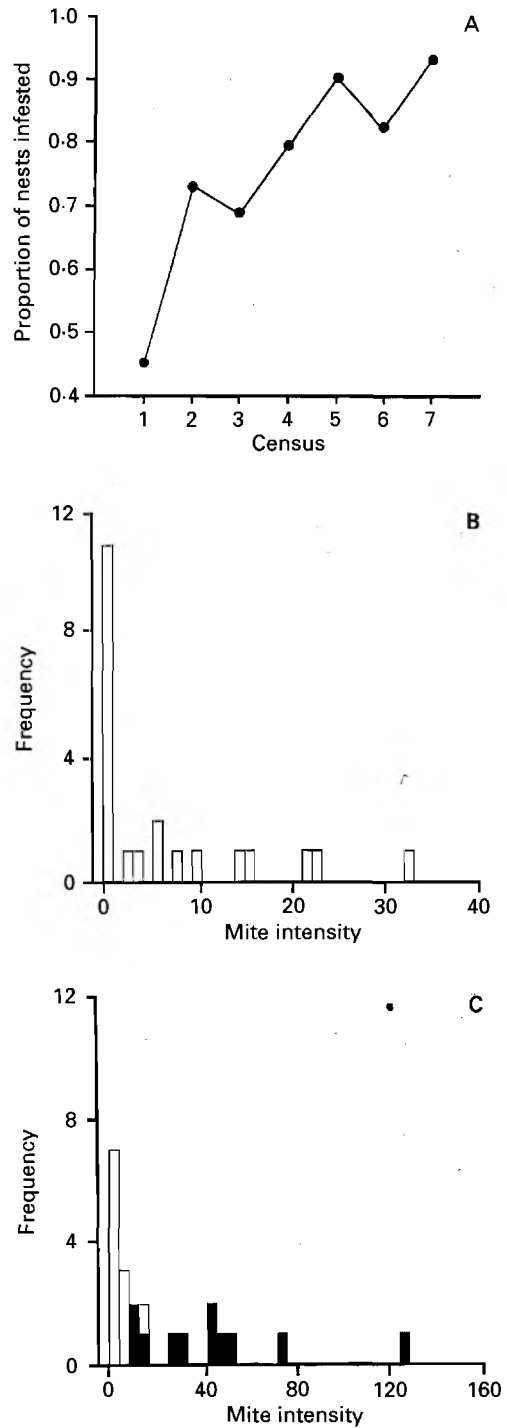

Fig. 1. (A) Increasing mite prevalence over the course of the study. Mites were censused at weekly intervals beginning 11 April; (B) frequency distribution of mites prior to fumigation in mid-April ($N = 22$ nests); (C) distribution of mites after fumigation. (□) Fumigated low-load nests; (■) sham-fumigated high-load nests. Values are the mean number of mites/nest on nestlings $\geqslant 15$ days of age averaged over weekly censuses from late April through mid-June.

Prevalence decreased in June owing to a sharp reduction in the occupancy of infested nests by young birds. The earlier increase in prevalence was due to widespread horizontal transmission of mites

among nest boxes (see Clayton & Tompkins, 1994). When treatments were assigned (on the basis of the first two censuses), 50 % of occupied nest boxes had mites (Fig. 1B). Although fumigation did not keep the low-load nests mite-free, it did keep the distribution of mites similar to that at the start of the experiment (Fig. 1C). Over the course of the experiment (results of 8 censuses averaged) low-load nests had a mean intensity of 3·3 mites (s.d. = 4·20) compared to a mean of 42·7 mites (s.d. = 33·42) in high-load nests (U = 3, P = 0·0002).

Louse loads. In May, prior to the louse experiment, louse prevalence was 100 % and mean intensity was 539 lice/bird (s.d. = 1023, N = 86). The lice were overdispersed among host individuals (Fig. 2A), with a distribution that did not differ significantly from a negative binomial distribution ($k = 1·02$; $\chi^2 = 2·46$, d.f. = 3, P = 0·52 (fitting method of Bliss, 1953)). By late July, within a few weeks of bitting, intensity had increased to 2068 lice (s.d. = 1970, N = 86) and overdispersion was considerably reduced (Fig. 2B). The maximum intensity of lice on bitted birds did not exceed natural intensities for birds in feral populations (Clayton, 1989).

Fumigation successfully controlled lice but did not eliminate them completely. The 20 low-load pairs had a mean intensity of 66 lice (s.d. = 37), compared to a mean of 2153 lice (s.d. = 1558) on the 23 high-load pairs (U = 0, P = 0·0001).

Repeated fumigation maintained similar proportions of high- and low-load birds throughout the study (Fig 2C). Of birds remaining in the enclosure during the follow-up period, the 10 low-load pairs had a mean intensity of 75 lice (s.d. = 46), compared to a mean of 1573 lice (s.d. = 764) on the 12 high-load pairs (U = 0, P = 0·0001).

The louse intensities of the offspring of low- and high-load pairs also differed significantly. Young of fumigated pairs had a mean intensity of 2·2 lice (s.d. = 2·77, N = 5 nests), compared to a mean of 23·5 lice (s.d. = 10·41, N = 4 nests) on young of sham-fumigated pairs (U = 0, P = 0·01). Once infested, the mean number of lice on nestlings correlated with the mean number of lice on their parents, regardless of their age (Kendall $T = 0·44$, P = 0·01, N = 17 nests; Fig. 3A). The robustness of this relationship increased after controlling for age ($T = 0·5$, P = 0·005, N = 17 nests; Fig. 3B). The correlation of louse intensity on parents and offspring reflects the vertical transmission of lice documented by Clayton & Tompkins (1994).

Effects of season, fumigant and bits on host fitness

The reproductive success of parasite-free birds in the spring of 1986 did not differ significantly from that in late summer. The mean number of young fledged from eggs laid April–May 1986 was 2·5 (s.d. = 1·32), compared to a mean of 2·4 (s.d. = 1·43)

fledged from eggs laid August–September (N = 32 pairs; Wilcoxon $T = 81·5$, P = 0·58). (Post-fledging survival was not measured in 1986.) This similarity is not surprising since the ambient temperatures at these times of year were also quite similar (April–June mean = 23 °C, s.d. = 6·43; Aug–Oct mean = 22 °C, s.d. = 6·57; $t = 0·70$, P = 0·48). Hence there was no seasonal variation in host reproductive success that could have confounded the comparison of mites and lice.

During the louse experiment all adult birds in the enclosure wore bits. Nevertheless, to assess potential side-effects of bits, the reproductive success of bitted birds during the louse study was compared to that of unbitted birds at other times. Two comparisons were made. First, the number of young fledged by unbitted pairs in 1986 did not differ significantly from the number fledged by the same pairs after bitting and fumigation in 1987. The mean fledging success from eggs laid 10 August–10 November 1986 was 2·3 (s.d. = 0·823), compared to a mean of 3·0 (s.d. = 1·56) from eggs laid over the same period in 1987 (N = 10 breeding pairs, Wilcoxon $T = 8·0$, P = 0·15). Note that the trend was for more young to be fledged after bitting and fumigation.

Second, the reproductive success of (unbitted) fumigated birds in the mite experiment did not differ from that of (bitted) fumigated birds in the louse experiment. Unbitted pairs successfully fledged an average of 0·64 (s.d. = 0·81) surviving young, compared to a mean of 0·75 (s.d. = 0·91) produced by bitted birds (U = 104·5, P = 0·80). These results further indicate that bits had no significant effect on reproductive success in the captive flock. They also serve as additional evidence against seasonal variation in reproductive success in spring compared to late summer.

Pyrethrum had no side-effects on the host. Recently hatched young drenched with pyrethrum had similar growth rates to those drenched with water (7 fumigated, 8 sham-fumigated; F = 0·22, P = 0·64) and all individuals fledged. Post-fledging body mass for the two groups was also similar (F = 0·17, P = 0·69), as were post-fledging survival rates (Fisher Exact P = 0·35).

Effects of mites and lice on host fitness

Reproductive success of birds at low- and high-load nests did not differ immediately before the mite experiment (12 February–12 March). Prior to treatment low-load pairs produced a mean of 0·27 (s.d. = 0·47) surviving fledglings, whereas high-load pairs produced a mean of 0·91 (s.d. = 1·04) survivors (U = 42, P = 0·16). Thus, mite infestation was not correlated with host fitness *a priori*. Note that the trend was for low-load birds to have poorer reproductive success than high-load birds prior to treatment.
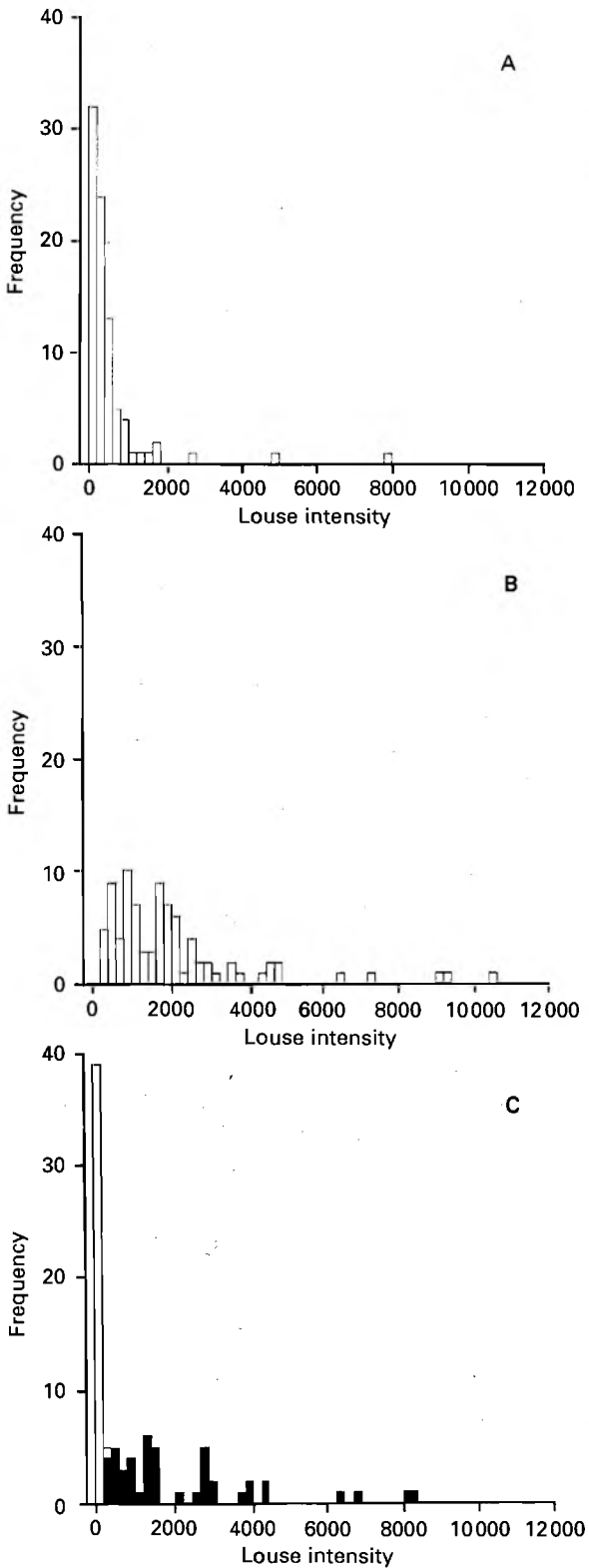
Fig. 2. (A) Frequency distribution of lice in May, prior to bitting ($N = 86$ birds); (B) distribution of lice in late July, several weeks after bitting; (C) distribution of lice at the end of the study, several months after fumigation. (□) Fumigated low-load birds; (■) sham-fumigated high-load birds.

The impact of mites on post-hatching components of fitness was analysed in two ways: (1) using data from all 22 nests in the main experiment and (2)
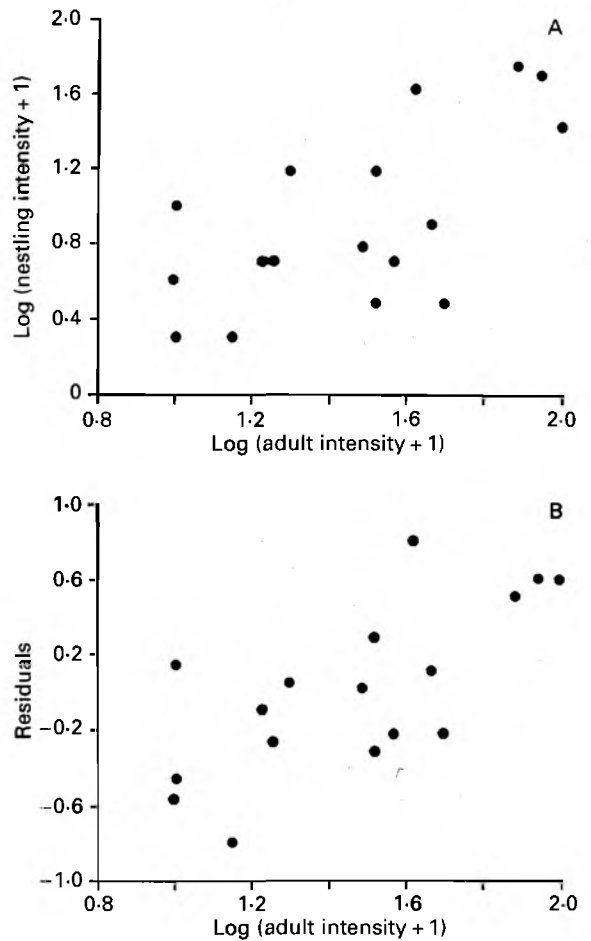

Fig. 3. (A) Relationship of mean intensity of lice on nestlings ($N = 17$ infested nests) to mean intensity of lice on their parents; (B) as for (A) but using residuals from a plot of louse intensity on nestling age to control for body size.

using data from nests that were mite-free until nestlings reached at least 15 days of age. Seven infested nests (mean intensity = $3·29$, s.d. = $2·36$) and 7 uninfested nests met this criterion. Analysis of this smaller sample permitted a more direct comparison of the impact of mites to the impact of lice, given that the latter did not infest birds under the age of 15 days (Clayton & Tompkins, 1994).

Egg laying. Mites had no effect on egg production. The number laid by the 11 low-load pairs (mean = $1·64$, s.d. = $0·81$) did not differ significantly from the number laid by the 11 high-load pairs (mean = $2·0$, s.d. = $0·89$; U = $50·5$, $P = 0·33$).

Lice also had no effect on egg production. During the main experiment the number of eggs laid by 20 low-load pairs (mean = $1·75$, s.d. = $0·79$) did not differ significantly from the number laid by 23 high-load pairs (mean = $1·61$, s.d. = $1·00$; U = $206·5$, $P = 0·45$). During the 2-month follow-up period the number laid by 10 low-load pairs (mean = $2·2$, s.d. = $1·03$) did not differ significantly from the number laid by 12 high-load pairs (mean = $2·67$, s.d. = $1·30$; U = 48, $P = 0·38$).
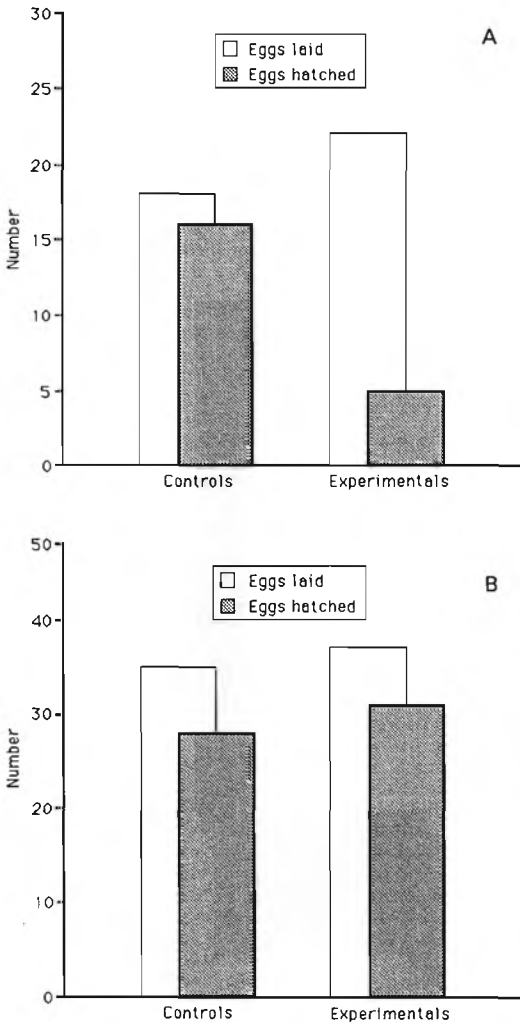
Fig. 4. Hatching success contingent upon number of eggs laid in (A) mite experiment and (B) louse experiment. Controls are low-load nests/birds; experimentals are high-load nests/birds.

Fig. 5. Mean ($\pm$s.e.) nestling growth for low-load ($\bigcirc$) and high-load ($\bullet$) nests in (A) mite experiment, where $N = 9$ low-load nests and 3 high-load nests unless otherwise indicated; (B) louse experiment, where $N = 15$ low-load nests and 16 high-load nests unless otherwise indicated.

Hatching success. Mites had a striking effect on hatching success (Fig. 4A; $\chi^2 = 17.38$, $P = 0.0001$). In contrast, lice had no effect on hatching success (Fig. 4B; $\chi^2 = 0.17$, $P = 0.91$). During the follow-up period low-load pairs hatched 17 of 22 eggs laid and high-load pairs hatched 22 of 32 laid ($\chi^2 = 0.47$, $P = 0.71$).

Nestling growth. Mites reduced nestling growth rates. Although there was no significant effect of mites when all data were included (F = 0.68, $P = 0.41$), limiting the analysis to data collected prior to Day 23 revealed a significant impact despite extremely small sample sizes (F = 3.91, $P = 0.05$, Fig. 5A). The justification for limiting the analysis was that 1 of only 3 high-load nests was lost from the sample owing to mortality by Day 23. A similar trend was apparent for the analysis restricted to birds infested after 15 days of age (F = 2.43, $P = 0.12$).

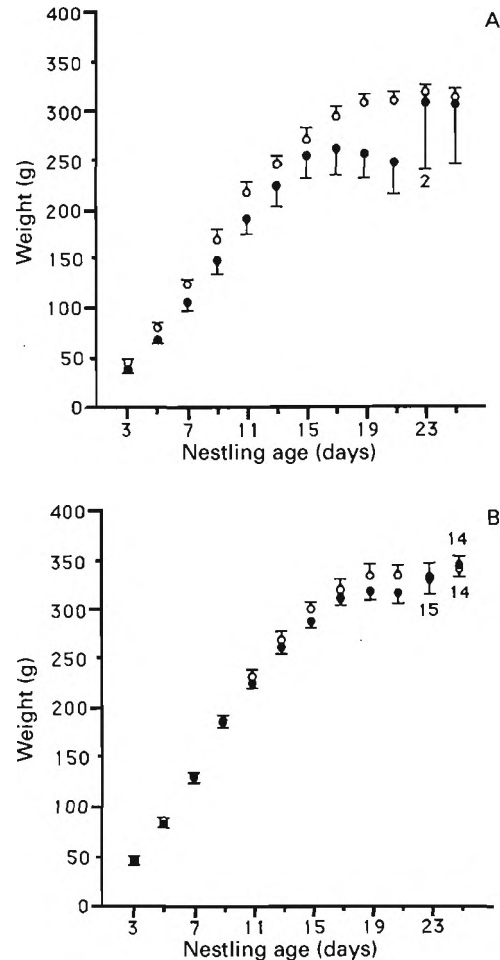In contrast, lice had no effect on nestling growth. The growth of low-load birds was similar to that of high-load birds during the main experiment, both when all data were included (F = 0.00, $P = 1.00$, Fig. 5B), as well as when the analysis was limited to data collected prior to Day 23 (F = 1.41, $P = 0.24$). Lice also had no effect on nestling growth during the follow-up period (F = 0.05, $P = 0.83$).

Fledging success. Mites had no significant effect on fledging success (Fig. 6A; Fisher Exact $P = 0.77$). Lice also had no significant effect on fledging success (Fig. 6B; $\chi^2 = 0.53$, $P = 0.76$). During the follow-up period 16 of 17 birds fledged from low-load nests and 18 of 22 birds fledged from high-load nests (Fisher Exact $P = 0.26$).

Post-fledging weight. Mites had no effect on post-fledging weights in the main experiment (F = 0, $P = 1.0$) but the analysis had to be truncated after the first post-fledging weighing because two-thirds of high-load birds died thereafter. Mites did significantly reduce post-fledging weights in the analysis restricted to birds infested after 15 days of age (F = 4.06, $P = 0.05$).
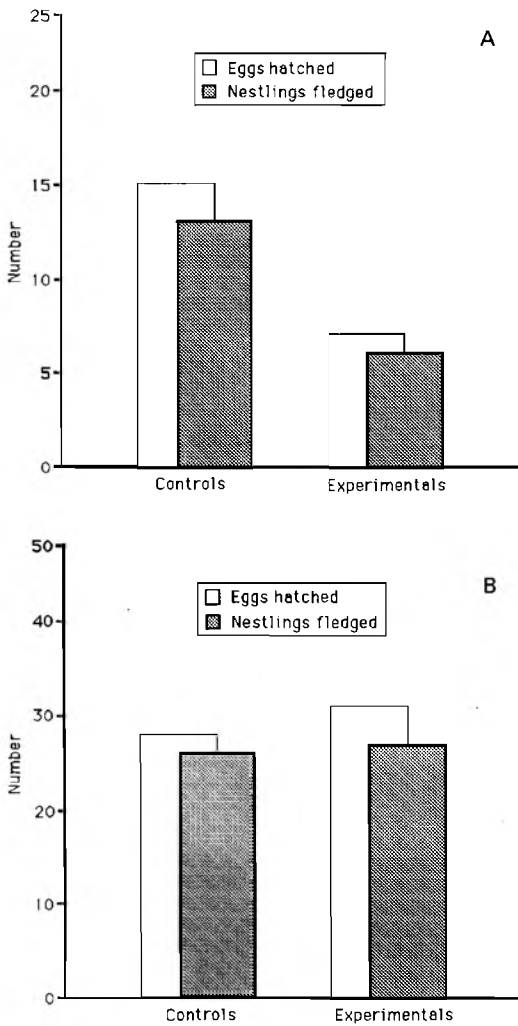
Fig. 6. Fledging success contingent upon number of eggs hatched in (A) mite experiment and (B) louse experiment. Controls are low-load nests/birds; experimentals are high-load nests/birds.
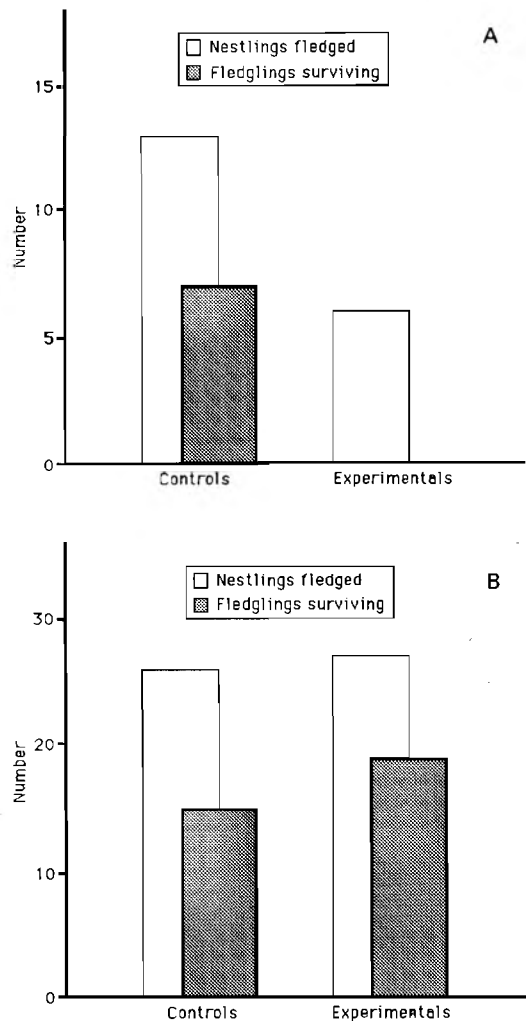

Fig. 7. Post-fledging survival contingent upon number of nestlings fledged in (A) mite experiment and (B) louse experiment. Controls are low-load nests/birds; experimentals are high-load nests/birds.

Lice had no significant effect on post-fledging weights during the main experiment ($F = 0.00$, $P = 0.96$) nor during the follow-up period ($F = 0.89$, $P = 0.38$).

Post-fledging survival. Mites reduced post-fledging survival (Fig. 7A; Fisher Exact $P = 0.034$). Over the course of the experiment, the low-load pairs produced a mean of 0.64 survivors (s.d. = 0.81)/pair, whereas high-load pairs produced no survivors. For the analysis restricted to young infested after 15 days of age, 7 of 14 fledglings from uninfested nests survived the 6-week period, compared to only 1 of 13 fledglings from infested nests (Fisher Exact $P = 0.02$).

Lice had no effect on post-fledging survival (Fig. 7B; $\chi^2 = 0.93$, $P = 0.50$). During the follow-up period 6 of 16 low-load birds survived compared to 9 of 18 high-load birds ($\chi^2 = 0.54$, $P = 0.70$). During the main experiment low-load birds produced a mean of 0.75 surviving fledglings/pair (s.d. = 0.91); high-load birds produced a mean of 0.83 survivors/

pair (s.d. 0.98; U = 223, $P = 0.85$). During the follow-up period low-load birds produced a mean of 0.60 survivors (s.d. = 0.84)/pair; high-load birds produced a mean of 0.75 survivors/pair (s.d. = 0.96; U = 56, $P = 0.76$).

Over the course of the main experiment, offspring survival was significantly correlated with mite intensity (Kendall $T = -0.21$, $P = 0.02$), whereas louse intensity was not correlated with offspring survival in either the main experiment (Kendall $T = 0.003$, $P = 0.97$) or during the follow-up period ($T = 0.12$, $P = 0.31$).

Adult weight and survival. Mites had no significant effect on adults. There were no deaths over the course of the experiment and group weights did not differ significantly. Low-load birds lost a mean of 13.32 g (s.d. = 25.25), compared to a mean loss of 12.55 g (s.d. = 21.1) by high-load birds (Unpaired, one-tailed $t = 0.11$, $P = 0.46$). Lice also had no effect on adult weight or survival. There were no deaths during the experiment or during the follow-up

period and lice had no persistent impact on adult weight. Although low-load birds tended to gain more weight than high-load birds by the October weighing (F = 3·40, $P = 0·07$), there was no overall effect of lice on adult weights by the February 1988 weighing (F = 0·88, $P = 0·35$).

Most adults continued to roost in the enclosure after the removal of window coverings in late January 1988. In mid-February all birds still roosting in the enclosure were captured and weighed. Similar proportions of low- and high-load birds were present from the louse experiment (29 of 40 low-load birds and 32 of 46 high-load birds, $\chi^2 = 0·09$, $P = 0·95$).

Lice had no significant effect on the susceptibility of birds to predation by racoons (*Procyon lotor*), which are common predators of feral pigeons in North America (Johnston, 1992). After removal of the window coverings, racoons occasionally captured roosting birds and by the end of the study we had recovered the banded remains of 9 victims. Four of these were low-load birds and 5 were high-load birds ($\chi^2 = 0·17$, $P = 0·96$).

DISCUSSION

Tests of the impact of parasites on host fitness are often complicated by the fact that parasites are generally overdispersed among host individuals (Anderson & Gordon, 1982). In such cases prohibitively large samples of hosts may be required to detect significant effects of parasites. One way around this problem is to convert the overdispersed distribution of parasite intensity into a more even distribution by manipulating parasite intensities within the range of natural variation. This approach enhances the statistical power of experiments designed to test the effects of parasites on host fitness, and circumvents problems of interpretation inherent in correlational data.

In this study louse intensities were manipulated through bitting and fumigation to produce roughly equal numbers of high- and low-load nests. Mite intensities needed to be manipulated only by fumigation to produce high- and low-load nests. The combination of techniques created similar mite and louse intensities among the birds in each experiment. Fumigant had no side-effects on the birds themselves. Bits had no apparent side-effects; however, every adult bird in the enclosure was bitted to ensure equal treatment. There was no significant seasonal variation in reproductive success between the periods in which the mite and louse experiments were conducted.

Fumigation to control louse loads was randomized. However, this was not the case for mite loads, which were controlled according to the pattern of mite infestation (see Materials and Methods section). This raises the possibility that the impact of mites on host reproduction was influenced by a third variable that was, in turn, influenced by the pattern of infestation. This did not appear to be the case. Mites first colonized nest boxes next to a crack in the wall of the barn that was the source of the mites. Over the next few days they spread rapidly to boxes adjacent to infested boxes significantly more often than to boxes adjacent to uninfested boxes (Clayton & Tompkins, 1994). Thus, the pattern of infestation was dictated by the physical position of the nest boxes, which had no significant effect on the reproductive success of birds immediately before the experiment (see Results section), nor during the previous year (unpublished data).

Mites were horizontally transmitted among nest boxes and so did not rely on contact between parent hosts and their offspring for transfer (Clayton & Tompkins, 1994). Rapid horizontal transmission caused an exponential increase in prevalence during the early weeks of the study. Lice, on the other hand, depended on direct contact between parents and their offspring for transfer, and so were vertically transmitted. In fact, lice depended on direct contact between the feathers of parents and their offspring, as revealed by the timing of transmission in relation to feather emergence (Clayton & Tompkins, 1994). Lice were never observed on the skin of a host. The correlation of parent and offspring louse intensity further shows that vertical transmission was the main, if not only, source of infestation. Of course, heritable resistance to lice could contribute to a parent–offspring correlation in louse intensity. However, heritable factors could not have been important in this case since experimentally induced variation in louse intensity was randomly assigned among adult breeding pairs.

Mites were extremely virulent. Without exception, the reproductive success of adults at nests with more than just a few mites was zero. The effect of mites was greatest early in the nesting cycle. Although mites had no impact on the number of eggs laid, they reduced hatching success by more than 75 %. The reason for this effect was that birds at heavily infested nests were too agitated to incubate, as shown for *Dermanyssus* infesting other species of birds (Moss & Camin, 1970). Adults at heavily infested nests responded with frequent turning, scratching, preening, leg-shaking and they spent less time incubating than birds at relatively uninfested nests (D. H. Clayton, personal observation). Physical irritation has been shown to reduce hatching success in other bird–ectoparasite systems (Duffy, 1983; Brown & Brown, 1986; Emlen, 1986).

Mites also reduced nestling growth (Fig. 5A) and post-fledging survival (Fig. 7A). These effects may have been the result of anaemia, which is known to be caused by *Dermanyssus* (Kirkwood, 1967) and other mites (Matthysse, Jones & Purnasiri, 1974; Clark, 1991). Mites may also have had an indirect effect on the hosts by vectoring endoparasites. *D.*

gallinae has been shown to vector a variety of protozoan, bacterial and viral diseases of birds (Moss, 1978). We did not investigate the proximal cause(s) of the impact of mites on growth and survival.

Lice had no effect on host fitness, despite a prolonged period of data collection with larger sample sizes than in the mite study. Lice had no impact on the number of eggs laid or on hatching success. This result is not surprising, given that Ischnocera on rock doves do not cause irritation. Birds with large numbers of lice do not preeen or scratch more than those with low numbers because the lice in question never go on the skin of the host (Clayton, 1990). In the current study birds with high louse intensities appeared to incubate as consistently as those with low intensities, although we did not quantify incubation times.

Lice also had no effect on nestling growth, fledging success, post-fledging survival, nor the weight or survival of adults. These results are interesting, given that louse-induced feather damage is known to have energetic costs even at relatively warm ambient temperatures. Booth *et al.* (1993) documented an 8·5 % increase in the metabolic rates of bitted, sham-fumigated rock doves over a range of ambient temperatures, including 22 °C – the mean temperature in our study. The amount of feather damage caused by lice in our study (reported by Clayton, 1990) was comparable to that in the study of Booth *et al.* (1993). Although the latter was primarily a field experiment, birds were taken captive and fed *ad libitum* for several days prior to the measurement of metabolic rates in the laboratory. Birds in our study were fed *ad libitum* throughout, which may have allowed them to compensate for any energetic cost of feather damage.

Such compensation is one explanation for why there was no significant effect of lice on winter survival in our study. High-load birds in the study of Booth *et al.* (1993) had significantly lower body mass than low-load birds, linked to a significant reduction in the over-winter survival of high-load birds in earlier work (Clayton, 1989). The pigeons in our study had ready access to shelter and our study was not as long term as the earlier one (Clayton, 1989).

Although conditions in the enclosure were more favourable than those in the field, our test of the impact of lice on host reproductive success appears to be an accurate reflection of the natural situation. A field experiment modelled on the one in this paper revealed no impact of lice on the reproductive success of free-ranging birds (Clayton, 1989). Hence, results for the captive flock are not merely a by-product of more favourable conditions in the enclosure. The severe impact of mites in this study further indicates that favourable conditions do not preclude the detection of parasite effects. We have no data on the impact of mites under field conditions. However, the negative effects of other species of *Dermanyssus* on wild birds (Moss & Camin, 1970) suggest that our findings are not an artifact of captive conditions.

The dissimilar effects of mites and lice could not have been due to seasonal differences as the reproductive success of control birds in the two experiments was quite similar. The dissimilar effects of mites and lice were also unlikely to have been artifacts of different parasite population sizes. Several pairs of adult birds with thousands of lice produced the maximum of two surviving offspring during the main louse experiment. In contrast, only nests with extremely low mite loads produced any surviving offspring.

The relative benevolence of Ischnocera appears to have at least two main components. First, restriction to feathers reduces irritation to the skin of the host, leading to more consistent incubation of eggs. Ischnocera have evolved a specialized niche restricted to feathers, derived from a more generalized niche on the body of the host (Waage, 1979). The latter was, in turn, probably derived from an even more generalized niche in the host's nest (Waage, 1979). Specialization to feathers carries benefits such as a predictable food supply. But it also carries costs such as limited ability to disperse to new hosts. Our data, in conjunction with a survey of the literature (Clayton & Tompkins, 1994), show that limited transmission is linked to reduced virulence, as suggested by theoretical work (Anderson & May, 1982; Ewald, 1983; Lehmann, 1993).

Second, dependence on host reproduction for transmission means that feather specialists, such as Ischnoceran lice or feather mites (Ateyo & Gaud, 1979), are unlikely to serve as vectors of virulent endoparasites (which could occur via ingestion of infected lice during preening, analogous to the ingestion of cestodes by dogs during grooming (Grundy, 1981)). Until recently (Bartlett, 1993), Ischnoceran lice had not been recorded as endoparasite vectors (Clayton, 1990). Pigeon Ischnocera have not been recorded as vectors, despite the fact that *Columbicola columbae* is a relatively well studied 'white rat' (Eichler *et al.* 1972). Transmission may thus constrain vector biology just as it appears to constrain more direct components of virulence. For sake of comparison, Amblyceran lice, which are more mobile than Ischnocera, are known to vector several kinds of endoparasites (Clayton, 1990).

The results of our mite experiment support the claim that ectoparasites can be costly, as emphasized by Lehmann in an important review (1993). The widespread assumption that ectoparasites are benign is clearly an oversimplification. However, the results of our louse experiment indicate that some ectoparasites are, in fact, benign with regard to host reproduction. It is therefore dangerous to draw

generalizations about costs of ectoparasitism, just as it would be dangerous to draw generalizations about costs of endoparasitism.

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