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

D. H. CLAYTON and D. M. TOMPKINS

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

(Received 15 March 1994; revised 19 July 1994; accepted 19 July 1994)

SUMMARY

We report experimental data comparing the effects of Mesostigmatid mites and Ichnoceran lice on the reproductive performance of a single group of captive rock doves (Columbia 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 Ichnocera are found on most species of birds, our results for lice constitute the first experimental test of the impact of Ichnocera 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, Columbia livia) in which we compared the effects of independently transmitted Mesostigmatid mites with the effects of vertically transmitted Ichnoceran lice. In a preliminary report (Clayton & Tompkins, 1994) we showed that mites are more virulents 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 Ichnoceran lice.

Experimental tests of the effects of Ichnocera on avian reproduction had not been published prior to our preliminary report (Clayton & Tompkins, 1994) despite the fact that Ichnocerna parasitize most species of birds (Marshall, 1981; Clayton, Gregory & Price, 1992). Derylo (1974a,b) reported a reduction in the egg production of Leghorn chickens parasitized by Ichnocera, but the subjects of study also had Amblyceran lice. In contrast to the feather-feeding Ichnocera, Amblyceran 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 Ichnocera.

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

gression models that accurately predict total louse load ($r^2 \geq 0.82$). 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 10% 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
fledged from eggs laid August–September (N = 32 pairs; Wilcoxon T = 815, 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 = 80, 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.
**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 ($F = 4.06$, $P = 0.05$).
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, χ² = 0.09, P = 0.95).

Lice had no significant effect on the susceptibility of birds to predation by raccoons (Procyon lotor), which are common predators of feral pigeons in North America (Johnston, 1992). After removal of the window coverings, raccoons 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 (χ² = 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 biting 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 banded 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 *Dermatobia* 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 nesting 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 *Dermatobia* (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.
generizations about costs of ectoparasitism, just as it would be dangerous to draw generalizations about costs of endoparasitism.

Funds were provided by NSF Grant BSR-8612575, NIH Grant GM 07197, Kaytee Products Inc., and L. Getz. D.M.T. was supported by a NERC studentship. Data were collected by D.H.C. as part of doctoral work at the University of Chicago. We are grateful to N. Burley, C. Cooper, L. Getz, P. Mankin, and D. Wake for facilities or accommodations. We are particularly grateful to D. Droge for starting the pigeon colony and allowing us to work with it. We thank J. Howe and Jean and Jim Nicholson for technical assistance, as well as S. Arnold, T. Attey, R. Clayton, R. Clayton Jr., J. Fitzpatrick, J. Kethley, R. Lande, M. Lloyd, A. & T. Peterson, M. Phelan, D. Schermske, J. West, and J. & L. White for other assistance or discussion. Thanks also to N. Gotelli, P. Harvey, A. Herre and A. Read for comments on the manuscript. D. H. C. especially thanks K. Clayton for assisting with all phases of the study and for tolerating numerous conversations in public about 'my lice'.

REFERENCES


