Ectoparasite virulence is linked to mode of transmission

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SUMMARY

Theory suggests that the evolution of parasite virulence is linked to the dynamics of parasite transmission. All else being equal, parasites transmitted vertically from parents to offspring should be less virulent than parasites capable of horizontal transmission to unrelated hosts. This is because the fitness of vertically transmitted parasites is tightly linked to the reproductive success of the host, whereas the fitness of horizontally transmitted parasites is relatively independent of host reproduction. The virulence–transmission relation has seldom been tested because of difficulties inherent in comparing virulences of different parasite–host systems. We compared the virulence of lice and mites infesting a single group of captive rock doves (*Columba livia*). Lice, which were vertically transmitted, had no detectable effect on host fitness, whereas horizontally transmitted mites drove host reproductive success to zero. These results, in conjunction with a survey of the literature, support the hypothesis that ectoparasite virulence is linked to the mode of transmission.

1. INTRODUCTION

Conventional wisdom holds that well-adapted parasites evolve reduced virulence because their fitness depends on that of the host (Smith 1934; Swellengrebel 1940; Simon 1960; Dubos 1965; Telford 1971; Burnet & White 1972; Hoeprich 1977; Alexander 1981; Palmieri 1982; Schmidt & Roberts 1985). However, this view is misleading as it fails to recognize the probable linkage of virulence to the dynamics of parasite transmission (Anderson & May 1982; Ewald 1983). In cases where parasites are transmitted to new hosts independently of host fitness, e.g. some horizontally transmitted parasites, the parasite may not suffer a reduction in fitness by harming its host. In contrast, in cases where parasites are transmitted vertically from parent hosts to offspring, the parasite may suffer a severe reduction in fitness by interfering with host reproduction.

Recent tests with endoparasites provide strong evidence for linkage of transmissibility and virulence. Bull *et al.* (1991) documented an evolutionary reduction in the virulence of bacteriophage restricted to vertical transmission; when horizontal transmission was added back to the system, virulence increased. Herre (1993) showed that virulence is strongly correlated with the opportunity for horizontal transmission among host-specific nematode parasites of fig wasps. These studies, in conjunction with the comparative work of Ewald (1993a), suggest that linkage of virulence and transmissibility is a general principle that holds across parasites, ranging from viruses to arthropods (Anderson & May 1979). However, the principle may not be a general one, as many additional factors could influence virulence (Levin & Svanborg Edén 1990). The purpose of our study was to examine the principle for ectoparasites by testing the explicit prediction that horizontally transmitted taxa are more virulent than vertically transmitted taxa (Ewald & Schubert 1989; Ewald 1993b; Lehmann 1993).

We compared the virulence of horizontally and vertically transmitted ectoparasites infesting the same captive flock of rock doves (feral pigeons). The horizontally transmitted parasites were blood-sucking mites (Acarina: Mesostigmata); the vertically transmitted parasites were feather-feeding lice (Phthiraptera: Ischnocera). No other ectoparasites were present during the study. To assess virulence we measured the impact of parasites on host reproductive success after manipulating parasite load experimentally. We also measured the transmissibility of each parasite. The two parasites were manipulated sequentially on the same flock of breeding birds. This approach controlled for among-host variation that could alter virulence, given that virulence is not an attribute of the parasite per se, but an outcome of the parasite–host interaction. Our experimental design also controlled for environmental variation that might alter virulence.

2. MATERIALS AND METHODS

(a) *Host population*

Data were collected in 1987 from birds in a free-flight loft near the University of Illinois, Urbana-Champaign, U.S.A. The 9.2 m × 3.7 m × 2.5 m enclosure, constructed in the upstairs of a barn, was originally stocked with 72 rock doves captured on rooftops and under bridges (Droge 1986).

During our study the flock contained 46 breeding pairs from original stock or their descendants. The birds nested in contiguous, open-faced boxes mounted on the wall of the loft (Levi 1957). Birds were continuously exposed to fresh air and sunlight (ambient temperature and photoperiod), but were protected from direct wind and precipitation. They were fed a commercial grain mixture (Kaytee Breeder and Conditioner Pigeon Feed #6™), and provided with grit, nesting material and water. See Clayton & Tompkins (1994) for further details.

(b) Mite experiment

We studied *Dermanyssus gallinae*, a member of the mite family Dermanyssidae (suborder Mesostigmata). This species is a common parasite of wild and domestic birds (Strandtmann & Wharton 1958; Phillips 1990) that frequently occurs in rock dove nests (Levi 1957), including the nests of feral populations in Illinois (Clayton 1989). *D. gallinae* spends most of its time in the nest material, emerging periodically to feed on the host's blood (Sikes & Chamberlain 1954). It usually feeds on nestlings, but will also attach to the abdomens of adults while they are incubating eggs or brooding young. The life cycle, completed in less than 10 days, consists of an egg, larva, two nymphal instars, and the adult (Benbrook 1965). Adults can survive for months without feeding.

Entire *D. gallinae* populations are difficult to quantify without destroying the host's nest. We therefore estimated mite populations by counting the number of mites observed on the bodies of nestlings during a thorough check lasting < 1 min for young nestlings and up to 3 min for fully feathered young. Mite loads of nestmates were averaged to produce a mean load for each nest. The number of mites on nestlings (or eggs) was significantly correlated with the number of mites in 12 nests that were destructively sampled with Berlese funnels ($r = 0.77$, d.f. = 10, $p = 0.004$).

Mites were first observed in nestboxes in April 1987; they were not present during 1986. The mites may have been introduced to the loft by house sparrows (*Passer domesticus*) nesting in the rafters of the barn. They were censused first on 11 April and weekly thereafter. Mite loads were manipulated following the second census (17 April) by fumigating 11 control nests (those with no mites during the first two censuses). The fumigant used was a 1.0% aqueous solution of pyrethrum, which is effective against *D. gallinae* (Zeman & Zelezny 1985), yet has no side effects on the host (Jackson 1985; Clayton & Tompkins 1994). An equal number of experimental nests (those with mites during the first two censuses) were sham fumigated with water. Birds were excluded temporarily from the nest to shield their (body-based) louse populations from the fumigant, which was soon deactivated by drying nests with a portable hair dryer. It was thus possible to control mites independently of lice. Control nests were refumigated periodically to prevent recolonization.

By June the mites were spreading throughout the pigeon colony, making it necessary to refumigate nests more frequently. To stop mites overrunning the colony, every nest in the loft was fumigated on 20 June, thus terminating the experiment.

(c) Louse experiment

We studied the lice *Columbicola columbae* and *Campanulotes bidentatus*, both members of the suborder Ischnocera (Phthiraptera (formerly Mallophaga)). These two species, commonly found on rock doves (Clayton 1989), are obligate parasites that complete their entire life cycle on the body of

the host (Clayton 1991). The life cycle requires 3–4 weeks, and consists of an egg, three nymphal instars, and the adult (Martin 1934). Eggs are glued to the host's feathers with a glandular cement. Both species feed exclusively on the barbules of abdominal contour feathers (Nelson & Murray 1971). To our knowledge, experiments to test the impact of these (or any other) species of Ischnocera on host reproductive success have not been published. Throughout this paper, louse 'load' refers to the combined populations of both species.

Nestling louse loads were estimated by using the procedure described 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 by using multiple regression models that predict total load from timed visual censuses of lice on various body regions ($r^2 \geqslant 0.82$) (Clayton 1991). The louse loads of adult birds were censused in May, July and again after termination of the experiment.

Louse loads were manipulated by using a two-step procedure designed to convert the overdispersed distribution of lice into a bimodal distribution of 'high-load' and 'low-load' hosts (Clayton & Tompkins 1994). First, preening ability, the main defence of birds against ectoparasites (Marshall 1981; Clayton 1991), 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 that prevents the full occlusion of the bill necessary for efficient preening. To control for any side effects of bits (none were apparent (Clayton & Tompkins 1994)), all birds in the 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 minor bill deformities (three of 150 wild-caught birds (Clayton 1989)). Bit-induced increases do not exceed the range of natural louse loads (Clayton 1989). All adults in the flock were bitted on 4–6 July. At the end of the experiment all birds had their bits removed.

The second step took place on 5–7 August. After ranking birds on the basis of previous reproductive success (D. H. Clayton & D. M. Tompkins, unpublished data), one of every two pairs was randomly fumigated with 1.0% pyrethrum (controls) and the other pair was sham fumigated with water (experimentals). In a few cases, randomly assigned treatments were reversed to balance the distribution of treatments with regard to previous mite infestation and physical position of nest boxes. In total, there were 20 fumigated pairs and 23 sham-fumigated pairs.

(d) Host fitness

We compared the impact of mites and lice on adult body mass and survival, as well as on several components of reproductive success. The latter included egg laying, hatching success, nestling growth, fledging success, and post-fledging survival. In this paper we report only the results for the two components influenced by at least one of the parasites. These components were hatching success and post-fledging survival; Clayton & Tompkins (1994) have further details. The post-fledging survival period was limited to 6 weeks following departure from the nest. It was not possible to monitor survival for longer than this because of the need to cull fledglings to prevent crowding.

Analyses of hatching success was for eggs laid over a period of one month starting 3 days after fumigation (20 April–20 May for mites, and 10 August–10 September for lice). The effect of lice on fledgling survival was analysed by using the

same cohort as for effects on hatching success. However. the effect of mites on survival was tested for nestlings that hatched 20 April–20 May. This restriction allowed all offspring in the mite experiment to reach fledging age by 20 June. when all nests in the loft were fumigated as described earlier.

3. RESULTS

a) *Mite loads and transmission*

Fumigation was successful at keeping control nests relatively free of mites. Over the course of the experiment (8 censuses averaged). the mean number of mites in fumigated 'low-load' nests was 3 s.d. = 4), compared with a mean of 43 mites s.d. = 33) in sham-fumigated. 'high-load' nests Mann-Whitney $U = 3$, $p = 0.0002$). There was no correlation between nestling age and mite load; mites attacked nestlings of all ages (figure 1a; Kendall $T = 0.10$, $p = 0.42$).

Mites moved horizontally among nest boxes. Of 15 boxes that were uninfested at first census. seven were infested by the following census. and eight remained uninfested (four of the boxes were not part of the mite experiment as they were destructively sampled with
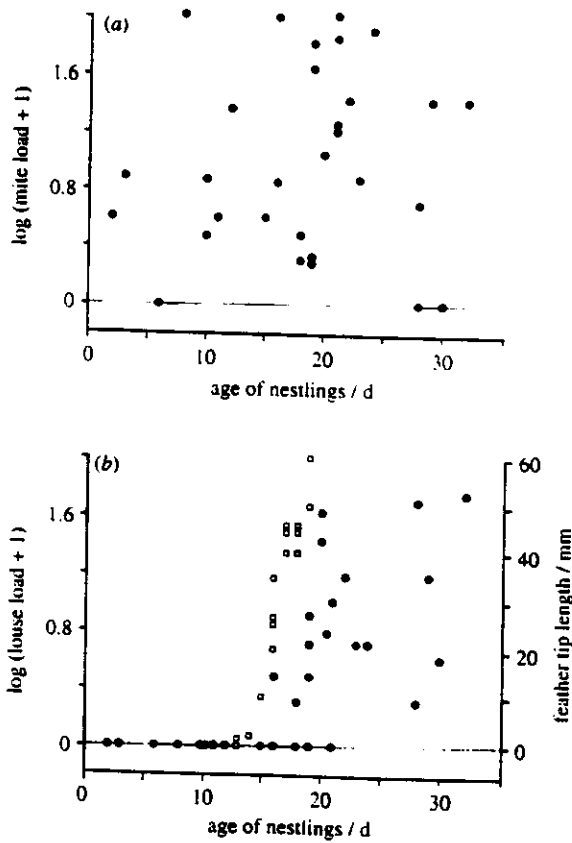

Figure 1. Relation of (a) mite and (b) louse load to nestling age ($n = 30$ nests). All nests were censused in May. and lice and mites at a given nest were censused on the same day. Parasite loads and ages of nest mates were averaged to produce mean values for each nest. (b) This also shows the relation of louse load to the emergence of the tips of developing wing feathers (open squares): feather tip data are from an independent sample of known-age birds.

Berlese funnels). All seven newly infested boxes were contiguous with previously infested ones. whereas only three of the eight uninfested boxes were contiguous with previously infested ones (Fisher exact test, $p = 0.02$). Boxes adjacent to sources of transmission were thus colonized significantly more often than those adjacent to uninfested boxes. The horizontal transmission was by movement on the part of the mites themselves. *D. gallinae* is capable of such movement (Sikes & Chamberlain 1954), and was observed running between boxes on several occasions during the study.

(b) *Louse loads and transmission*

The combination of bitting and fumigation resulted in fumigated birds having much lower louse loads than sham-fumigated birds. The 20 fumigated, 'low-load' pairs had a mean of 66 lice (s.d. = 37), compared with a mean of 2153 lice (s.d. = 1558) on the 23 sham-fumigated, 'high-load' pairs ($U = 0$, $p = 0.0001$). The maximum number of lice on high-load birds did not exceed the maximum recorded for birds in feral populations (Clayton 1989).

The louse loads of offspring of the two groups of adults also differed significantly. Young produced by low-load pairs had a mean load of 2 lice (s.d. = 3, $n = 5$ nests), compared with a mean of 23 lice (s.d. = 10, $n = 4$ nests) on young produced by 'high-load' pairs ($U = 0$, $p = 0.01$). The mean number of lice on nestlings was significantly correlated with the mean number of lice on their parents (Kendall $T = 0.44$, $p = 0.01$, $n = 17$ nests).

Unlike mites, lice were never found away from the body of the host. In fact, they were confined to the feathers and were never observed on the host's skin. Because adult birds seldom contacted other adults, transmission of lice was mainly between parents and their offspring, and presumably also between mated adults. Transmission to nestlings was delayed until after the tips of developing feathers emerged from the sheaths (figure 1b). Most transmission occurred after nestlings reached 15 days of age, when feather tips had emerged ≥ 1 cm. Given this dependence on feathers for transmission. louse load was strongly correlated with nestling age (figure 1b: Kendall $T = 0.52$, $p = 0.0001$).

c) *Effect of mites on host fitness*

Mites had no detectable effect on adults; there were no deaths over the course of the experiment, and the body masses of low- and high-load birds did not differ significantly. The former lost a mean of 13.32 g (s.d. = 25.25), compared with a mean loss by the latter of 12.55 g (s.d. = 21.1) (unpaired, one-tailed $t = 0.11, p = 0.46$).

The reproductive success of low-load and high-load nests did not differ significantly before the mite experiment (12 February–12 March). Adults with future low-load nests produced a mean of 0.27 (s.d. = 0.47) surviving fledglings, whereas those with future
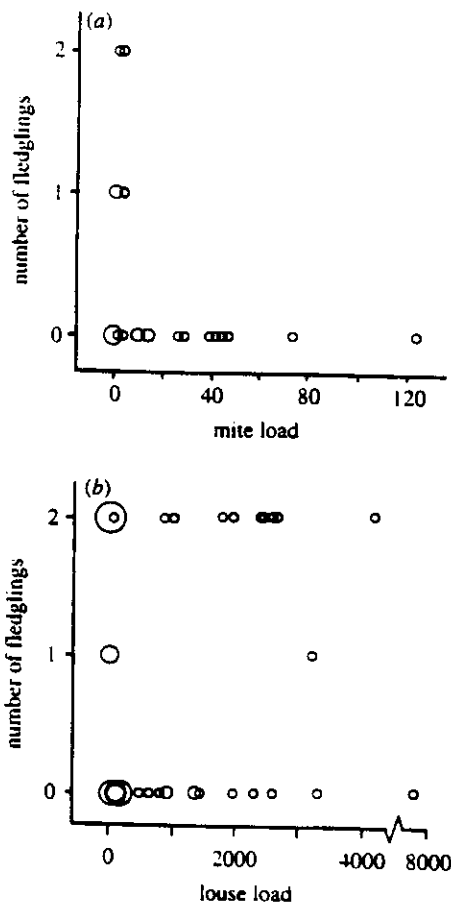
Figure 2. Number of surviving young in relation to mean load of (a) mites (n = 22 nests), and (b) lice (n = 43 adult pairs). Diameter of points is proportional to the number of nests or adult pairs (range = 1–5).

high-load nests produced a mean of 0.91 (s.d. = 1.04) survivors (U = 42, p = 0.16). Prior reproductive success was thus unrelated to mite loads in the experiment.

During the experiment, mites drastically reduced the hatching success of high-load nests compared with low-load nests. Of 18 eggs in low-load nests, 16 hatched, compared with only five of 22 eggs in high-load nests ($\chi^2 = 17.38, p = 0.0001$). Mites also reduced post-fledging survival. Seven of 13 young fledged by low-load pairs survived the 6 week period, whereas none of the six young fledged by high-load pairs survived (Fisher exact $p = 0.034$). In total, low-load pairs produced a mean of 0.64 survivors (s.d. = 0.81), whereas high-load pairs produced no survivors (figure 2a). Mite load was inversely correlated with the number of surviving offspring (Kendall $T = -0.21$, $p = 0.02$; figure 2a).

The impact of mites on post-fledging survival was still significant when the analysis was restricted to nests remaining mite-free until their nestlings were ≥ 15 days of age (at which time nestlings can also become infested with lice (figure 1b)). This criterion was met by seven infested nests (mean load = 3, s.d. = 2) and seven uninfested nests with similarly aged nestlings (some of these were not part of the main mite experiment). As before, mites significantly reduced post-fledging survival. Seven of 14 young fledged by

low-load pairs survived the 6 week period, compared with just one of 13 young fledged by high-load pairs (Fisher exact $p = 0.02$).

(d) Effect of lice on host fitness

Lice had no detectable effect on the survival or body mass of high-load adults. They also had no effect on hatching success: low-load pairs hatched 28 of 35 eggs, compared with 31 of 37 eggs hatched by high-load pairs ($\chi^2 = 0.17, p = 0.91$). Neither did lice influence post-fledging survival: 15 of 26 low-load young survived the 6 week period, compared with 19 of 27 high-load young ($\chi^2 = 0.93, p = 0.50$). Over the course of the experiment, low-load pairs produced a mean of 0.75 survivors (s.d. = 0.91), whereas high-load pairs produced a mean of 0.83 survivors (s.d. = 0.98; $U = 223$, $p = 0.85$). Louse load was not correlated with the number of surviving offspring ($T = 0.003$, $p = 0.97$; figure 2b).

4. DISCUSSION

Mites were horizontally transmitted among nest boxes, and so did not rely on contact between parent hosts and offspring for transfer. Direct dispersal among boxes was confirmed by the higher probability of infestation for boxes adjacent to already infested boxes, as well as by direct observation of dispersing mites.

In contrast, lice depended for transfer on direct contact between the feathers of parents and offspring, and so were vertically transmitted. It is unlikely that much horizontal transmission took place, as nestlings were seldom contacted by adults other than their parents. The significant correlation of parent and offspring loads further suggests that vertical transmission was the principle source of infestation. Although heritable resistance to lice might contribute to a parent–offspring correlation under normal circumstances, it could not have been important here because adult loads were randomly manipulated before the experiment.

Mites had no effect on adult body mass or survival. However, they had a devastating impact on reproductive success (figure 2a). The effect was still significant after the analysis was restricted to nests uninfested until after the nestlings reached 15 days, the age at which nestlings can also become infested with lice (figure 1b). Our results are similar to those obtained in field experiments with *Dermanyssus progne-philus*, a congener of *D. gallinae* which reduces the reproductive success of martins (Moss & Camin 1970).

The main proximal cause of the impact of *D. gallinae* in our study was agitation to incubating adults, leading to a 75% reduction in hatching success. Adults at heavily infested nests engaged in more turning, grooming and stamping of their feet than adults at uninfested nests (D. H. Clayton, unpublished observation). In some cases the eggs were actually abandoned. Similar agitation is known to reduce hatching success in a number of other bird–ectoparasite systems (Duffy 1983; Brown & Brown 1986; Emlen 1986).

Mites also reduced post-fledging survival. Not a single offspring from nests with more than five mites

Table 1. *Relation between transmission and virulence of ectoparasites on birds*

(This is based on studies where experimental manipulations of parasite load were done, allowing effects of particular parasite taxa to be distinguished.)

host	parasite	transmission[a]			virulence[b]			reference
		horizontal	intermediate	vertical	high	medium	low	
Progne subis (purple martin)	*Dermanyssus prognephilus* (martin mite)	×			×			(Moss & Camin 1970)
Columba livia (rock dove)	*Dermanyssus gallinae* (red fowl mite)	×			×			this paper
Hirundo pyrrhonota (cliff swallow)	*Oeciacus vicarius* (swallow bug)	×			×			(Brown & Brown 1986)
Delichon urbica (house martin)	*Oeciacus hirundinis* (house martin bug)	×			×			(de Lope et al. 1993)
Parus major (great tit)	*Ceratophyllus gallinae* (hen flea)	×			×			(Richner et al. 1993)
Hirundo rustica (barn swallow)	*Ornithonyssus bursa* (tropical fowl mite)		×					(Moller 1990)
Sturnus vulgaris (European starling)	*Ornithonyssus sylviarum* (Northern fowl mite)		×			×		(Fauth et al. 1991)
Apus apus (common swift)	*Crataerina pallida* (swift louse fly)		×				×	(submitted)
Apus apus (common swift)	*Dennyus hirundinis* (swift louse)			×			×	(submitted)
Columba livia (rock dove)	*Columbicola columbae* (slender pigeon louse)			×			×	this paper
Columba livia (rock dove)	*Campanulotes bidentatus* (golden feather louse)			×			×	this paper

[a] Horizontal, most transmission horizontal; intermediate, transmission both horizontal and vertical; vertical, most transmission vertical.
[b] High, parasite reduces host reproductive success by ≥ 30%; medium, parasite reduces nestling body mass but has no detectable effect on fledglings; low, no effect on any component of reproductive success.

survived the 6 week post-fledging period (figure 2a). The impact on survival may have been a delayed effect of anaemia caused by large amounts of blood being removed by *D. gallinae* (Kirkwood 1967). One cannot merely assume that blood loss was the culprit, however, as mite-induced anaemia does not necessarily reduce post-fledging survival in birds (Fauth et al. 1991). The severe impact of *D. gallinae* on host reproductive success was not a foregone conclusion.

Lice had no effect on adults or their reproductive success (figure 2b). It is not surprising that Ischnocera had no impact on the hatching success or survival of offspring. As they do not venture onto the skin (Clayton 1991), Ischnocera do not have the potential to agitate the host. High-load birds do not spend more time grooming than low-load birds (Clayton 1990) and, as they do not feed on blood, Ischnocera do not have the potential to cause anaemia.

Preliminary data show that Ischnocera also have no effect on host reproduction under field conditions (Clayton 1989), despite the fact that such conditions are known to exacerbate the effects of bird parasites (de Lope et al. 1993; Lehmann 1993). This is not to say that Ischnocera never affect host fitness. On the contrary, they reduce the over-winter survival of adult pigeons, owing to the thermoregulatory cost of the feather damage they cause (Booth et al. 1993). However, first-year birds probably do not accumulate significant damage because they have a post-juvenile moult that continues until the immediate onset of winter (Levi 1957; Ginn & Melville 1983). It is thus unlikely that Ischnocera affect host fitness until after the first breeding season, allowing the lice to be transmitted to a new generation of hosts. A preliminary test of this hypothesis could be made by comparing the amount of feather damage on young and old birds.

The dissimilar effects of mites and lice on pigeons were not artefacts of seasonal differences in reproductive success during the two experiments. Ambient temperature did not differ significantly between the mite experiment (April–June, mean = 23 °C, s.d. = 6.43) and the louse experiment (August–October, mean = 22 °C, s.d. = 6.57; $t = 0.70$, $p = 0.48$). Moreover, the reproductive success of control birds (fumigated) in the two experiments did not differ significantly: mite controls produced a mean of 0.64 s.d. = 0.81) surviving fledglings, compared with a mean of 0.75 s.d. = 0.91) produced by louse controls ($U = 104.5$, $p = 0.80$).

The dissimilar effects of mites and lice are also unlikely to have been artefacts of different parasite population sizes. Several pairs of adult birds with thousands of lice produced the maximum of two surviving offspring (figure 2b). In contrast, only nests with extremely low mite loads produced any surviving offspring.

Our results show conclusively that horizontally transmitted pigeon mites are far more virulent than vertically transmitted lice. However, it may be that the species studied here are not representative of ectoparasites in general. We therefore surveyed the literature for tests of the impact of ectoparasites on the reproductive success of birds in natural populations.

We included only experimental studies because the aggregated distribution of parasites means that observational data are insufficient to show conclusively that parasites have no impact on the host Booth *et al.* 1993).

The results of our survey agree with the results of our experimental work (table 1). Horizontally transmitted ectoparasites are more virulent than vertically transmitted ectoparasites. However, too few data exist to conduct a phylogenetically controlled comparative analysis (Harvey & Pagel 1991). Additional data on the effects of vertically transmitted ectoparasites other than lice are particularly needed. For example, a test of the impact of feather mites, which are vertically transmitted (Atyeo & Gaud 1979) and relatively benign, would be useful. Data on the effects of Amblycera, another suborder of lice, would also be worthwhile, as some Amblycera can be transmitted horizontally and vertically. For example, *Menacanthus stramineus*, restricted to horizontal transmission in henhouses (DeVaney *et al.* 1980), is responsible for 46°₀ reductions in poultry egg production (DeVaney 1976).

Our results, in conjunction with the results of other studies (table 1), show that ectoparasite virulence is proportional to the amount of horizontal transmission. Ectoparasites capable of independent transmission are extremely virulent, whereas those dependent on direct contact between hosts are not virulent. Linkage between virulence and mode of transmission thus applies to ectoparasites as well as endoparasites, supporting the relation as a general rule across major parasite–host systems.

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