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VERTICAL TRANSMISSION OF FEATHER LICE BETWEEN ADULT BLACKBIRDS *TURDUS MERULA* AND THEIR NESTLINGS: A LOUSY PERSPECTIVE

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ABSTRACT: There is limited information about the natural history of the transmission of feather lice (Phthiraptera) from parent birds to their young. This article therefore examines the transmission of 4 species of feather lice from parent blackbirds to their nestlings in an English population, and addresses questions formulated from the perspective of the lice. The lice that disperse onto the several young in the nest were mostly found on the larger chicks, those with higher survival prospects. The lice dispersing to chicks were overwhelmingly nymphs, which cannot be sexed morphologically, and so the prediction that the adult lice dispersing would be disproportionately female, potential founders of a new population, was only supported for the most numerous species, *Brueelia merulensis*. There was no evidence that louse dispersal to chicks was density dependent and more likely when the parents were more heavily infested. Finally, I predicted that lice might aggregate on female blackbirds, which undertake more brooding, to increase their chance of transmission to nestlings. For 1 louse species, *B. merulensis*, prevalence, but not louse intensity, was higher on female than male blackbirds. For 2 other louse species, *Philopterus turdi* and *Menacanthus eurysternus*, no differences between male and female blackbirds were detected.

Feather lice (Phthiraptera) are abundant ectoparasites of birds. As obligate ectoparasites that are commonly host specific, their entire life cycle, from eggs to nymphs and then to adults, is spent on the plumage of their hosts. This life cycle and the inability of lice to survive long away from the host (Rothschild and Clay, 1952) challenges these parasites to develop means of transferring themselves quickly and directly from 1 host to another.

Such direct transmission can potentially be either horizontal or vertical. There is evidence for both. For example, there is evidence for the rapid horizontal transmission of lice during the few seconds needed for mating by common pheasants *Phasianus colchicus* (Hillgarth, 1996) and during brief contact between full-grown common cuckoos *Cuculus canorus* (Brooke and Nakamura, 1998). In the latter case, vertical transmission can be excluded, because there is no contact between the brood-parasitic parent and its young. At the same time, it is likely that vertical transmission of lice occurs in many, and perhaps the majority, of bird species, and it has been demonstrated in a few (Lee and Clayton, 1995; Darolova et al., 2001). Vertical transmission involves the movement of lice from a parent onto a young bird, probably most often during brooding. Additionally, lice have been recorded as being carried by such mobile ectoparasites as hippoboscid flies, and this ''hitchhiking,'' known as phoresy, is a means whereby lice could reach uninfested hosts (Rothschild and Clay, 1952; Harbison et al., 2008). Transmission by phoresy could be either vertical or horizontal.

The consequences of vertical versus horizontal parasite transmission are potentially profound in terms of the likely impact on hosts. There are good theoretical reasons for supposing that, in general, horizontally transmitted parasites may be more damaging to hosts than vertically transmitted parasites (Ewald, 1983; Bull et al., 1991; Stewart et al., 2005), and Clayton and Tompkins (1994) have shown that feather lice, which are commonly transmitted vertically, are more benign than mites that are horizontally transmitted.

Dwelling in, and sometimes eating, birds' feathers, feather lice can potentially damage the plumage, sometimes so severely as to reduce host survival (Clayton, 1990; Brown et al., 1995; Lee and Clayton, 1995). However, even moderate infestation levels may influence the quality of birds' plumage, and thus generate visible differences between individuals, which could form the basis for sexual selection (Hamilton and Zuk, 1982). Accordingly, several studies have explored relationships between mating success and measures of louse infestation under the hypothesis that more lightly infested individuals may enjoy higher mating success (Møller, 1991; Kose et al., 1999; Kose and Møller, 1999; Barbosa et al., 2002). These studies have generated some support for the hypothesis, but have tended to ignore selective pressures that might be acting on the lice (rather than the hosts). Thus, although a researcher approaching the issue from the standpoint of sexual selection might argue that mating success and louse load will be negatively correlated, another researcher, more mindful of the lice, might argue that an individual louse could benefit from living on the host with higher reproductive success. If that host were male, it might afford the louse or its offspring more opportunities to reach new female hosts during mating. If the host were female, it might rear more young, each of which would be a potential and possibly uninfested host for lice.

Aspects of the tension between the hosts' and ectoparasites' perspective are evident in the ''tasty chick'' hypothesis, originally posited to explain a possible advantage to hosts of brood hierarchies. If the latest chick to hatch is least competent immunologically, and therefore most ''tasty,'' it may preferentially attract parasites, to the advantage of its siblings (Christe et al., 1998, Roulin et al., 2003). However, Bize et al. (2008) pointed out that the lower nutritive resources of the smallest chicks may partially negate the advantage to the parasite of the reduced immunocompetence of those chicks.

I therefore studied vertical transmission of feather lice in common blackbirds *Turdus merula*, asking questions about the process from the perspective of the lice. First, do the lice that move onto the young in the nest aggregate on the larger chicks, rather than smaller chicks? Because larger blackbird chicks have higher survival prospects (Magrath, 1991), this aggregation would reduce the chance that the lice would find themselves in peril on a dead host.

Second, are the lice that infect the chicks more female-biased than the source population? Because of the influence of local mate competition (Hamilton, 1967), louse populations are commonly female biased (Rothschild and Clay, 1952; Rózsa et al., 1996). Although male lice that move onto a host chick could potentially

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TABLE I. Number of blackbirds, either breeding adults of the stated sex or their nestlings, sampled in various years, and number on which lice were recorded as present.

	No. sampled	No. where given species detected			
		Brueelia merulensis	*Philopterus turdi*	*Menacanthus eurysternus*	*Ricinus elongatus*
1996					
Males	6	1	4	0	0
Females	7	4	2	1	0
Nestlings (comprising 25 broods)	78	39	12	4	0
1997					
Males	11	2	3	0	1
Females	9	6	3	0	0
Nestlings (comprising 39 broods)	122	38	11	6	0
1998					
Males	9	4	5	2	1
Females	12	8	5	1	0
Nestlings (comprising 15 broods)	47	22	5	7	0

find themselves without mates and, therefore, at risk of zero reproductive success, dispersing fertilized female lice could produce eggs that would hatch into nymphs facing minimal competition from unrelated conspecifics. This might render dispersal more advantageous to female than male lice.

Third, is the extent of dispersal from parents to chicks dependent on the intensity of infestation of the parents? This is simply density-dependent dispersal. Finally, do the lice, at least during the blackbird breeding season, aggregate on the female rather than the male blackbirds? Because male blackbirds rarely incubate the eggs or brood the young (Snow, 1958; Cramp, 1988), a louse on a female blackbird would have more opportunities for dispersing to new hosts, i.e., chicks with feathers. This suggestion of aggregation by lice on female blackbirds assumes that lice would be able to determine host sex. Although there is no evidence regarding whether such a determination is possible or the mechanism by which it might be achieved, the fact that louse breeding is co-ordinated with the host breeding season (Foster, 1969; Hamstra and Badyaev, 2009) suggests the possibility of subtle host–louse interactions.

MATERIALS AND METHODS

The study was conducted from 1996 to 1998 in southeastern England, mainly in the maintained gardens of Anglesey Abbey, near Cambridge (52°14′N, 0°15′E), and in nearby gardens and hedgerows. Blackbird nests were found April–June on an ad hoc basis, usually during nest building or incubation. If the nests survived, the chick(s) reached a stage, at about 8 days old, when contour feathers were starting to cover the head and back, and the flight feathers were beginning to emerge from their sheaths. (Smaller chicks had few feathers, and larger chicks could not be handled safely.) At this point, I attempted to catch male and female parents. Even if these were not the genetic parents, and I have no evidence on the point, they were certainly the social parents, and the most likely source of any feather lice transmitting to the young. Captured birds were deloused following the protocol of Fowler and Cohen (1983). Briefly, the bird, its head held in an airtight collar, was suspended for 10 min over a container filled with chloroform vapor into which the ectoparasites fall. From the container, the lice were transferred to tubes of alcohol. The head of the bird, not sampled by the Fowler and Cohen apparatus, was searched visually for lice, and any detected were removed before the bird was released.

Immediately after the attempt to catch the parent blackbirds had been successful or abandoned, I deloused the chicks in the nest. At the same time, body mass, wing length, and length of that part of the outermost large primary emergent from the shaft were measured for each chick.

Subsequent to fieldwork, the lice were mounted for determination of species, assessment of whether adult or nymph, and, if adult, determination of sex. A sample of slides showing mounted examples of the 4 louse species (see Results) identified by Oldřich Sychra is deposited in the University Museum of Zoology, Cambridge (accession numbers CU2010:4.1-3).

RESULTS

Distribution of lice within blackbird broods

Table I shows the number of birds sampled by year, and the number of individuals infested with the 4 feather louse species recorded during this study. The 4 species were *Brueelia merulensis* (Denny, 1842) and *Philopterus turdi* (Denny, 1842) (both Ischnocera: Philopteridae), *Menacanthus eurysternus* (Burmeister, 1838) (Amblycera: Menoponidae), and *Ricinus elongatus* (Olfers, 1816) (Amblycera: Ricinidae). The most common species was *B. merulensis* and, therefore, some analyses are restricted to this species.

I investigated whether the number of *B. merulensis* detected on a chick was related to its position in the brood hierarchy. The question was explored by calculating within broods where at least 1 chick was infested with *B. merulensis*, the Kendall correlation coefficient (Siegel, 1956) between louse intensity and either body mass or length of exposed primary. The numerators and the denominators of the τ value for the individual broods were then summed to give the fractions presented in Table II, following Brooke (1978). If there was no relationship between louse intensity and position in the brood hierarchy, these fractions would be one-half. A χ^2 test then tests the significance of deviations from this expectation. Overall, louse intensity was positively correlated with both wing and mass. Therefore, the lice tended to be found on the larger chicks whose plumage was most advanced. It is not evident from these data whether the lice simply gathered where there were feathers and, therefore, a greater surface area of suitable habitat, or whether the greater survival

TABLE II. Kendall correlation coefficients (between intensity of *Brueelia merulensis* and chick weight or length of exposed primary shaft across all blackbird broods in various years. *P*-values determined by χ^2 tests.

	Weight	*P*	Primary shaft	*P*
1996	39.5/60	<0.02	39/60	<0.05
1997	29/48	NS	30.5/48	<0.10
1998	23/36	NS	23/36	NS
Over 3 yr	91.5/144	<0.01	92.5/144	<0.001

chances of the heavier chicks was a factor promoting the adherence of lice to such chicks. However, there was no indication of louse aggregation on the lighter chicks.

Age and sex of lice dispersing to blackbird chicks

The populations of adult lice on both adult and nestling blackbirds were consistently female-biased, a common situation among feather lice (Rózsa et al., 1996; Brooke and Nakamura, 1998). Only for *B. merulensis* is it possible to make a useful comparison of the sex ratio of adult lice on adult and nestling blackbirds. The ratio is more strongly biased toward female lice on the nestlings ($\chi^2 = 5.26$, 1 df, $P < 0.05$; Table III). Thus, there may be slightly stronger dispersal by adult female lice than males, but the effect is not pronounced, and no similar effects are detectable in the other louse species. Table III also shows that the lice of *B. merulensis* and *P. turdi* moving from the parent blackbirds onto the nestlings are disproportionately nymphs, hence consistently higher adult:nymph ratios on parents than on nestlings.

Dispersal to chicks in relation to infestation of adult blackbirds

Only for *B. merulensis* were numbers on both adult and nestling blackbirds adequate to allow investigation of the relationship between adult and brood louse intensities (Table III).

Considering first the relationship between adult and brood nymph loads, the latter summed across all chicks within the brood, there was a correlation between female intensity and brood intensity ($r_s = 0.601$, N = 27, $P < 0.005$), between male intensity and brood intensity ($r_s = 0.574$, n = 26, $P < 0.005$), but not between combined parent intensity and brood intensity ($r_s = 0.453$, n = 12, $P > 0.05$) in the 12 pairs where louse data were obtained from both male and female parents. However, the significant relationships above were largely driven by cases where there were no nymphs on any male, female, or brood. Once such cases are excluded, there was no correlation between female intensity and brood intensity ($r_s = 0.008$, n = 13, $P > 0.05$), or between male intensity and brood intensity ($r_s = 0.154$, n = 5, $P > 0.05$).

Only in 1998 were adult *B. merulensis* found on chicks. In that year, excluding cases where no adult *B. merulensis* were found on either the brood or the parent blackbird(s) caught, there was no significant correlation between the number of adult *B. merulensis* on the female blackbird and her brood, again summing data from all chicks in each brood ($r_s = 0.382$, n = 7). Corresponding data on adult male blackbirds (n = 4) are too sparse for analysis. Overall, these data do not support the hypothesis that the dispersal of lice onto nestling blackbirds is influenced by the number of lice on the parent blackbirds. That being so, there is no support for density-dependent dispersal, with dispersal proportionately more likely the higher the parental load.

Comparison of louse loads of breeding male and female blackbirds

Female blackbirds were significantly more likely to be infected with *B. merulensis* than males, but there were no significant differences in the prevalences of the other 2 louse species, *P. turdi* and *M. eurysternus* (Table IV). The mean number of adult *B. merulensis* occurring on a blackbird where the species was found was 16.4 ± 19.5 (SD) (n = 7) on males and 31.7 ± 47.6 (n = 18) on females (Mann–Whitney $U = 56$, $P > 0.1$). The corresponding numbers of nymphal *B. merulensis* were 21.1 ± 28.8 (n = 7) on

TABLE III. The total number of lice of the various species recorded on male and female adult blackbirds (data for the 2 sexes combined in the table) and on nestlings during this study. The final column compares, with χ^2 or Fisher exact tests, the adult:nymph ratio on adult and nestling blackbirds for the given louse species.

	No. adult females	No. adult males	Louse sex ratio (female:male)	No. nymphs	Adult:nymph ratio	Significantly different ratio?
Brueelia merulensis						
Adult blackbird	403	157	2.57:1	347	1.96:1*	<0.001
Nestlings	124	28	4.43:1	896	0.170:1	
Philopterus turdi						
Adult blackbird	41	15	2.73:1	21	3.00:1†	<0.001
Nestlings	7	4	1.75:1	40	0.275:1	
Menacanthus eurysternus						
Adult blackbird	3	1	3.00:1	2	3.00:1‡	NS
Nestlings	460	102	4.52:1	643	0.874:1	
Ricinus elongatus						
Adult blackbird	6	0	n/a	8	0.75:1	–
Nestlings	None recorded					

* Includes 121 adults that could not be sexed after specimen deterioration.
† Includes 7 adults that could not be sexed after specimen deterioration.
‡ Includes 2 adults that could not be sexed after specimen deterioration.

TABLE IV. The percentage of breeding male and female blackbirds carrying lice (adults and/or nymphs). Combined data 1996–1998. Sample sizes were 26 for males and 28 for females (see Table I).

	Male	Female	Significance of difference
Brueelia merulensis	26.9	64.3	$P < 0.02$
Philopterus turdi	46.1	35.7	NS
Menacanthus eurysternus	7.7	7.1	NS

male blackbirds and 11.1 ± 14.3 (n = 18) on females (Mann–Whitney $U = 56.5$, $P > 0.1$). Thus, for neither adult nor nymphal lice, and the latter are the dispersing age group, were intensities higher on female blackbirds where prevalence was higher.

DISCUSSION

More lice were found on the larger blackbird nestlings, those more likely to survive. This would be especially advantageous to the lice if death of smaller fledglings was most likely within a few weeks of leaving the nest, before the lice had time to breed and disperse to further hosts. Magrath (1991) reported such a pattern, with daily survival of fledglings improving markedly about a month after fledging.

Within a blackbird brood, the smallest chicks may be barely feathered at a time when their larger siblings are well feathered and liable to "explode" out of the nest if handled. This means that it is difficult to know whether the observed congregation of lice on larger chicks is simply a consequence of their being more fully feathered and possibly older, or whether it represents a strategy by the lice for enhancing their survival. It is also possible that parents are better able to remove lice from barely feathered chicks. The point could be further explored by an experimental study, rather than a correlative study as here. Another approach would be to study hole-nesting birds, such as great tits *Parus major*, where well-feathered young remain in the nest for a week, or more, and where it is also known that the smaller young are less likely to survive (Perrins, 1965). If there were more lice on the larger chicks, this would be unlikely to be because the smaller chicks were less well feathered.

Having hypothesised that female lice were the sex more likely to disperse to nestlings, I found that adult female *B. merulensis* were more likely to disperse than males. However, the effect was not strong and not replicated in the other louse species, where sample sizes were smaller. However, vertical transmission was much more likely by nymphs than by adult lice. Because nymphal lice cannot be sexed morphologically with a microscope, the sex of the nymphs transmitting to the young blackbirds was not determined in this study. It would be interesting to explore the possibility of differential transmission of male and female nymphal lice by applying molecular techniques to determine their sex.

As also reported by Darolova et al. (2001) for European bee-eaters *Merops apiaster*, there was no correlation between louse abundance on blackbird adults and nestlings, at least when families lacking lice altogether were removed from the analysis. Presumably a louse faces a trade-off between remaining on its current host, where it encounters competition from other lice, both conspecific and heterospecific (Harbison et al., 2008), but host survival is likely, and dispersing to a new host where competition is potentially lower, but host survival is less assured. Possibly the absence of a correlation between louse abundance on adults and chicks indicates that, in general, louse abundance on hosts does not reach a level where competition is a major driver of dispersal.

I predicted that louse prevalence would be higher on female blackbirds than males, on the grounds that females have more contact with the young and, therefore, offer more transmission possibilities to the lice than males. This prediction was supported for *B. merulensis*, but *P. turdi* and *M. eurysternus* showed no significant difference in prevalence between the blackbird sexes. Support was, therefore, equivocal (see also Wheeler and Threlfall, 1986). With the same train of thought in mind, it would be interesting to test the possibility that, where males had most contact with young, e.g., polyandrous bird species, louse prevalence would be higher on males than females; where the 2 sexes played an equal role in rearing the young, prevalence would be similar in the 2 sexes; and where females had more contact (as in blackbirds), prevalence would be higher on females. This would require extensive screening of louse intensity, duly controlled for season because of evidence that louse abundance varies with time of year and host breeding season (Foster, 1969; Hamstra and Badyaev, 2009). However, the essential idea, that ectoparasite prevalence may be influenced by the opportunities for transmission, is supported by observations of mites (*Spinturnix* spp.), which select communally roosting female bats *Myotis daubentoni* in preference to solitary roosting males (Christe et al., 2007).

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