Chris,
Many thanks for your help Mike

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The acquisition of host-specific feather lice by common cuckoos (*Cuculus canorus*)

M. de L. Brooke[1]* and Hiroshi Nakamura[2]

[1] Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.
[2] Faculty of Education, Shinshu University, Nishinagano, Nagano 380, Japan

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Abstract

This study addresses the question of how three species of flightless feather lice (Phthiraptera) specific to a brood parasitic bird, the common cuckoo (*Cuculus canorus*), are transmitted from one cuckoo generation to the next in the absence of any direct contact between parent and young. None of 21 cuckoo nestlings examined shortly before fledging carried cuckoo lice; nor were any lice found in 19 nests in which cuckoos had laid. Cuckoos returning to Japan for their first breeding season were as likely to be lousy as, and carried similar louse loads to, older birds. These field observations are consistent with data arising from examination of museum skins from European breeding areas and from African wintering areas, and it is concluded that cuckoos acquire their lice between leaving the nest in summer and returning to the breeding grounds the following spring. This acquisition probably occurs via direct body-to-body contact between cuckoos, a supposition bolstered by some observations.

Key words: *Cuculus canorus*, Phthiraptera, host specificity, phoresy

INTRODUCTION

Feather lice (Phthiraptera) are flightless obligate ectoparasitic insects which spend their entire lives adhering to the plumage or skin of their avian hosts. The majority of feather lice species are specific to a particular host species or genus (Rothschild & Clay, 1952; Marshall, 1981). The transmission of feather lice from one generation of brood parasitic birds to the next generation therefore poses a puzzle. If the feather lice of the parasite and of the host that raises it belong to different species, the parasite chick cannot receive its lice from its host. In the absence of any contact with its parents, how then does the young parasite acquire its lice?

Since cuckoos throughout the world harbour three genera of lice, namely *Cuculoecus*, *Cuculicola*, and *Cuculiphilus*, the question has been posed in respect of cuckoos by a number of authors (Rothschild & Clay, 1952; Dogiel, 1964; Marshall, 1981), but not answered. The young cuckoo, in the order Cuculiformes, is raised by passerine birds in the order Passeriformes, which harbour different genera of lice. As far as is known, neither the female cuckoo nor her mate visit the host nest after laying. There is therefore no apparent opportunity for transfer of cuculiform lice between parent and young cuckoo. It could be that the cuckoo lice leave the female cuckoo while she is laying and then linger in the host nest or on the host until the young cuckoo has grown feathers to which the lice could attach. This explanation has problems. The lice would have to detect the exact period, of only about 10 seconds duration (Wyllie, 1981), when the female cuckoo was laying. They would then have to survive off their usual host until the young cuckoo had hatched and grown, a period of 3–4 weeks, whereas, as far as is known, feather lice do not normally survive away from their hosts for more than a matter of days (Ledger, 1980; Marshall, 1981; Lehane, 1991).

Two alternative explanations have been proposed. The first is that transfer of feather lice occurs during mating. Under this scenario, the young cuckoo would leave the nest free of cuckoo lice and would remain free for its first year of life (assuming first breeding at one year old). When the first-year cuckoo mated with infested, older birds it would acquire lice (Hillgarth, 1996). This mode of transmission yields testable predictions. Cuckoos in the nest and in their first year would be louse-free (excluding possible temporary infestation with host louse species). Then, during the course of the first breeding season, a steadily increasing proportion of these birds would become infested, but louse loads would possibly be lower than those of older, adult birds which had been infested for at least a year. On the basis of finding fledgling cuckoos to be louse-free and mature cuckoos shot the following summer to be lousy, Dogiel

*All correspondence to: M. de L. Brooke, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.

(1936, 1964) has championed this explanation. However, his work did not demonstrate that first-year cuckoos, which had not mated, arrived louse-free at the breeding grounds. The second explanation involves phoresy whereby the lice would attach to flatflies (Hippoboscidae), as is not infrequently observed (Clay & Meinertzhagen, 1943; Rothschild & Clay, 1952; Keirans, 1975). By securing a flight aboard a flatfly, from an infested cuckoo to an uninfested cuckoo, the lice could potentially reach new hosts. If this mode of transmission operated, it might be that cuckoo nestlings would occasionally become infested. But most infestation would presumably occur post-fledging, and it would not then be distinguishable from infestation occurring by direct bird-to-bird contact.

This study reports observations on common cuckoos (*Cuculus canorus*) designed to distinguish between these various alternatives. The three louse species found on this bird are *Cuculoecus latifrons*, *Cuculicola latirostris* (both belonging to the suborder Ischnocera), and *Cuculiphilus fasciatus* (suborder Amblycera). *Cuculoecus* is a louse primarily found on the head and neck (Rothschild & Clay, 1952), while the other two lice occur more widely over the body.

STUDY AREAS AND METHODS

The methods used in our study of common cuckoos relate to the various transmission possibilities mentioned above.

(a) Do cuckoo nestlings leave the nest without cuckoo lice? To assess this, 21 nestling cuckoos were checked for feather lice using the method of Fowler & Cohen (1983). Briefly, the bird, its head held in an airtight collar, is suspended for 10 min over a container filled with chloroform vapour into which ectoparasites fall. They are collected for mounting and microscopic examination. The nestlings (13 in reed warbler *Acrocephalus scirpaceus* nests in Oxfordshire and Cambridgeshire, England (1994–1996), 7 in great reed warbler *A. arundinaceus* nests in Nagano Prefecture, Japan (1995), and 1 in an azure-winged magpie *Cyanopica cyana* nest in Japan (1995)) were checked at roughly the largest size they could be handled without prompting premature fledging. Thus primaries were showing beyond the sheaths and wing length ranged from 77–128 mm ($n = 20$).

To assess whether cuckoo nestlings were more or less likely to acquire the host-specific lice than the hosts' own young, nestling reed warblers (1–3 per nest) were deloused in Cambridgeshire in 1994 and nestling great reed warblers (2 per nest) were deloused in Japan in 1995. As with the cuckoo nestlings, the young warblers were examined at roughly the largest size they could be handled without prompting premature fledging. Mist-netted adult and juvenile reed warblers were also examined for lice in July and August 1994. The method of obtaining lice from warblers was as described for young cuckoos, except treatment with chloroform lasted only 5 min.

Since it is probably true that Fowler & Cohen's method does not secure all ectoparasites on a bird (Clayton & Walther, 1997), a failure to find lice on nestling cuckoos could represent a "false negative" owing to imperfect sampling of low louse infestation levels. To check this and the possibility that lice leave the laying female cuckoo to linger in the host nest in anticipation of a young cuckoo, we also checked for feather lice in the actual nests where cuckoos had laid. This examination was conducted on 19 reed warbler nests obtained from Oxfordshire and Cambridgeshire in 1996. As soon as practicable after the nest had failed at the egg stage ($n = 1$) or at the chick stage ($n = 10$), or after the cuckoo chick had fledged ($n = 8$), the entire nest was cut out of the reeds and brought into the laboratory. It was then examined carefully under a binocular microscope for 10 min. This examination was done immediately, and repeated 1 day later, 2 days later and 5 days later. During this period in the laboratory, 13 of the nests were kept in polythene bags while 6 were suspended on a metal grille under a 60 W light and over water in a Berlese funnel (Southwood, 1966).

(b) Are lice acquired during mating? To explore this possibility, free-flying cuckoos were caught during the breeding season in canopy-level nets in *Acacia* groves along the Chikuma River, Nagano, Japan, where the principal host is the great reed warbler (Nakamura, 1990). The birds were separated into those in their first year (i.e. those hatching the previous calendar year) and those that were older by the presence in the former group of variable numbers of juvenile secondaries and coverts (Baker, 1993). The birds were then ringed to avoid repeat delousing and deloused using Fowler & Cohen's (1983) method for 10 min. While the bird was suspended over chloroform, its head was examined and any *Cuculoecus* found removed with forceps. The feather lice were initially preserved in alcohol. Subsequently, they were mounted, identified by reference to the collections of the Natural History Museum, London, and sexed by examination of the genitalia. Nymphs were differentiated from adult lice by smaller head capsules (measured under the microscope) and incomplete development of the genitalia.

The main sample comprised 35 birds caught by the authors between 27 May and 2 July 1995, a period stretching from a few days before the start of cuckoo laying until towards the end of the cuckoo laying period. Detailed analysis of the ectoparasites is restricted to the lice from these birds since the delousing treatment was standard. In addition, 6 birds (3 at Wicken Fen, Cambridgeshire, 1 at Knettishall, Suffolk and 2 at Dungeness, Kent) were caught in England in 1994 and another 3 at Wicken Fen in 1995.

(c) Are lice acquired outside the breeding season via phoresy and/or by direct contact between birds? Since cuckoos are not readily captured alive outside the breeding season, and since we did not wish to collect birds, we could only sample louse loads via museum skins. We visited the Natural History Museum, Tring (NHM), and combed cuckoo skins with a nit comb.

Each skin was combed for about 5 min and any lice obtained were identified. Although not without drawbacks, for instance lice may abandon a dead bird before its prepared skin reaches the museum and dead lice may be inadvertently exchanged between skins in the same museum drawer, the method did yield lice (the maximum number obtained from 1 bird was 3) and, as will emerge below, the results were compatible with the field studies.

RESULTS

(a) Neither warbler-specific nor cuckoo-specific feather lice were obtained from any of the 20 cuckoo nestlings examined from the nests of *Acrocephalus* warblers. However, warbler-specific lice were found on warbler chicks; *Menacanthus* sp. (Amblycera) occurred on 5 of 57 reed warbler nestlings examined from 24 nests, and *Bruelia* sp. (Ischnocera) occurred on four of 52 great reed warbler nestlings examined from 26 nests. Thus the prevalence of warbler-specific lice (9/109) on warbler chicks was higher, but not significantly higher, than on cuckoo chicks in warbler nests (0/20). The prevalence on reed warbler nestlings was similar to that on fledged juvenile (3/26) and adult (1/18) reed warblers mist-netted in July and August, suggesting that, for the warblers, contact within the nest is a primary means of louse transmission (Lee & Clayton, 1995).

The single cuckoo nestling sampled from an azure-winged magpie nest yielded one specimen of *Philopterus* sp. (Ischnocera), belonging to a louse genus often associated with corvids (Hopkins & Clay, 1952).

No feather lice whatsoever were found in the 19 reed warbler nests examined.

(b)

(i) The Japanese sample and its bearing on louse transfer during cuckoo mating

The principal sample of 35 cuckoos caught in Nagano Prefecture, Japan, comprised 15 first-year and 20 older cuckoos. All the cuckoos were found to carry cuckoo-specific feather lice (Table 1), and the likelihood that any one of the three louse species would be found on a particular cuckoo was not significantly affected by the age of the cuckoo (Table 1a). There was also no difference between louse species in prevalence, either on first-year or older cuckoos.

While all cuckoos bore lice, first-year cuckoos were somewhat more likely to have only one species of louse, while older cuckoos were more likely to be infested with two species. There was no difference between cuckoo age classes in the proportion of birds infested with all three louse species (Table 1b).

For none of the three louse species was there a significant difference in the number of lice, either adult or nymphs, retrieved from first-year and older cuckoos (Table 2).

There is thus no evidence that first-year cuckoos differed from older birds in the prevalence of louse infestation or in the number of lice harboured, or in adult/nymph ratios which might reflect the recent breeding history of the louse population. Some such differences would be anticipated if the first-year birds had acquired their cuckoo-specific lice by mating with older birds during the sampling period, 27 May to 2 July.

If mating were a primary route of louse transfer, then we predicted that first-year birds in the early part of the breeding season would be less heavily infested than those caught in the latter part. We cannot use prevalence as a measure since all first-year birds, whenever caught, were infested (Table 1). We have, however, divided the 15 first-year cuckoos into the eight caught before 22 June (actually 4–21 June) and the seven caught after 23 June (24 June–2 July). The former group did not have significantly fewer lice (Table 3).

Table 1. The prevalence of feather lice on common cuckoos caught in Nagano Prefecture, Japan, in spring 1995

	Cuckoos		
	First-year	Older	Significance (χ^2 test, 1 *d.f.*)
(a) Proportion carrying:			
Cuculicola	10/15	17/20	NS
Cuculoecus	12/15	18/20	NS
Cuculiphilus	10/15	13/20	NS
(b) Proportion of cuckoos with:			
One louse species	8/15	3/20	<0.05
Two louse species	2/15	12/20	<0.05
Three louse species	5/15	5/20	NS
At least one louse species	15/15	20/20	NS

Table 2. Numbers of feather lice (mean ± S.D.; range) on common cuckoos caught in Nagano Prefecture, Japan, in spring 1995. No differences between first-year and older cuckoos (i.e. within rows) were significant (2-tailed Mann–Whitney tests)

		Cuckoos	
		First-year ($n = 15$)	Older ($n = 20$)
Louse species			
Cuculicola	Adults	7.6 ± 13.75 (0–47)	14.3 ± 25.88 (0–113)
	Nymphs	4.3 ± 7.96 (0–30)	20.6 ± 48.79 (0–226)
Cuculoecus	Adults	5.9 ± 13.87 (0–57)	3.3 ± 3.13 (0–12)
	Nymphs	2.9 ± 4.54 (0–14)	1.7 ± 2.03 (0–5)
Cuculiphilus	Adults	1.4 ± 2.87 (0–11)	1.8 ± 3.55 (0–15)
	Nymphs	4.4 ± 8.50 (0–33)	6.9 ± 19.64 (0–91)

Table 3. Numbers of feather lice (mean ± S.D. for adults and nymphs combined) on first-year common cuckoos caught in Nagano Prefecture, Japan, in spring 1995. No differences between cuckoos in the two time periods were significant (2-tailed Mann–Whitney tests)

	Cuckoos caught	
	Before 22 June ($n = 8$)	After 23 June ($n = 7$)
Louse species		
Cuculicola	11.1 ± 15.71	12.9 ± 26.32
Cuculoecus	13.8 ± 22.24	3.1 ± 4.94
Cuculiphilus	8.0 ± 13.80	3.3 ± 6.50

(ii) Other comments on the Japanese sample

From Table 2, adult/nymph ratios generally appear higher in the head louse, *Cuculoecus*, the largest of the species, than in the other two species. Among 30 birds carrying *Cuculoecus*, adult/nymph ratios exceeded unity in 20 cases. The corresponding values for *Cuculicola* and *Cuculiphila* were 13/27 (v 20/30; $\chi^2 = 1.31$, 1 *d.f.*, NS) and 5/23 ($\chi^2 = 8.81$, 1 *d.f.*, $P < 0.01$), respectively.

As has been recorded in a variety of studies of avian lice (Marshall, 1981; Clayton, Gregory & Price, 1992; Rózsa, Rékási & Reiczigel, 1996), the sex ratio of the three louse species found on cuckoos was skewed in favour of females (Table 4). In a majority of birds, a majority that was significant for *Cuculicola* and *Cuculoecus* ($P < 0.01$, sign test), female lice outnumbered male lice. For each species of louse, the total number of female and male lice deviated significantly from parity ($P < 0.01$), and the ratio of females to males was fairly similar in the three louse species ranging from 2.11 in *Cuculiphilus* to 2.56 in *Cuculoecus* ($\chi^2 = 0.603$, 2 *d.f.*, $P > 0.1$),

Twenty-seven of the Japanese cuckoos could be sexed confidently by their plumage and, more conclusively, by their call when released. There were no significant differences in the numbers of lice on the 16 males and 11 females.

(iii) British samples

The details of the lice obtained from the cuckoos trapped in England are given in Table 5. Although the data are sparse, some interesting points emerge. First, the first-year bird caught in May at Dungeness, a bird observatory on the south coast of England, was almost certainly on migration and therefore had not mated (assuming that cuckoos do not copulate away from the breeding grounds). It was nevertheless lousy. Furthermore, all four first-year cuckoos caught at Wicken Fen carried lice, although the dates of capture were at the very start of the nesting season (first cuckoo egg dates at Wicken Fen normally in the last week of May; pers. obs.). Second, the Dungeness juvenile caught in mid-July did not yield lice. This is compatible with the failure to find cuckoo-specific lice on any cuckoo nestlings. Third, the failure to record *Cuculoecus* was probably because of inconsistent searching of the birds' heads during the delousing treatment. There is no reason to suppose this louse species does not infest British cuckoos since it was obtained during the museum combing of cuckoos shot in the breeding season in Britain (see c below).

(c) We combed the skins of 50 fledged juvenile cuckoos from Great Britain (> 80% of the holding in the NHM) and another six from continental Europe (the entire holding). Only one skin yielded a louse, identified as *Cuculicola*. This bird was collected in 1935 at Lochgilphead, Argyllshire, Scotland on the exceptionally late date of 10 November. Nevertheless, the record was accepted by Witherby *et al.* (1938). Six juvenile cuckoos collected between September and November in Saudi Arabia, where they were likely to be on migration (Moreau, 1972), yielded no lice. The NHM's entire holding of first-year common cuckoos obtained in winter quarters in Africa ($n = 37$) was combed, and lice were found on four skins. The proportion with lice was as follows: July/Aug. 0/1; Sept./Oct. 1/12; Nov./Dec. 2/14; Jan./Feb. 0/6; Mar.–May 1/4. The earliest louse found was a specimen of *Cuculiphilus* on a young cuckoo obtained in Somalia on 18 September. All three cuckoo louse species were represented on the birds obtained in Africa. Finally all British common cuckoos ($n = 42$) and a further seven from continental Europe, all obtained in the breeding season as adults (late April–end June), were combed. Again, all three louse species were represented. The overall prevalence of lice in this combined sample of first-year and older birds was 6/49 and, therefore, not significantly different from the prevalence of 4/37 on first-year birds wintering in Africa. Thus the prevalence of lice on first winter and

Table 4. Sex ratio of adult feather lice obtained from common cuckoos caught in Nagano Prefecture, Japan, in spring 1995. Note that the number of infested cuckoos (first three numerical columns) is slightly lower than in Table 1 because of the small number of birds that had only immature lice of a particular species

	No. of cuckoos with:			Total no. of lice	
	More female than male lice	Equal numbers	More male than female lice	Female	Male
Cuculicola	20	2	4	275	125
Cuculoecus	22	1	6	115	45
Cuculiphilus	11	3	1	38	18

Table 5. Feather lice recorded on nine common cuckoos trapped in England. Cuckoos classified below as "older" were more than one year old

Date	Place	Age of cuckoo	Louse species found
15 May 1994	Wicken Fen	Older	None
23 May 1994	Dungeness	First year	*Cuculicola*
1 June 1994	Wicken Fen	Older	*Cuculicola*, *Cuculiphilus*
1 June 1994	Wicken Fen	First year	*Cuculicola*
2 June 1994	Knettishall	Older	*Cuculicola*
15 July 1994	Dungeness	Juvenile	None
22 May 1995	Wicken Fen	First year	*Cuculicola*
22 May 1995	Wicken Fen	First year	*Cuculicola*
22 May 1995	Wicken Fen	First year	*Cuculicola*, *Cuculiphilus*

breeding season cuckoos was 10/86, higher ($\chi^2 = 3.33$, 1 *d.f.*, 1-tailed $P < 0.05$) than the prevalence, 1/56, on juvenile cuckoos still in the breeding area or on their first migration.

Despite the admitted problems associated with combing skins (see 'Study areas and methods'), the pattern of occurrence revealed by skins is compatible with the field observations. In the early autumn, few if any juvenile cuckoos are lousy. As the autumn progresses, lice are acquired. This acquisition can apparently occur either in Africa or occasionally in Europe. By the time birds leave Africa to begin spring migration, louse prevalence is probably similar to that observed on the breeding grounds, nearly 100%, judging by the observations of mist-netted birds in England and Japan.

DISCUSSION

Our study of cuckoo nestlings and of nests in which cuckoos had laid essentially confirmed previous findings (Dogiel, 1936, 1964; Clay & Meinertzhagen, 1943) in establishing that the young cuckoo leaves the nest without cuckoo lice. Compatible with these observations is the fact that the skins of young, but fledged cuckoos combed in the Natural History Museum were louse-free, with the single exception of a bird shot unusually late, in November in Scotland. Also louse-free was a single free-flying juvenile sampled in July. Thus the conclusion that acquisition of lice does not occur within the host nest seems secure.

Moreover, only one young cuckoo, sampled from an azure-winged magpie nest, carried a host louse (see also Dubinin, 1951; Dogiel, 1964). Although we cannot know how long this louse would have survived, the fact that no free-flying cuckoos sampled in our study harboured non-cuckoo feather lice suggests that any such host lice usually do not persist for long. However, Lindholm, Venter & Ueckermann (1998) have recently discovered that host lice can be found on diederik cuckoos *Chrysococcyx caprius* at least a year old. Since the cuckoos sampled were male, making any contact with the hosts unlikely, it seems the lice had remained on the birds since they fledged.

While acquisition of cuckoo lice has often been assumed to occur during mating (Dogiel, 1964; Marshall, 1981; Page, Clayton & Paterson, 1996), the present results refute that assumption. All first-year common cuckoos carried cuckoo lice, including one likely to be on migration and those sampled early in the breeding season on the nesting grounds. We did not detect any difference in the numbers or age distribution of lice carried by first-year and older cuckoos. The only significant difference between the two classes was that first-year birds more commonly had one species of louse and more rarely had two species of louse than older birds. This difference may simply reflect the lesser age of the first-year birds, and therefore the shorter time available to acquire the full set of louse species. While lice may transfer between birds during mating (Hillgarth, 1996), our field data do not argue for contact during copulation as the principal means by which the cuckoo lice reach new cuckoo hosts. In nearly 100% of cases, lice have reached the cuckoo by the start of the breeding season, and therefore, we presume, before mating.

This scenario is supported by the results of combing skins. Lice can occasionally be found on the skins of young birds obtained on the breeding grounds in late autumn, and more frequently on the skins of young birds from Africa. By the time the birds are ready to return on migration to the breeding grounds, skins obtained from Africa are apparently as likely to yield lice as skins obtained on the Palaearctic breeding grounds. This picture is identical for all three species of cuckoo lice.

Another point of identity is that the sex ratios among adult lice of the three species are significantly female biased, but to a similar degree. Sex ratio bias, mostly towards females, has been noted in a proportion of feather louse populations studied (Marshall, 1981; Clayton *et al.*, 1992). Female bias has been interpreted as a consequence of local mate competition (Hamilton, 1967), arising because the louse populations on individual birds are more or less isolated from other such populations and therefore inbred. This reasoning leads to the prediction that the greater the degree of isolation, the greater the female bias, a suggestion supported by a comparison between bird species (Rózsa *et al.*, 1996). Since the sex ratio biases of all three species of cuckoo lice are similar, it may be that the three species transfer by similar methods so that populations on different cuckoos are isolated to a similar degree. Neither the sex ratio results, nor indeed any other part of the data, suggest major differences in transmission between the two Ischnoceran lice and the one Amblyceran species (Keirans, 1975; Clayton *et al.*, 1992).

If young cuckoos leave the nest louse-free and return to the breeding grounds carrying lice, the timing of louse acquisition has been narrowed to a period of

approximately nine months. Two non-exclusive possibilities for the method of acquisition are direct contact and phoresy. Both methods would lead to a progressive build-up in louse infestation, as hinted by the combing studies. Both routes would presumably be available only infrequently and so cause inbreeding and hence female bias in the louse populations on individual hosts. How likely are these methods?

Although we ourselves have no experience of common cuckoos in the Asiatic and African wintering grounds, the consensus of bird-watching colleagues is that the birds are not often seen, and then usually singly. However, there are records both from Africa (Moreau, 1972) and from migration points (Christie, 1979; Hurrell, 1980; Rogers, 1980; Cramp, 1985) of aggregations of tens of birds gathering excitedly at caterpillar outbreaks. D. A. Christie (pers. comm.), amplifying his published observations, writes "I do certainly recall seeing three [cuckoos] perch for some 10 seconds in very close contact, two of these definitely in body contact; and another sub-group of five or six perched for no more than a couple of seconds, with at least three of these birds so close together that full body contact was inevitable." Such occasions can therefore involve the contact needed for louse transfer. In addition to any transfer at daytime feeding aggregations of cuckoos, there is the possibility of transfer at communal dustbaths or at roosts if ever the birds roost communally (Marshall, 1981).

Clay & Meinertzhagen (1943) report examining five young cuckoos in Britain and Estonia in late summer. None had Mallophaga. However, one had nine, two had five, one had two and one had no hippoboscids. One of the hippoboscids *Ornithomyia avicularis* carried a female of the louse *Bruelia merulensis*, a species which is a parasite of the blackbird (*Turdus merula*). Since Meinertzhagen's veracity as an observer has been questioned (Knox, 1993), these records merit cautious assessment. Even if they do suggest regular use of cuckoos by hippoboscids, they do not provide an instance of a hippoboscid carrying a cuckoo louse (see also Eichler, 1939). To our knowledge, there are no such records. Even if there were, hippoboscids are generally less specific in their host preferences than are feather lice (Maa, 1966; Marshall, 1981). It would therefore be surprising if cuckoo lice used hippoboscids as the sole means of transferring to new hosts.

Records of phoresy generally involve Ischnoceran feather lice, while Amblyceran species may crawl between hosts (Keirans, 1975). The fact that our data on prevalence and sex ratios suggest no difference between the transmission methods of the two Ischnoceran and one Amblyceran species infesting cuckoos is a further argument that phoresy is not the primary means of transmission. But we certainly cannot exclude the possibility of phoresy.

We conclude that transfer of the feather lice of the common cuckoo does mostly occur horizontally, either by direct contact between birds and/or by phoresy before the breeding season. It will be difficult to devise experiments to distinguish the relative importance of these alternatives.

A final point is that this evidence of horizontal transmission by the lice of a bird species which is not generally gregarious implies that horizontal transmission could also occur in other bird species, especially those that are more sociable than cuckoos. Thus the presumption that feather lice primarily move between hosts by vertical transmission may be premature. If lice, indeed, commonly move by both vertical and horizontal routes, then the theoretically-based belief that vertically-transmitted lice are less virulent than other, horizontally-transmitted ectoparasites may need to be refashioned (Ewald, 1993; Clayton & Tompkins, 1994).

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