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Persistence of passerine ectoparasites on the diederik cuckoo *Chrysococcyx caprius*

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Abstract

Using the African diederik cuckoo *Chrysococcyx caprius* and four sympatric passerine foster species in the subfamily Ploceinae, we show that nestling cuckoos are infested by feather lice and mites derived from the ectoparasite fauna typical of the foster species. Adult cuckoos had five species of lice and mites normally found on ploceines, which demonstrates that these ectoparasites are able to survive on foreign hosts. This is the first record of persistence of passerine ectoparasites on a cuckoo. Adult diederik cuckoos also harboured four species of mites and lice specific to cuckoos; since these were not detected on nestlings, cuckoo-specific lice and mites apparently transfer to cuckoos after they leave the nest. Contrary to prediction, ectoparasites with a life cycle involving a permanent association with their host (feather mites and lice) were more likely to transfer to cuckoo nestlings than ectoparasites which spend part of their life cycle away from their host (haematophagous mites and phoretic skin mites). New host records are established for the lice genera *Brueelia*, *Cuculoecus*, *Machaerilaemus*, *Myrsidea*, *Philopterus* as well as for the mite species *Microlichus americanus*, *Ornithonyssus bursa*, *Ornithocheyla megaphallos*, *Pellonyssus reedi*, *Pteronyssoides passeris*, *Pternonyssus glossifer*, *Trouessartia baupi*, *T. carpi*, *Xolalges plocei*, *X. scaurus* and the mite genus *Passeroptes*.

Key words: mites Acarina, feather lice Phthiraptera, host switching, *Euplectes orix*, *Ploceus intermedius*

INTRODUCTION

Avian brood parasites offer a natural system for the study of host specificity of ectoparasites. Parasitic cuckoos (Cuculiformes: Cuculidae) are particularly useful study species since they parasitize birds of a different order, the Passeriformes, or passerine birds. Cuckoos lay their eggs in the nests of passerines and abandon them, leaving all parental care to the nest owners. In most species, newly hatched cuckoos evict all other eggs or young from the nest and are reared alone (Rowan, 1983). As ectoparasites such as feather mites (Arachnida: Acarina) and lice (Insecta: Phthiraptera) are primarily transmitted vertically, between parent and offspring (Atyeo & Gaud, 1979; Lee & Clayton, 1995), nestling cuckoos have ample opportunity to acquire ectoparasites directly from their foster-parents. However, mites and lice typical of passerine birds have only infrequently been found on nestlings or fledglings of the common cuckoo *Cuculus canorus* (Clay & Meinertzhagen, 1943; Dubinin, 1951; Brooke & Nakamura, 1998) and have never been reported on adult parasitic cuckoos (Hopkins & Clay, 1952; Zumpt, 1961; Dogiel, 1964; Atyeo & Gaud, 1979; Ledger, 1980). This absence from cuckoos has often been used to exemplify the inability of highly specialized ectoparasites, such as feather mites and lice, to persist on "foreign" hosts (Rothschild & Clay, 1952; Atyeo & Gaud, 1979; Marshall, 1981; Page, Clayton & Paterson, 1996). Physical or physiological incompatibility between passerine ectoparasites and cuckoos or the superior competitive ability of cuckoo-specific ectoparasites over "straggling" passerine-specific ectoparasites are thought to inhibit the establishment of passerine-specific lice and mites on cuckoos (Rothschild & Clay, 1952; Rózsa, 1993).

Permanent ectoparasites, such as feather lice and feather mites, complete their entire life cycles on the host and are highly host-specific (Fain, 1994). By contrast, temporary parasites, species which leave the host for part of the life cycle (e.g. nest-living haematophagous mites), generally have low host specificity (Marshall, 1981; Fain, 1994) and may not rely on physical contact between host individuals for transmission (Fain, 1965;

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Clayton & Tompkins, 1994). Temporary parasites should be less dependent on any particular species for survival and reproduction than permanent parasites, and therefore should be more successful on cuckoo nestlings. Comparison of species of mites found on nestling cuckoos, their foster species, and adult cuckoos can test the relationship between permanence of the host–parasite association during the parasite life cycle and ability to survive on different host species.

Another question arising from the study of cuckoo ectoparasites has stemmed from the observation that several species of mites and lice have been found only on adult cuckoos but never on nestling cuckoos or their foster species (Hopkins & Clay, 1952; Zumpt, 1961; Dogiel, 1964; Atyeo & Gaud, 1979; Ledger, 1980). How do ectoparasites which are only found on cuckoos disperse from one cuckoo to another when parent cuckoos never meet their young? Cuckoo-specific parasites must rely on alternative means of dispersal. One possibility is that female cuckoos leave ectoparasites behind in the nest when they lay their eggs. Feather lice have been found on eggs of some species of Charadriiform waders (Mester, 1971; Rankin, 1982), possibly in order to disperse from one bird to its mate (Mester, 1971). This explanation appears unlikely, as it does not account for the observed absence of cuckoo-specific ectoparasites on nestling cuckoos. Instead, cuckoo-specific ectoparasites are thought to be transferred between cuckoos during sexual or other contact (Dogiel, 1964; Brooke & Nakamura, 1998), through phoresy, the dispersal of mites and lice through temporary attachment to more mobile animals, such as hippoboscid flies (Clay & Meinertzhagen, 1943; Keirans, 1975), or through shared bathing or roosting sites (Marshall, 1981). Direct evidence is lacking.

We compared the ectoparasite fauna of nestling and adult diederik cuckoos *Chrysococcyx caprius* and their passerine foster species, with equal attention to feather lice and mites, to determine if nestling cuckoos acquire the ectoparasite fauna characteristic of their foster species or of adult cuckoos. We also quantified, for the first time, the ectoparasites of nestlings and adults of the diederik cuckoo and two of its foster species *Euplectes orix*, the red bishop, and *Ploceus intermedius*, the lesser masked weaver, and present incidental records of two other foster species, *P. subaureus*, the yellow weaver, and *P. ocularis*, the spectacled weaver. The four foster species are classified in the family Passeridae, subfamily Ploceinae (Sibley & Monroe, 1990). The diederik cuckoo is known to have 10 foster species in the Ploceinae (Rowan, 1983).

MATERIALS AND METHODS

Field sites

We collected ectoparasites from diederik cuckoos and ploceines in Pietermaritzburg (29°39′S, 30°23′E), KwaZulu/Natal, South Africa, with the following exceptions: one nestling *P. intermedius* was examined at each of Ashburton (29°41′S, 30°27′E) and Empangeni (28°45′S, 31°54′E), KwaZulu/Natal, and one diederik cuckoo nestling in a *P. subaureus* nest was examined at Empangeni. We examined live birds during 2 consecutive breeding seasons, in November to February 1993/94 and in November to December 1994.

Sampling procedure

We used a fumigation apparatus to collect ectoparasites from birds non-destructively (Fowler & Cohen, 1983). Each bird was suspended for 10 minutes in a fumigation jar such that its body was inside the jar and exposed to chloroform while its head was outside, allowing the bird to breathe. Ectoparasites fell off the bird on to filter paper lining the bottom of the jar. After releasing the bird, the filter paper holding the ectoparasites was carefully removed from the jar and its contents transferred to numbered alcohol-filled vials. The clear glass jar was then brushed out and closely inspected, as was the brush, to prevent contamination. New filter paper was used each time and jars were washed daily.

Ploceines and diederik cuckoos were captured in mist-nets near breeding colonies and were classified as juveniles or adults based on plumage (Maclean, 1993). They were sexed, ringed, and fumigated, regardless of breeding status. As cuckoos were much less abundant than ploceines, no more than one adult cuckoo was captured per day. To prevent contamination, no other birds were fumigated on the same day as an adult cuckoo. Nestlings of all species were fumigated when about 75% of the total length of the ninth outermost primary feather was in web, at about 2 weeks of age for *P. intermedius* and *E. orix* and $2\frac{1}{2}$–3 weeks for diederik cuckoos. Body feathers were well developed by this stage and the young were nearly ready to fledge. Mites and lice were likely to have transferred to nestlings by this time, as feather lice infest nestlings as soon as tips of feathers are available (Lee & Clayton, 1995) and feather mites transfer from parent to offspring when primary feathers are 50–75% developed (Atyeo & Gaud, 1979). All nestlings in each nest were ringed, but only one was fumigated.

From each sample of ectoparasites, mites and feather lice were separated for mounting and identification. Each specimen was identified to species level if possible, or else to genus or family level. None of the feather lice could be identified to species because reliable taxonomic descriptions of African species in these genera are not available (Ledger, 1980). Age and sex was recorded for most of the lice which were collected. Specimens of all louse species are now held at the collection of the Onderstepoort Veterinary Institute while most of the mite species are held at the Plant Protection Research Institute, South Africa.

We follow Margolis *et al.* (1982) in referring to

Table 1. Counts of birds infested with feather lice. Diederik cuckoo nestlings are listed according to the species in whose nest each was found. No lice were collected from nestling *Ploceus ocularis* ($n = 3$), *P. subaureus* ($n = 2$) or cuckoo nestlings reared by these species ($n = 1$ each). The following abbreviations were used for age of bird: ad = adult, juv = juvenile and ne = nestling. *n* is the number of birds examined

			Suborder Ischnocera: Family Philopteridae				Suborder Amblycera: Family Menoponidae		
Bird species	Age	*n*	*Brueelia* sp. A	*Brueelia* sp. B	*Philopterus* sp. A	*Cuculoecus* sp. A	*Myrsidea* sp. A	*Machaerilaemus* sp. A	*Cuculiphilus* sp. A
Euplectes orix	ad	29		11	19		3		
	juv	2			25				
	ne	30		15	1		5	2	
Cuckoo in *E. orix*	ne	7		5					
Ploceus intermedius	ad	25	19		1		1		
	juv	2	1						
	ne	9	6	2	1*		2		
Cuckoo in *P. intermedius*	ne	7	1						
Cuckoo (free-flying)	ad	5		1	2*	5			3

* The specimens were subadults of the *Philopterus* genus that could not be assigned to sp. A with certainty

parasite "prevalence" as the proportion of birds which are parasitized, "intensity" as the number of parasites collected per bird, including uninfested individuals, and parasite "load" as a general term encompassing both prevalence and intensity.

Statistical analyses were performed using Statview 4.02.

RESULTS

Ectoparasite fauna of the diederik cuckoo and its host species

Feather lice

Diederik cuckoo nestlings did not carry any cuckoo-specific lice but were infested with the *Brueelia* species typical of the foster species that reared it, which differed between *E. orix* and *P. intermedius* (Table 1). By contrast, adult cuckoos were infested with species of the genera *Cuculoecus* and *Cuculiphilus*, neither of which was found on ploceines. *Cuculiphilus snodgrassi* is the only feather louse previously reported from the diederik cuckoo, while *Cuculoecus latifrons* is known to infect common cuckoos (Ledger, 1980). In addition, adult cuckoos carried two genera of lice also present on *E. orix* and *P. intermedius*, namely *Philopterus* and *Brueelia*, which have not been reported on cuckoos (Hopkins & Clay, 1952; Dogiel, 1964; Ledger, 1980). The four louse genera that were found on *E. orix* and *P. intermedius* have not previously been collected from these species but are known to infest other members of the Ploceinae (Ledger, 1980). The two foster species which were examined in small numbers, *P. ocularis* and *P. subaureus*, had no lice, nor did cuckoo nestlings reared in nests of these species.

The relationship between intensity of infestation on the five adult cuckoos and the persistence of ploceine lice was examined qualitatively. The most heavily infested adult cuckoo carried only cuckoo-specific lice, the second ranked cuckoo carried one ploceine louse species and two cuckoo-specific species, while the third ranked cuckoo carried two ploceine louse species and one cuckoo-specific species. The two remaining adults carried one and two species of cuckoo-specific lice only.

There was little indication that the ratio of male to female lice differed from unity on ploceine hosts (adults and nestlings combined: $\chi^2_c = 3.2$, $d.f. = 1$, $P = 0.08$ (*Brueelia* sp. A); $\chi^2_c = 0.9$, $d.f. = 1$, $P = 0.4$ (*Brueelia* sp. B); $\chi^2_c = 0.08$, $d.f. = 1$, $P = 0.9$ (*Philopterus* sp.)). When each bird, rather than each louse, is considered an independent datum, a significant number of birds harboured more female than male *Brueelia* sp. A. (adults, and nestlings combined: sign test, 2 male biased vs. 12 female biased, $P = 0.01$). Data for adults and nestlings were pooled as no differences between them in male to female ratios were found in either analysis.

In nestling ploceines, adult lice outnumbered nymphs ($\chi^2_c = 4.1$, $d.f. = 1$, $P = 0.04$ (*Brueelia* sp. A), $\chi^2_c = 4.5$, $d.f. = 1$, $P = 0.02$ (*Brueelia* sp. B), $\chi^2_c = 34.4$, $d.f. = 1$, $P < 0.001$ (*Philopterus* sp.)). In adults, more adult lice than nymphs were found in *Brueelia* sp. A ($\chi^2_c = 6.0$, $d.f. = 1$, $P = 0.02$) but no differences were found in *Brueelia* sp. B ($\chi^2_c = 0.03$, $d.f. = 1$, $P > 0.9$) or in *Philopterus* sp. ($\chi^2_c = 0$, $d.f. = 1$, $P > 0.99$). Again considering each bird as an independent datum, more adult than nymphal Ischnoceran lice were found in nestlings and adults, but significant differences were only found in nestlings and adult birds carrying *Philopterus* sp. (nestlings: 19 adult biased vs. 2 nymph biased, $P = 0.0002$; adults: 12 vs. 2, $P = 0.01$), and adults carrying *Brueelia* sp. B (8 vs. 1, $P = 0.04$). Adult male, female, and nymphal lice were collected both from nestling and adult diederik cuckoos.

Table 2a. Counts of birds infested with mites. Abbreviations as in Table 1

			Mite species code as in Table 2b																	
Bird species	Age	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Euplectes orix	ad	29	17		1			7		1				10		8		4			
	juv	2																			
	ne	30	27			1	2	14	1	18	10		1	6		23		3	1		1
Cuckoo in *E. orix*	ne	7	1					4						1		1		2			
Ploceus intermedius	ad	25	19					5							1						
	juv	2	1					4					1								
	ne	9	8					1		1			1	1							
Cuckoo in *P. intermedius*	ne	7	4													1					
Ploceus ocularis	ne	3	2							2	1										
Cuckoo in *P. ocularis*	ne	1																			
Ploceus subaureus	ne	2	2									1									
Cuckoo in *P. subaureus*	ne	1																			
Cuckoo (free-flying)	ad	5	1	1										2			1			1	

Table 2b. Key to *Acarina* species of Table 2a

				Previously documented on*	
Code	Suborder	Family	Species	Passeridae	Cuculidae
1	Mesostigmata	Macronyssidae	*Pellonyssus reedi* (Zumpt & Patterson)	+	–
2			*Ornithonyssus bursa* Berlese	+	–
3		Rhinonyssidae	*Ptilonyssus ploceanus* Fain	+	–
4		Phytoseeidae	*Typhlodromus* sp.	–	–
5	Trombidiformes	Cheyletiellidae	*Ornithocheyla megaphallos* Lawrence	+	–
6	Sarcoptiformes	Trouessartiidae	*Trouessartia baupi* Gaud	+	–
7			*Trouessartia carpi* Till	–	–
8		Epidermoptidae	*Microlichus americanus* Fain	–	–
9			*Microlichus* undescribed sp.**	–	–
10			*Passeroptes* sp.	+	–
11		Pteronyssidae	*Pteronyssus glossifer* Gaud	+	–
12			*Pteronyssoides passeris* (Gaud)	+	–
13			*Pteronyssoides* sp.	+	–
14		Xolalgidae	*Xolalges plocei* Gaud & Mouchet	+	–
15			*Xolalges scaurus* (Trouessart, 1985)	–	+
16		Proctophyllodidae	*Pterodectes papillo* Gaud & Mouchet	+	–
17		Acaridae	*Tyrophagus putrescentiae* (Schrunk)	–	–
18		Pterolichidae	*Coraciacarus cuculi* (Megnin & Trouessart)	–	+
19		Analgidae	?		

* Sources: Zumpt, 1961; Fain, Gaud & Philips, 1987
** A. Fain, pers. comm.

Mites

Nesting diederik cuckoos in *E. orix* nests carried the same mite species as *E. orix* (Table 2). In nests of *P. intermedius*, cuckoos carried the most common mite species of *P. intermedius*, with the exception of *Xolalges plocei* which was detected only on *E. orix*. However, *X. plocei* has been collected from several *Ploceus* species (Zumpt, 1961) and is therefore likely to infest some *P. intermedius* which were not sampled. No mites were found on the single cuckoo nestlings in *P. ocularis* and *P. subaureus* nests.

Adult diederik cuckoos were infested with two species of mite which are only known to parasitize the Cuculiformes, *Coriacarus cuculi* and *Xolalges scaurus*. *C. cuculi* has been previously detected on diederik cuckoos while both species are ectoparasites of the common cuckoo (Zumpt, 1961). Adult cuckoos also carried three species of mites not previously recorded on any cuckoo. Two of these species, *Pellonyssus reedi* and *Pteronyssoides passeris*, were found on both *E. orix* and *P. intermedius* hosts. The other, *Ornithonyssus bursa*, was not collected from ploceines in this study but is known from other Ploceinae (Zumpt, 1961). As

Table 3. Prevalence and intensity of parasitic mites and feather lice on ploceine species which rear diederik cuckoos and on the cuckoos themselves. The diederik cuckoo nestlings ($n = 2$) sampled in nests of *Ploceus ocularis* and *P. subaureus* were free of parasites and were not listed separately

			Parasitic mites			Feather lice		
Bird species	Age	*n*	Prevalence No. infested (%)	Intensity Mean ± S.D.	Maximum intensity	Prevalence No. infested (%)	Intensity Mean ± S.D.	Maximum intensity
Euplectes orix	adult	29	22 (76)	22.7 ± 73.6	395	22 (76)	8.1 ± 10.6	44
	juvenile	2	0 (0)	0	0	1 (50)	1.0 ± 1.4	2
	nestling	30	29 (97)	39.6 ± 40.7	140	27 (90)	10.6 ± 13.2	59
	all	61	51 (84)	30.3 ± 58.6		50 (82)	9.1 ± 8.1	
Cuckoo in *E. orix*	nestling	7	5 (71)	23.4 ± 33.3	89	4 (57)	2.7 ± 2.3	5
Ploceus intermedius	adult	25	20 (80)	6.2 ± 8.0	30	19 (76)	8.7 ± 10.0	29
	juvenile	2	1 (50)	4.0 ± 5.7	8	1 (50)	16.0 ± 22.6	32
	nestling	9	8 (89)	37.6 ± 31.1	94	7 (78)	4.8 ± 4.3	12
	all	36	29 (81)	13.9 ± 21.4		26 (72)	8.1 ± 9.7	
Cuckoo in *P. intermedius*	nestling	7	5 (71)	1.3 ± 1.0	2	1 (14)	2.6 ± 6.8	18
Ploceus ocularis	nestling	3	2 (67)	26.3 ± 28.8	57	0 (0)	0	0
Ploceus subaureus	nestling	2	2 (100)	88.5 ± 119.5	173	0 (0)	0	0
Above ploceines	all	102	84 (82)	25.5 ± 49.9		76 (75)	8.2 ± 10.9	
Cuckoo	all nestling	16	10 (63)	16.3 ± 30.5	89	5 (31)	2.1 ± 4.6	18
	adult	5	4 (80)	2.0 ± 2.0	5	5 (100)	4.8 ± 4.4	12

nestlings, cuckoos could have acquired from their foster-parents the passeriform mite species but not the cuculiform mite species.

Additional new host records are established for several species of mites (Zumpt, 1961; Fain, Gaud & Philips, 1987). *Ploceus intermedius* is a new host record for all mite species collected from it: *Pellonyssus reedi*, *Trouessartia baupi*, *Microlichus americanus*, *Pteronyssus glossifer*, and *Pteronyssoides passeris*. *Euplectes orix* is a new host record for *T. baupi*, *T. carpi*, *M. americanus*, and *Xolalges plocei*. *Ploceus subaureus* is a new host record for *Pellonyssus reedi* and the genus *Passeroptes*. Finally, *Ploceus ocularis* is a new host record for *Pellonyssus reedi* and *M. americanus*.

Three mite species which were recovered exclusively from nestlings are not parasitic. *Ornithocheyla megaphallos* (Cheyletiellidae) is a predator of bird ectoparasites (Zumpt, 1961) which probably forages on temporary parasites such as haematophagous mites. *Tyrophagus putrescentiae* (Acaridae) feeds on a variety of plant and soil nematodes (Bilgrami, 1994). Finally, the Phytoseiidae, represented by *Typhlodromus* sp., are normally found on plants. These latter two species probably feed amongst plant material in nests and may have been found on nestlings by chance.

Other species

A parasitic larva of the tropical nest fly *Passeromyia heterochaeta* (Villeneuve 1915) of the Muscidae was found on one nestling *E. orix*. One hippoboscid fly was collected from a recently fledged *E. orix*, two were collected from both an adult and juvenile *P. intermedius*, one from a nestling *P. intermedius*, and one from a nestling *P. subaureus*. The following non-parasitic insects were all collected from nestling *E. orix* and a small number of other nestlings: Coleoptera larvae, Collembola, nymphal Hemipterans (Homoptera) and a parasitic wasp (order Hymenoptera: family Mymaridae).

Parasite loads

(a) Prevalence

The prevalence of mite and louse infestation among adult and nestling ploceines ranged from 67 to 100% (Table 3). Nestlings had higher prevalence than adults of *E. orix* ($\chi_c^2 = 3.8$, $d.f. = 1$, $P = 0.05$), but there was no difference in *P. intermedius* ($\chi_c^2 = 0.01$, $d.f. = 1$, $P = 0.9$), nor in the diederik cuckoo ($\chi_c^2 = 0.03$, $d.f. = 1$, $P = 0.9$).

(b) Intensity

Diederik cuckoo nestlings had significantly smaller intensities of infestation of both parasitic mites (Mann-Whitney *U*-test, $Z = -3.8$, $P = 0.0002$) and feather lice ($Z = -3.0$, $P = 0.0025$) than did all ploceine nestlings. Adult and nestling diederik cuckoos did not differ in parasitic mite intensity ($Z = -0.1$, $P = 0.93$), but adults had significantly greater intensities of feather lice than nestlings ($Z = -2.2$, $P = 0.03$). Differences in louse intensities between cuckoo and ploceine nestlings and nestling and adult cuckoos were due to the lower

prevalence of infestation of diederik nestlings. When uninfested birds were excluded from the analysis, the significant differences in louse intensities disappeared, but this was not the case in mites.

The two ploceine species *E. orix* and *P. intermedius* had similar intensities of infestation of both parasitic mites ($Z = -1.0$, $P = 0.30$) and feather lice ($Z = -0.4$, $P = 0.72$). In both species, nestlings had higher mite intensities than adults (*E. orix*: $Z = -4.0$, $P < 0.0001$; *P. intermedius*: $Z = -3.2$, $P = 0.0002$) but similar louse intensities (*E. orix*: $Z = -1.0$, $P = 0.32$; *P. intermedius*: $Z = -0.4$, $P = 0.72$). The mite and louse intensities of adult males and females were not significantly different (*E. orix* mites: $n_1 = 14$, $n_2 = 15$, $Z = 0.3$, $P = 0.74$; lice: $Z = -1.1$, $P = 0.25$; *P. intermedius* mites: $n_1 = 17$, $n_2 = 8$, $Z = -1.6$, $P = 0.11$; lice: $Z = -0.7$, $P = 0.50$). All adult cuckoos that were sampled were male so no comparisons between sexes could be made.

Mite intensities were compared between nestling cuckoos and their foster species according to guild, or feeding specialization, which is reflected in their taxonomic divisions. Haematophagous mites (Macronyssidae and Rhinonyssidae) were less numerous on diederik cuckoo nestlings than on *E. orix* ($n_1 = 7$, $n_2 = 61$, $Z = -2.9$, $P = 0.004$) or *P. intermedius* ($n_1 = 7$, $n_2 = 36$, $Z = -2.3$, $P = 0.02$). However, the intensity of feather mite (Trouessartidae, Pteronyssidae, Xolalgidae, Proctophyllodidae and Analgidae) infestation did not differ between cuckoo nestlings and *E. orix* ($Z = -0.6$, $P = 0.54$) or *P. intermedius* ($Z = -0.3$, $P = 0.77$). Similar results were found when mite intensities of only nestling *E. orix* and *P. intermedius* were compared to those of nestling cuckoos. No skin mites (Epidermoptidae) were found on any nestling or adult diederik cuckoo.

DISCUSSION

Ectoparasites of *E. orix* and *P. intermedius*

Most nestling and adult ploceines were infested with mites and feather lice. The ploceines *E. orix* and *P. intermedius* were infested with several mite and louse species which were common to the two species. Both bird species are sympatric in much of their range, gregarious, breed colonially in similar habitat, and overlap in food preferences (Maclean, 1993). Similarity in ecology and habitat can promote mixed infestations (Clayton, 1990). Nestlings tended to have greater intensities of infestation of mites than adults, presumably because nest-living mites contributed disproportionately to nestling loads compared to adult loads. Louse intensities were similar between nestlings and adults. Mean intensities of eight to nine lice per adult *E. orix* and *P. intermedius* are slightly higher than the average of seven lice recorded for tropical and temperate lice (Clayton, Gregory & Price, 1992).

More adult than nymphal lice were collected from both adult and nestling ploceines. This result parallels those of Wheeler & Threlfall (1986) and Clayton *et al.* (1992) for adult tropical and temperate lice. In nestling ploceines, however, the results differ from that of the louse *Dennyus hirundinis* (L.). The age ratio of *D. hirundinis* changed from primarily nymphs in nestling swifts *Apus apus* at two weeks of age (when feather tips began to appear) to an equal ratio of nymphs to adults by 24–35 days old. No eggs were found on swifts by this age, which suggested that most dispersal to nestlings was by newly-hatched nymphs (Lee & Clayton, 1995). In comparison, feather web was first seen on nestling *P. intermedius* at age 6–7 days ($n = 5$), and ectoparasites were sampled from *P. intermedius* and *E. orix* at age 11–16 days ($n = 20$). As fewer days were available for maturation of nymphal ploceine lice before sampling, and age ratios were biased in favour of adults, it appears that ploceine lice have a different life-history strategy from *D. hirundinis*.

No sex differences were found, either in parasite intensities of male versus female hosts, or in prevalence of infestation by male or female lice, with the possible exception of *Brueelia* sp. A. Clayton *et al.* (1992) predicted that biased sex ratios would be favoured in Ischnoceran lice because of local mate competition (Hamilton, 1967). Although only 44.4% ($n = 279$) of all Ischnocerans collected on ploceines were male, sex ratios of feather lice were not significantly biased in two of three Ischnoceran louse species.

Ectoparasites of the diederik cuckoo

Cuckoo-specific ectoparasites

Adult cuckoos had two species each of cuckoo-specific mites and lice which were not found on nestling cuckoos. Therefore, adult female cuckoos do not appear to leave ectoparasites behind in the host nest at the time of egg-laying. Instead, it is likely that direct contact between cuckoos after fledging is the main means of ectoparasite transfer. In the common cuckoo, direct contact between cuckoos outside of the breeding season appears to allow transfer of cuckoo-specific lice to unmated juveniles (Brooke & Nakamura, 1998). Direct contact between hosts is likely to be the means of transfer of the cuckoo-specific ectoparasitic nasal mite *Sternostoma cuculorum* Fain. This mite infests the diederik cuckoo (Fain, 1957) but was not detected in this study. If *S. cuculorum* behaves similarly to its congener *S. tracheacolum* Lawrence, then females move from the respiratory system to the bill, nares and head plumage of their host from where they can potentially transfer to a new host (Bell, 1996). Thus, ectoparasite dispersal could be promoted by courtship feeding, in which males feed females with caterpillars during the breeding season. Courtship feeding was frequently observed in the diederik cuckoo (Lindholm, 1997) and is found in all genera of parasitic cuckoos (Rowan, 1983). Brief sexual contact has been shown to permit the transfer of lice between adult ring-necked pheasants *Phasianus*

colchicus (Hillgarth, 1996), and therefore could also be important in the transmission of ectoparasites between adult cuckoos. Finally, phoresy provides an alternative means of dispersal which may have been used by mite species (Fain, 1965; Hunter & Rosario, 1988) and Ischnoceran louse species (Keirans, 1975).

Cuckoo-specific feather mites and lice do not appear to become established on adult cuckoos at equal rates, as only two cuckoos had gained cuckoo-specific feather mite species, while all five cuckoos carried at least one cuckoo-specific feather louse. Differences in persistence of lice and feather mites could be due to differences in relative competitive abilities, in relative rates of transmission, or in relative host responses to infestation. An alternative explanation is that lice are more readily collected in the sampling apparatus than feather mites, a suggestion made by Fowler & Cohen (1983). The possibility that there is variation between and within species of lice or mites in their susceptibility to collection cannot be excluded.

Host-switching

Nestling cuckoos were infested by the same species of mites and lice as their ploceine foster-species. Adult cuckoos had three species of mites and two species of lice which are common to ploceines, in addition to cuckoo-specific parasites. It was previously believed that cuckoo nestlings were only rarely infested with any ectoparasite found on their foster-parents and that any such parasite would not survive on the cuckoo (Clay & Meintertzhagen, 1943; Ash, 1960; Dogiel, 1964). Our data show that this is certainly not the case in the diederik cuckoo.

A successful host switch requires establishment and continued reproduction on the new host (Barker, 1994). The similarity of louse and mite communities on nestling cuckoos, compared with those on their foster species (Tables 1 & 2) is evidence of the establishment of ploceine-specific mites and lice on cuckoos. Intensities of lice and mites were lower on adult cuckoos than on adult ploceines, suggesting that ploceine ectoparasites are eventually more successful on their usual hosts than on cuckoos. There was not sufficient evidence to determine the extent of competition on adult cuckoos between lice specific to cuckoos and those common to ploceines. The presence of the same species of mites and of adults and nymphs of the same genera of lice on adult cuckoos as on ploceines is suggestive of reproduction on the new host. The known generation time for lice and mites is about one month (Sweatman, 1957; Marshall, 1981) and the known time to starvation for lice ranges from three days to three weeks (Marshall, 1981). Alternatively, adult cuckoos could have lost any ectoparasites acquired as nestlings and been re-infested at a later time. Male cuckoos are unlikely to acquire ploceine-specific ectoparasites from direct encounters with ploceines or nests, as only female diederik cuckoos approach and enter nests and suffer attacks by ploceine nest owners (Rowan, 1983; pers. obs.). The simplest explanation is that the adult male cuckoos which were sampled retained some species which they acquired as nestlings. This study is one of the first empirical demonstrations of the natural occurrence of host-switching of ectoparasites between distantly related birds. Why host-switching has not been recorded in studies of the common cuckoo (e.g. Brooke & Nakamura, 1998) is puzzling.

Host specificity of mites and lice

Diederik cuckoo nestlings were infested at lower overall intensities of infestation than ploceine nestlings, and carried fewer species of ectoparasites. Each nestling cuckoo either acquired no lice, or the one species which was found on the largest number of nestlings of its foster-species. In contrast, acquisition of mites varied by guild.

Epidermoptid (skin) mites, found on many nestling *E. orix*, were never found on cuckoos. Mites of the *Microlichus* genus, which made up 99.5% ($n = 221$) of the specimens of Epidermoptidae recorded, are not permanent parasites of birds, as the life cycle includes hyperparasitism of hippoboscid flies or feather lice (Fain, 1965). The most prevalent epidermoptid mite in this study, *M. americanus*, is not strongly host-specific as it has been collected from several passeriform hosts and a gruiform host (Fain *et al.*, 1987).

Haematophagous mites of the Macronyssidae infest birds and their nests, from where they emerge to take blood meals from nestlings (Rothschild & Clay, 1952). These mites are unlikely to rely on an exclusive relationship with their host species for survival, as several nest-living haematophagous species are known to attack mammals (Zumpt, 1961; Evans & Till, 1966) and one is known to disperse by running between nests (Clayton & Tompkins, 1994). One of the species which infested adult cuckoos, *Ornithonyssus bursa*, the tropical fowl mite, is known from several avian orders (Zumpt, 1961). The most prevalent species encountered on ploceines, *Pellonyssus reedi*, was recovered from several nestling and one adult cuckoo, and has been collected from several families of birds (Zumpt, 1961). Despite a low level of host-specificity, haematophagous mites were found in significantly smaller numbers on nestling cuckoos than on their foster-species. This difference suggests a reduced preference of haematophagous mites for cuckoos compared to ploceines.

Feather mites, as a guild, infested diederik cuckoo nestlings as heavily as *E. orix* and *P. intermedius*. The four most prevalent species of feather mites infesting ploceines were also found on cuckoo nestlings. Contrary to expectation, feather mites showed no detectable preference for ploceines over cuckoos. However, only one species of ploceine feather mite, *Pteronyssoides passeris*, was found on adult cuckoos, which suggests reduced survivorship of ploceine feather mites on cuckoos over time.

Predictions of which types of species would be transferred from ploceine to cuckoo, if any were to be transferred, were generally found to be incorrect. Species thought to be somewhat "generalist", the haematophagous mites and phoretic skin mites, were under-represented or absent from cuckoo nestlings, while species thought to be more highly specialized, the feather lice and feather mites, were found on cuckoo nestlings at similar loads to the species which reared them. Both "generalist" and "specialist" species were found on adult cuckoos. Host specificity of feather lice and feather mites in general appears to be less strict than has been commonly believed.

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