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A REVIEW OF THE PHORETIC RELATIONSHIP BETWEEN MALLOPHAGA (PHTHIRAPTERA: INSECTA) AND HIPPOBOSCIDAE (DIPTERA: INSECTA)

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Abstract: Isolated instances of phoresy between certain species of Mallophaga and the dipterous family Hippoboscidae have been recorded numerous times in various journals for over 100 years. Herein are reviewed and summarized published cases of phoresy from 11 non-passerine bird orders, 22 passerine families, and 58 cases lacking definite host data.

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Phoresy is a transitory association between 2 species in which one animal attaches to another and is carried away from a potentially suboptimal environment. In the case of Mallophaga, a smaller biting louse attaches by its mandibles to a larger hippoboscid, or louse fly, and is transported away from a presumed less favorable environment, usually a dead bird. Shelter is afforded the mallophagan,

but it does not feed on the hippoboscid nor, if an immature stage, exhibit ontogeny while attached.

Farish & Axtell (1971) in their definition of phoresy substituted the passive word "dispersal" for the more widely accepted term "transportation." The distinction is important; "transportation" has the teleological implication of directed movement toward an ultimate goal, whereas "dispersal" has the broader nondirectional implication and in fact may be a survival mechanism providing random distribution over a large area. Dispersal may, in addition, be selectively advantageous in promoting crossing and a greater potential for recombination.

The stimulus that induces a mallophagan to attach to a hippoboscid remains unknown. However, the number of reported cases (TABLE 1, 2, 3) is so extensive, especially in view of the infrequent collection of hippoboscids, that Ansari's (1947) statement, 'transport of Mallophaga by the bird flies is purely accidental, and is not a common feature" is difficult to accept. Indeed, Bennett (1961) reported that 41 (22%) of 180 *Ornithomya anchineuria* carried lice and that phoresy was so common that records were not kept of it in ensuing years. In other studies, Corbet (1956) examined 156 flies, 68 (43.5%) of which carried lice; Markov (1938) found lice on 14 (25.5%) of 55 flies.

TABLE 1. Records of Mallophaga on hippoboscids collected from non-passerine birds.*

ORDER	RECORDS	LITERATURE CITATIONS
Ciconiiformes (*Casmerodius, Botaurus*)	3	Peters (1935), Thompson (1936), Bequaert (1945), Maa (1969b)
Falconiformes (*Accipiter, Cathartes, Circus, Falco*)	4	Thompson (1947), Bequaert (1953, 1957), Corbet (1956), Hill et al. (1967)
Galliformes (*Tetrao*)	1	Forsius (1912)
Columbiformes (*Columba, Zenaidura, Phapiteron, Leptotila, Oreopellia*)	13	Adie (1915), Martin (1934), Hathaway (1943), Ansari (1947), Hopkins (1947), Ward (1953), Bequaert (1953, 1957), Couch (1962), Maa (1969c)
Psittaciformes (*Pionus, Alisterus*)	3	Bequaert (1953), Maa (1966, 1969b)
Cuculiformes (*Cuculus, Centropus*)	3	Eichler (1939), Maa (1966)
Strigiformes (*Surnia, Glaucidium*)	2	Blagoveshtchensky (1950), Bequaert (1957)
Apodiformes (*Apus*)	1	Eichler (1939, 1944)
Trogoniformes (*Trogon, Harpactes*)	5	Guimarães (1944), Maa (1969c)
Coraciiformes (*Dacelo, Melidora, Halcyon, Momotus*)	14	Thompson (1936), Bequaert (1953), Maa (1966, 1969a, c)
Piciformes (*Megalaima, Ramphastos, Colaptes, Dendrocopus*)	14	MacArthur (1948), Ash (1952), Bequaert (1953), Maa (1966, 1969b), Main & Anderson (1970)

*Where number of records exceeds no. of literature citations, 1 or more citation(s) records multiple cases of phoresy; where no. of citations exceeds no. of records, this usually indicates that additional information was added subsequent to initial record(s).

About 16% of the 405 recorded cases of phoresy have occurred on 11 of the 27 non-passerine bird orders (TABLE 1). Summarized in TABLE 2 are 284 cases occurring on 22 passerine families and in TABLE 3 are phoresy records lacking host data. Ninety percent of the 405 cases of phoresy cited in TABLE 1–3 involve hippoboscids of the genera *Ornithomya* (290), *Ornithoica* (50) and *Icosta* (23).

Ornithomya spp. bearing phoretic lice have been collected from all non-passerine orders cited in TABLE 1 except the Ciconiiformes, Psittaciformes, Cuculiformes, and Apodiformes. Members of all but 9 of the 22 passerine families (TABLE 2) have had *Ornithomya* spp. with phoretic Mallophaga collected from them. The 9 families from which louse-carrying *Ornithomya* have not been reported are Cotingidae, Pittidae, Camperhagidae, Oriolidae, Dicruridae, Paradisaeidae, Zosteropidae, Pycnonotidae, and Ploceidae. Of the 21 species of *Ornithomya*, 6 have been collected with lice attached, i.e., *avicularia, anchineuria, chloropus, fuscipennis, parva,* and *rouboudi.*

There are 23 species of *Ornithoica*, of which 8 (*exiles, stipituri, tridens, vicina, pusilla, rabori, bestativa,* and *simplicis*) have been collected with Mallophaga attached. They have been collected on the non-passerine orders (TABLE 1) Psittaciformes, Cuculiformes, Coraciiformes, and Piciformes and 13 passerine families (TABLE 2), excluding the Hirundinidae, Dicruridae, Zosteropidae, Irenidae, Troglodytidae, Mimidae, Motacillidae, Laniidae, and Ploceidae.

Icosta (=*Lynchia* of authors, cf Maa 1969b) is the largest genus of Hippoboscidae with about 65 species. The following have been found with phoretic Mallophaga: *americana, ardeae* and *albipennis* (Ciconiiformes), *angustifrons* (Falconiformes, Strigiformes), *chalcolampra* (Psittaciformes), *trita* (Piciformes), *fenestella* (Pittidae, Dicruridae), *formosae* (Corvidae), *sensilis* (Pycnonotidae), *rufiventris* and *ardeae* (unknown host), and *Icosta* sp. (Ploceidae).

The remaining 42 cases involve hippoboscids of the genera *Ornithophila* (17), all *metallica* on Coraciiformes and 8 passerine families; *Pseudolynchia* (7), all *canariensis* on *Columba livia* except 1 collection from a house wall; *Ornithoctona* (6), *erythrocephala* on Columbiformes, Psittaciformes, and Coraciiformes, *australasiae* on Zosteropidae and Sturnidae, and *fusciventris* on Fringillidae; *Stilbometopa* (4), *podopstyea* on Columbiformes and *ramphastonis* on Trogoniformes

TABLE 2. Records of Ischnocera on hippoboscids collected from members of the Passeriformes.*

Family (Genus)	Records	Literature citations
Cotingidae (*Pyroderus*)	1	Bequaert (1943)
Pittidae (*Eucichla, Pitta*)	4	Jacobson (1911), Ferriere (1926), Maa (1966, 1969a, b)
Hirundinidae (from nest)	1	Seguy (1938)
Camperhagidae (*Coracina*)	1	Maa (1966)
Oriolidae (*Oriolus*)	2	Maa (1966)
Corvidae (*Cyanocitta, Aphelocoma, Cyanocorax, Garrulus, Perisoreus, Urocissa, Dendrocitta, Pica, Corvus*)	35	Aubé (1857), Forsius (1912), Banks (1920), Johnson (1922), McAtee (1922), Spencer (1928), Thompson (1934, 1937), Bequaert (1943), Clay & Meinertzhagen (1943), Callot (1946), Büttiker (1949), Blagoveshtchensky (1950), Bequaert (1953), Baker & Blackie (1963), Maa (1966, 1969a, b, c), Main & Anderson (1970, 1971)
Dicruridae (*Dicrurus*)	2	Maa (1969a, b)
Cracticidae (*Cracticus, Strepera*)	2	Harrison (1913), Thompson (1936), Maa (1966)
Ptilinorhynchidae (*Sericulus*)	2	Harrison (1913), Thompson (1936), Maa (1966)
Paradisaeidae (*Ptiloris, Paradisaea*)	2	Maa (1966, 1969a)
Muscicapidae (*Pellorneum, Garrulax, Heterophasia, Turdus, Oenanthe, Copsychus, Hylocichla, Nesocichla, Zoothera, Sylvia, Myiophoneus, Pachycephala, Poecilodryas*)	67	Wanach (1910), Thompson (1933, 1935, 1936, 1937, 1947, 1952), Spencer (1938), Bequaert (1943), MacArthur (1948), Clay (1949), Blagoveshtchensky (1950), Ash (1952, 1960), Edwards (1952), Bequaert (1953), Corbet (1956), Wilson (1964), Maa (1966, 1969a, c), Main & Anderson (1970)
Zosteropidae (*Hypocryptadius*)	1	Maa (1969c)
Pycnonotidae (*Pycnonotus, Criniger, Hypsipetes*)	7	Maa (1966, 1969a, b)
Irenidae (*Irena*)	1	Maa (1969c)
Troglodytidae (*Troglodytes*)	2	Corbet (1956), Main & Anderson (1970, 1971)
Mimidae (*Dumatella, Toxostoma*)	3	Ewing (1927), Thompson (1936), MacArthur (1948), Bequaert (1953)
Motacillidae (*Anthus*)	3	Corbet (1956)
Laniidae (*Tchagra, Lanius*)	3	Clay & Meinertzhagen (1943), Eichler (1946), Maa (1969a)
Sturnidae (*Sturnus, Acridotheres, Mino, Basilornis, Gracula*)	124	Mjoberg (1910), Thompson (1934, 1947), Markov (1938), Eichler (1939), Clay & Meinertzhagen (1943), Ansari (1947), Edwards (1951, 1952), Rothschild & Clay (1952), Corbet (1956), Clay (1957), Corbet (1961), Maa (1966, 1969a, b, c)
Icteridae (*Icterus, Quiscalus, Molothrus*)	3	Herman (1937a, b, 1945), Thompson (1947), Bequaert (1953), Main & Anderson (1970)
Ploceidae (*Euplectes*)	1	Thompson (1935)
Fringillidae (*Emberiza, Zonotrichia, Spizella, Diuca, Pipilo, Pselliophorus*)	17	Ewing (1927), Reed (1932), Thompson (1936, 1937), Clay & Meinertzhagen (1943), Bequaert (1953, 1954), Davies (1958), Main & Anderson (1970)

*See footnote TABLE 1.

and Piciformes; *Microlynchia* (2), both *pusila* on Columbiformes and *Crataerina pallida* (1) on Apodiformes. Five cases of phoresy were recorded on undetermined hippoboscid genera (Clay & Meinertzhagen 1943, Bequaert 1943, Hopkins 1947).

In most published reports of phoresy, generic determinations of the Mallophaga involved are usually lacking, an understandable situation since most published records are by authors interested in hippoboscids rather than Mallophaga. Therefore, any attempt to determine a pattern regarding phoresy involving diverse mallophagan taxa would be precarious.

However, within the Passeriformes available records indicate that the ischnoceran genus *Brueelia* has been collected from hippoboscids most often, followed by *Sturnidoecus* and rarely *Philopterus*. With the exception of several records of *Columbicola columbae* on *Pseudolynchia canariensis* from the pigeon, data regarding phoretic Mallophaga within the non-passerine orders are too scanty for analysis.

When a bird host dies and begins to cool, ischnocerans cling to the feathers and also die, whereas amblycerans generally attempt to leave the dead host. Because they attempt to disperse outward from an inhospitable environment, one would expect to find amblycerans rather than ischnocerans attached to hippoboscids, but of the approximately 405 records of bird lice attaching to hippoboscids, only 1 has been an amblyceran (Hopkins 1947).

A possible explanation for this attachment behavior may be the differences in the alignment of mandibles in the 2 groups. Amblyceran mandibles move approximately parallel to the ventral surface of the head, whereas those of ischnocerans are articulated to allow movement in a dorsoventral plane or approximately perpendicular to the ventral surface of the head. Thus, the alignment, articulation, and movement of ischnoceran mandibles may more readily facilitate attachment of this group of lice than the amblyceran group to the abdominal integument and setae of hippoboscids.

A 2nd possible explanation of attachment be-

TABLE 3. Phoresy records between Ischnocera and Hippoboscidae lacking data concerning avian hosts.*

HIPPOBOSCIDAE	RECORDS	LITERATURE CITATIONS
Ornithomya avicularia	5	Sharp (1890, 1895), Warburton (1928), Thompson (1933, 1934), Blagoveshtchensky (1950)
Ornithomya anchineuria	44	McAtee (1922), Bennett (1961), Main & Anderson (1970, 1971)
Ornithomya chloropus	1	Blagoveshtchensky (1950)
Ornithomya parva	3	Reed (1932)
Ornithomya sp.	1	Hardy (1964)
Ornithophila metallica	1	Thompson (1936)
Icosta ardeae	1	Dubinin (1947), Blagoveshtchensky (1959)
Icosta rufiventris	1	Maa (1969a)
Pseudolynchia canariensis	1	Hiregaudar & Khambata (1954)

*See footnote TABLE 1.

havior within the Amblycera and Ischnocera might be found in the origins of the 2 groups. Clay (1970) considers the order Phthiraptera to contain 2 general groupings: (a) Amblycera, (b) Ischnocera, Anoplura, and Rhynchophthirina. She offers supporting evidence for separating these groups with scanning electron microscope studies of antennal sense organs. Two dissimilar methods for dispersal from a dead host may have arisen within these 2 dissimilar groups of Phthiraptera, namely phoresy (Ischnocera) and crawling away (Amblycera).

In reviewing the subject, it was found that at least 44% of the cases of phoresy involved the attachment of at least 2 ischnocerans to a single louse fly. In addition there are several records of numerous lice upon 1 fly; Harrison (1913) and Baker & Blackie (1963) report 14, Bequaert (1953) records 15, Spencer (1928) 16, and Peters (1935) cites 31. Multiple attachments greatly enhance the value of phoresy as a survival mechanism, provided the fly reaches a suitable host.

Because almost all species of bird lice are extremely host specific, whereas hippoboscids, including *Ornithomya*, are not, many authors have suggested that phoresy would offer little survival value to the louse. However, Corbet (1956) showed that the interchange of flies was more often between birds of the same species than between those of different species. This was not through any host specificity of the flies, but because birds of the same species tend to congregate together. Thus, the more gregarious the bird species, the more frequent the transfer of flies.

Within the Phthiraptera in which all developmental stages are passed upon the host (protelean parasites with free-living adults are unknown among the exopterygota), direct host-to-host transfer offers a greater promise of survival than any other means of dispersal. On the other hand, because death occurs in every host, these wingless ectoparasites are faced with a last-ditch situation of crawling away, climbing to the tips of hairs or feathers in search of a passing animal, or phoresy. Perhaps phoresy is a survival and dispersal mechanism that is exploited more often than has been heretofore evident.

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