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The Feather Holes on the Barn Swallow *Hirundo rustica* and Other Small Passerines are Probably Caused by *Brueelia* Spp. Lice

Zoltán Vas, Tibor Csörgő, Anders P. Møller*, and Lajos Rózsa†‡, Loránd Eötvös University, Department of General Zoology, Pázmány Péter s. 1/C, Budapest, H-1117, Hungary; *Université Pierre et Marie Curie, CNRS UMR 7103, Laboratoire de Parasitologie Evolutive Bat. A, 7ème étage, 7 quai St. Bernard, Case 237, Paris Cedex of, 75252, France;† Hung Academy Sciences–Hung National History Museum, Animal Ecology Research Group, Ludovika t. 2-6, Budapest, H-1083, Hungary. ‡ to whom correspondence should be addressed. *e-mail: lajos.rozsa@gmail.com*

ABSTRACT: Barn swallows *Hirundo rustica* often have characteristic feather holes on wing and tail feathers. During the past 15 yr, several influential papers have been based on the assumption that these holes were chewed by the louse *Machaerilaemus malleus*. We gathered feather-hole data from barn swallows and other passerines at 2 sites in Hungary and correlated the presence of holes with louse infestations and, more specifically, with the occurrence of *M. malleus* versus other species of avian lice. The shape of frequency distribution of holes was left-biased, and this bias was more pronounced in large swallow colonies that in a random sample, in accordance with the view that the causative agent of the 'feather hole symptom' is a contagious macroparasite. However, both intra- and interspecific comparisons suggest that the causative agent of the symptom had probably been misidentified. The occurrence of *Brueelia* spp. 'wing lice' provides the best fit to the distribution and abundance of feather holes, both in barn swallows and across some other small passerines. This identification error does not challenge the results of the former evolutionary–ecological studies based on this model system, although it has important implications from the viewpoint of louse biology.

More than 15 yr ago, Møller (1991) described characteristic feather holes found on the rectrices, primaries, and secondaries of the barn swallow *Hirundo rustica* L. (Fig. 1). Based on a positive correlation between hole numbers and intensity of infestation, he suggested that the holes were feeding traces of avian lice, either *Machaerilaemus malleus* (Burm, 1838) (syn: *Hirundoecus malleus*) or *Myrsidea rustica* (Giebel, 1874), or both. Hole counts were shown to be highly repeatable and, thus, counts appeared to be useful measures to quantify the intensity of infestation. Since then, a number of influential papers have been published on the evolutionary, ecological, and behavioral aspects of host–parasite interactions based on the assumption that holes were chewed by *M. malleus*.

More specifically, host sexual selection (Kose et al., 1999), feather breakage (Kose and Møller, 1999), flight performance (Barbosa et al., 2002), immunity levels and arrival dates (Møller, de Lope, and Saino, 2004), and song characteristics (Garamszegi et al., 2005) were shown to covary with the number of holes. Møller, Martinelli, and Saino (2004) have used cross-fostering experiments to show that infestation levels were heritable. A few authors cautioned, however, that the origin of feather holes has never been tested accurately (Pap et al., 2005).

Amblyceran and Ischnoceran lice (chewing lice, once called Mallophaga) comprise the most widespread ectoparasites of birds. They are the only parasitic insects that complete their entire life cycle on the body surface of birds, showing low levels of pathogenicity (Clayton and Tompkins, 1994, 1995). However, lice still influence major aspects of the life history of their hosts such as flight performance (Barbosa et al., 2002), metabolism (Booth et al., 1993), life expectancy (Brown et al., 1995; Clayton et al., 1999), and sexual selection (Clayton, 1990; Kose and Moller, 1999; Kose et al., 1999) in wild birds. There are 2 major taxa of chewing lice. Amblycerans partly feed on feathers, but also consume living tissues such as blood and other excretions (Mey et al., 2007). In contrast, iscnocerans rely almost exclusively on grazing of feather barbs and have little, if any, contact with living tissues of the host.

There are, in fact, reasons to doubt that *M. malleus* could be the causative agent of these holes. First, according to published data based on traditional collection methods, *M. malleus* appears to be either absent or very rare in the western Palearctic (0 infested swallows of 133 examined) (Touleshkov, 1964; Schumilo and Lunkaschu, 1972; Touleshkov, 1974; Rékási and Kiss, 1980) and it has only a single documented occurrence in the mid-Palearctic (1 infested bird of 10 birds collected in Tadzykistan, 1934) (Blagoveshtchensky, 1951). On the contrary, feather holes are highly prevalent on swallows, with ca. 85–95% of birds infested (see e.g., Pap et al., 2005). Although traditional sampling methods involving visual searching with forceps probably resulted in an underestimation of the prevalence and load of lice, this bias is expected to be relatively small for large-bodied, oval-shaped species like *M. malleus* (though early instars are small and easily overlooked).

Second, *Machaerilaemus* spp. are most closely related to *Austromenopon* spp. (Marshall, 2003). These lice are globally widespread on procellariiforms and charadriiforms. On the contrary, *Machaerilaemus* spp. appears to be more widespread among passeriforms living in North America (54 known host species in 8 families) than in passeriforms of all other continents (10 known host species in 5 families) (Price et al., 2002). Outside of North and South America, half of the known host species are hirundinids (swallows), including the only 2 hosts present in the western Palearctic (Price et al., 2002). The European species parasitize sand martins *Riparia riparia* (L.) (Balát, 1966; Adam and Chisamera, 2006) and also, possibly barn swallows, birds that are widely distributed throughout North America, Europe, Asia, and Africa. One possible explanation of this distribution pattern is to suppose that *Machaerilaemus* spp. lice may have originated in the Americas and invaded Europe with hirundinid hosts, where they remained scarce and failed to colonize additional hosts. However, feather holes have also been described from other small passerines in Europe, such as the house sparrow *Passer domesticus* (L.) (Moreno-Rueda, 2005), a species not known to harbor *Machaerilaemus* spp. lice.

Finally, being a large-bodied and oval-shaped amblyceran louse, *M. malleus* is apparently not adapted to stay on the vane (aerodynamic surface) of the major tail and wing feathers. This microhabitat on the body surface is typically inhabited by narrow-bodied lice, whereas large and oval-shaped lice tend to live on the skin or in the dense downy layer of the plumage (see Johnson and Clayton, 2003; Mey, 2003). In small passerines, only ischnoceran lice are known to exhibit this body shape and habitat preference. Of course, this argument cannot exclude the possibility that holes are chewed during feather development while the developing new vane surface is still within the downy layer.

Motivated by these observations, the present study seeks to correlate the presence of holes on primary feathers and rectrices with louse infestations and, more specifically, with the occurrence of *M. malleus* versus other species of avian lice. We quantified feather holes of barn swallows in a breeding colony at a cattle farm (Világospuszta, Hungary, May–August 2006) and at a bird-ringing center in Ócsa, Hungary, August–October 2003–2006. At the first site, we did not use chemical fumigants and, thus, we could track changes in the number of holes on recaptured adult birds harboring relatively undisturbed louse assemblages. At the latter site, we also tested other small passerines for the lack or presence of feather holes. Here, we collected lice using fumigants applied on the whole plumage of swallows (Clayton and Walther, 1997). We used a commercial spray (Chemotox Bogancs, manufactured by Caola, Budapest, Hungary) containing a pyrethroid synergized with piperonyl-butoxide.

Feather holes occurred in 97.2% (103/106) of barn swallows (juvenile and adult, nestlings excluded) captured at Világospuszta and in 87.7% (592/675) of barn swallows (juvenile and adult, no nestlings) captured at Ócsa; both locations are in Hungary. The distribution of feather holes exhibited a typical left-biased shape that is characteristic of the distribution of macroparasites among host individuals (Crofton, 1971). More specifically, the level of aggregation—as exemplified by adult birds—was clearly more pronounced in Ócsa during migration than in the breeding colony at Világospuszta (Fig. 2) or in the sample described by Pap et al. (2005). These latter breeding colonies were unusually large for central European barn swallows. On the contrary, the sample from

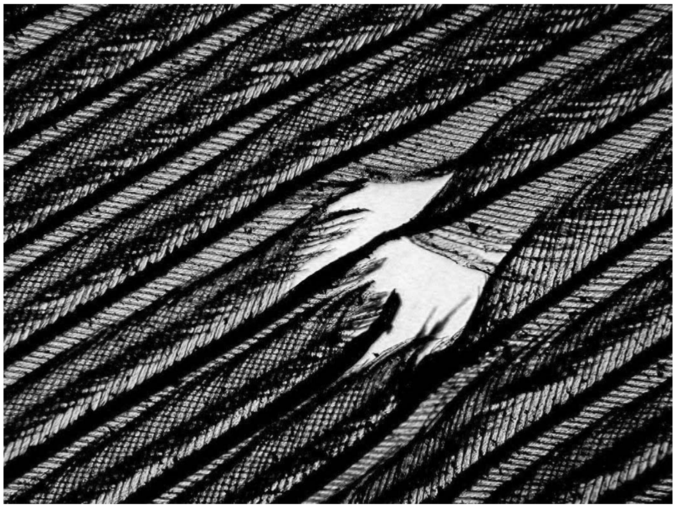

FIGURE 1. A feather hole on the rectrix of a barn swallow. Note that 1 barb is cut through and partially lost. The barbules are absent at the damage site, but fixed to each other above the hole.

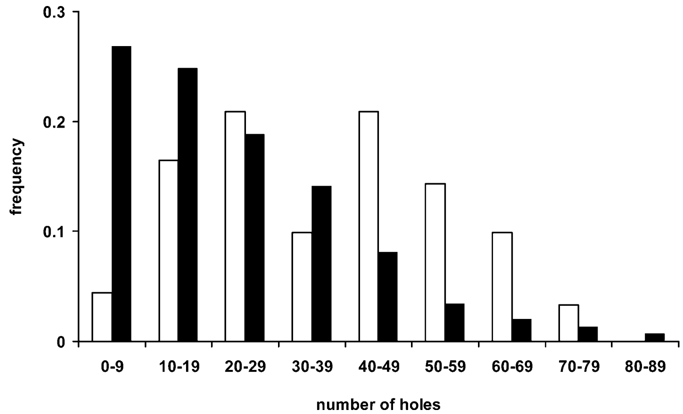

FIGURE 2. Frequency distribution of feather holes on adult barn swallows caught at a large breeding colony at Világospuszta (grey, n = 91) and during migration at Ócsa (black, n = 149).

Ócsa most probably consisted of a random mixture of territorial, semi-colonial, and colonial breeders. Thus, the difference of hole frequency distributions between our 2 samples corresponds nicely with the known relationship between host coloniality and frequency distribution of avian lice (Rékási et al., 1997), probably arising due to an increased transfer of lice among colony members (Darolová et al., 2001; Valera et al., 2003; Whiteman and Parker, 2004).

At Világospuszta, we counted the feather holes of captured and recaptured adult birds (n = 34). Birds do not molt remiges and retrices during summer. A few negative values, i.e., apparent loss of a few holes, were caused by the imperfect repeatability of counts. However, hole numbers tended to increase on the fully developed primaries, secondaries, and rectrices (1-sample t-test, t = 5.27, df = 33, $P < 0.0001$). This excludes the possibility that holes were only chewed on the vanes of feathers during their development (Fig. 3).

A surprising observation at Világospuszta was the total lack of feather holes on the 60 nestlings checked. Either the causative agent of symptoms infests the offspring only after they have already fledged or, alternatively, they are present on nestlings but feed on nutrient sources other than the developing aerodynamic vanes. Soon after the birds fledged, the first holes appeared (10 infested of the 13 first-year birds). Similarly, holes were almost totally absent from nestlings in Denmark (A. P. Møller, pers. obs.).

At Ócsa, collection with fumigants revealed that *M. malleus* is either a rare species or is totally absent in the area (0 of 61 individuals), yet birds at this site have feather holes. The most frequent louse found was *Brueelia domestica* Kellogg & Chapman 1899 (12 of 61 individuals). Since this is a narrow-bodied ischnoceran species that is easy to overlook by traditional collection methods based on a visual search, it is not at all surprising that former literature indicated a much lower prevalence (4 of 94 individuals) of this species (Blagoveshtchensky, 1951; Touleshkov, 1964; Schumilo and Lunkaschu, 1972; Touleshkov, 1974; Rékási and Kiss, 1980). Even our prevalence data seem to be highly underestimated for *B. domestica*, as we often found living individuals in the cloth bags used to store barn swallows prior to ringing (10–60 min storage periods are typical). On the contrary, no *M. malleus* was ever found in these bags. Further, *B. domestica* individuals might have been lost during ringing, prior to collection of lice.

Finally, interspecific comparisons may also provide insight into the origin of feather holes. The holes on barn swallows and sand martins provide little information in this context, since they are potential hosts to species of both *Machearilaemus* and *Brueelia* lice (Price et al., 2003). On the other hand, we also found characteristic holes on house martin *Delichon urbica* (L.), tree pipit *Anthus trivialis* (L.), nightingale *Luscinia megarhynchos* (Brehm, 1831), blackcap warbler *Sylvia atricapilla* (L.), garden warbler *S. borin* (Boddaert, 1783), house sparrow *Passer domesticus*, and tree sparrow *P. montanus* (L.). All these birds are known to harbor *Brueelia* spp. but not *Machaerilaemus* spp. lice (Price et al., 2003).

Furthermore, within the congeneric species pairs of blue tit *Parus caeruleus* L. versus great tit *P. major* L., and river warbler *Locustella fluviatilis* (Wolf, 1810) versus Savi's warbler *L. luscinioides* (Savi, 1824), the former species are not known to harbor *Brueelia* spp. lice while the latter ones do (Price et al., 2003). Accordingly, we found feather holes only in the latter species. We also found some feather holes on a very few individuals of sedge warbler *Acrocephalus scirpaceus* (Hermann, 1804) and moustached warbler *A. melanopogon* (Temminck, 1823); these species are not known to harbor *Brueelia* spp. up to the present day, perhaps due to the low intensity of study of their parasite fauna. In any case, none of the above species harbored *Machaerilaemus* spp.

Naturally, the passerines listed above also host other genera of lice such as species of *Menacathus*, *Myrsidea*, *Philopterus*, *Ricinus*, and *Sturnidoecus*. However, contrary to *Brueelia* spp., none of these genera occur on all bird species characterized by feather holes (Price et al., 2003). In the case of our barn swallow samples, *Philopterus microsomaticus* Tandan 1955 and *M. rustica* were both represented by a single individual. Furthermore, ectoparasitic mites occurred very scarcely.

To summarize, the correlational evidence shown above supports the hypothesis that feather holes are feeding traces of macroparasites, and chewing lice in particular. More specifically, the occurrence of *Brueelia* spp. lice provides the best fit to the distribution and abundance of feather holes, both in barn swallows and across several small passerines. These small, elongate lice appear to be capable of hiding between the

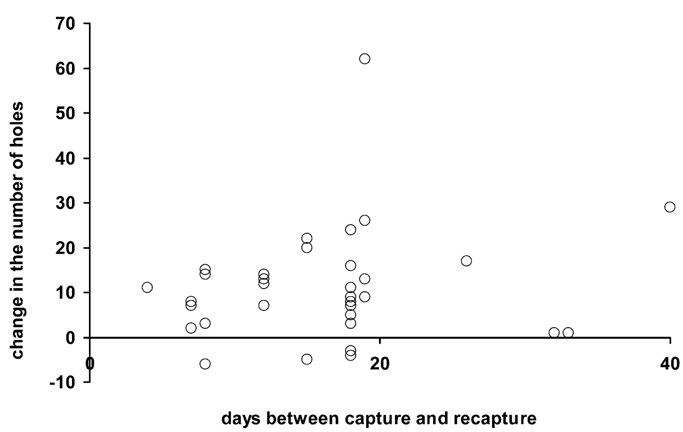

FIGURE 3. An increase of the number of holes between capture and recapture (in days, all within the range 20 May to 11 August) in barn swallows breeding at Világospuszta cattle farm (n = 34). Negative values indicate imperfect repeatability of counts.

barbs of wing and tail feathers. Accordingly, *Brueelia* spp. and some similar-shaped ischnoceran genera are often referred to as 'wing lice' in the literature (Johnson and Clayton, 2003; Mey, 2003). We conclude that the causative agent of the 'feather hole symptom' of small passerines was misidentified in 1991. This identification error does not challenge the validity of the numerous evolutionary–ecological studies based on this model system because the major message of these articles refers to host–parasite systems in general. However, we feel that the correct identification of lice has important implications from the viewpoint of phthirapterists, those who study the ecology, behavior, and evolution of lice.

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