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

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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 for both barn swallows and across 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: *Hirundoeicus malleus*) or *Myrsiedia 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, Martellini, and Saino (2004) have used crossed-fostering experiments to show that infestations of 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 bird fitness and, more specifically, the level of aggregation—as exemplified by adult birds—was clearly more pronounced in Öcsa 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
Ocsa 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 oflice among colony members (Darolová et al., 2001; Valera et al., 2003; Whiteman and Parker, 2004).

At Vílagospuszta, we counted the feather holes of captured and re-captured adult birds (n = 34). Birds do not molt remiges and rectrices 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 Vílagospuszta 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 Ocsa, collection with fumigants revealed that Brueelia domestica Kellogg & Chapman 1899 (12 of 61 individuals). Since this is a narrow-bodied ischnoceran species that is easy to over-look 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 Machaeriaenius 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 Lus-cinda megarhynchos (Brechm, 1831), blackcap warbler Sylvia atricapilla (L.), garden warbler S. borin (Boddart, 1783), house sparrow Passer domesticus, and tree sparrow P. montanus (L.). All these birds are known to harbor Brueelia spp. but not Machaeriaenius 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 Savî’s warbler L. luscinoides (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 scir-paceus (Hermann, 1804) and moustached warbler A. melampegon (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 Machaeriaenius spp.

Naturally, the passerines listed above also host other genera of lice such as species of Menacathus, Myrsidea, Philopterus, Ricinus, and Sturnidocus. 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 Tandam 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...
bars of wing and tail feathers. Accordingly, Brucella 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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LITERATURE CITED


