



The origin of feather holes: a word of caution

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Antagonistic processes between parasites and their hosts are hallmarks of evolutionary ecology. A group of parasites is adapted to feed on feather keratin. In doing so, they inflict a variety of costs on avian hosts by causing feathers to degrade faster. Feather holes represent a class of feather damage that is attributed to the chewing bites of Phthirapteran lice. Consequently, hole counts were used as an approximation of lice infestation intensity when studying bird–lice interaction. Here, I express some reservations regarding this practice. I survey the literature concerning feather holes and the state of the hole–lice concept, highlight some uncertainties regarding its reliability, offer possible alternative explanations for the origin of holes, and suggest directions for future investigations. I conclude that the origin of holes is still unknown, and so a prudent approach is desirable when interpreting the relationship between avian phenotype or fitness and lice infestation inferred from hole counts.

Parasitic organisms (including pathogens) represent one of the most powerful selection forces (Schmid-Hempel 2011). Birds interact with numerous parasites, of which a substantial share consists of plumage-dwelling species ranging from bacteria through fungi to arthropods. Some can harm the plumage of hosts (keratinolytic bacteria, syringicolous mites, feather lice). One mode of allegedly parasite-induced feather damage is represented by feather holes, which are small, apparently round defects in flight feathers (remiges, rectrices) that denote sections of barbs where barbules are missing (Fig. 1).

Avian ecologists and evolutionists who strive to understand host–parasite dynamics may rely on simplistic measures (soft traits) to approximate biological traits that are more difficult to measure (hard traits). However, the use of such simplification can be a flawed endeavour if not substantiated critically. One such case is that of the occurrence of feather holes that are attributed to the feather-grazing activity of chewing lice (Phthiraptera: Amblycera, Ischnocera) based on a correlative study by Møller (1991). Based on this correlation, several later studies used the feather hole count as a substitute soft trait to infer louse infestation intensity, the hard trait (Supplementary material Appendix 1, Table A1).

Here, I address the proximate cause of feather holes, which remains little understood, by 1) reviewing the literature on the correlates of lice infestation inferred from hole counts, 2) presenting the pros and cons of three alternative hypotheses about the origin of feather holes, and 3) recommending possible avenues for future study.

Lice infestation inferred from hole counts

The literature dealing with feather holes as an indicator of either lice parasitaemia or simply feather quality (35 studies) is summarised in the Supplementary material Appendix 1, Table A1. These studies focused on morphology, condition, sexual selection, host–parasite coevolution (e.g. host physiology) and fitness; and the barn swallow *Hirundo rustica* was the best-studied organism. Although the sign of certain associations is inconsistent across studies (e.g. with morphology, condition, physiology), well-established relationships are also emerging: 1) common environment does not explain the number of holes, while genetic relatedness does. 2) Juvenile birds have larger hole loads than adult (except senescent) birds. 3) The expression of sexual traits is inversely related to the number of holes. 4) Reproductive or survival performance is lower when the incidence of feather holes is high.

Causative agent of feather holes

The lice origin of holes was routinely reiterated in avian ecology despite the lack of compelling experimental evidence to support this assumption, a shortcoming raised nearly a decade ago by Pap et al. (2005). Later, some were cautious about the lice origin of feather holes (Pap et al. 2007, Vas et al. 2008, Møller 2010) and Clayton et al. (2010) cast some doubt on this as well. Vágási et al. (2011) presented data for the first time that did not corroborate the hypothesis regarding the lice origin of holes and offered

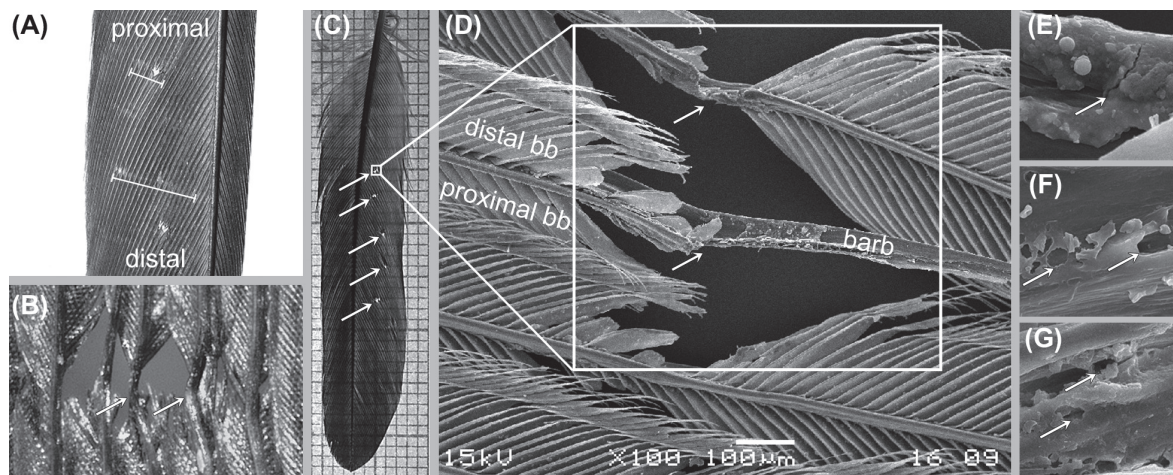


Figure 1. Feather holes of house martin *Delichon urbica* feathers. (A) Some holes are positioned along light fault bars (white section marks) and are elongated quasi horizontally; (B) the denuded portions of barbs are frequently bent (see also D); (C) feather with several holes; (D) close-up view of the damaged barbs and barbules (bb) on a scanning electron micrograph; (E)–(G) crop details of damaged barbs (marked with arrows on D) with multiple signs of fractures, micro-cracks and surface damages.

two alternative hypotheses delineated based on the causative agents: 1) feather-degrading bacteria, and 2) feather fault or breakage. Below, I describe the evidence for and against each of the three hypotheses.

Hypothesis 1: the chewing lice origin of feather holes

This hypothesis suggests that chewing lice bite holes in the vanes of pennaceous flight feathers (Møller 1991; Fig. 2A). This claim arguably rests on the observation that feather lice feed on feather keratin of plumulaceous body feathers (Clayton 1990).

Pros

First, there is a positive correlation between the number of holes and the abundance of Amblyceran lice (Møller 1991). Second, the frequency distributions of lice and holes among host individuals have a similar shape (Møller 1991) and, in populations in which hosts breed colonially, the frequency distribution of holes is less skewed (Pap et al. 2005, Vas et al. 2008). Third, lice prefer staying on white rectrix spots, which are claimed to be more easily damaged by them, and holes are more frequent on these feather parts (Kose et al. 1999). Fourth, holes are associated with the infestation by *Brueelia* spp. lice (Ischnocera) in comparisons of sister avian taxa (Vas et al. 2008).

Cons

These associations, however, do not substantiate the hypothesis clearly, as they are all correlative. The major concerns identified can be structured according to the following subheadings.

Identity of damaging lice taxa. Recently, Ischnoceran lice were proposed in general and the *Brueelia* genus in particular as hole-makers (Vas et al. 2008). The Ischnoceran fraction of the lice removed by Møller (1991) with chloroform vapour is unknown, and the denominated Amblyceran species was later discarded as a potential

delinquent (Vas et al. 2008). As suggested by Clayton et al. (2010), it would be informative to repeat the studies describing the lice–hole abundance correlation found by Møller (1991) and feather preference of lice showed by Kose et al. (1999) with the new candidate genus.

Sample size, host populations and species. First, the hole–lice association was based on a small sample size (DF = 18, $p < 0.01$) and assessed for a single barn swallow population (Møller 1991). Given the aggregated frequency

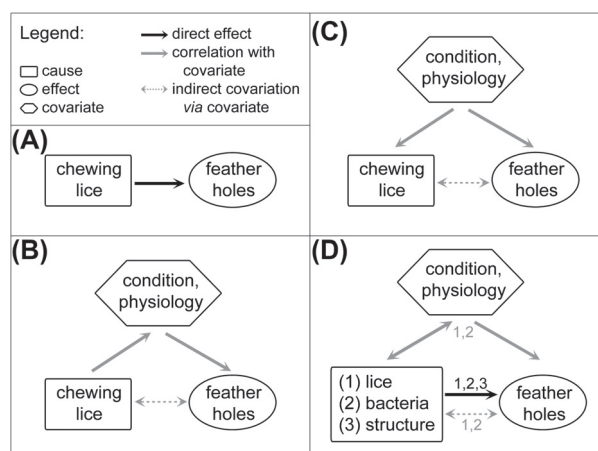


Figure 2. Putative scenarios of the causation of feather holes. (A) 'Cause–effect' scenario: the conventional wisdom that lice chew the holes; (B) 'mediator scenario': parasites affect the 'state' of hosts, which in turn influences feather quality (cf. arrowheads with C); (C) 'false co-variation scenario': a third-party variable is related to both lice infestation and feather damages, but through independent routes (e.g. 'good-quality' birds better withstand a parasite attack and grow higher quality feathers that are e.g. less holey); (D) 'current state-of-the-art': compression of previous scenarios. This scenario represents our current knowledge and it is so intricate because a) the cause is unknown and might be multiple (1, 2, 3) and b) causes 1 and 2 might be related directly (black numbers) or through co-variation (type B or C, grey numbers). Note that cause 3 affects directly the damage of feathers.

distribution of parasites, small sample sizes can be problematic and increase the probability of overlooking indirect relationships (Booth et al. 1993, Jovani and Tella 2006). Second, hole count as substitute for lice abundance was later adopted for many other swallow populations and other avian hosts (Supplementary material Appendix 1, Table A1) without verifying the hole–lice correlation. However, differences among host population and species might well exist at the level of both parties (parasite identity, infestation level and host defence, condition). It is also possible that the causative agent differs in space or among hosts (hypotheses 2 and 3).

Lack of experimental support. Correlations cannot distinguish between cause and effect. A third-party trait (e.g. condition) can mediate the co-variation between the two parameters under investigation (Vágási et al. 2011; Fig. 2B) or even co-vary simultaneously with both leading to a false correlation between the two (Fig. 2C). These cases imply the decoupling of the cause (lice) from effect (holes). If mediators such as condition play a role, the direction of correlation between two traits tells little owing to a ‘big house, big car’ paradox (van Noordwijk and de Jong 1986). This uncertainty is inherent in the discussions of several papers in which condition is identified as a potential confounder.

Free-living barn swallows treated with a general insecticide (pyrethrin) did not differ from controls in terms of changes in hole load in one month (P. L. Pap pers. comm., $n = 24$, $p = 0.93$). However, the absolute breakthrough would be to test experimentally whether feather lice puncture holes directly or their effect is manifested indirectly (Fig. 2A–C). If lice chew the holes, loss of feather mass and temporal increase in hole counts is predicted for intact feathers (in vitro) or birds (in vivo) experimentally infested by lice. Such experimentation might gain insight also into the pace at which holes are created. Sometimes the abundance of holes is relatively stable over time (Møller 1991, Vágási et al. 2011). The apparent temporal pauses in hole count accrual is surprising because Ischnoceran lice cannot cease feeding on feathers, their sole carbon source.

How to eat flight feathers? Ischnoceran lice damage only the thin barbule filaments of the plumulaceous part of down feathers, but never those at distal pennaceous part (Clayton 1990) due to the physical constraint imposed by mandible size (Bush et al. 2006, Bush and Malenke 2008). Given that the best current candidate lice *Brueelia* spp. are slender-bodied Ischnocerans, it seems unlikely that they have mandibles robust enough to masticate the barbules (and sometimes the barbs) of flight feathers (Fig. 1). Finally, chewing lice do not hesitate to eat almost entirely the downy barbules that they are capable to graze (Clayton 1990); hence, small feather punctures demand an explanation.

Host defence mechanisms. It has been suggested that white feathers are more susceptible to lice chewing (Kose and Møller 1999, Kose et al. 1999) because they are devoid of melanin pigments that endow feathers with strength (Bonser 1995). Although lice prefer to stay on white feather spots in vitro, lice-related damage was not assessed (Kose et al. 1999). Moreover, lice do not harm white feathers any more severely than black feathers (Bush

et al. 2006), and plumage colouration does not explain the load of holes or lice (Moreno-Rueda 2005, Bush et al. 2006). Uropygial gland secretions were supposed to serve lice-deterrent function because birds with larger glands harbour fewer holes (Moreno-Rueda 2010). However, the accessibility of gland oils did not protect hosts from lice in vivo (Moyer et al. 2003) and the size of the uropygial gland was not associated with the number of Ischnoceran genera (Møller et al. 2010).

Hypothesis 2: feather holes induced by keratinolytic parasites

This hypothesis holds that keratinolytic parasites induce the formation of feather holes (Vágási et al. 2011; Fig. 2D), which stems from the fact that feather-degrading bacteria (FDB) evolved proteolytic keratinase enzymes that catalyze the process of hydrolytic break-down of the keratin (Gunderson 2008).

Pros

First, the activity of FDB initiates scratches and fractures of the keratin cortex (Shawkey et al. 2007), and both FDB and fungi can digest feather barbules in vitro (Cristol et al. 2005, Gunderson 2008, Ruiz-Rodríguez et al. 2009, Lingham-Soliar et al. 2010), though not so in vivo (at least the *Bacillus licheniformis*; Cristol et al. 2005). Unlike in the case of chewing lice, these effects are independent of feather tract (body or flight feather) or outer structure (plumulaceous or pennaceous). Furthermore, the distribution of FDB among hosts is aggregated like that of holes.

Second, fungi can lyse the keratin membrane of bat wings and initially create holes (Voigt 2013). In agreement with this, the abundance of FDB is strongly and positively correlated with feather hole burden in house sparrows *Passer domesticus* even after controlling for possible mediating variables like condition (A. Fülöp, G. Á. Cziráj, P. L. Pap and C. I. Vágási unpubl., $DF = 121$, $p = 0.007$).

Third, contrary to lice, defence by means of melanin pigments (Burt and Ichida 2004, Gunderson et al. 2008) and uropygial gland secretions (Shawkey et al. 2003, Gunderson 2008, but see Cziráj et al. 2013) might succeed against FDB. Lice load is not influenced by surgical gland removal, yet feathers become more damaged in birds without glands (Moyer et al. 2003). The above results might explain the correlation between holes and colouration and gland size (see hypothesis 1) by putting FDB in the role of parasite instead of chewing lice (Fig. 2D).

Fourth, FDB are potentially more pervasive among birds than *Brueelia* spp. lice are (Burt and Ichida 1999, Johnson et al. 2002, Gunderson 2008). Moreover, bacteria with proteolytic capacity were found in soil and water (Saag et al. 2011a). These biological traits of bacteria might fill the large gap found between *Brueelia* spp. lice and hole prevalence (Vágási et al. 2011). They might also explain why some water- or diving birds, such as the dipper *Cinclus cinclus*, bear holes (100% prevalence, C. I. Vágási and P. L. Pap pers. obs.) despite lacking *Brueelia* spp. at all (Price et al. 2003).

Cons

First, the abundance of holes did not increase during the annual cycle in great tits *Parus major* (Vágási et al. 2011). Active mostly in the canopy, great tits are less exposed to FDB (Burtt and Ichida 1999, Saag et al. 2011b). Model organisms with higher exposure to FDB would better suit a longitudinal study of damage accumulation and FDB load based on repeated measures of the same individuals.

Second, little is known about whether FDB disrupt the keratin matrix under natural conditions and about the keratinolytic potential of different bacteria strains (Gunderson 2008). For instance, FDB had no effect on feather deterioration in vivo, but only in vitro (Cristol et al. 2005). Finally, FDB degrade feathers to dust within one week of in vitro inoculation (Gunderson et al. 2008), hence the small size of feather holes does not correspond to the keratinolytic potential of FDB.

Experimental manipulation of the FDB load and the bird's capability to coat the plumage with uropygial gland oils (i.e. birds are allowed or not to coat their plumage) could give insights into the influence of FDB on hole numbers. Taking advantage of modern phylogenetic comparisons, testing the interspecific correlation between bacteria and hole load would also be a good test of this hypothesis.

Hypothesis 3: feather holes as fault spots or minor breaks

This hypothesis posits that feather holes depend entirely on feather structure, not parasites. Specifically, holes are either short fault bars (i.e. fault spots, sensu Murphy et al. 1989) developed during feather synthesis or minor breaks that are initiated after feather growth where the vane is locally compromised by e.g. disturbed moult process, weak inner structure or scratch initiation (Vágási et al. 2011). In contrast with the previous two hypotheses, where an indirect (i.e. mediated) link between the parasitic agent and holes are also plausible, this hypothesis assumes a direct link by default: compromised feather structure gives rise to holes (Fig. 2D).

Pros

First, the appearance of fault bars on scanning electron micrographs (Murphy et al. 1989) is remarkably similar to that of holes (Fig. 1D–G). Several pieces of evidence make this comparison reasonable. Murphy et al. (1989) found that sometimes fault spots form instead of fault bars. They argued that the constriction of feather muscles could squeeze the soft shaft of unpinched feather and, in essence, fault spots could result from local muscle constriction and fault bars from circumferential muscle constriction. Accordingly, fault bars are at an angle slightly inclined towards the base of the feather (i.e. proximal end, calamus), which corresponds with the helical development of feathers and fault bar simulations (Prum 1999, Prum and Williamson 2001). In other words, fault bars are defect isochrones. Interestingly, holes are usually elongated (i.e. multiple adjacent barbs defected) and the axis of this elongation is at an angle to the rachis similar to that of fault bars (Fig. 1A, C). Barbs of both fault bars and feather holes are bent or buckled, showing signs of possible squeeze

of feathers (Murphy et al. 1989; Fig. 1B, D). Holes are frequently in line with light fault bars (sensu Sarasola and Jovani 2006; Fig. 1A; pers. obs. on several species). The presence of fault bars predicts higher hole load in great tits (Vágási et al. 2011), and there is a very strong correlation between the number of fault bars and feather holes in house sparrows (A. Fülöp, G. Á. Cziráj, P. L. Pap and C. I. Vágási unpubl., $n = 155$, $p = 0.003$). Finally, Jovani and Diaz-Real (2012) found that fault bars of white storks *Ciconia ciconia*, especially in juveniles, are highly concentrated close to the tip of the feather, just as feather holes are in the case of great tits (Vágási et al. 2011). The fault spot scenario implies that feather holes are created in situ during feather growth and not subsequently, which might explain the temporal consistency of hole numbers in certain barn swallow populations (Møller 1991) and in great tits (Vágási et al. 2011).

Alternatively or in combination with the fault spot notion, feather muscle constriction or other perturbations of feather growth could cause small-scale defects where the feather vane is unperceivably weaker immediately after moult. Later, however, feathers could more easily fail at such places owing to intense usage. Failure could arise from small scratches of the cortex, which can initiate crack propagation and ultimately lead feathers to succumb structurally under cyclic load (Bonser 1995) or due to friction against abrasive surfaces. It might be that the parts where holes emerge are more prone to scratch initiation, mainly if feather structure is locally compromised, and these scratches cause fractures to limited numbers of barbs that result in a spot-like breakage (Fig. 1D–G). In concert with this, feather holes are much concentrated close to the tip of the feather, where buckling is the most powerful (Vágási et al. 2011). Furthermore, feather damage propagation (wear, breakage) is also more likely at sections where the keratin matrix is poor in or devoid of melanin pigments (Bonser 1995). Experimental exposure of feathers with non-visible faults but having either healthy or locally weak structures to numerous bending cycles in a fatigue apparatus (Vágási 2013) could be a promising test. This alternative scenario extends the timing of formation of holes to the period after feather growth. This could explain the increase of holes over time in some barn swallow populations (Vas et al. 2008), which is a notorious aerial species and long-distant migrant (i.e. flight feathers bend frequently and extremely), but not in the great tit (Vágási et al. 2011), which is an arboreal non-migratory species that presumably flies considerably less.

Second, fault bars and spots are acknowledged as being caused by stress (Bortolotti et al. 2009, Jovani and Diaz-Real 2012). Given the ubiquity of stress stimuli, this might explain the pervasiveness of holes among avian species in general and among hosts that are free of *Brueelia* spp. lice (e.g. great and blue tit *Cyanistes caeruleus*, dipper) or FDB.

Studies have only recently uncovered the causes of fault bars (Murphy et al. 1989), the relationship between fault bars and stress (Bortolotti et al. 2009), and the fine-scale details of their formation (Jovani and Diaz-Real 2012). However, questions regarding the causes and formation of feather holes and the relationship between stress and feather holes remain unanswered, which makes feather holes

a topic ripe for similar investigations. Some questions that might open new dimensions include: 1) do feathers or feather sections with or without holes have different concentrations of feather corticosterone? 2) Do sites with holes (i.e. small fractures) have different nanometer-scale structures than contiguous sites without holes (keratin ridge density, melanin granulation, indentation hardness)? 3) Does the combined study of ptilochronology (feather growth bands) and position of holes provide insight into the origin of holes?

Cons

The most important con is the finding of Vas and Fuisz (2010), who subjected barn swallows to two different ringing agendas: either normal or abridged length. Birds recaptured after one month all had increased hole loads, but those exposed to longer ringing (i.e. normal length) had hole loads with smaller increments. The authors concluded that ringing procedure reduces louse infestation.

Concluding remarks

The origin of feather holes is currently unknown. The pervasive view according to which holes are made by chewing lice is premature, and the alternative hypotheses are also speculative. It is also noteworthy that these hypotheses are not diametrically opposed: multi-causal origin within or among host species is plausible, and the alternative hypotheses should be taken into account concurrently.

The indirect results supporting the conventional wisdom regarding the lice origin of holes is currently a 'red herring', as indicated by two fallacies. Some studies committed the logical fallacy of assuming that lice chew the holes and then took a biological trait of lice relevant for the question under examination and produced results regarding hole load and finally inferred that these together hint at the lice origin of holes. On the other hand, interpretational fallacy is committed when results based on direct measurement of lice infestation and the substitute measure (i.e. hole count) are put side-by-side with the same power to discuss host-lice coevolution. In addition, in some of the discussions, results on flight feather holes and lice-induced damages of body feathers are conflated.

The potential vague use of hole counts to infer lice infestation has implications for various evolutionary questions. Holes apparently indicate condition, but we still have to determine which aspect of condition: 1) resistance against parasite infestation (lice or FDB), 2) resistance against deterioration because of environmental factors other than parasites (stress bars, friction, buckling), 3) a trait that went undetected so far, or 4) a combination of these. Current knowledge is best described by the many potential paths in Fig. 2D, which raises the question of what is being studied: the causes and fitness consequences of lice or hole abundance. If lice or bacteria perforate the feathers, then these studies address the host-parasite arms race, in which both parties are exposed to selection imposed by the other party. If holes are structural defects, then selection is acting only on hosts to minimize the costs, and holes cannot take countermeasures; hence studying host-parasite coevolution based on hole counts (Supplementary material

Appendix 1, Table A1) is unfounded. A specific example is parasite-mediated sexual selection: the choosy sex differentiates partners based on honest signalling of lice resistance, in this case inferred from hole counts. If it turns out that FDB are responsible for holes instead of lice, the theoretical framework does not change, but if holes have a non-parasitic origin then we leave the boundary of parasite-mediated sexual selection.

Recording a substitute of lice infestation is an undue simplification when lice, including *Brueelia* spp., can be counted directly and reliably e.g. by visual examination (Koop and Clayton 2013). Phthirapterists who study bird-lice interactions avoid simplistic measures and record lice infestation rate per se (Booth et al. 1993) because even this practice can be deceiving (Moyer et al. 2002). I urge the use of such protocols, even though they are more time-consuming, when host-lice co-evolution is studied. Nevertheless, counting holes could still provide valuable information about feather quality (Pap et al. 2007, Vágási et al. 2011).

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References

- Bonser, R. H. C. 1995. Melanin and the abrasion resistance of feathers. – *Condor* 97: 590–591.
- Booth, D. T., Clayton, D. H. and Block, B. A. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. – *Proc. R. Soc. B* 253: 125–129.
- Bortolotti, G. R., Marchant, T., Blas, J. and Cabezas, S. 2009. Tracking stress: localisation, deposition and stability of corticosterone in feathers. – *J. Exp. Biol.* 212: 1477–1482.
- Burt, E. H. Jr and Ichida, J. M. 1999. Occurrence of feather-degrading bacilli in the plumage of birds. – *Auk* 116: 364–372.
- Burt, E. H. Jr and Ichida, J. M. 2004. Gloger's rule, feather-degrading bacteria, and color variation among song sparrows. – *Condor* 106: 681–686.
- Bush, S. E. and Malenke, J. R. 2008. Host defence mediates interspecific competition in ectoparasites. – *J. Anim. Ecol.* 77: 558–564.
- Bush, S. E., Kim, D., Moyer, B. R., Lever, J. and Clayton, D. H. 2006. Is melanin a defence against feather-feeding lice? – *Auk* 123: 153–161.
- Clayton, D. H. 1990. Mate choice in experimentally parasitized rock doves: lousy males lose. – *Am. Zool.* 30: 251–262.
- Clayton, D. H., Koop, J. A. H., Harbison, C. W., Moyer, B. R. and Bush, S. E. 2010. How birds combat ectoparasites. – *Open Ornithol. J.* 3: 41–71.

- Cristol, D. A., Armstrong, J. L., Whitaker, J. M. and Forsyth, M. H. 2005. Feather-degrading bacteria do not affect feathers on captive birds. – *Auk* 122: 222–230.
- Czirják, G. Á., Pap, P. L., Vágási, C. I., Giraudeau, M., Mureşan, C., Mirleau, P. and Heeb, P. 2013. Preen gland removal increases plumage bacterial load, but not that of feather-degrading bacteria. – *Naturwissenschaften* 100: 145–151.
- Gunderson, A. R. 2008. Feather-degrading bacteria: a new frontier in avian and host–parasite research? – *Auk* 125: 972–979.
- Gunderson, A. R., Frame, A. M., Swaddle, J. P. and Forsyth, M. H. 2008. Resistance of melanized feathers to bacterial degradation: is it really so black and white? – *J. Avian Biol.* 39: 539–545.
- Johnson, K. P., Adams, R. J. and Clayton, D. H. 2002. The phylogeny of the louse genus *Brueelia* does not reflect host phylogeny. – *Biol. J. Linn. Soc.* 77: 233–247.
- Jovani, R. and Tella, J. L. 2006. Parasite prevalence and sample size: misconceptions and solutions. – *Trends Parasitol.* 22: 214–218.
- Jovani, R. and Diaz-Real, J. 2012. Fault bars timing and duration: the power of studying feather fault bars and growth bands together. – *J. Avian Biol.* 43: 97–101.
- Koop, J. A. and Clayton, D. H. 2013. Evaluation of two methods for quantifying passeriform lice. – *J. Field Ornithol.* 84: 210–215.
- Kose, M. and Møller, A. P. 1999. Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barn swallow (*Hirundo rustica*). – *Behav. Ecol. Sociobiol.* 45: 430–436.
- Kose, M., Mänd, R. and Møller, A. P. 1999. Sexual selection for white tail spots in the barn swallow in relation to habitat choice by feather lice. – *Anim. Behav.* 58: 1201–1205.
- Lingham-Soliar, T., Bonser, R. H. C. and Wesley-Smith, J. 2010. Selective biodegradation of keratin matrix in feather rachis reveals bioengineering. – *Proc. R. Soc. B* 277: 1161–1168.
- Møller, A. P. 1991. Parasites, sexual ornaments, and mate choice in the barn swallow. – In: Loye, J. E. and Zuk, M. (eds), *Bird–parasite interactions: ecology, evolution, and behaviour*. Oxford Univ. Press, pp. 328–343.
- Møller, A. P. 2010. Host–parasite interactions and vectors in the barn swallow in relation to climate change. – *Global Change Biol.* 16: 1158–1170.
- Møller, A. P., Erritzøe, J. and Rózsa, L. 2010. Ectoparasites, uropygial glands and hatching success in birds. – *Oecologia* 163: 303–311.
- Moreno-Rueda, G. 2005. Is the white wing-stripe of male house sparrows *Passer domesticus* an indicator of the load of Mallophaga? – *Ardea* 93: 109–114.
- Moreno-Rueda, G. 2010. Uropygial gland size correlates with feather holes, body condition, and wingbar size in the house sparrow. – *J. Avian Biol.* 41: 229–236.
- Moyer, B. R., Gardiner, D. W. and Clayton, D. H. 2002. Impact of feather molt on ectoparasites: looks can be deceiving. – *Oecologia* 131: 203–210.
- Moyer, B. R., Rock, A. N. and Clayton, D. H. 2003. Experimental test of the importance of preen oil in rock doves (*Columba livia*). – *Auk* 120: 490–496.
- Murphy, M. E., Miller, B. T. and King, J. R. 1989. A structural comparison of fault bars with feather defects known to be nutritionally induced. – *Can. J. Zool.* 67: 1311–1317.
- Pap, P. L., Tökölyi, J. and Szép, T. 2005. Frequency and consequences of feather holes in barn swallows *Hirundo rustica*. – *Ibis* 147: 169–175.
- Pap, P. L., Barta, Z., Tökölyi, J. and Vágási, C. I. 2007. Increase of feather quality during moult: a possible implication of feather deformities in the evolution of partial moult in the great tit *Parus major*. – *J. Avian Biol.* 38: 471–478.
- Price, R. D., Hellenthal, R. A., Palma, R. L., Johnson, K. P. and Clayton, D. H. 2003. The chewing lice: world checklist and biological overview. – *Illinois Nat. Hist. Surv. Special Publ.* 24.
- Prum, R. O. 1999. Developmental and evolutionary origin of feathers. – *J. Exp. Zool. B* 285: 291–306.
- Prum, R. O. and Williamson, S. 2001. Theory of feather growth and evolution of feather shape. – *J. Exp. Zool. B* 291: 30–57.
- Ruiz-Rodríguez, M., Valdivia, E., Soler, J. J., Martín-Vivaldi, M., Martín-Platero, A. M. and Martínez-Bueno, M. 2009. Symbiotic bacteria living in the hoopoe's uropygial gland prevent feather degradation. – *J. Exp. Biol.* 212: 3621–3626.
- Saag, P., Tilgar, V., Mänd, R., Kilgas, P. and Mägi, M. 2011a. Plumage bacterial assemblages in a breeding wild passerine: relationships with ecological factors and body condition. – *Microb. Ecol.* 61: 740–749.
- Saag, P., Mänd, R., Tilgar, V., Kilgas, P., Mägi, M. and Rasmann, E. 2011b. Plumage bacterial load is related to species, sex, biometrics and fledging success in co-occurring cavity-breeding passerines. – *Acta Ornithol.* 46: 191–201.
- Sarasola, J. H. and Jovani, R. 2006. Risk of feather damage explains fault bar occurrence in a migrant hawk, the Swainson's hawk *Buteo swainsoni*. – *J. Avian Biol.* 37: 29–35.
- Schmid-Hempel, P. 2011. *Evolutionary parasitology. The integrated study of infections, immunology, ecology and genetics*. – Oxford Univ. Press.
- Shawkey, M. D., Pillai, S. R. and Hill, G. E. 2003. Chemical warfare? Effects of uropygial oil on feather-degrading bacteria. – *J. Avian Biol.* 34: 345–349.
- Shawkey, M. D., Pillai, S. R., Hill, G. E., Siefferman, L. M. and Roberts, S. R. 2007. Bacteria as an agent for change in structural plumage color: correlational and experimental evidence. – *Am. Nat.* 169: S112–S121.
- Vágási, C. I. 2013. Costs of moult: feather quality, signals and physiology. – PhD thesis, Univ. of Debrecen, Debrecen, Hungary.
- Vágási, C. I., Pap, P. L., Tökölyi, J., Székely, E. and Barta, Z. 2011. Correlates of variation in flight feather quality in the great tit *Parus major*. – *Ardea* 99: 53–60.
- van Noordwijk, A. J. and de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. – *Am. Nat.* 128: 137–142.
- Vas, Z. and Fuisz, T. I. 2010. Ringing procedure can reduce the burden of feather lice in barn swallows *Hirundo rustica*. – *Acta Ornithol.* 45: 203–207.
- Vas, Z., Csörgő, T., Møller, A. P. and Rózsa, L. 2008. The feather holes on the barn swallow *Hirundo rustica* and other small passerines are probably caused by *Brueelia* spp. lice. – *J. Parasitol.* 94: 1438–1440.
- Voigt, C. C. 2013. Bat flight with bad wings: is flight metabolism affected by damaged wings. – *J. Exp. Biol.* 216: 1516–1521.

Supplementary material (Appendix JAV-00359 at < <http://www.avianbiology.org/readers/appendix>>). Appendix 1.