

# Feather-degrading bacteria, uropygial gland size and feather quality in House Sparrows *Passer domesticus*

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1 ATTILA FÜLÖP,<sup>1,2,\*</sup> GÁBOR Á. CZIRJÁK,<sup>3</sup> PÉTER L. PAP<sup>1,2</sup> & CSONGOR I. VÁGÁSI<sup>1,2,\*</sup>

<sup>1</sup>MTA-DE 'Lendület' Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Egyetem tér 1, H-4032, Debrecen, Hungary

<sup>2</sup>Evolutionary Ecology Group, Hungarian Department of Biology and Ecology, Babeş-Bolyai University, Clinicilor Street 5–7, RO-400006, Cluj Napoca, Romania

<sup>3</sup>Department of Wildlife Diseases, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Straße 17, DE-10315, Berlin, Germany

Feathers are dead integumentary structures that are prone to damage and thus show gradual degradation over the course of a year. This loss of quality might have negative fitness consequences. Feather-degrading bacteria are some of the most prevalent feather-degrading organisms, yet the relationship between feather-degrading bacteria load and flight feather quality has rarely been assessed. We studied this relationship in free-living House Sparrows during breeding and non-breeding annual lifecycle stages. We also considered the size of the uropygial gland, given the antimicrobial function of its secretions, and the effect of body condition. The number of feather holes was positively associated with feather-degrading bacteria load and was negatively related to uropygial gland size and body condition during the breeding season in both sexes. In the non-breeding season we found the same relationships, but only in females. The degree of feather wear was unrelated to any of the variables measured during the breeding season, whereas it was negatively associated with uropygial gland size and positively with feather-degrading bacteria load in the non-breeding season, but only in females. Our results suggest that feather-degrading bacteria may induce the formation of feather holes, but play only a minor role in the abrasion of flight feathers.

**Keywords:** feather hole, feather wear, feather structure, keratinolytic microorganisms, preen oil.

Feathers are epidermal appendages that characterize theropod dinosaurs, including birds. Because they are dead structures, they are incapable of regeneration and therefore their structure abrades gradually with persistent use, particularly in the case of flight feathers (the remiges and rectrices; Vágási *et al.* 2011, Flinks & Salewski 2012). Feather abrasion and feather holes are the most commonly encountered signs of structural damage. Of these, feather abrasion (or wear) is the gradual shortening of the flight feather tips (Merilä & Hemborg 2000, Vágási *et al.* 2011), whereas feather holes are small defects (diameter 0.5–1 mm) of the vane (Vas *et al.* 2008, Vágási 2014).

\*Corresponding authors.

Emails: fafeldolgozo@gmail.com; csvagasi@gmail.com

Feather structural damage could decrease flight feather quality and/or create asymmetry in the wing and tail. Consequently, such damage might impose fitness costs via reduced flight performance (e.g. manoeuvrability, take-off speed or wing-beat frequency; Swaddle *et al.* 1996, 1999, Swaddle & Witter 1998, Barbosa *et al.* 2003).

Feather structure can be impaired by both abiotic and biotic environmental factors. Feather abrasion is recognized as a direct consequence of mechanical friction (Burt 1986, Francis & Wood 1989, Jenni & Winkler 1994). In addition, Moreno-Rueda (2011) proposed that the degree of abrasion might also be exacerbated by ectoparasites (e.g. chewing lice, feather-degrading bacteria). Feather holes are usually considered to be the feeding traces of chewing lice (Møller 1991) but a

Dispatch: 31.12.15	CE: Hari
No. of pages: 9	PE: Iniya Selvi
WILEY	
12342	Manuscript No.
IBI	Journal Code
	

1 recent review suggests this conclusion to be  
 2 contentious, as damage could be caused by other  
 3 parasites (e.g. feather-degrading bacteria) and/or  
 4 mechanical agents (Vágási 2014, see also Vágási  
 5 *et al.* 2011). These assumptions, however, have  
 6 never been explored.

7 Feather-degrading bacteria (FDB) are a wide-  
 8 spread group of microorganisms that live on the  
 9 plumage of birds (Burt & Ichida 1999, Gunderson  
 10 2008). They possess keratinolytic enzymes that  
 11 hydrolyse the keratin matrix (Ramnani *et al.*  
 12 2005), leading to complete degradation of feathers  
 13 *in vitro* (Ichida *et al.* 2001, Ramnani *et al.* 2005,  
 14 Ruiz-Rodríguez *et al.* 2009). However, this inter-  
 15 action might be more intricate than depicted by  
 16 *in vitro* studies, as some peculiarities of FDB break  
 17 down *in vivo* (Czirják *et al.* 2013), and the *in vivo*  
 18 association between FDB and plumage condition is  
 19 still largely unexplored (Gunderson 2008, excep-  
 20 tions are Jacob *et al.* 2014a, Leclaire *et al.* 2015).

21 Birds are equipped with multiple defence  
 22 mechanisms that have evolved to protect them  
 23 against biotic impacts on their feathers, such as  
 24 feather structure and coloration, body maintenance  
 25 behaviours and moult (reviewed by Gunderson  
 26 2008, but see also Bonser 1995, Burt & Ichida  
 27 1999, Saranathan & Burt 2007, Giraudeau *et al.*  
 28 2010a, Burt *et al.* 2011). One prominent adapta-  
 29 tion is the oily secretion of the uropygial gland  
 30 (UG) (Jacob & Ziswiler 1982). The UG is an epi-  
 31 dermal holocrine gland of birds that produces  
 32 preen oil, which is spread onto the plumage during  
 33 preening. Various functions are attributed to the  
 34 preen oil, such as improving the resistance of flight  
 35 feathers to mechanical friction (Moreno-Rueda  
 36 2011) and acting as an antimicrobial barrier to ker-  
 37 atinolytic microorganisms (Jacob *et al.* 1997,  
 38 Shawkey *et al.* 2003, Soler *et al.* 2008, Møller  
 39 *et al.* 2009, Martín-Vivaldi *et al.* 2010). It has also  
 40 been shown that UG size is inversely related to  
 41 the number of feather holes (Moreno-Rueda 2010,  
 42 2014), suggesting that the volume of preen oils  
 43 available might influence the formation of holes.  
 44 Although most studies attribute an important role  
 45 to preen oil in improving feather quality, the rela-  
 46 tionship of feather damage, FDB and UG size has  
 47 remained little studied.

48 We studied free-ranging House Sparrows *Passer*  
 49 *domesticus* to assess the relationships between FDB  
 50 load and flight feather quality by also taking into  
 51 account the potential mediating effects of UG size  
 52 and body condition. Birds were sampled in two dif-

ferent stages of their annual cycle, breeding and  
 non-breeding, which differ markedly in terms of  
 feather damage (Vágási *et al.* 2011), FDB preva-  
 lence (Burt & Ichida 1999) and UG volume (Pap  
*et al.* 2010). We assessed whether: (1) feather qual-  
 ity is related to FDB abundance, UG size and body  
 condition, (2) UG size and body condition are asso-  
 ciated with FDB load and (3) these relationships  
 differ between seasons and sexes. Based on the  
 expectation that keratinolytic parasites could  
 induce the formation of feather holes by disrupting  
 a feather's structural integrity (Vágási 2014), we  
 predicted a positive relationship between feather  
 damage (i.e. degree of feather wear and feather  
 hole load) and FDB abundance. We expected a  
 negative relationship between the feather damage  
 and UG size, in line with former studies (Moreno-  
 Rueda 2010, 2011, 2014). Finally, we predicted a **3**  
 positive relationship between FDB abundance and  
 UG size, as some recent studies indicated that UG  
 size increases with experimentally elevated micro-  
 bial pressure (Jacob *et al.* 2014b, Leclaire *et al.*  
 2015, but see Møller *et al.* 2009).

## METHODS

### General procedures **4**

We caught respectively 48 (26 males and 22  
 females) and 74 (39 males and 35 females) House  
 Sparrows with mist-nets (Ecotone, Poland) during **5**  
 the breeding (May 2012) and non-breeding sea-  
 sons (November 2012) at a farm near Bălcaciu  
 Village, central Transylvania, Romania (46°11'28"  
 N, 24°3'41"E). All birds captured in May were  
 adults (i.e. at least 1 year old); however, individu-  
 als caught in November were either adults or first-  
 year individuals. While males can be aged based  
 on the 'mask of seniority' (Nakagawa & Burke  
 2008), first-year and adult females cannot be dis-  
 tinguished based on plumage characters after the  
 complete post-juvenile moult. To overcome pseu-  
 doreplication, we did not sample the individuals  
 recaptured in November.

Birds were ringed and standard biometric data  
 were recorded: tarsus length ( $\pm 0.01$  mm with  
 digital callipers), body mass ( $\pm 0.1$  g with a Pesola  
 spring balance) and UG size. The volume of the  
 UG ( $\text{mm}^3$ ) is the product of maximum width,  
 length and height ( $\pm 0.01$  mm with digital cal-  
 lipers; see Pap *et al.* 2010). To increase the preci-  
 sion of our data, UG size was measured twice and

then averaged for each individual. Measurement precision was very high as shown by the large repeatability of UG volume both during the breeding ( $r = 0.964$ , 95% confidence interval (CI) = 0.943–0.984,  $P < 0.001$ ) and non-breeding seasons ( $r = 0.961$ , 95% CI = 0.944–0.979,  $P < 0.001$ ). Gland volume correlates with the amount of secretion produced in House Sparrows (Pap *et al.* 2010), therefore volume is a good proxy of the secretory capacity of the UG (Møller *et al.* 2009).

### Feather quality

Flight feather quality was characterized by two measures of feather damage: the degree of feather wear and the number of feather holes. Feather wear was scored separately for each of the 18 remiges of the left wing (the outermost primary is vestigial in sparrows) following Prater *et al.* (1977) as follows: 0 = unworn (i.e. immaculate feather tip), 1 = slightly, 2 = moderately, and 3 = very abraded (i.e. a considerably shorter feather, even with breakage at the tip). The scores of individual feathers were summed for an overall wing wear index. Feather holes were counted separately on the remiges of the left wing and on tail feathers, then individual counts were summed to obtain a total hole load (see also Vágási *et al.* 2011). Both parameters were quantified by the same person (CIV).

### Abundance of feather-degrading bacteria

Immediately after capture, we collected approximately five belly feathers following the method described by Czirják *et al.* (2013). We collected feather samples only from the belly, as it has been shown previously that bacterial abundances from different body regions of the same individual are positively correlated (Pearson's product-moment correlation of belly feathers vs. primary and secondary remiges:  $t = 3.424$ ,  $df = 128$ ,  $P < 0.001$ ,  $r = 0.289$ , 95% CI of  $r = 0.123$ – $0.439$ , A. Fülöp, G. Á. Czirják, P. L. Pap & C. I. Vágási unpubl. data from the same population; see also Gundersen *et al.* 2009). We took every measure to exclude the exogenous contamination of feathers. Briefly, before handling the birds, we washed our hands with ethanol (70%) and waited for this to evaporate completely to avoid the unintentional

killing of any bacteria on the feathers. Then we collected the feather samples using forceps that had been sterilized with ethanol (70%) and heat (flamed for at least 10 s). Feather samples were stored in sterile cryotubes and kept at 4 °C in a dark cool box until arriving at the laboratory (within 10 h), where samples were stored at – 20 °C until microbiological analyses took place. Further details are described elsewhere (Czirják *et al.* 2013).

The abundance of FDB (interchangeably used with FDB load) was measured under sterile conditions in the laboratory using the microbiological techniques described by Czirják *et al.* (2010). A detailed description of the methodology can be found in Appendix S1. FDB load was expressed as the number of colony-forming units per mg of feather (CFU/mg feather). These values were also used in the subsequent statistical analyses. All laboratory procedures and counts were performed blind with respect to the identity of individual birds and conducted by the same person (A.F.).

### Statistical analyses

Statistical analyses were carried out using the R statistical environment, version 3.1.1 (R Core Team 2014). Body condition was expressed as scaled mass index (SMI; Peig & Green 2009), which is a size-corrected body condition index calculated by the function  $SMI = \text{body mass} \times (19.14/\text{tarsus length})^{1.65}$ , where 19.14 is the mean tarsus length of the sample, and 1.65 is the slope of a model II standard major axis regression of log mass on log tarsus length calculated from the sampled individuals (R package 'lmodel2'; Legendre 2014). Prior to analyses, FDB load was  $\log_{10}$ -transformed to improve its distribution, and SMI, UG size and FDB load were scaled such that the mean = 0 and sd = 1 using the 'scale' function in R, which subtracts the sample mean from each individual's value and divides this by the sample sd.

To assess seasonal and sex differences in the measured traits we used generalized linear models (GLMs) with quasi-Poisson error distribution for the feather quality markers (feather holes and wear) and linear models (LM) with Gaussian distribution for SMI, UG size and FDB load. Traits were entered in separate models as dependent variables, with season, sex and their interaction as independent terms. Relationships between feather quality traits (feather holes and wear), entered as

dependent variables in the models, and sex, FDB load, UG size and SMI were assessed using GLMs with quasi-Poisson error distribution separately for the two seasons (breeding/non-breeding). The interactions between sex and other continuous predictors were also tested in all models. FDB load was analysed separately for the two seasons using LMs with Gaussian distributions. FDB load was entered as a dependent variable, whereas sex, UG size, SMI and the interaction of sex with UG size and SMI were included as independent terms.

In all cases, we first built saturated models that were simplified to minimum adequate models (MAMs) using a backward stepwise elimination procedure dropping non-significant ( $P > 0.05$ ) predictors and/or interactions with the largest  $P$ -value during each step. Exceptions were those non-significant main effects that were part of a significant interaction. Requirements of MAMs related to linearity, outliers and residual distribution were checked by plot diagnosis, and the potential multicollinearity issue between predictors was assessed by computing the variance inflation factor (VIF; R package 'car'; Fox & Weisberg 2011). Because all  $VIF < 4.61$ , we concluded that there was no multicollinearity that might alter our conclusions. Only the MAMs are presented in the main text (results of the full models are given in Tables S1–S4).

The reference levels for the factors season and sex are breeding season and males, respectively. Thus, negative values for season indicate that the averages are smaller during the non-breeding season, and negative values associated with sex indicate that sex-specific averages tend towards females. Model estimates ( $\beta$ )  $\pm$  se are reported throughout, and results are considered significant if  $P \leq 0.05$ .

## RESULTS

Each House Sparrow was infested with FDB (i.e. prevalence was 100% in both seasons) and the median, mean and sd for FDB load were 16.33, 25.71 and 22.93 during breeding (range: 4.40–123.75) and 17.81, 43.90 and 66.46, during non-breeding (range: 2.41–383.42), respectively.

### Seasonal and sex differences

The extent of feather wear and the number of feather holes was significantly greater during the

breeding season compared with the non-breeding season (wear:  $\beta = -2.765 \pm 0.171$ ,  $t = 16.130$ ,  $P < 0.001$ ; holes:  $\beta = -1.050 \pm 0.184$ ,  $t = 5.691$ ,  $P < 0.001$ ). The number of feather holes was significantly greater in males than in females ( $\beta = -0.478 \pm 0.184$ ,  $t = 2.590$ ,  $P = 0.010$ ), whereas feather wear was similar between the sexes.

Body condition (i.e. SMI) was similar between seasons and sexes. The size of the UG differed between seasons sex-dependently (UG  $\times$  sex interaction:  $\beta = -0.780 \pm 0.254$ ,  $t = 3.069$ ,  $P = 0.002$ ); sexes were similar in UG volume during the non-breeding season ( $\beta = -0.012 \pm 0.129$ ,  $t = 0.097$ ,  $P = 0.923$ ), but females had larger UG than males during the breeding period ( $\beta = 0.767 \pm 0.244$ ,  $t = 3.137$ ,  $P = 0.002$ ). Variation in FDB loads was not explained by either season or sex.

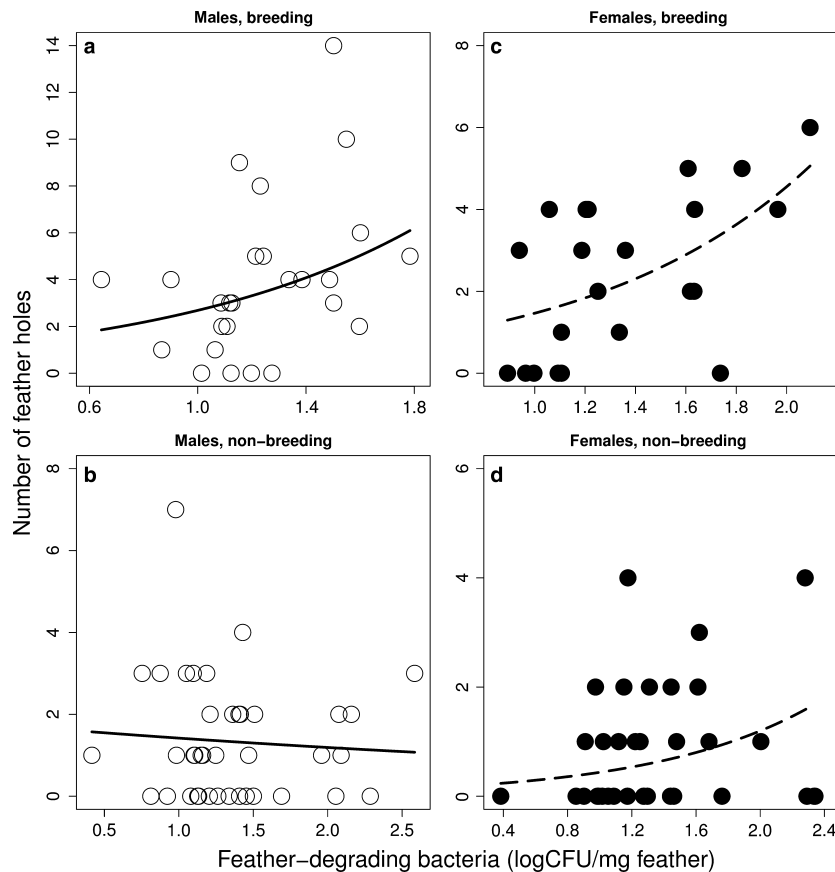
### Feather quality during breeding

The number of feather holes was negatively related to body condition (i.e. SMI) and UG size, and was positively associated with FDB load (Fig. 1a,c, Table 1). The extent of feather wear was not explained by any of the predictors (Table 1).

### Feather quality during non-breeding

The number of feather holes differed significantly between the sexes, males having more holes than females. The number of feather holes was also related to UG size and FDB load in a sex-dependent way, as shown by the significant two-way interactions (Table 1). In males, the number of feather holes was unrelated to SMI ( $\beta = -0.168 \pm 0.194$ ,  $t = 0.866$ ,  $P = 0.392$ ), UG ( $\beta = -0.077 \pm 0.185$ ,  $t = 0.418$ ,  $P = 0.678$ ) or FDB ( $\beta = -0.080 \pm 0.200$ ,  $t = 0.398$ ,  $P = 0.693$ ; Fig. 1b), whereas in females it was significantly negatively related to SMI ( $\beta = -0.399 \pm 0.185$ ,  $t = 2.153$ ,  $P = 0.039$ ) and UG size ( $\beta = -0.633 \pm 0.196$ ,  $t = 3.226$ ,  $P = 0.002$ ), and positively to FDB load ( $\beta = 0.485 \pm 0.188$ ,  $t = 2.430$ ,  $P = 0.021$ ; Fig. 1d).

The degree of feather wear was significantly negatively related to UG size, and was sex-dependently related to FDB load, as indicated by the significant sex  $\times$  FDB interaction (Table 1). The degree of feather wear was not related to SMI



**Figure 1.** Relationships between the abundance of feather-degrading bacteria and the number of feather holes in House Sparrows *Passer domesticus* for the different sexes and seasons ((a) breeding males; (b) non-breeding males; (c) breeding females; (d) non-breeding females).

( $\beta = -0.042 \pm 0.272$ ,  $t = 0.155$ ,  $P = 0.877$ ), UG size ( $\beta = -0.235 \pm 0.263$ ,  $t = 0.892$ ,  $P = 0.378$ ) or FDB load ( $\beta = -0.140 \pm 0.287$ ,  $t = 0.490$ ,  $P = 0.627$ ) in males, but it was significantly negatively related to UG size ( $\beta = -0.827 \pm 0.275$ ,  $t = 2.999$ ,  $P = 0.005$ ), and positively to FDB abundance ( $\beta = 0.884 \pm 0.271$ ,  $t = 3.261$ ,  $P = 0.002$ ) in females.

### Feather-degrading bacteria load

Feather-degrading bacteria load was sex-dependently related to UG size during the breeding season, as shown by the significant sex  $\times$  UG interaction ( $\beta = 0.519 \pm 0.243$ ,  $t = 2.128$ ,  $P = 0.039$ ); FDB load was not related to UG size in males ( $\beta = 0.004 \pm 0.209$ ,  $t = 0.024$ ,  $P = 0.981$ ), but was significantly positively related in females ( $\beta = 0.641 \pm 0.215$ ,  $t = 2.982$ ,  $P = 0.007$ ). Dur-

ing the non-breeding season, FDB load was significantly positively associated with UG size ( $\beta = 0.615 \pm 0.228$ ,  $t = 2.689$ ,  $P = 0.008$ ) in both sexes (sex  $\times$  UG interaction:  $\beta = 0.442 \pm 0.480$ ,  $t = 0.922$ ,  $P = 0.360$ ).

## DISCUSSION

### Feather holes

Our findings show that the number of feather holes has a negatively relationship to UG size and a positive relationship to FDB abundance in the breeding season. Even though the entire plumage is moulted at the end of breeding, these relationships were also observed for the freshly grown feathers in females in the non-breeding season. Earlier studies have referred to feather holes mostly as feeding traces of feather lice, and thus

**Table 1.** Minimum adequate models (MAMs) of generalized linear models of flight feather quality traits of House Sparrows *Passer domesticus* during the breeding and non-breeding seasons. For the main effect of the fixed factor 'Sex', males are included in the intercept, therefore the reported estimates show the extent to which females differ from males. The sign of estimates indicates the direction of associations.

Response/predictor	Estimate $\pm$ se	<i>t</i>	<i>P</i>
<b>Breeding</b>			
<i>Feather holes</i>			
(Intercept)	1.380 $\pm$ 0.133	10.370	< <b>0.001</b>
SMI	- 0.243 $\pm$ 0.112	2.159	<b>0.036</b>
UG	- 0.365 $\pm$ 0.115	3.175	<b>0.002</b>
FDB	0.512 $\pm$ 0.148	3.453	<b>0.001</b>
<i>Feather wear</i>			
(Intercept)	3.015 $\pm$ 0.043	68.900	< <b>0.001</b>
<b>Non-breeding</b>			
<i>Feather holes</i>			
(Intercept)	0.201 $\pm$ 0.238	0.843	0.402
Sex (female)	- 1.416 $\pm$ 0.510	2.772	<b>0.007</b>
UG	- 0.182 $\pm$ 0.291	0.627	0.533
FDB	- 0.057 $\pm$ 0.150	0.381	0.704
Sex $\times$ UG	- 1.195 $\pm$ 0.523	2.281	<b>0.025</b>
Sex $\times$ FDB	0.525 $\pm$ 0.262	2.004	<b>0.049</b>
<i>Feather wear</i>			
(Intercept)	- 0.573 $\pm$ 0.361	1.586	0.117
Sex (female)	0.097 $\pm$ 0.347	0.281	0.779
UG	- 0.989 $\pm$ 0.329	3.001	<b>0.003</b>
FDB	- 0.071 $\pm$ 0.253	0.281	0.779
Sex $\times$ FDB	0.733 $\pm$ 0.318	2.301	<b>0.024</b>

FDB, intensity of infestation by feather-degrading bacteria; SMI, scaled mass index; UG, uropygial gland volume. Significant *P*-values are highlighted in bold.

several studies used the number of holes as a substitute for lice load (Vágási 2014). Additionally, it has been assumed that UG secretions contain insecticides, which hamper the proliferation of lice (Moyer *et al.* 2003, Møller *et al.* 2010). Therefore, the negative relationship between the number of feather holes and UG size has been explained based on the basis that preen oil is a defence mechanism against chewing lice (Moreno-Rueda 2010). However, these explanations are not straightforward or well-substantiated in the literature (Vágási 2014).

We report for the first time that FDB load is positively related to feather hole incidence in agreement with an alternative hypothesis for the origin of feather holes (Vágási *et al.* 2011, Vágási 2014). This is also indicated by the negative relationship between feather hole load and UG size given the protective role of UG secretions against FDB (see below). Because feather lice infestation

was not quantified in our study, we cannot exclude the lice origin of the feather holes. However, the lice origin of feather holes seems to be unlikely in this species for the following reasons. Vas *et al.* (2008) reported that feather holes of small passerines are probably caused by *Brueelia* spp. lice, but in a previous study we found that House Sparrows from the same population were not infested by *Brueelia* spp. lice (Pap *et al.* 2013a). Furthermore, it has been suggested that Ischnoceran lice such as *Brueelia* spp. are probably incapable of chewing the large barbules and/or barbs of flight feathers (compared with body feathers) due to physical constraints imposed by mandible size (Vágási 2014). The suggestion that FDB are the major causative agents of feather holes, however, requires experimental demonstration and its generality in birds could be studied by means of phylogenetic comparison.

We found a positive association between FDB loads and UG volume in females during breeding and in both sexes in the non-breeding season. This indicates that the preen oil might have an important function in the regulation of plumage-dwelling microbial communities (Shawkey *et al.* 2003, Soler *et al.* 2008, Martín-Vivaldi *et al.* 2010, but see Czirják *et al.* 2013, Giraudeau *et al.* 2013). Our findings differ from those of Møller *et al.* (2009), who recovered a negative relationship between UG size and FDB abundance in breeding Barn Swallows *Hirundo rustica*. This might stem from the fundamental differences in life-history (e.g. terrestrial vs. aerial foraging) and ecological (e.g. sedentary vs. long-term migrant) attributes of the two species, which might lead to species-specificity in the amount of preen oil produced (Jacob & Ziswiler 1982, Vincze *et al.* 2013). However, our results are in line with two experimental studies performed on Great Tits *Parus major* and Feral Pigeons *Columba livia* (Jacob *et al.* 2014b, Leclaire *et al.* 2015). Both studies found that birds exposed to higher bacterial infection possessed larger UG. Taken together, the UG may partly have evolved, or been seconded, as a defence mechanism against FDB.

The number of feather holes was negatively related to body condition in both sexes during breeding, and only in females during the non-breeding season. Our results indicate that feather hole emergence can reflect body condition, and that feather quality depends on the individual's general state of health, both of which can be

1 influenced by parasites (Saag *et al.* 2011, Jovani  
2 *et al.* 2014). However, we found no relationship  
3 between body condition and FDB load. This sug-  
4 gests that body condition is a determinant of flight  
5 feather quality in House Sparrows, which may act  
6 independently from FDB or through other para-  
7 sites (Pap *et al.* 2013b).

### 9 Feather wear

10 We found that feather wear was not related to any  
11 of the model predictors during the breeding sea-  
12 son, when its extent is considerably higher than  
13 during the non-breeding season (i.e. after the com-  
14 plete annual moult). Feather wear, however, was  
15 negatively related to UG size and positively to  
16 FDB abundance in females during the non-breed-  
17 ing season. Our results from the breeding season  
18 are in line with previous studies indicating that  
19 feather abrasion is the consequence of mechanical  
20 friction (Burt 1986, Francis & Wood 1989, Jenni  
21 & Winkler 1994), rather than the harmful effect  
22 of FDB, as we found no relationship between bac-  
23 terial load and the intensity of feather wear. How-  
24 ever, the lack of relationship between UG and  
25 wear is in contrast with a previous study on the  
26 same species, in which a negative relationship was  
27 reported (Moreno-Rueda 2011). Discrepancies  
28 between the two studies might be attributed to  
29 the different timing of the studies, pre-breeding by  
30 Moreno-Rueda (2011) and breeding in this study.  
31 Note that the size of the UG is significantly smal-  
32 ler in both sexes during the pre-breeding period  
33 than during breeding, and there is no sex-differ-  
34 ence in UG size during pre-breeding, but during  
35 breeding females possess significantly larger glands  
36 than males (this study, Pap *et al.* 2010, Moreno-  
37 Rueda 2011). Such seasonal and sex-dependent  
38 variations in UG size might influence its relation-  
39 ship with feather abrasion.

40 The relationships between feather wear and UG  
41 size and between feather wear and FDB load,  
42 which were apparent in females during the non-  
43 breeding season, indicate a rather slight protective  
44 role of preen oil against feather wear and tear. The  
45 beneficial effect of preen oil on plumage function-  
46 ality was demonstrated by the stronger or faster  
47 physical feather deterioration in birds that had  
48 experimentally blocked or naturally smaller glands  
49 (Elder 1954, Jacob & Ziswiler 1982, Moyer *et al.*  
50 2003, Giraudeau *et al.* 2010b, Moreno-Rueda  
51 2011). Still, we found a minor indication that the

wear of flight feathers can be mitigated by the  
preen secretion.

### CONCLUSION

We demonstrate that damage to flight feathers,  
expressed as abundance of feather holes and extent  
of feather wear, is associated with diverse intrinsic  
factors such as body condition, UG size and FDB  
load, and that these relationships vary seasonally  
and/or sex-dependently. Our findings indicate that  
UG might play an important role in the regulation  
of plumage bacterial abundance, and hence medi-  
ate the potentially negative impact of FDB on  
flight feather quality. Experimental studies are  
needed to prove causation.

Lórinç Bărbos, Annamária Fenesi, Attila Marton  
and Zsófia Mezey are thanked for helping us catch  
birds. Alina Sesarman, Endre Jakab, Laura Pătraş,  
Cornelia Ochiş and Bianca Ianc provided logistical  
help during laboratory work. Csaba Paizs lent us  
the ultrasonic cleaner. All the laboratory work was  
carried out at the Molecular Biology Centre, Insti-  
tute of Interdisciplinary Experimental Research,  
Babeş-Bolyai University, with the support of Octa-  
vian Popescu and Annette Damert. Javier Pérez-  
Tris, Gregorio Moreno-Rueda, Rauri Bowie and an  
anonymous reviewer provided constructive criti-  
cism. Gareth Dyke kindly helped to polish our  
English. A.F. was financially supported by an  
excellence student scholarship of the Babeş-Bolyai  
University (30068/20/19.01.2012), G.Á.C. by  
funds from Leibniz Institute for Zoo and Wildlife  
Research, P.L.P. and C.I.V. by a research grant  
(PN II. RU TE 291/2010) from the Romanian  
Ministry of Education. During writing A.F. was  
financed by an OTKA grant (K112527), P.L.P. by  
a János Bolyai Research Scholarship of the Hun-  
garian Academy of Sciences and C.I.V. by the  
Postdoctoral Fellowship Programme of the Hun-  
garian Academy of Sciences. Transport between  
the Hungarian and Romanian teams was financed  
by a bilateral Tét grant (RO-HU 679/2013).

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Received 18 June 2015;  
revision accepted 16 December 2015.  
Associate Editor: Javier Perez-Tris.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Detailed methodology of the microbiological techniques used to quantify feather-degrading bacterial abundances.

**Table S1.** The full GLMs demonstrating seasonal (breeding and non-breeding) and sex differences for feather quality traits of House Sparrows *Passer domesticus*.

**Table S2.** The full LMs demonstrating seasonal (breeding and non-breeding) and sex differences for scaled mass index, uropygial gland volume and intensity of infestation by feather-degrading bacteria in House Sparrows *Passer domesticus*.

**Table S3.** The full GLMs of feather quality traits of House Sparrows *Passer domesticus* during the breeding and non-breeding seasons.

**Table S4.** The full LMs on the determinants of feather-degrading bacterial load of House Sparrows *Passer domesticus* during the breeding and non-breeding seasons.

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