Correlates of variation in flight feather quality in the Great Tit *Parus major*

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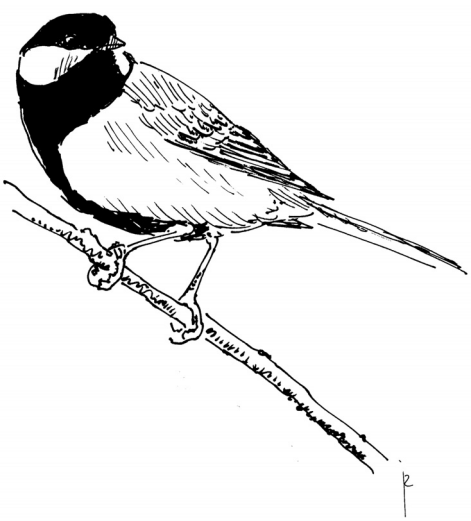

The most important function of moult in birds is the renewal of deteriorated feathers. Worn and holey remiges may incur fitness costs, yet little is known about the factors responsible for the degree of feather wear and sources of variation in feather hole incidence. Here, we report results on variation in feather quality based on a study of three consecutive annual cycles of a Great Tit *Parus major* population. We found that month, age, sex, weight and the presence of feather holes are the main sources of variation in degree of wear. Juveniles and individuals with lower feather quality (measured through rachis diameter) and with fault bars present had higher feather hole loads. Feather abrasion peaked in the breeding season and was higher in females probably due to higher workload. The lower feather quality of juveniles compared to adults probably arises because of fast ontogeny in contrast to adults' prolonged moult. Our results indicate that feather deformities are positively interrelated and can be used as proxies of feather quality. Our findings on the correlates of feather holes seem partially contradictory with the widespread view that holes are feeding marks of chewing lice. We propose that feather holes are instead minor feather handicaps, at least in Great Tits.

Key words: annual cycle, fault bar, feather deformities, feather hole, feather wear, flight feather quality, *Parus major*

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One of the primary functions of complete moult in birds is the renewal of old, deteriorated flight feathers, since damaged feathers may impair flight performance and ultimately reduce fitness. The gradual shortening of wing length and increasing dullness of flight feather colour following moult is a widespread and well-known phenomenon in birds (e.g. used for age classification; Svensson 1992). Yet less attention has been paid towards understanding which factors are responsible for the intensity of feather abrasion (but see Merilä & Hemborg 2000, Serra 2001). In a Collared Flycatcher *Ficedula albicollis* population Merilä & Hemborg (2000) found that age, sex and reproductive effort are the main factors that predict the degree of abrasion of the primaries. In several Grey Plover *Pluvialis squatarola* wintering populations, birds with a prolonged moulting period had less abraded feathers compared to individuals with fast moulting (Serra 2001). However, these investigations were conducted in only one season (breeding and wintering, respectively), thus information about the pattern of annual accumulation of feather wear is scarce. Similarly, the suspected dependence of feather deformities (such as feather holes and fault bars) on physical condition and feather quality and their predicted positive effects on feather wear are topics largely neglected. Although flight feathers abrade mainly at their tip (in our population 3–4 mm when heavily abraded, but without breakages), which consist of less than 5% of the total surface of the feathers, the abovementioned topics are worth investigating, because the reduced wing area (i.e. increased wing load) and the altered wingtip shape may influence the

flight performance of birds. For instance, studies on European Starlings *Sturnus vulgaris* demonstrated that birds with shortened and more rounded wingtips (which characterize the birds just before their annual complete moult) had a lower take-off angle and reduced flight speed (Swaddle *et al.* 1996, Swaddle & Lockwood 2003, Williams & Swaddle 2003). These capacities are predictors of escape success from a pursuing predator (Kullberg *et al.* 1998) in that they decrease the likelihood of escape when reduced. Therefore, understanding which factors contribute to feather usage may open an avenue to study the fitness consequences of worn feathers.

Impairment of flight ability could also result from the appearance of feather deformities during the period between two moults. Such abnormalities are the feather holes (with a diameter of approximately 0.5–1 mm) which appear on the vanes of flight feathers and are the consequences of missing barbs / barbules (Fig. 1 in Vas *et al.* 2008). Although this deformity is used as a proxy for feather quality (Pap *et al.* 2005, 2007), the relationship between feather hole abundance and feather quality has not been addressed. Considering the proximal causes of feather hole incidence, Kose & Møller (1999) found that the length of the outermost tail feather, a secondary sexual character in male Barn Swallows *Hirundo rustica*, negatively correlates with the occurrence of holes, suggesting that feather deformities are condition-dependent. Holes are thought to be the feeding traces of chewing lice (e.g. Møller 1991), but the available indirect results are ambiguous (Pap *et al.* 2005, Vas *et al.* 2008). Moreover, the causes and consequences of feather holes have only been investigated in Barn Swallows (e.g. Kose & Møller 1999, Barbosa *et al.* 2002, Pap *et al.* 2005, Møller 2010), a passerine which forages on the wing and is a long-distance migrant. It is also unclear which factors create variation in the frequency of feather holes.

Here, we report correlative results for a resident Great Tit *Parus major* population. Great Tits start breeding from mid April and nestlings generally fledge until early July. Between June and September, adults perform their annual complete post-breeding moult (primaries are replaced from the 1st innermost towards the 10th outermost), while juveniles replace only the tertials, rectrices, and their body feathers and wing coverts during the partial post-juvenile moult (Cramp & Perrins 1993, Pap *et al.* 2007, 2010). Birds were followed throughout three consecutive annual cycles by monthly sampling, allowing us to compare the breeding and the non-breeding season on a fine time-scale. Our aims were to examine (1) the main sources of variation in feather wear and incidence of feather holes; (2) whether different feather deformities (feather wear, feather holes and fault bars) are associated; (3) the possible causal link between 'true' feather quality variables (e.g. rachis width, barbule density; see Dawson *et al.* 2000) and feather hole load. We predicted that, during the annual cycle breeding activity will greatly deteriorate the quality of flight feathers due to increased locomotion in an abrasive environment and because there is less time available for self maintenance (i.e. preening). We also expect sex differences in feather usage since parental effort in tits is biased towards females (Cramp & Perrins 1993). Further, if feather deformities are dependent on feather quality (which is dependent on condition; see Pap *et al.* 2008), then they are expected to be positively related to each other. Provided that the condition of juveniles is generally lower and they develop the whole plumage in an extremely short period, we predicted that their feathers are of inferior quality compared to adults.

METHODS

Study population and procedures

We studied a Great Tit population situated in a 40-ha orchard of various old fruit-trees between March 2004 and May 2007 near Stana village, Transylvania, central Romania (46°89'N, 23°14'E). During three consecutive annual cycles, we captured Great Tits (n = 964, recaptures n = 448) with mist nets (Ecotone, Poland). After capture, we sexed and aged birds following Svensson's (1992) criteria. Here, 'juveniles' are birds before, whereas 'adults' are those after their first complete post-breeding moult. Note that in this categorisation, the 'juveniles' group contains both first- and second-year birds. The latter are reproductively active, but still prior to their first complete moult. We decided to choose this age division because, although second-year birds do breed, they differ from adults with respect to flight feather quality as they retain their primaries and secondaries during the first years' partial post-juvenile moult (see above; Pap *et al.* 2007). We were able to determine the sex and age of all individuals, because we present data only for the period outside the aforementioned moulting period, namely from September of one year to May of the next year (see below why we restricted the analyses to this period). We collected standard physical measurements: wing length (±0.5 mm with a ruler), tarsus length (±0.01 mm with a digital calliper), weight (±0.1 g with a Pesola spring balance), and the rachis diameter of the 8th primary

(±0.01 mm, measured with digital calliper at the tip of the 8th primary covert; 1st primary being the innermost), which is a proxy for feather quality (see Dawson *et al.* 2000). We calculated a condition-index using the residuals of the regression between tarsus length and weight.

Feather quality measurements

We categorized the degree of flight feather wear after 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). We scored all flight feathers separately, although in the analyses we only used the primaries, because of their greater function in flight compared to secondaries (Barta *et al.* 2006, Merilä & Hemborg 2000), and since they are significantly more worn than other flight feathers (pers. obs.). We computed a primary wear index by summing the abrasion score of nine fully developed primaries (the outermost primary is vestigial). Feather wear was not examined in adults and second-year juveniles between June and August when they were performing the annual complete post-breeding moult. Although newly fledged first-year juveniles shed only the tertials and rectrices during the partial post-juvenile moult, their feather wear data were also excluded if gathered in the above mentioned period, because at this time the wear index was on average zero with almost no variation. Thus we analysed the period between the end of the moult in the given year and beginning of the moult in the next year (i.e. September–May in our population). In order to test the assumption that feather wear depends on feather quality, we counted the number of fault bars (Fig. 1 in Sarasola & Jovani 2006) and feather holes (Fig. 1 in Vas *et al.* 2008) on the whole wing. Variation in the intensity of feather deformities can indicate individual condition, yet this has rarely been tested (but see Bortolotti *et al.* 2002, Pap *et al.* 2007). To provide more robust data, we assessed feather wear, the number of feather holes and fault bars on both wings, and then used the mean values in the subsequent analyses. In contrast to feather wear, feather holes are more evenly distributed across the different wing feathers (see Pap *et al.* 2007), therefore we used the number of holes on the whole wing. Another reason for using this parameter was the low occurrence of holes in the case of adults (see also Pap *et al.* 2007).

In order to evaluate the quality of the primaries more precisely, we collected the innermost primaries of both left and right wings in a subset of birds (n = 82), which were analysed later in the laboratory. From every pair of primaries a digital photograph was taken under standard light conditions and camera settings. From these recordings we measured the rachis diameter at the base of the feather vane. In case of feathers with at least one feather hole, we first digitalized the contour of the vanes and the line of the rachis; thereafter we geometrically transformed the points of the contour and rachis to set the naturally curvilinear rachis to be straight. Subsequently, the relative longitudinal position of the hole was measured, where the proximal (shaft) end of the vane was 0 and the distal end (tip) was 1. Photographs taken under microscope were used to quantify the density of barbules (measured at 3 barbs along a portion of 530 pixels length and then averaged). For these purposes (relative hole position, rachis width and barbule density measurement) we used the ImageJ software (Rasband 2008). All digital measurements were done by the same person (ES).

Statistical analyses

We performed two separate analyses for the two dependent variables (primary feather wear and whole wing feather hole number). The data were analysed by fitting generalized linear mixed effect models (GLMMs) with Poisson distribution of error terms and logarithmic link function. The identity (ID) of individuals, study year and ringer (CIV, PLP and JT) were entered as random factors, sex and age as factors, while month, biometrical variables and condition were included as covariates. The distributions of fault bars and feather holes among individuals were highly skewed even after data transformations, thus we converted them into binomial variables (present / absent) when analysing the effect of holes and fault bars on feather wear and the effect of fault bars on feather hole numbers. Initially we entered all explanatory variables and their second order interactions into the models and then used stepwise backward removal of those variables with $|z|$ scores < 2. Thus, only those explanatory variables were retained in the final minimal model that fulfilled the $|z| > 2$ criterion. We used this conservative criterion for significance testing instead of the actual probabilities because the derivation of these probabilities is not well founded theoretically (Pinheiro & Bates 2000, Crawley 2007). All analyses were carried out with the 'lmer' function ('lme4' package; Bates 2008) in the R statistical environment version 2.11.1 (R Development Core Team 2010).

RESULTS

Feather wear

Time of year (expressed in months) significantly explained the abrasion of primaries (Table 1). Birds had unworn feathers after their complete annual moult (adults) or fledging (juveniles), as expected. Feather wear score increased non-linearly during the annual cycle reaching its maximum during the breeding season, before the onset of post-breeding moult (Fig. 1A). The effect of age was significant during the whole annual cycle, since adults had less worn primary feathers than juveniles (Fig. 1A; Table 1). The pattern of seasonal change differed between the age classes, as indicated by the significant month × age interaction. This is caused by the absence of wear in adults as opposed to juveniles in September, but adults become nearly as worn as juveniles until May (Fig. 1A). Nonetheless, restricting the analysis to May revealed that adults had less worn primaries than juveniles (GLMM, estimate = –0.28, SE = 0.07, z = –3.83). Males and females differed in their degree of primary wear: females had less abraded feathers (Table 1) over the whole annual cycle, but their wearing trajectories diverged during the annual cycle as shown by the significant month × sex interaction (Fig. 1A; Table 1). Consequently, females become more abraded until May (May estimate = 0.15, SE = 0.07, z = 2.02).

Weight was negatively related to feather wear, indicating that the flight feathers of birds with higher body mass were less intensively abraded (Table 1). Wing length (estimate = –0.01, SE = 0.01, z = –0.26), tarsus length (estimate = –0.03, SE = 0.04, z = –0.79) and condition (estimate = 0.04, SE = 0.05, z = 0.89) did not explain any variation in the intensity of primary abrasion. Birds with higher rachis diameter had marginally more worn primaries (estimate = 0.87, SE = 0.49, z = 1.78). In the presence of feather holes, feather abrasion was more extensive (Table 1) and females with feather holes present tended to have more worn feathers (hole × sex: estimate = 0.13, SE = 0.08, z = 1.75). The presence of fault bars (estimate = 0.03, SE = 0.06, z = 0.52) was not related to the degree of wear.

Feather holes

The variation in the number of feather holes among individual Great Tits did not depend on month (estimate = 0.01, SE = 0.02, z = 0.43), thus the number of feather holes remained unchanged during the whole annual cycle (Fig. 1B). Juveniles had significantly higher hole loads than adults throughout the annual

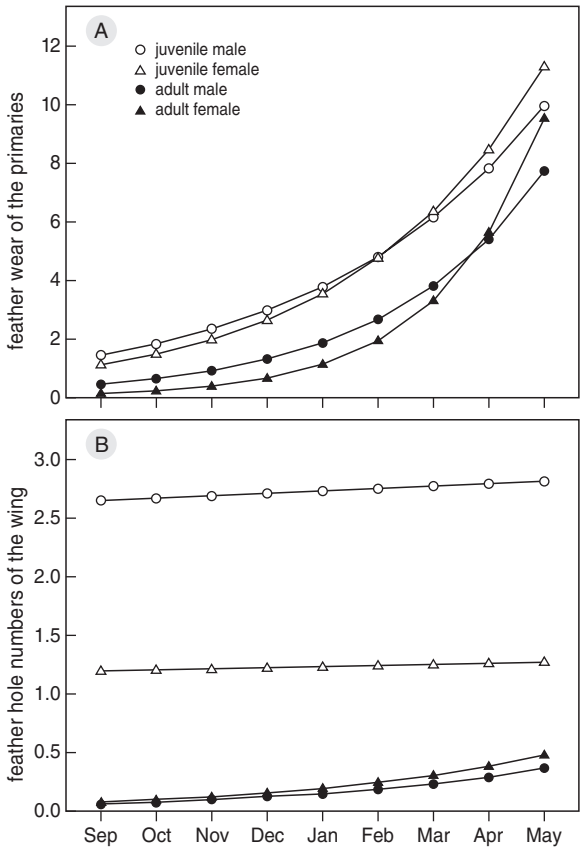

Figure 1. Seasonal variation of (A) feather wear of primaries and (B) feather hole numbers of the whole wing in juveniles and adults. The data plotted are estimates predicted by the model and transformed back to the original variable scale; lines are fits from the model.

Table 1. Estimated parameter values with SE and z-values of explanatory variables in the generalized linear mixed effect model to explain the intensity of feather wear of the primary feathers. The final model is presented.

Source	Estimate	SE	z
Intercept	1.49	0.38	3.95
Month	0.24	0.02	14.29
Age	–1.27	0.21	–6.13
Sex	–0.30	0.15	–2.06
Month × age	0.11	0.03	3.63
Month × sex	0.05	0.02	1.98
Age × sex	–1.03	0.40	–2.61
Weight	–0.07	0.02	–4.12
Feather holes	0.15	0.04	3.69

The variances of the random effects in the final model: birds' ID = 0.11, ringer = 0.03, year = 0.03.

cycle (Fig. 1B; Table 2). The significant age × sex interaction shows that juvenile males had significantly more feather holes than juvenile females, while the sex of adults had no effect (Fig. 1B).

Rachis diameter and wing length were significantly negatively related to the number of feather holes (Table 2), while weight (estimate = 0.04, SE = 0.04, z = 1.06), tarsus length (estimate = –0.14, SE = 0.13, z = –1.08) and condition (estimate = 0.03, SE = 0.04, z = 0.67) were unrelated to the number of holes in the wing. If fault bars were present, the incidence of feather holes was significantly higher (Table 2).

On the removed flight feathers, holes were more often present in the distal (65 out of 77 holes) than proximal part of the feather vane (12 out of 77 holes) and this differed significantly from a uniform distribution (χ^2_6 = 29.2, P < 0.001; Fig. 2). Feathers with thinner rachis had more holes (Spearman's rank correlation, r_S = –0.28, P = 0.0005; Fig. 3), while the density of barbules did not correlate with hole frequency (r_S = –0.12, P = 0.13). Results pertaining to rachis diameter corroborated the results based on data collected during field inspection (see above and cf. Table 2).

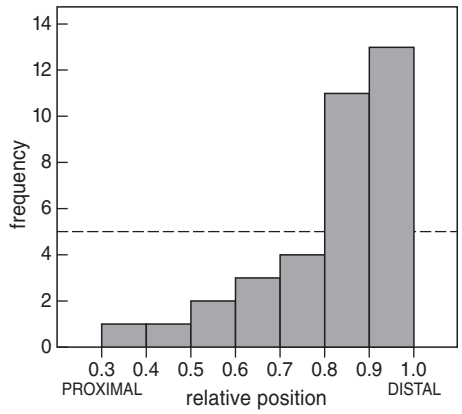

Figure 2. Frequency distribution of the relative feather hole position (0 = proximal end, shaft of the primary, 1 = distal end, tip of the primary). The dashed line represents the expected value calculated from the χ^2-test.

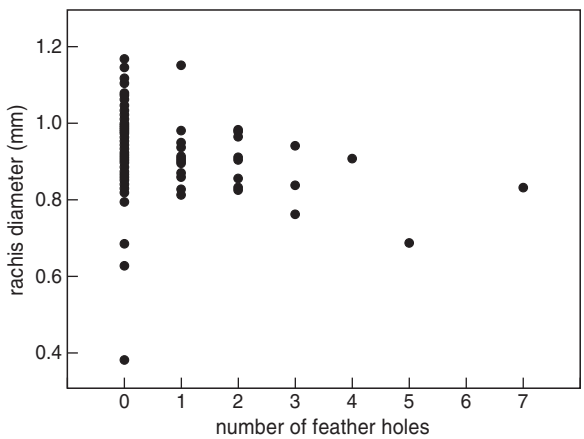

Figure 3. The relationship between rachis diameter and the number of feather holes measured on Great Tit feathers.

DISCUSSION

The fine scale time effect revealed that the abrasion rate of feathers became disproportionately accentuated during the annual cycle, reaching a peak in the breeding season. This non-linear increase can be ascribed to the higher workload and elevated locomotor activity during reproduction (Drent & Daan 1980). During peak chick provisioning, parents perform hundreds of daily trips between nest and feeding sites, meanwhile airborne particles, dense vegetation, and the cavity entrance and inner wall may abrade the primaries. Breeding-related costs can also explain the finding that females became more intensively worn during breeding. Parental duties of tits (Paridae) are female biased in terms of nest building, incubation inside an abrasive cavity and chick feeding rate (Cramp & Perrins 1993, Sanz *et al.* 2000). Moreover, the abrasion rate was marginally higher in females with feather holes present. This could be due to the non-uniform distribution of holes within individual primaries. Since the majority

Table 2. Estimated parameter values with standard errors and z-values of explanatory variables in the generalized linear mixed effect model to explain the intensity of feather hole incidence of the whole wing. Here only the final model is presented (month was also included owing to its interaction with age).

Source	Estimate	SE	z
Intercept	7.36	2.63	2.79
Age	–3.99	0.37	–10.65
Sex	–0.79	0.19	–4.15
Month	0.01	0.02	0.43
Month × age	0.22	0.05	3.94
Age × sex	1.08	0.30	3.64
Rachis diameter	–4.84	1.12	–4.33
Wing length	–0.09	0.03	–2.47
Fault bars	0.32	0.14	2.32

The variances of the random effects in the final model: birds' ID = 3.73, ringer = 0.003, year = 0.03.

of feather holes were situated close to the tip of the primaries, this may result in the breakage of the barbs positioned toward the tip (i.e. enhancing the abrasion status) mainly in the highly demanding period of reproduction.

Age was another significant predictor: juveniles bore feathers of lower quality, a pattern that was consistently true for each feather deformity (degree of abrasion, number of holes and fault bars; Pap *et al.* 2007). Juveniles have a short developmental period when all vital functions develop simultaneously, and these may compromise each other owing to resource-based trade-offs. Besides, the primaries and secondaries are retained during the partial post-juvenile moult, being shed only the next year. In comparison, adults grow their flight feathers during the prolonged complete post-breeding moult, when apparently only somatic growth occurs. These results corroborate our previous results showing a positive relationship between feather hole load and number of brood mates and relative laying date (Pap *et al.* 2007).

Our study provides evidence that the number of feather holes can be used as a proxy of flight feather quality (measured through rachis diameter; see Dawson *et al.* 2000) at least in juveniles where their prevalence is adequately high. We also showed that feather deformities are positively interrelated. These associations arise probably through the joint dependence of these variables on feather quality, which is affected by body condition during moult (Pap *et al.* 2008). This, in effect, means that birds in poor condition during moult grow lower quality remiges, which became more rapidly and intensely damaged. These possible long-term effects could have a pronounced impact on Great Tits, as feather deformities increase the breakage of feathers (Kose & Møller 1999, Sarasola & Jovani 2006) and are known to impair flight capacity (Barbosa *et al.* 2002, Swaddle & Lockwood 2003) by altering the wing load or the aerodynamic conditions.

According to a widespread paradigm, feather holes are feeding traces of Ischnoceran chewing lice (Phthiraptera), a conclusion based on correlative data involving mainly Barn Swallows (e.g. Møller 1991). Comparing sister taxa, Vas *et al.* (2008) suggested that feather holes in Barn Swallows and other passerines are probably caused by *Brueelia* spp., as only host species infected with these lice had holey feathers. However, our results are diametrically opposed to this, as hole prevalence was 62.2%, while we found no *Brueelia* spp. and no lice at all ($n = 23$ Great Tits examined visually combined with fumigation; C. Adam, P.L. Pap and C.I. Vágási, pers. obs.). Similarly, Shumilo & Lunkaschu (1972) inspecting 51 Great Tits found only *Menacanthus sinuatus* (Amblycera) and *Philopterus pallescens* (Ischnocera) with low prevalence (7.8% and 5.9%, respectively). In addition, we found that feather holes were situated disproportionately closer to the tip of the primaries, which questions the chewing lice origin of feather holes, since we expect ectoparasites to feed preferentially closer to the base of the remiges, where aerodynamic forces are the lowest, i.e. the risk of accidental falling is negligible. Although keratin remains were found in the stomachs of lice, these could derive from already broken feather fragments and/or body feathers. Moreover, among Barn Swallows, the number and distribution of feather holes strongly correlates with that of chewing lice (Møller 1991). Such correlations could also be found if highly parasitized birds are of inferior condition (Møller *et al.* 2004), and hence have lower-quality feathers (Pap *et al.* 2008) that have more handicaps (e.g. holes). Furthermore, the distribution pattern of fault bars among tits is also highly skewed (see Pap *et al.* 2007 for the same population), although bars are known to be caused by stressors acting during feather production rather than by ectoparasites. Finally, if chewed by lice, we would expect the number of holes to increase during the annual cycle, while this did not happen in our study. Based on our results, we propose an alternative explanation. Feather holes are possibly feather handicaps that emerge due to minor breaks on feather vanes occurring where the strength of barbs / barbules is locally compromised. Breaks could arise due to the failure of feathers to resist high mechanic stress (cyclic loads; Weber *et al.* 2010) on the tip of flight feathers (e.g. during breeding) or because barbs / barbules are weakened by feather-degrading bacteria. The first mechanical assumption is supported by our results (see above). For the second, there is evidence that colony-forming feather-degrading bacteria can cause breaks on barbs / barbules (Shawkey *et al.* 2007), which may result in formation of feather holes. However, this scenario remains to be tested, as bacteria are less likely to occur on wing feathers compared to ventral contour feathers (Burtt & Ichida 1999). Furthermore, Great Tits are found to have a reduced mean number of bacilli phylotypes (Saag *et al.* 2008), and it is still unknown, whether keratinolytic bacteria spores are able to develop on the feathers of living birds (Muza *et al.* 2000), because preen oils have a sanitation function in inhibiting bacteria growth (Shawkey *et al.* 2003). Altogether, we suggest more caution regarding the origin of feather holes, until well-designed, rigorous experimental studies are performed.

To summarize, we have shown that breeding may incur significant costs in terms of flight feather usage. Primaries of females are more abraded than those of males during the breeding season. The frequency of feather abnormalities may depend on the condition and feather quality of the birds. We have also found that feather abnormalities were positively interrelated: Great Tits with feather holes had more abraded primaries, and those with fault bars on flight feathers had a higher incidence of feather holes. These results may serve as starting-point for future studies aiming to explore how condition-dependent feather quality may be translated to age-specific reproductive output, among individual differences in fitness-related traits and the evolution of repair or mitigating mechanisms (e.g. moult, melanin-pigment allocation) that reduce the possible adverse effects of feather deformities.

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REFERENCES

Barbosa A., Merino S., de Lope F. & Møller A.P. 2002. Effects of feather lice on flight behavior of male barn swallows (*Hirundo rustica*). Auk 119: 213–216.

Barta Z., Houston A.I., McNamara J.M., Welham R.K., Hedenström A., Weber T.P. & Feró O. 2006. Annual routines of non-migratory birds: optimal moult strategies. Oikos 112: 580–593.

Bates D. 2008. lme4: Linear mixed-effects models using S4 classes. URL: http://lme4.r-forge.r-project.org.

Bortolotti G.R., Dawson R.D. & Murza G.L. 2002. Stress during feather development predicts fitness potential. J. Anim. Ecol. 71: 333–342.

Burtt E.H., Jr. & Ichida J.M. 1999. Occurrence of feather-degrading bacilli in the plumage of birds. Auk 116: 364–372.

Cramp S. & Perrins C.M. 1993. The birds of the western Palearctic, vol. 7. Oxford University Press, Oxford.

Crawley M.J. 2007. The R book. John Wiley & Sons, Chichester, UK.

Dawson A., Hinsley S.A., Ferns P.N., Bonser R.H.C. & Eccleston L. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proc. R. Soc. Lond. B 267: 2093–2098.

Drent R.H. & Daan S. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225–252.

Kose M. & 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.

Kullberg C., Jakobsson S. & Fransson T. 1998. Predator-induced take-off strategy in great tits (*Parus major*). Proc. R. Soc. Lond. B 265: 1659–1664.

Merilä J. & Hemborg C. 2000. Fitness and feather wear in the Collared Flycatcher *Ficedula albicollis*. J. Avian Biol. 31: 504–510.

Møller A.P. 1991. Parasites, sexual ornaments, and mate choice in the barn swallow. In: Loye J.E. & Zuk M. (eds) Bird–parasite interactions: ecology, evolution, and behaviour. Oxford University Press, New York, pp 328–343.

Møller A.P. 2010. Host–parasite interactions and vectors in the barn swallow in relation to climate change. Glob. Change Biol. 16: 1158–1170.

Møller A.P., de Lope F. & Saino N. 2004. Parasitism, immunity, and arrival date in a migratory bird, the barn swallow. Ecology 85: 206–219.

Muza M.M., Burtt E.H., Jr. & Ichida J.M. 2000. Distribution of bacteria on feathers of some Eastern North American birds. Wilson Bull. 112: 432–435.

Pap P.L., Tökölyi J. & 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. & 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.

Pap P.L., Vágási C.I., Czirják G.Á. & Barta Z. 2008. Diet quality affects postnuptial molting and feather quality of the house sparrow (*Passer domesticus*): interaction with humoral immune function? Can. J. Zool. 86: 834–842.

Pap P.L., Vágási C.I., Tökölyi J., Czirják G.Á. & Barta Z. 2010. Variation in haematological indices and immune function during the annual cycle in the Great Tit *Parus major*. Ardea 98: 105–112.

Pinheiro J.C. & Bates D.M. 2000. Mixed-effects models in S and S-PLUS. Springer-Verlag, New York.

Prater A.J., Marchant J.H. & Vuorinen J. 1977. Guide to the identification and aging of Holarctic waders. BTO Guide 17, BTO, Tring, UK.

R Development Core Team 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org.

Rasband W.S. 2008. ImageJ, release version 1.37. National Institutes of Health, Bethesda, Maryland. URL http://rsbweb.nih.gov/ij.

Saag P., Mänd R., Tilgar V., Mägi M. & Kilgas P. 2008. Feather degrading bacteria as a factor potentially affecting breeding performance in great tits *Parus major*. 12th International Behavioral Ecology Congress, Ithaca, p. 259.

Sanz J.J., Kranenbarg S. & Tinbergen J.M. 2000. Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). J. Anim. Ecol. 69: 74–84.

Sarasola J.H. & 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.

Serra L. 2001. Duration of primary moult affects primary quality in Grey Plovers *Pluvialis squatarola*. J. Avian Biol. 32: 377–380.

Shawkey M.D., Pillai S.R. & 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. & Roberts S.R. 2007. Bacteria as an agent for change in structural plumage color: correlational and experimental evidence. Am. Nat. 169: S112–S121.

Shumilo R.P. & Lunkaschu M.I. 1972. Mallophaga from wild terrestrial birds of the Dnester-Prut region. Moldavian Academy of Sciences. (In Russian)

Svensson L. 1992. Identification guide to European passerines, 4th edn. Stockholm.

Swaddle J.P. & Lockwood R. 2003. Wingtip shape and flight performance in the European Starling *Sturnus vulgaris*. Ibis 145: 457–464.

Swaddle J.P., Witter M.S., Cuthill I.C., Budden A. & McCowen P. 1996. Plumage condition affects flight performance in Common Starlings: implications for developmental homeostasis, abrasion and moult. J. Avian Biol. 27: 103–111.

Vas Z., Csörgő T., Møller A.P. & 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.

Weber T.P., Kranenbarg S., Hedenström A., Waarsing J.H. & Weinans H. 2010. Flight feather shaft structure of two warbler species with different moult schedules: a study using high-resolution X-ray imaging. J. Zool. 280: 163–170.

Williams E.V. & Swaddle J.P. 2003. Moult, flight performance and wingbeat kinematics during take-off in European starlings *Sturnus vulgaris*. J. Avian Biol. 34: 371–378.

SAMENVATTING

Vogels ruien om oude, versleten veren te vervangen door nieuwe. Versleten slagpennen met gaten kunnen ten koste gaan van de kans op overleving en voortplanting. Toch is er maar weinig bekend over de factoren die verantwoordelijk zijn voor de mate van slijtage aan veren en wat de veroorzakers zijn van gaten in veren. Deze studie beschrijft mogelijke oorzaken van variatie in veerkwaliteit bij de Koolmees *Parus major* en is gebaseerd op drie achtereenvolgende jaarcycli. De auteurs laten zien dat variatie in de mate van veerslijtage voornamelijk samenhangt met de tijd van het jaar, de leeftijd, het geslacht en het gewicht van de vogel en met de aanwezigheid van gaten in de veren. Juveniele vogels en individuen met een lage veerkwaliteit en met zogenaamde fault bars (veerafwijkingen) hebben daarbij meer gaten in hun veren dan andere vogels. Veerslijtage vond vooral plaats tijdens het broedseizoen en was het grootst bij vrouwtjes, hoogstwaarschijnlijk als gevolg van hun grotere werkdruk. De auteurs verklaren het verschil in veerkwaliteit tussen juveniele en adulte vogels door het versnelde ruiproces dat bij juveniele vogels optreedt. Verschillende maten van gebreken en slijtage in de veren correleerden met elkaar en kunnen dus gebruikt worden als een indicator voor veerkwaliteit. Het idee dat gaten in veren een mate voor veerkwaliteit zijn, staat in contrast met de huidige gedachte dat deze gaten vraatsporen zijn van veerluizen. De auteurs stellen echter dat deze gaten, in het geval van de Koolmees, kleine misvormingen zijn die bij de ontwikkeling van de veren zijn ontstaan. (KvO)

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