

Frequency and consequences of feather holes in Barn Swallows *Hirundo rustica*

PÉTER LÁSZLÓ PAP,^{1*} JÁCINT TÖKÖLYI² & TIBOR SZÉP³

¹Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, H-4010 Debrecen, Hungary

²Department of Zoology, Babeş-Bolyai University, RO-3400 Cluj Napoca, Clinicilor Street 5–7, Romania

³Department of Environmental Sciences, College of Nyíregyháza, PO Box 166, H-4401 Nyíregyháza, Hungary

The relationship between feather quality, estimated through the prevalence and intensity of feather holes, and the breeding performance and survival of the Barn Swallow *Hirundo rustica* was studied over a 5-year period. In addition, we present some indirect data on the role of chewing lice in producing the feather holes. The balanced distribution of feather holes (high prevalence, low aggregation) corresponds with the pattern of distribution of lice on colonial birds, and in the Barn Swallow. Feather holes were significantly and positively associated with the arrival dates of the birds, as both males and females with an increased number of feather holes started laying later. Females that survived the winter had significantly fewer holes than non-surviving females, whereas there was no difference in feather hole number between surviving and non-surviving males. Given that there was no association between the number of feather holes and body condition indices, except for the tail length of male Barn Swallows, we suggest that the negative effect of feather holes on the fitness of the birds is mainly apparent during periods of intensive locomotor activity, such as migration. Alternatively, if feather holes are an indicator of quality, those birds with a high intensity of feather holes may have been of poor quality. These birds may have been less able to cope with the environmental conditions, resulting in the lower survival and later arrival of the birds to the breeding grounds. The negative relationship between the length of the outermost tail feathers of males and the incidence of feather holes suggests that the tail is a condition-dependent secondary sexual characteristic.

Feather length is a crucial factor determining the fitness of birds by altering flight and manoeuvre capacity (Swaddle *et al.* 1996). Feather damage is closely related to feather quality (Bonser 1995), which is determined by intrinsic (e.g. genetic, developmental) and extrinsic (e.g. habitat preference, locomotor activity) factors (Dawson *et al.* 2000, Merilä & Hemborg 2000). Feathers are damaged by mechanical abrasion (e.g. wear, feather breakage), photochemical processes and ectoparasites, such as chewing lice (Clayton 1990, Jenni & Winkler 1994).

As with any other feature of life history, reproduction represents a significant cost to the host, which

can be expressed in various ways (Stearns 1992). Enhanced parental activity of breeding birds, which leads to an increased use of traits such as flight feathers, results in a trade-off between reproduction and self-maintenance. In birds, increased reproductive effort might increase feather wear due to the intensity of foraging trips, together with a loss of feather mass as well as increased feather damage caused by feather lice as the parents have insufficient time to preen adequately. Despite evidence of feather damage, few attempts have been made to investigate the sources of variation in feather quality and the effect of feather quality on the breeding performance and survival of birds (but see Dawson *et al.* 2000, Merilä & Hemborg 2000). An experimental study on the migratory Collared Flycatcher *Ficedula albicollis* has shown that parents trade-off parental activity with feather wear, and ultimately feather quality seems to

*Corresponding author. Present address: Department of Zoology, Babeş-Bolyai University, RO-3400 Cluj Napoca, Clinicilor Street 5–7, Romania.

Email: peterpl@hasdeu.ubbcluj.ro

affect the survival capacity of the birds (Merilä & Hemborg 2000). Similarly, feather quality estimated as the number of feather holes of the male Barn Swallow *Hirundo rustica* has been related to individual variation in breeding performance throughout mate selection (Kose & Møller 1999), although direct evidence of the effect of feather holes on fitness is still largely lacking. The reduced fitness of birds with more feather holes can be related partly to the detrimental effect of feather holes on the flight performance of the birds through the transmission of air through feathers. This could alter the aerodynamic efficiency, and increase the risk of feather breakage (Kose & Møller 1999, Barbosa *et al.* 2002). Thus, the quality of flight feathers should be crucial to individuals performing intensive locomotor activity, such as that undertaken by aerial insectivorous and migratory birds.

It had been thought that the feather holes of Barn Swallows were produced by chewing lice (Mallophaga; Møller 1991, Kose & Møller 1999). However, apart from a positive correlation between the numbers of feather holes and of individual lice (*Phthiraptera*, *Machaerilaemus malleus*, formerly *Hirundoecus malleus*), the fact that most feather holes occurred in the white parts of the largely black tail feathers of Barn Swallows, and that the white spots of feathers are preferred by lice (Møller 1991, Kose & Møller 1999, Kose *et al.* 1999), we can find no study in which the origin of feather holes has been tested.

The aim of this study is two-fold: first, we present some indirect evidence that chewing lice produced feather holes, by comparing indices of distribution and aggregation of feather holes with data on lice, and we describe factors that might affect the variation in the number of feather holes of individuals. Secondly, we examine the relationship between feather holes and several fitness measures of the Barn Swallow. We studied the possible short- and long-term effect of feather holes on breeding performance of the birds during a 5-year period by examining the relationship between feather holes, differential morphological variables and breeding parameters, and by analysing retrospectively the different number of feather holes in surviving and non-surviving birds.

METHODS

The study was carried out in Balmazújváros (47°37'N, 21°21'E), eastern Hungary, during the breeding seasons 1999–2003. The Swallows bred either in one of

three colonies or solitarily on farms, and were studied from their arrival in April to the start of their second clutch at the end of July. During this time more than 95% of the breeding birds were captured and individually marked with a combination of colour rings and with a numbered metal ring. For each nest the breeding birds were identified from their colour ring combinations and by capturing them with a nest trap. While trapping, one of the authors (P.L.P.) used standard measurements including: wing length and outermost tail feather length (0.5 mm precision using a ruler), tarsus length (0.01 mm precision using a pair of callipers) and body mass (0.1 g precision using a spring balance) (Svensson 1984). Considering bilateral morphological variables, the left and right sides were measured and we used the average value of the two measurements in the analyses. The number of feather holes on left and right primaries and on tail feathers were counted separately. For the present study we used the pooled values for feather holes from the wing and tail feathers.

The breeding performance of the birds was assessed by inspecting the nests every second day, and determining the laying date of the first egg, the clutch size and the brood size when the nestlings were 12 days old. In three years (2000–02) we estimated the condition of 12-day-old nestlings by measuring the body mass, wing length and tarsus length, and we recorded the feeding rate of males and females on days 10–12 after hatching for 1 h between 07:00 and 12:00 h, the time of day when feeding rate is highest. We recorded feeding rates only on sunny days. We performed the same capture–recapture effort each year, and standardized the measurements and feather hole counting on the birds. Thus the results obtained during the 5-year study could be compared.

Previous observations on this species (Møller 1994) and our capture–recapture data indicate a high breeding philopatry. As the capture rate of the marked birds was high and constant over the study period, the survival of the birds between years can be assessed accurately, permitting the relationship between feather-hole number and fitness to be studied. Survival of the birds was assessed only for those captured as breeders in both capture and recapture years (1999–2002). For birds captured at least twice in different years, their data from a single year were included randomly in all analyses, except in the analysis of feather-hole repeatability. This was undertaken to avoid pseudoreplication, as the birds presented very similar values in different years (see Results for analyses of repeatability of feather holes).

As feather holes showed a normal distribution, we used parametric statistics in the analysis.

To describe the distribution patterns of feather holes, we used several indices from the parasitological literature following the recommendations of Rózsa *et al.* (2000). The following measures were applied: prevalence (%) was estimated as the proportion of hosts with feather holes within the samples examined; mean intensity as the arithmetic mean of the number of feather holes per individual with feather holes; and indices of aggregation such as k of the negative binomial distribution and D the index of discrepancy. The value of k decreases and D increases with increasing levels of aggregation. Feather-hole quantification was carried out using the program 'Quantitative Parasitology 2.0' (Reiczigel & Rózsa 2001).

RESULTS

Distribution and repeatability of feather holes on males and females

Prevalence of feather holes was high for both sexes: 99% of both males and females (345/348 males and 321/325 females) had feather holes. The mean intensity of feather holes was 28.7 and 28.2 for males and females, respectively. Feather holes showed a normal distribution for both sexes (Kolmogorov–Smirnov test, males: $d = 0.05$, $P > 0.2$; females: $d = 0.06$, $P > 0.1$, Fig. 1), but the data tended to skew in accordance with a negative binomial model. The aggregation indices k and D were 2.71 and 0.312 for males and 2.20 and 0.339 for females. The total number of holes did not differ significantly between sexes (Student's t -test, $t = 0.5$, $n = 671$, $P = 0.62$). This was the case also for the relative number of holes, because after controlling for tail length and wing length the difference between sexes remained non-significant ($F_{1,663} = 2.49$, $P = 0.06$). Repeatability between years of feather-hole number was low to moderate, but significant (males: $R = 0.27$, $F_{77,119} = 1.94$, $P < 0.001$; females: $R = 0.41$, $F_{80,116} = 2.70$, $P < 0.001$). Because a complete moult would have occurred between observations, this indicates that the susceptibility of individuals to obtaining feather holes was consistent over time.

Breeding performance and survival

To test the relationship between laying date, feather-hole number and condition indices we used a stepwise

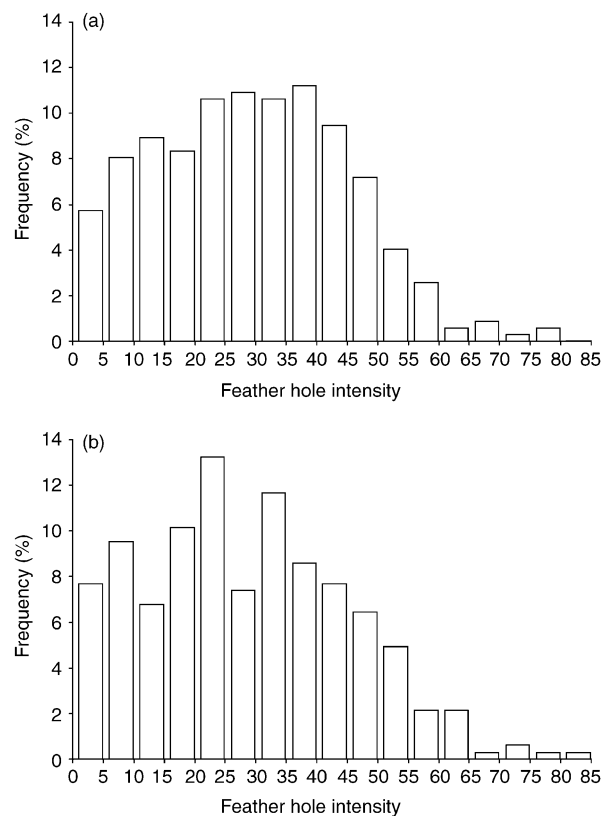


Figure 1. Frequency distribution of feather holes on male (a) and female (b) Barn Swallows.

generalized linear model (GLM), in which first we introduced all possible explanatory variables (number of feather holes, year, wing length, tail length, tarsus length and body mass), and then, using a backwards procedure, we eliminated all continuous predictor variables lower than the critical value (see Zar 1984, p. 342). The potentially confounding variable (year) was included in the model as a categorical explanatory variable, as the number of feather holes and different morphological variables varied between years for males (one-way ANOVA, feather holes: $F_{4,343} = 4.89$, $P < 0.001$; wing length: $F_{4,361} = 4.71$, $P = 0.001$; tarsus length: $F_{4,355} = 3.54$, $P = 0.008$; body mass: $F_{4,352} = 3.55$, $P = 0.008$) and females (feather holes: $F_{4,320} = 5.38$, $P = 0.0003$; wing length: $F_{4,338} = 6.36$, $P < 0.0001$; body mass: $F_{4,332} = 3.85$, $P = 0.005$). The number of feather holes was related significantly to the female's laying date in both sexes (Table 1a, Fig. 2), whereas, with the exception of female tail length, morphological variables known as condition indices were far less important in explaining variation in the laying date.

Table 1. Results of the stepwise GLMs of the relationship (a) between laying date and condition indices and the number of feather holes in males and females and (b) between number of feather holes and condition indices in male Barn Swallows. Tail length, wing length, tarsus length and body mass are considered as condition indices and we show only the selected variables. For females there was no effect of feather holes on any condition indices.

Variable	MS	df	F	P
(a) Laying date				
Male				
Feather holes	1232.4	1	9.03	0.003
Year	345.2	4	2.53	0.04
Model	$F_{5,183} = 12.43, r^2 = 0.06, P < 0.001$			
Female				
Tail length	1014.5	1	7.4	0.007
Feather holes	3596.5	1	26.24	< 0.001
Model	$F_{2,200} = 19.29, r^2 = 0.16, P < 0.001$			
(b) Number of feather holes				
Male				
Tail length	945.6	1	4.04	0.045
Year	1091.1	4	4.66	0.001
Model	$F_{5,340} = 4.66, r^2 = 0.06, P < 0.001$			

Analysing the relationship between the number of feather holes and the breeding performance of males and females, while controlling for potentially confounding variables (laying date, wing length, tail length, tarsus length and body mass) in a stepwise GLM (see Table 1a), we found no significant effect on clutch size, brood size, breeding success or the condition of the nestlings. We found similar results for feeding activity of males and females, because there was no relationship between the number of feather holes and parental activity (males: $F_{3,124} = 0.41, P = 0.75$; females: $F_{3,116} = 2.1, P = 0.1$).

Over the 4 years we found that non-surviving females consistently had more feather holes than did surviving females (two-way ANOVA, year: $F_{3,142} = 1.79, P = 0.15$; survival: $F_{1,142} = 4.58, P = 0.04$, Fig. 3), suggesting a negative effect of feather holes on the survival prospects of female Barn Swallows. The difference between groups remained significant even after controlling for tail length ($F_{1,139} = 4.75, P = 0.03$), wing length ($F_{1,141} = 4.77, P = 0.03$) and tarsus length ($F_{1,141} = 4.44, P = 0.04$). We found no such difference for males ($F_{1,128} = 0.06, P = 0.87$, Fig. 3), even after controlling for tail length, wing length and tarsus length ($P > 0.1$). In contrast to females, the difference between surviving and non-surviving males with respect to the number of feather holes was not consistent between years ($F_{3,128} = 3.77, P = 0.013$):

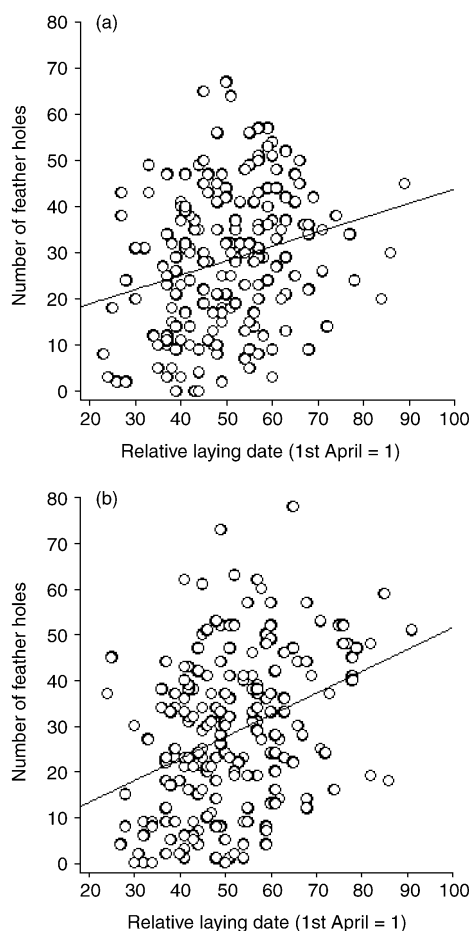


Figure 2. Feather hole number of male (a) and female (b) Barn Swallows in relation to laying date. Male: $F_{1,183} = 12.43, P < 0.001$, slope (se) = 0.252 (0.072); female: $F_{1,202} = 31.06, P < 0.001$, slope (se) = 0.365 (0.066).

in some years the surviving birds had more feather holes, whereas in other years the non-surviving birds had more feather holes, although this was not statistically significant.

Relationship between body condition and number of feather holes

We analysed the relationship between feather holes (dependent variable) and different morphological variables separately for both sexes, in a stepwise GLM, while controlling for potentially confounding variables (see above). We found no significant relationship between feather-hole number and different morphological variables, except that for males the tail length declined with increasing feather-hole number (Table 1b).

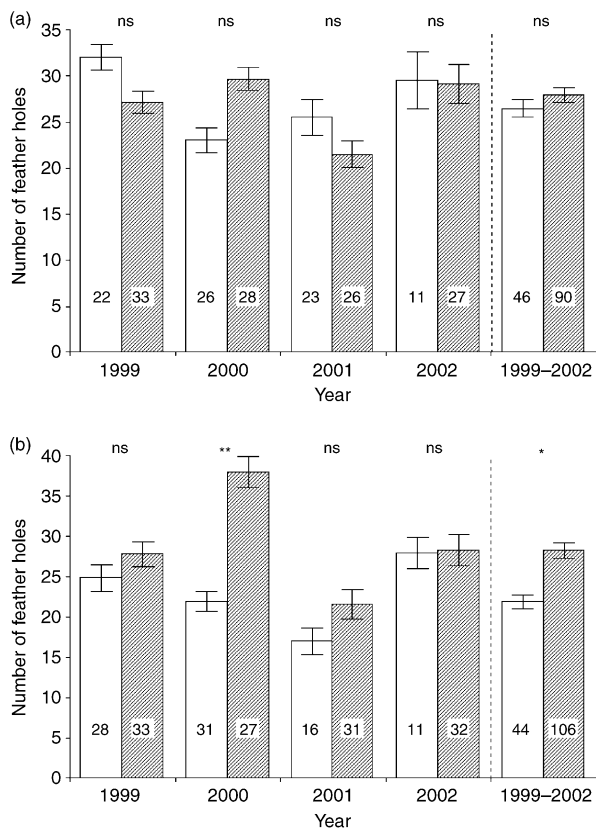


Figure 3. Difference in the number of feather holes between surviving and non-surviving male (a) and female (b) Barn Swallows between 1999 and 2002 and in the pooled data (mean \pm se). Open – surviving, shaded – non-surviving.

Correlation of feather holes within pairs of birds

If feather holes are produced by lice as suggested above (see Introduction), given that lice are transmitted among hosts through direct contact (Clayton & Tompkins 1994, Hillgarth 1996), we should expect a positive correlation in the number of feather holes between birds within pairs. We tested the possibility that birds can be infected from their mates in two ways. First, testing the relationship across pairs of birds in year i and the number of holes counted in the same year (i) we found no significant correlation in feather-hole number ($r = 0.1$, $n = 235$, $P = 0.15$). Secondly, as the birds perform a complete moult during winter, the feather holes counted during the breeding period must have been produced since the last moult. As a consequence, if the birds are infested at least partially from their mates in year i , then a correlation between the infestation rate – based on

the number of feather holes – and between birds in a pair might be revealed 1 year later. Analysing the relationship between feather holes of males and females that formed a breeding pair in the previous year ($i - 1$), but counted in year i , the correlation again showed no significant relationship ($r = 0.32$, $n = 28$, $P = 0.1$), indicating either that there is a low transmission rate of lice between mates during the breeding season, or that this effect is masked by the horizontal transmission of lice between individuals during the roosting period in the winter grounds.

DISCUSSION

Aggregation is a well-known property of parasite distributions, which is best described by the negative binomial model (Bush *et al.* 2001). This means that most individual hosts have few parasites, while a few individuals have many parasites. The distribution of lice depends on various extrinsic factors such as the host's social behaviour. Comparative studies on birds have shown that louse aggregation is reduced in colonial species (Rózsa *et al.* 1996, Rékási *et al.* 1997). In relation to territorial birds, the low aggregation of parasites on colonial hosts is reflected by an increased prevalence and a decreased level of aggregation, which is reflected by an increase in k and a decrease in D . The 'uniform' distribution of lice on colonial birds is presumably due to an increased opportunity for horizontal transmission (Rózsa *et al.* 1996). If we consider feather holes as an accurate index of louse infestation (Møller 1991), the distribution values observed by us are lower than the average values observed for lice in other studies, but are still within the range of louse prevalence and aggregation observed in colonial birds (Rékási *et al.* 1997). Furthermore, the high prevalence of feather holes described here is close to the values for two louse species observed by Camplani *et al.* (1999) in three Barn Swallow populations (on average 84.2% and 97.1% for two louse species). Thus our data on feather holes agree with the general pattern observed for lice on colonial birds and specifically with that of the semi-colonial Barn Swallow. Despite this evidence, other possible sources of origin for the feather holes cannot be excluded. For example, developmental anomalies during the moulting period (Bortolotti *et al.* 2002) can produce feather abrasions similar to feather holes, resulting in an overestimate of their prevalence and a change in distribution pattern. Direct experiments are required to elucidate the importance of feather lice as the cause of feather holes. Furthermore,

it is important to consider the relative importance of the two most common louse species found on the Barn Swallow with respect to the occurrence of feather holes. Whereas in some studies the feather holes are considered to be produced by the species *Machaerilaemus malleus* (Møller 1991, Kose & Møller 1999, Kose *et al.* 1999), others considered them to be produced by *Myrsidea rustica* (Barbosa *et al.* 2002), the latter a species also found in the earlier studies.

Assuming that feather holes are indeed produced by lice, the repeatability of feather-hole intensity between years indicates the persistence of lice, and as a consequence a long-term effect of lice on birds, especially on females (but for an alternative explanation of the relationship between feather holes and fitness see below). As a consequence it should be adaptive for females to avoid infested males during the breeding season. The feature of white patches in tail feathers (Kose & Møller 1999) and the negative relationship between feather-hole number and the length of the outermost tail feathers of male Barn Swallows could act as a signal for females allowing them to avoid infested individuals. The negative relationship between feather-hole number and tail length indicates that males may reliably signal their parasite load, and that the tail length remains an honest signal of phenotypic quality, because they are particularly demanding to grow for individuals of low quality (Møller 1994). Our results comply with Kose and Møller's (1999) findings, because both studies found a significant negative relationship between the length of the outermost tail feathers and feather-hole number of males, but not of females.

Our results suggest that for both male and female Barn Swallows, feather holes have a significant effect on fitness, as birds with more feather holes delayed laying, and the survival rate of these females was significantly reduced. However, a drawback of this non-experimental study is that alternative explanations cannot be excluded. For example, the difference in the number of feather holes between surviving and non-surviving females, and the negative relationship between the number of feather holes and laying date might be explained as follows: poor quality birds with low survival prospects and delayed breeding are more susceptible to infection, and as a consequence they will show a high intensity of feather holes. Under this scenario there would be no causal effect of feather holes on the fitness of the birds. Our results seem not to support this alternative explanation, because we found no significant relationship between

the number of feather holes and condition indices of females, except for tail length of males.

Our results on the negative relationship between feather holes and fitness are consistent with the most recent findings on the importance of feather holes on flight performance of the Barn Swallow (Barbosa *et al.* 2002). However, the mechanism behind this is still unclear. A possible explanation for the implications of feather holes should be their effect in altering the flight performance of the birds (Barbosa *et al.* 2002). Another implication of feather holes is that as the outermost tail feathers of the forked tail of Barn Swallow grow thin they are particularly predisposed to be damaged (Kose & Møller 1999) and lead to a fluctuating asymmetry. Finally, because the white spots in the tail of the Barn Swallow are melanin-free, they are preferred by chewing lice, resulting in a disproportional high number of feather holes. Ultimately, the white spots are more susceptible to feather breakage than the melanized parts of the feather (Kose & Møller 1999). Feather breakage seems to impose strong natural selection on the host, given the aerodynamic cost of the asymmetric tail feathers (Møller & Swaddle 1997). Our result on the negative relationship between tail length and feather-hole intensity agrees with the negative association found by Møller (1994) between tail length and feather breakage of male Barn Swallows.

Assuming that feather holes are produced by feather lice, this raises some interesting questions. Previous studies on wild birds performed mostly during the breeding season demonstrated that chewing lice have only minor direct effects on the fitness of the host (Clayton & Tompkins 1995, Lee & Clayton 1995, Tompkins *et al.* 1996; but see Booth *et al.* 1993). This view is probably based on just a few influential papers, which support the benign effect of lice (see Clayton & Tompkins 1995, Tompkins *et al.* 1996). Feather lice cannot elicit an immune reaction from the host as can the relatively well-studied haematophagous mites, louse flies, fleas and ticks, which have serious effects on bird fitness. Consequently, the short-term effect of lice on the physiology and the breeding performance of the hosts should be low. However, by overexploiting the resources of birds they can damage the feathers significantly, and may affect the homeostasis and flight capability of birds (Booth *et al.* 1993, Barbosa *et al.* 2002). In this case, we should expect a long-term effect of parasitism on fitness, especially during an intensive locomotor period, such as migration. Here we have shown that the number of feather holes correlates with laying

date and survival of Barn Swallows, both features being strongly related to the migratory activity of birds generally. Thus our results raise the importance of studies on the fitness consequences of parasitism of feather lice during the whole life-cycle of birds. In comparing the fitness consequence of parasitism on migratory and non-migratory birds we should expect a more severe effect on the former group. This waits to be tested.

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