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Increase of feather quality during moult: a possible implication of feather deformities in the evolution of partial moult in the great tit *Parus major*

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Here we investigate the change in feather quality during partial post-juvenile and complete post-breeding moult in great tit *Parus major* by measuring the change in the number of fault bars and feather holes on wing and tail feathers. Feathers grown during ontogeny usually are of lower quality than feathers grown following subsequent moults at independence. This is reflected by higher number of fault bars and feather holes on juveniles compared to adults. Fault bars are significantly more common on tail and proximal wing feathers than on the distal remiges, indicating a mechanism of adaptive allocation of stress induced abnormalities during ontogeny into the aerodynamically less important flight feathers. On the contrary, feather holes produced probably by chewing lice have a more uniform distribution on wing and tail feathers, which may reflect the inability of birds to control their distribution, or the weak natural selection imposed by them. The adaptive value of the differential allocation of fault bar between groups of feathers seems to be supported by the significantly higher recapture probability of those juvenile great tits which have fewer fault bars at fledging on the aerodynamically most important primaries, but not on other groups of flight feathers. The selection imposed by feather holes seems to be smaller, since except for the positive association between hatching date, brood size and the number of feather holes at fledging, great tits' survival was not affected by the number of feather holes. During post-juvenile moult, the intensity of fault bars drops significantly through the replacement of tail feathers and tertials, resulting in disproportional reduction of the total number of fault bars on flight feathers related to the number of feathers replaced. The reduction in the number of fault bars during post-juvenile moult associated with their adaptive allocation to proximal wing feathers and rectrices may explain the evolution of partial post-juvenile moult in the great tit, since the quality of flight feathers can be increased significantly at a relatively small cost. Our results may explain the widespread phenomenon of partial post-juvenile moult of flight feathers among Palearctic passerines. During the next complete post-breeding moult, the total number of fault bars on flight feathers has remained unchanged, indicating the effectiveness of partial post-juvenile moult in reducing the number of adaptively allocated fault bars. The number of feather holes has also decreased on groups of feathers replaced during partial post-juvenile moult, but the reduction is proportional with the number of feathers moulted. In line with this observation, the number of feather holes is further reduced during post-breeding moult on primaries and secondaries, resulting in an increase in feather quality of adult great tits.

The process of moult in birds is an adaptive mechanism to keep the plumage in good quality (Jenni and Winkler 1994). The pattern of moult emerges as the result of trade offs between the costs and benefits of plumage renewal (Barta et al. 2006). For instance, moult can be constrained by the energetic costs of feather synthesis, and the maintenance of efficient flight and thermoregulation during moult (Dietz et al. 1992, Lindström et al. 1993, Hedenström and Sunada 1999). On the other hand, during the course of the year the quality of feathers is constantly deteriorating due to physical abrasion and breakage, resulting in an increasing demand for feather replacement as the quality of feathers decreases. One of the consequence of these diverse trade-offs is the large variability of the timing, number and extension of moults observed between different populations and between species (Baker 1993, Jenni and Winkler 1994). For example, there is a large variability between species in the extension of moult of the remiges (wing feathers) and rectrices (tail feathers) shortly after fledging, with some species retaining all flight feathers grown during ontogeny for nearly one year until the subsequent post-breeding season, while others replacing some tertials and rectrices, or even the whole plumage (Svensson 1992, Jenni and Winkler 1994).

One of the possible explanations for the adaptive value of post-juvenile moult is the advantage to replace the low quality juvenile feathers with more resistant ones. The feathers grown during the nestling period are considered to be of low quality because of the food shortage caused by the intense competition between siblings, the stress induced by parasites, and the unforeseeable climatic events, and the conflict between the energetic requirement for the rapid, simultaneous development of feathers and other vital traits. The findings that feather quality of the remiges and rectrices, measured as the texture, weight, number of feather holes and fault bars, tends to improve during the individuals' life (Slagsvold 1982, Jenni and Winkler 1994, Møller and de Lope 1999, Jovani and Blas 2004) support this argument.

It is, however, still unclear why only well defined groups of flight feathers (the tertials and rectrices) are replaced when the post-fledging moult is partial. The hypothesis of adaptive allocations of fault bars (feather deformities caused by developmental stress during feather synthesis) suggests that through natural selection birds evolved mechanisms to reduce the load of fault bars produced during the intense, simultaneous development of flight feathers of nestlings on the feathers with the highest strength requirements and function during flight (Jovani and Blas 2004). Therefore one would expect that nestlings allocate the limited resources during the development of flight feathers towards the primaries and secondaries. This process, however, because of the limitedness of resources, would result in tertials and rectrices of lower quality which might impose serious fitness cost during the winter. We propose that the partial post-juvenile moult may serve as a means to further decrease the costs of the intense nestling growth. Partial post-juvenile moult allows the juveniles to substantially reduce the amount of deformities by replacing feathers of low quality when food becomes more available to them. At the same time they do not have to pay the remarkable cost of a complete moult; flight efficiency is maintained because primaries and secondaries remain intact.

The quality of feathers can be characterized by the resistance against mechanical abrasion, photochemical processes and parasites. First, fault bars caused by stress during feather development (Slagsvold 1982, Negro et al. 1994) increase the risk of feather damage (Sarasola and Jovani 2006) which can, through reduction of wing and tail area, seriously impair the flight performance of the birds (Lind and Jakobson 2001, Senar et al. 2002). Second, relatively small differences early in the course of the year in the abrasion of the aerodynamically most important outermost primaries might affect the breeding performance of the birds through the timing of reproduction and breeding attempts as a current annual routine model indicates (Barta et al. 2006). Third, parasites like chewing lice (Phthiraptera) and the feather degrading bacteria can also reduce seriously the quality of feathers (Booth et al. 1993, Kose and Møller 1999, Barbosa et al. 2002, Shawkey et al. 2003, Lucas et al. 2005, Pap et al. 2005). As a consequence of the significant costs of feather damage individuals are under strong selection to maintain or even increase the quality of feathers, and/or to reduce the effect of feather damage on their function. Essentially, there are three solutions to reduce the costs imposed by the feather damage: (1) to replace the old, damaged feathers through annual moult (Jenni and Winkler 1994), (2) through mechanism of adaptive allocation of feather abnormalities to reduce the load of damages on feathers with high strength requirements during flight (Jovani and Blas 2004, Serrano and Jovani 2005), and (3) the combination of these two. Feather damages caused by accidental events and by feather degrading parasites (e.g. chewing lice, bacteria, fungi) are probably above the control of the individual, that is why these losses can be repaired only through periodic replacement of feathers. On the other hand, the negative effects caused by feather degradation due to abrasion or stress induced abnormalities (known as fault bars) can be diminished through adaptive allocation of biochemical components (e.g. melanin) into feathers exposed to increased friction (Bonser 1995), or by mechanism favoring allocation of feather deformities in feathers with low strength requirements during flight and/or in feathers with low costs of replacement. In the last case, these feathers with selectively allocated abnormalities can be replaced with low costs through partial moult (e.g. partial post-juvenile moult) following feather development.

Here we followed the change in feather quality during subsequent partial and complete moults of the flight feathers of the great tit *Parus major*, by studying the distribution and frequency of fault bars and feather holes, which are considered as two important components of feather quality. Furthermore, we investigated the implication of adaptively allocated stress induced feather deformities to feathers with reduced importance in flight in the evolution of the partial post-juvenile moult.

Methods

We studied a local great tit population in the surroundings of Stana village (46°89′N, 23°14′E, Transylvania, Romania) between June 2004 and March 2006. The study site is situated in a 40 ha orchard of various old fruit-trees (mainly plum and apple). The orchard is surrounded by pastures and arable fields, and a nearby woodland area is about 4 km from the study site. In 2004 we had mounted 180 nest boxes in the orchard to study the breeding biology of the species. During this period we regularly captured and ringed the birds resulting in more than 900 marked individuals. The age and sex of the birds were determined according to the criteria described by Svensson (1992). We defined three age categories: juveniles being after fledging and before post-juvenile moult, first year-old birds which are after the post-juvenile moult and before their first post-breeding moult, and adults defined as birds after the first post-breeding moult. The quality of the wing and tail feathers was assessed by counting the number of fault bars and feather holes on each feather. Fault bars are narrow and translucent bands perpendicular to the feather rachis. Feather holes are small round shaped holes on the vane of the wing and tail feathers with a diameter between 0.5 and 1 mm. Feather holes seem to reduce the aerodynamic efficiency and increase the risk of feather breakage (Kose and Møller 1999, Barbosa et al. 2002).

As in tits the outermost primary is less than 10% in size of the next proximal primary we only counted the number of feather holes and fault bars on the 9 fully grown primaries, on the 6 secondaries, on the 3 tertials and on the 12 tail feathers. In order to increase the robustness of our data, we counted fault bars and feather holes on both wings, and then we pooled the data of the two wings for the subsequent analyses.

After fledging, great tits perform a post-juvenile moult, during which part of the body and flight feathers are replaced. Among flight feathers, tertials and rectrices are usually moulted in various amounts, which differs according to sex, population, fledging date and year (Jenni and Winkler 1994, Bojarinova et al. 1999). In our population apparently 100% of the fledged birds replace the tertials and rectrices starting from July to the end of September. Adults commence the complete post-breeding moult at the end of the breeding season at the beginning of June, replacing all wing and tail feathers until the end of September. The change in feather quality was measured on the same individuals captured before and after the post-juvenile or post-breeding moult. To analyze the change in feather quality we used the mean number of fault bars and feather holes separately calculated for primaries, secondaries, tertials, and rectrices. The reason for using the average for groups of feathers is twofold. First, we are mainly interested in the changes of qualities between feather groups replaced during different moult sessions. Second, calculating the average number of deformities per groups of feathers improves the distributional properties of the otherwise very skewed distribution of fault bar and feather hole data (Pap et al. 2005, Serrano and Jovani 2005, pers. obs.). A considerable number of juvenile birds were captured during active post-juvenile moult when some of the tertials and tail feathers were dropped. For these birds we included only the data on those feathers in the analyses which were measured both before and after moult.

In 2005 we followed the breeding biology of the great tits in natural holes and in nest boxes. Nests were checked systematically from April, and date of clutch initiation, clutch size and number of fledged young was noted. Nestlings were weighed 15 d after hatching (hatching day = 0), and their body mass, tarsus length and wing length were measured. We followed 25 nests, in 21 of which at least one nestling had fledged. After fledging we recaptured as many birds as possible by mist netting in order to study the effect of condition during ontogeny on the quality of flight feathers.

Statistical analyses

Through the analyses, except when stated otherwise, we used non-parametric tests because of the aggregated distribution of fault bars and feather holes. To analyse the effects of nestling attributes on feather deformities we built generalized linear mixed models (GLMMs) with Poisson error distribution and log link function and with the nests from where the individual fledged and body mass, wing length, tarsus length, brood size at fledging as random factor. Because a significant number of nestlings ringed and measured in the nest were recaptured during and after post-juvenile moult, in these analyses we could use as a dependent variable the number of fault bars and feather holes only on primaries and secondaries (as the tertials and rectrices are replaced during the post-juvenile moult). The GLMM analyses were done in the R statistical environment (R Development Core Team 2004), using the glmmPQL function of the MASS library (Venables and Ripley 2002).

Results

Change of feather quality during moults

Fault bars of juvenile great tits captured before their post-juvenile moult were non-uniformly distributed between the groups of wing feathers (Friedman ANOVA test, prevalence: $\chi^2_{2,64} = 13.6$, $P < 0.005$; mean abundance: $\chi^2_{2,66} = 19.6$, $P < 0.001$) and between remiges and rectrices (Table 1). Within wing, the prevalence and mean abundance of fault bars increased from primaries to tertials with intermediate value for secondaries (Fig. 1a). Among all groups of feathers the prevalence and the mean number of fault bars were the highest on tail feathers. The distribution of feather holes differed from that of fault bars (Fig. 1b). Among groups of wing feathers the difference in prevalence and mean abundance of feather holes was significant (Friedman ANOVA test, prevalence: $\chi^2_{2,70} = 49.8$, $P < 0.001$; mean abundance: $\chi^2_{2,76} = 62.0$, $P < 0.001$), with the highest prevalence and mean abundance found on secondaries, followed by primaries and tertials (Table 1). The prevalence and mean abundance of feather holes on tail feathers was similar to primaries and secondaries (Table 1).

During post-juvenile moult the number of fault bars on groups of feathers moulted decreased significantly (Wilcoxon matched pairs test, tertiary: $Z = 3.15$, $n = 68$, $P < 0.01$, tail: $Z = 4.03$, $n = 58$, $P < 0.001$, Fig. 2a), while their number remained unchanged on primaries and secondaries (primary: $Z = 0.82$, $n = 73$, $P = 0.41$, secondary: $Z = 0.39$, $n = 73$, $P = 0.70$) between capture and recapture (an average duration of 179 ± 7.2 (mean ± SE) d), as expected. Following partial post-juvenile moult, the number of feather holes decreased significantly only on tail feathers ($Z = 5.18$, $n = 58$, $P < 0.001$, Fig. 2b), while the decrease in their number on tertials was only marginally significant ($Z = 1.87$, $n = 68$, $P = 0.06$). The number of feather holes on primaries and secondaries remained unchanged (primary: $Z = 0.18$, $n = 73$, $P = 0.86$, secondary: $Z = 0.86$, $n = 73$, $P = 0.39$). During the post-juvenile moult, because of the high number of fault bars found on tertials and tail feathers, the total number of fault bars decreased disproportionately more than expected based on the uniform distribution of fault bars

Table 1. Wilcoxon matched pair tests of the difference in prevalence and mean number of fault bars and feather holes between different groups of flight feathers of the juvenile great tits captured before post-juvenile moult. The data of those birds is included with at least one fault bar or feather hole.

	Z	n	P
Prevalence			
Fault bars			
Primary vs secondary	3.52	64	<0.001
Primary-secondary vs tertiary	3.55	64	<0.001
Primary-secondary vs tail	6.42	64	<0.001
Feather holes			
Primary vs secondary	2.44	70	<0.05
Primary-secondary vs tertiary	6.37	70	<0.001
Primary-secondary vs tail	1.52	67	0.13
Mean abundance			
Fault bars			
Primary vs secondary	3.88	66	0.001
Primary-secondary vs tertiary	4.23	66	<0.001
Primary-secondary vs tail	6.67	66	<0.001
Feather holes			
Primary vs secondary	2.31	76	<0.05
Primary-secondary vs tertiary	6.85	76	<0.001
Primary-secondary vs tail	1.00	75	0.32

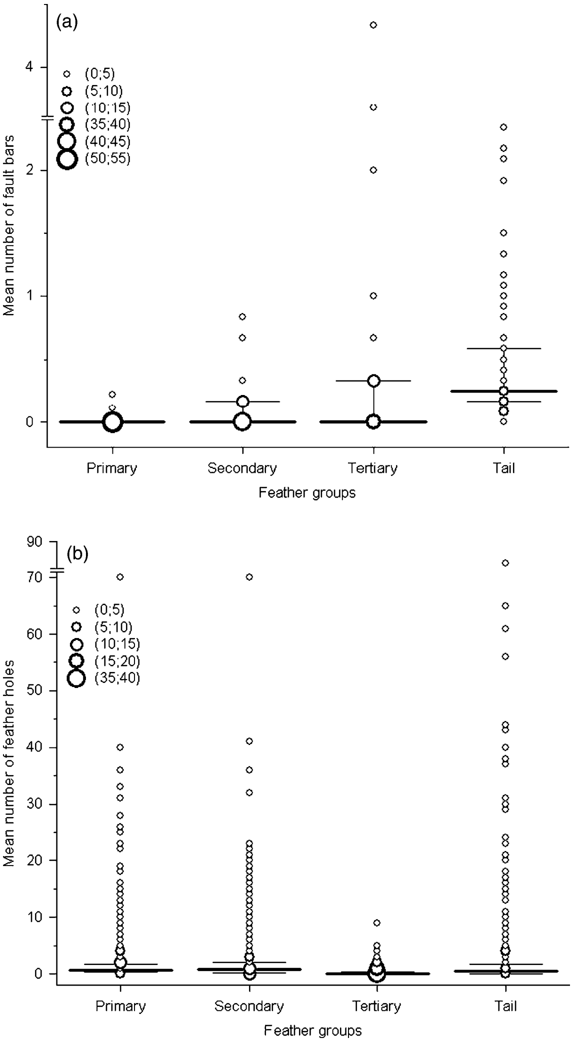

Fig. 1. Mean number of fault bars (a), and feather holes (b) on different groups of feathers of juvenile great tits captured before partial post-juvenile moult (median and inter quartile range, circles indicate data values).

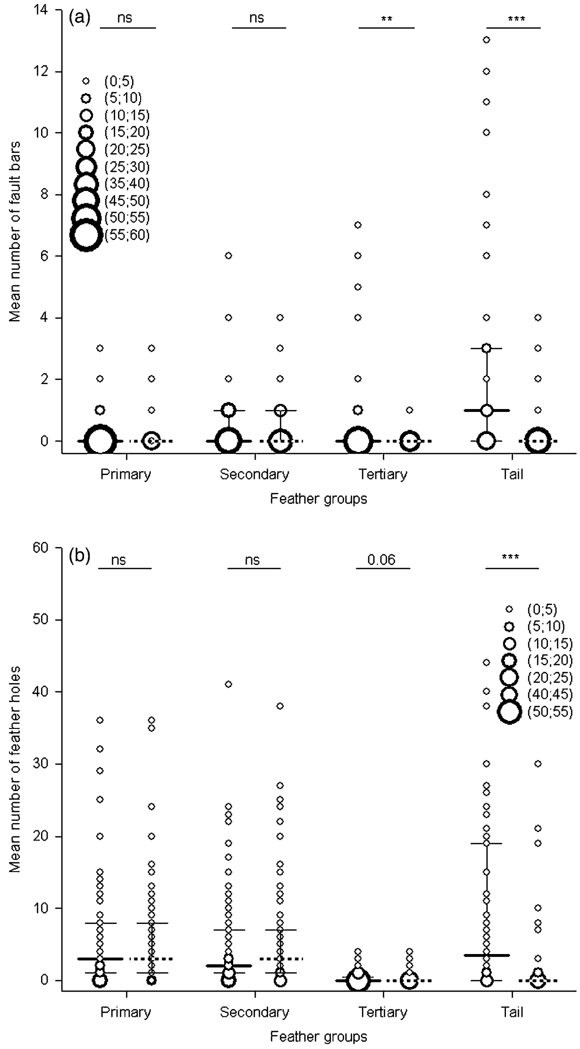

Fig. 2. Change in the mean number of fault bars (a), and feather holes (b) on different groups of feathers during partial post-juvenile moult of the great tits. Continuous and broken thick lines indicate median number of fault bars and feather holes before and after moult, respectively (median and inter quartile range, circles indicate data values). Note, that during post-juvenile moult only the tertials and tail feathers are replaced. Significance level for Wilcoxon matched pair tests are shown above columns (**P <0.01, ***P <0.001, ns – not significant). n = 73 for primaries and secondaries, n = 68 for tertials, and n = 58 for tail feathers.

on wing and tail feathers (Z = 2.59, n = 57, P = 0.01). On the contrary, the number of feather holes decreased proportionally during post-juvenile moult related to a uniform distribution on wing and tail feathers (Z = 0.45, n = 57, P = 0.65).

During complete post-breeding moult of the first year-old birds, the total number of fault bars (summed over all flight feathers) tended to decrease but the change was non-significant (Z = 1.65, n = 23, P = 0.10). The separate analyses of the change in the number of fault bars on different groups of feathers revealed that on secondaries the change was significant (Z = 2.02, n = 24, P = 0.04), while on primaries and tail feathers it was not (primary: Z = 0.00, n = 24, P = 1.00, tail feathers: Z = 0.84, n = 23, P = 0.40). In the case of the tertials, the low prevalence of fault bars (0% before and 4% after moult, n = 24) prevented separate analyses. The number of feather holes decreased significantly during post-breeding moult (Z = 2.93, n = 23, P < 0.005, Fig. 3), which is related to the significant change in the number of feather holes on primaries (Z = 3.23, n = 24, P = 0.001) and secondaries (Z = 3.18, n = 24, P = 0.002). The number of feather holes on tertials and tail feathers did not change during post-breeding moult (tertials: Z = 1.60, n = 24, P = 0.11, tail: Z = 0.66, n = 23, P = 0.51).

Feather quality, condition during ontogeny and survival

We cannot show any effects of conditions (body mass, tarsus length and wing length) during the developmental period in the nest on the number of fault bars on primaries and secondaries of the great tit (data not shown). However, birds recaptured after post-juvenile

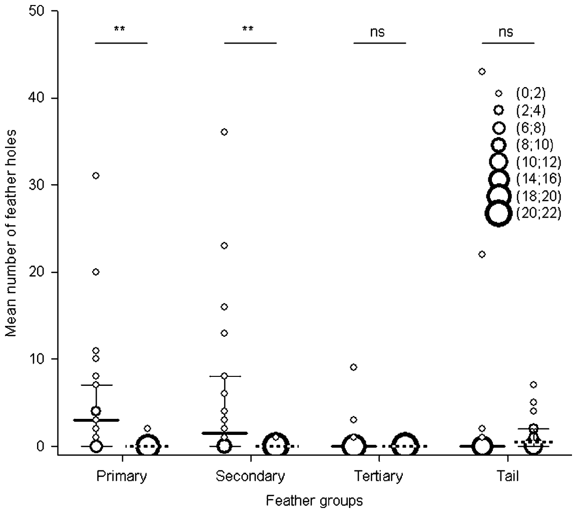

Fig. 3. Change in the mean number of feather holes on different groups of feathers during complete post-breeding moult of first year-old great tits. Continuous and broken thick lines indicate the median number of feather holes before and after moult, respectively (median and inter quartile range, circles indicate data values). Note, that during post-breeding moult all wing and tail feathers are replaced. Significance level for Wilcoxon matched pair tests are shown above columns (**P < 0.01, ns – not significant). n = 24 for primaries, secondaries and tertials, and n = 23 for tail feathers.

moult have a lower number of fault bars on their primaries before moult than birds which we could not recapture (rank sum: 2926 vs 2024, Table 2). The number of fault bars on secondaries, tertials and rectrices did not differ at capture between the recaptured and not recaptured birds. Conditions during ontogeny predicted the number of feather holes at independence, since the brood size and hatching date were positively associated with the number of feather holes on primaries and secondaries (GLMM; brood size: $t = 2.88$, $df = 10$, $P = 0.02$, hatching date: $t = 4.41$, $df = 10$, $P = 0.001$). Contrary to the relationship between status of recaptured or not and number of fault bars, the number of feather holes did not significantly differ between the two groups (Table 2).

Discussion

Fault bars

We have found that during ontogeny, when flight feathers are developing approximately simultaneously, fault bars are mainly appeared on proximal wing feathers and rectrices supporting the “adaptive fault bar allocation hypothesis” proposed by Jovani and Blas (2004). Our results confirm the findings of the few studies on this topic, namely the high occurrence of fault bars on feathers with reduced aerodynamic importance (Jovani and Blas 2004, Serrano and Jovani 2005, Sarasola and Jovani 2006). The non-uniform distribution of feather abnormalities can be adaptive, since feather breakage produced by fault bars (Sarasola and Jovani 2006) may impair significantly the flying capacity of individuals, and the effect of the reduced surface area of feathers is more pronounced on the distal part of the wing than on the proximal one. If one assumes that birds not recaptured at the study site have reduced fitness related to the recaptured ones our results seems to support that the fault bars on remiges can result in a fitness cost (Bortolotti et al. 2002), with an increased effect on distal part of the wing. Birds not recaptured at the study site should perish during the harsh winter, or they may disperse out of the natal area. In case of increased dispersion of individuals with many fault bars we cannot judge that these birds had decreased fitness related to the local recruitments, but data on great tits indicate that nestlings having better condition during development have an increased recruitment rate related to the low quality individuals (Tinbergen and Boerlijst 1990). Thus the superior quality of the recaptured birds seems to be a reasonable assumption. Of course a more appropriate test on the effects of fault bars on fitness would require an experimental approach. On the other hand, allocating fault bars preferentially into the tertials and tail feathers may still impose strong natural selection costs due to the reduced maneuvering capacity of the birds with broken feathers, which is likely to be asymmetric and hence give rise to aerodynamic costs (reviewed in Møller and Swaddle 1997). Our results do not confirm the fitness cost of fault bars on tertials and rectrices in terms of survival and/or dispersion, however, due to the short period between fledging and partial post-juvenile moult (approximately 40–50 d, see also Bojarinova et al. 1999) feather deformities should have a limited effect on the performance of the birds. We showed that during post-juvenile moult, when tertials and tail feathers are replaced in apparently all juveniles in our great tit population, the number of feather abnormalities found on moulted flight feathers

Table 2. Mann-Whitney U tests of the difference in number of fault bars and feather holes on different groups of feathers between recaptured and not recaptured juvenile great tits. Great tits were initially captured before and during the post-juvenile moult (June–August) and recaptured several months later during winter and spring at the study site. n_1 = recaptured, n_2 = not recaptured.

	Z	n_1, n_2	P
Fault bars			
Groups of feathers not replaced during post-juvenile moult			
Primary	2.01	35, 64	<0.05
Secondary	1.41	35, 64	0.16
Groups of feathers replaced during post-juvenile moult			
Tertiary	0.23	35, 64	0.82
Tail	0.99	36, 60	0.32
Wing and tail feathers	0.18	28, 48	0.86
Feather holes			
Groups of feathers not replaced during post-juvenile moult			
Primary	1.09	34, 64	0.28
Secondary	1.06	34, 64	0.29
Groups of feathers replaced during post-juvenile moult			
Tertiary	0.95	34, 64	0.34
Tail	−0.01	36, 58	0.99
Wing and tail feathers	0.06	28, 48	0.95

decreased significantly. Following the partial post-juvenile moult, great tits decrease disproportionately the total number of fault bars related to a uniform distribution of growth abnormalities, with probably reduced costs in terms of flight capacity, predation risk and energy expenditure due to feather synthesis. Feather breakages produced by fault bars can have a long-term influence on the flying capacity of the birds, since feathers damaged during the non-moulting period cannot be replaced. Thus, by moulting those groups of flight feathers on which the frequency and number of fault bars is high, individuals can significantly increase their fitness expectation through improved plumage quality at a relatively low cost (see above). After fledging, by getting experienced, great tits performing their first partial moult can increase the quality of flight feathers, thus increasing their future prospect of survival. The mechanism of reducing feather deformities through adaptive fault bar allocation combined with partial post-juvenile moult seems to efficiently reduce feather abnormalities produced during fast postembryonic growth, since we found no effects of the number of fault bars on those feathers which are replaced during post-juvenile moult on survival. Furthermore, in the subsequent complete post-breeding moult of the first year-old great tits the number of fault bars decreases only marginally. Our results may explain the widespread phenomenon of partial post-juvenile moult of flight feathers among Palearctic passerines (Cramp 1988, 1992, 1993, Jenni and Winkler 1994). One possible way to test this hypothesis is to compare the extent of adaptive fault bar allocation between species with different extensions of post-juvenile moult.

Feather holes

Feather holes are considered to be produced by chewing lice, at least in the case of the barn swallow (Kose and Møller 1999, Møller and de Lope 1999, Barbosa et al. 2002, Pap et al. 2005). Feather holes appear on flight feathers during feather development in the nest and shortly after fledging (Pap et al. pers. obs.), after which their number remain unchanged (see Results). This may indicate that lice only chew the newly developing feathers. This observation, however, contradicts with the continuous feeding activity of feather lice over the annual cycle on rock dove *Columba livia* (Booth et al. 1993), however in this experiment louse were observed to feed on body feathers. Contrary to the fault bars, feather holes are more uniformly distributed between groups of feathers. If feather holes were produced by chewing lice, then their distribution would probably be determined primarily by the structure and quality of different groups of feathers (Kose and Møller 1999), and/or by the grooming behavior of the host (Rózsa 1993). Note also, feather holes are produced during the developmental period of the feathers, when the difference between groups of feather in terms of air turbulences and microclimate is probably low. In any case, their distribution is expected to be more uniform than that of the fault bars which are under intrinsic control, which was confirmed in the present study and by observations on the barn swallow (Pap and Tökölyi pers. obs.). Alternatively, the uniform distribution of feather holes can be related to the weak selection force imposed by feather holes on the flight ability of the birds, making unnecessary the evolution of mechanisms favoring adaptive allocation of feather holes to the groups of feathers with reduced aerodynamic importance. Our results indicate that feather holes are related with condition during development, but the selection imposed by them on the flying capacity of the great tit is probably low. Thus our results seem to support the plausibility of the weak selection compelled by feather holes. During post-juvenile moult, as in the case of fault bars, the number of feather holes decrease on groups of feathers moulted. In line with the observation about uniform distribution of feather holes between groups of feathers, their number is decreasing in proportion with the number of feathers replaced during the post-juvenile moult. Thus, contrary to the change in the number of fault bars during post-juvenile moult, the total number of feather holes on flight feathers remains considerable, which is related to their proportional frequency on the non-moulted primaries and secondaries. Based on studies conducted on the barn swallow, feather holes are known to reduce the fitness of the birds through delayed breeding and reduced survival (Pap et al. 2005), which is related probably to the impaired aerial performance of the birds with many feather holes. However, as mentioned before, the effect of feather holes on the fitness of the great tit is probably small which might be explained by the fact that great tits spend much less time in the air during foraging than the swallows do. Thus this might prevent any selection imposed by feather holes to replace feathers with many holes through the overbalanced costs related to the complete moult.

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