

Host–symbiont relationship and abundance of feather mites in relation to age and body condition of the barn swallow (*Hirundo rustica*): an experimental study

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Abstract: We analyzed the host–symbiont relationship and factors determining the abundance of feather mites among individual barn swallows (*Hirundo rustica* L., 1758) in two different host populations during the breeding season and postbreeding period. By experimentally removing the feather mites from the flight feathers of the birds with an insecticide, we showed that these symbiotic organisms have neither harmful nor beneficial effects on the fitness of the host, supporting the view that mites are commensals. This was indicated by the lack of any difference in the change in wing-feather length, tail-feather length, fluctuating asymmetry in tail-feather length, breeding performance, and survival of the birds between the fumigated and control groups 1 year after the experiment. During the postbreeding period juveniles harbored fewer mites than adults and the difference was also significant between the 1-year-old birds and those over 1 year old in the breeding population. The number of mites did not change after the second year of life of the birds. We hypothesize that the difference in abundance of mites between the age classes can be explained by the low reproductive potential of the mites, which are not able to populate the exploitable space until the second year of life of the host. Alternatively, young birds might provide fewer resources than old birds. The significant negative association between the number of mites and the laying date of female barn swallows seems to support the conclusion that the abundance of mites is condition-dependent. Because there was no relationship between other condition indices for males and females and number of mites, further research is needed to confirm this conclusion.

Résumé : Nous avons analysé la relation hôte–symbiote et les facteurs responsables de l’abondance des acariens des plumes chez des hirondelles rustiques (*Hirundo rustica* L., 1758) individuelles, dans deux populations d’hôtes durant la saison de reproduction et la saison qui suit. En retirant expérimentalement les acariens des plumes des pen- nées des oiseaux au moyen d’un insecticide, nous montrons que ces organismes symbiotiques n’ont d’effet ni favorable ni nuisible sur la fitness de l’hôte, ce qui appuie l’opinion que ces acariens sont des commensaux. Ce fait est appuyé par l’absence complète, 1 an après l’expérience, de différences dans la longueur des rémiges de l’aile, la longueur des pen- nes de la queue, l’asymétrie fluctuante de la longueur des pen- nes de la queue, la performance reproductive et la survie chez les oiseaux qui ont subi la fumigation et les oiseaux témoins. Durant la période qui suit la reproduction, les jeu- nes portent moins d’acariens que les adultes; il y a aussi une différence significative entre les oiseaux d’un an et ceux qui ont plus d’un an dans la population reproductive. Le nombre d’acariens ne varie plus après la seconde année de vie des oiseaux. Nous posons en hypothèse que les différences d’abondance des acariens entre les classes d’âge s’expliquent par le faible potentiel reproductif des acariens qui ne sont pas capables de coloniser tout l’espace utilisable avant la seconde année de vie de l’hôte. Il se peut aussi que les jeunes oiseaux fournissent moins de ressources que les oiseaux plus âgés. L’association significative négative entre le nombre d’acariens et la date de ponte des hirondelles rustiques femelles semble appuyer l’idée que l’abondance des acariens dépend de la condition de l’hôte. Comme il n’existe pas de relation entre les autres indices de condition des mâles et des femelles et le nombre d’acariens, il fau- drait de nouvelles études pour appuyer cette conclusion.

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Introduction

Feather mites are one of the most common ectosymbionts of birds, with high variance in both prevalence and intensity of infestation among individuals (e.g., Figuerola 2000; Proctor 2003). Despite the high abundance of feather mites on birds (Proctor and Owens 2000), this group of obligate avian symbionts is not well studied, especially in relation to their role in the host's life history (Proctor and Owens 2000). Feather mites are considered to be commensals, mutualistic organisms, or parasites with a mild effect (e.g., Pérez-Tris et al. 2002; Lindström et al. 2004; Shutler et al. 2004), and their influence on the host is expected to be minimal. That there are different life forms of the feather mites seems to be reflected in the few correlational studies carried out, which showed negative (e.g., Rózsa 1997; Thompson et al. 1997; Harper 1999), positive, or no relationship (Blanco et al. 1997, 1999; Dowling et al. 2001; Møller et al. 2004) between the number of mites and the fitness measures of the host. However, correlational studies have the drawback that they cannot overcome important caveats in regard to the functional relationship between feather traits and parasites. One experimental study (Figuerola et al. 2003) showed a negative effect of feather mites on the plumage color of the serin (*Serinus serinus* L., 1766). In summary, there is a great need for experimental studies of mites (see Proctor and Owens 2000) in which their abundance is manipulated.

Considering the nature of the host–symbiont relationship (see above), the effect of feather mites on the fitness of the host is crucial in the appearance and evolution of defense mechanisms used by the host against symbionts. Ultimately, this can affect the abundance of mites on the host. For example, if a symbiotic organism diverts an important proportion of the host's resources, as is typical of many parasites, a quick response from the host is expected, leading to the decrease in the parasite population (e.g., Møller 2000). The huge diversity of immunological, ecological, and behavioral forms of defense in birds supports this theory (Clayton and Moore 1997). On the other hand, if the symbionts have no or little effect on the fitness of the host, the evolution of defense mechanisms would not be expected. The apparent lack of correlation between the response of the host and the intensity of infestation by feather mites supports this hypothesis (Blanco et al. 1997; Dowling et al. 2001). In this case, the variation in the number of feather mites among hosts is due to factors other than host defense, like the availability of resources or the reproductive capacity of the mites (e.g., Blanco and Frías 2001).

Feather mites of the barn swallow (*Hirundo rustica* L., 1758) are presumed to be commensals, with no harmful effect on the fitness of the birds (Blanco and Frías 2001; Møller et al. 2004). The mites feed on algae, fungi, pollen, and the secretion from the uropygial gland, which covers the feathers and removes oil and microorganisms (Blanco et al. 2001). Feather mites live primarily on the ventral surface of the wing and tail feathers, between the barbs.

Taking into consideration the lack of experimental studies on the role of feather mites on the fitness of the host, we address the following questions in our study of the relationship between barn swallows and feather mites: (i) do feather

mites affect the fitness of the host, and (ii) which factors are responsible for the variation in the number of feather mites among individual barn swallows. We manipulated the number of mites on adult breeding barn swallows by fumigating the wing and tail feathers with an insecticide (experimental group), and then compared the change in their morphological and reproductive parameters and survival rate 1 year later with those of a control group (sprayed with water). Furthermore, we analyzed the relationship between condition indices of the birds and the number of feather mites on the same breeding population during the breeding season and on a different population during the postbreeding period.

Methods

Study areas and measurements

Two barn swallow populations in two different areas were studied: a breeding population near Balmazújváros, Hungary (47°37'N, 21°21'E), between 2002 and 2004, and a postbreeding population ca. 200 km east of the first study area, near Sic, Romania (46°55'N, 23°52'E), in 2004. Breeding barn swallows were captured by intensive mist-netting and with nest traps during the first breeding attempt between May and July. After birds were marked with a unique combination of one epigraphic aluminium ring and two different colored rings, standard measurements were taken. We measured the lengths of the left and right wing feathers, left and right outermost tail feathers — a condition-dependent sexual character (Møller 1994), and left tarsus, and body mass. We averaged the lengths of the left and right wing feathers and left and right outermost tail feathers and calculated the fluctuating asymmetry (FA) of the tail feathers, which is the unsigned value of the left minus the right tail feathers. The FA of bilateral characters is widely used as a stress indicator (e.g., Brown and Brown 2002), and we supposed that any effect of mites on the fitness of the birds would be reflected in an altered FA of the tail feathers. We used the FA of only the outermost tail feathers because of the great accuracy of measurement and the high variance in FA (males: CV = 107%; females: CV = 118%). We frequently inspected the nests during the breeding season to determine laying date, clutch size, and brood size, and to assign nest ownership by reading the colored-ring combination or capturing adult birds at the nests. Postbreeding birds were captured during June and July 2004 with mist nets mounted in a large reed bed, taking advantage of the barn swallows' communal roosting during this period of the year. The age (adult or juvenile) of the birds during the postbreeding period was determined on the basis of external characters (Svensson 1992).

After measurements had been made, the number of feather mites was assessed by a semiquantitative method at both study sites. That is, we counted (P.L. Pap for the breeding population and P.L. Pap and J. Tökölly for the postbreeding population) feather mites separately on individual primaries on both wing and on tail feathers for up to 10 mites; above this number the intensity of infestation was assessed by scoring the mite clusters on a scale using intervals of 5 (i.e., 15, 20, 25, etc.). Feather mites live on the ventral surface of the feather vanes, and can be distinguished individually without magnification. The use of semiquantitative

assessment was necessary, since barn swallows are heavily infested, some bearing hundreds of mites. The use of this visual-inspection semiquantitative method produces measurement errors, owing to the difficulty of distinguishing between live mites and skin casts (Proctor and Owens 2000), and there is a general problem with the repeatability of estimates. We verified the efficacy of this method in two ways. First, in a sample of barn swallows from the breeding colony in Hungary in 2003, we compared counts obtained using this technique with those obtained from the same birds using a dust-ruffling method (Clayton and Drown 2001). To remove feather mites we used a common repellent against arthropod parasites developed for veterinary use (see below). The intensity of infestation by feather mites, based on visual inspection of the three outermost primaries, correlated significantly with the number of feather mites on the collecting plate (Spearman's rank correlation, $r_{[48]} = 0.65$, $P < 0.0001$), confirming the accuracy of the counting method used. Second, on a subset of breeding birds from Hungary in 2004, we re-counted the feather mites on the flight feathers of the same birds several days after the initial measurement, in order to calculate the repeatability of our assessment. The high repeatability again indicates the reliability of the method used ($R = 0.97$, $F_{[10,11]} = 75.3$, $P < 0.0001$). Two species of feather mites, *Trouessartia crucifera* Gaud, 1957 and *Trouessartia appendiculata* (Berlese, 1886) (Acari: Analgoidea), collected from the wing feathers of the Hungarian breeding barn swallows were identified by Ronald Schmäschke (University of Leipzig, Leipzig, Germany). We have no information about the identity of feather mites from the Romanian barn swallow population. Mites of the genus *Trouessartia* seem to be widespread on barn swallows, since, besides those from the Hungarian breeding population, we collected them on barn swallows in three different South African localities (P.L. Pap, T. Szép, J. Tökölyi, and S. Piper, unpublished data).

In 2002 and 2003, we counted feather mites on breeding barn swallows only on the three outermost primaries, while in 2004, both wing feathers (primaries, secondaries, and tertiaries) and tail feathers were inspected at both study sites. Thus, except for the experimental data and the analyses of postbreeding birds, we used only the numbers from the three outermost primaries. The number of feather mites on only the three outermost primaries serves as an accurate predictor of the total number of mites on the flight feathers because 57% of the mites are on these three feathers, and the relationship between the number of mites on the three outermost primaries and in total is strongly significant (Spearman's rank correlation, $r_{[151]} = 0.92$, $P < 0.0001$). The values obtained from the left and right wing feathers were averaged to increase the robustness of the data.

To test the effect of feather mites on the fitness of the birds, we conducted an experiment in 2003 in which half of the adult birds captured during the first breeding season in the Hungarian colonies were fumigated with an insecticide (0.17% permethrin and 0.07% bioresmetrin (Insecticide 2000, Waldner GmbH, Vienna, Austria) (experimental group), while birds in the control group were sprayed with water. After the fumigation procedure we put the birds in a bag for 10 min to dry. A sample of birds was recaptured sev-

eral weeks after the first capture, to test the effectiveness of the insecticide used. A sharp difference in infestation rates between the fumigated and water-sprayed birds was found, with significantly fewer mites on birds in the fumigated group (Mann-Whitney U test, $Z_{[10,17]} = 3.89$, $P = 0.0001$). The following year we recaptured the breeding barn swallows that had survived and measured the same variables as in the previous year. We measured the effect of the experiment on morphological variables, breeding performance, and survival of the birds. Survival could be reliably assessed, since philopatry to breeding colonies is very high in this species, and breeding dispersal is very low (Møller and Szép 2002; Pap et al. 2005).

Data analyses

To analyze the effect of the experiment on the fitness of the host, we compared morphological variables, breeding parameters, and survival rates of the birds from the two groups in the year after the experiment, and the change in wing- and tail-feather lengths between the year of experiment and the following year, in this way controlling for the initial size of the character. In the analyses of the relationship between the number of feather mites, morphological variables, and breeding parameters of the birds, we used the data collected from the 3 years between 2002 and 2004. In these analyses we used the data from an individual only once, to avoid pseudoreplication, by randomly including data from only one year. Several potential categorical and continuous predictor variables were included in a general linear model (GLM) to test factors responsible for the variation in number of feather mites among individuals. We used a backward stepwise procedure eliminating all non-explanatory variables included in the model, where the critical value was set to 0.05. Year, age, and, in the case of postbreeding birds, time of capture (the birds were captured at sunrise and at sunset) were included as categorical predictors, and date of capture, time of capture (in case of breeding birds), wing-feather, tail-feather, and tarsus lengths, and, in the case of breeding birds, laying date and clutch size were included as continuous predictors of the number of feather mites (dependent variable). We included year as a factor in the model, since birds varied significantly in their number of feather mites among years (Kruskal-Wallis test, $H_{[2,451]} = 11.05$, $P < 0.01$).

In the case of postbreeding birds, data from adult and juvenile males and females were pooled, owing to uncertainty in determining the sex. The age of postbreeding birds was defined as adult (more than 1 year old) or juvenile (born in the study year), while breeding birds were categorized as 1, 2, 3, or 4 years old. Ageing of breeding adult barn swallows was possible, since we have conducted intensive capturing and ringing of the breeding population since 1999; more than 95% of the birds are marked, and as mentioned before, the breeding philopatry of the birds is high. So newly ringed birds were defined as 1 year old, while the age of the recaptured birds was determined on the basis of ring number. We had only a few 5-year-old birds, so their data could not be included in the analyses because of the small sample size. Whenever necessary, data transformation was used to normalize data, and in cases where the transformation did not normalize the data, we used nonparametric tests.

Results

In both the breeding and postbreeding populations studied in 2004, when all the feather mites on the flight feathers were counted, the birds were heavily infested, since 97% and 98% of adult birds had mites on the flight feathers. The intensity of feather mites was 125.4 ± 86.9 (mean $\pm$ SD; maximum 390) and 168.8 ± 85.1 (maximum 372) for the breeding and postbreeding population, respectively ($t = 3.12$, $n_1 = 152$, $n_2 = 52$, $P = 0.002$). We tested the consistency of infestation within individual birds by analyzing the changes in number of mites on the same individuals in the Hungarian population that were recaptured in different years between 2002 and 2004. The repeatability of the number of mites within individuals is slight but significant ($R = 0.24$, $F_{[54,61]} = 1.97$, $P = 0.005$). The low repeatability could have been caused, at least partially, by the fact that the number of mites increases between the first year of life of the birds and the second year (see below), reducing the consistency of the number of mites within individuals. When the data from those birds that were at least 2 years old were analyzed separately, repeatability increased to moderate ($R = 0.44$, $F_{[16,21]} = 3.47$, $P = 0.004$). We found significant variation among individual adult barn swallows in the total number of mites in 2004, with skewness of 0.64 ($n = 157$) and 0.08 ($n = 52$) and kurtosis of -0.14 and -0.49 in the breeding and postbreeding population, respectively. This indicates that, at least in the case of the breeding population, most of the birds were either not infested or only moderately infested, while just a few birds harbored many mites.

Next we analyzed the relationship between the number of mites and factors that could affect this number. First, considering the low reproductive potential of feather mites (Proctor 2003), we hypothesized that juveniles have fewer mites than adults during the postbreeding period. As we expected, juvenile barn swallows had fewer mites on the flight feathers than adults ($F_{[1,99]} = 107.5$, $P < 0.0001$; Fig. 1a), but unexpectedly, the difference remained significant also between the 1-year-old birds and those that were more than 1 year old in the breeding Hungarian barn swallow population ($F_{[1,188]} = 16.49$, $P < 0.0001$; Fig. 1b). However, after the second year of life, the number of feather mites did not change (Tukey's post-hoc test for unequal sample sizes, $P > 0.05$ in all cases). We repeated these analyses on the same individuals captured as 1-year-olds and recaptured 1 year later. Again, birds harbored fewer mites in their first year than 1 year later ($F_{[1,39]} = 23.63$, $P < 0.0001$), corroborating the results of the previous analyses. Second, we analyzed the relationship between the number of feather mites and morphological and breeding parameters of the birds in both the breeding and postbreeding populations. The GLM analyses (see Methods) showed that among the morphological variables and breeding parameters, only the laying date of females significantly predicted the number of mites, birds that laid earlier being more heavily infested than late breeders (Table 1, Fig. 2).

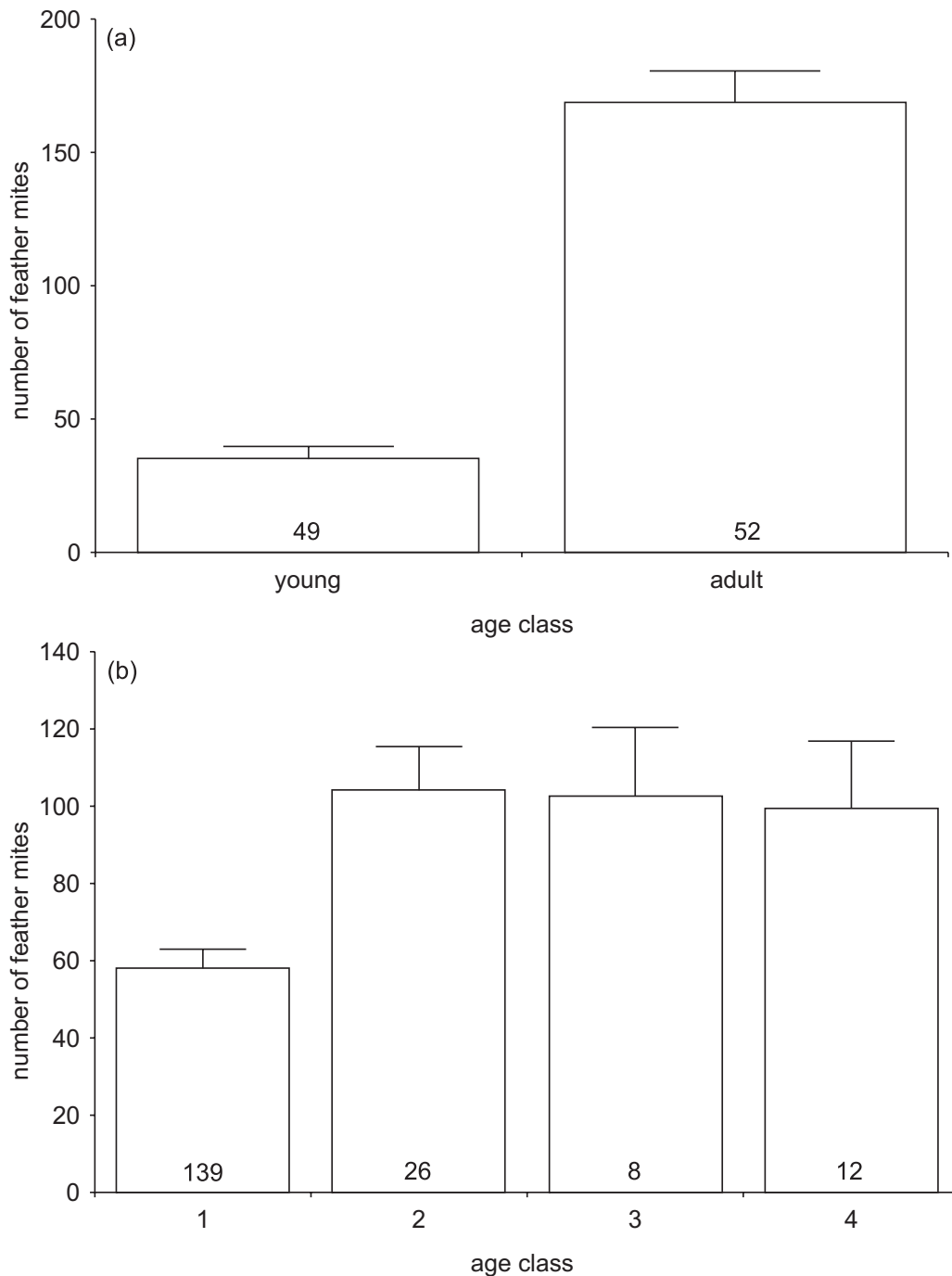
Fumigation with the insecticide had a significant effect on the total number of feather mites on the wing and tail feathers 1 year after the experiment, since birds in the experimental group had significantly fewer mites than those in the control group (59.9 ± 50.7 vs. 176.8 ± 95.1 ; $n_1 = 29$, $n_2 =$

32; $F = 34.84$, $P < 0.0001$). When we compared the breeding performance and morphological variables of the birds 1 year after the experiment, we found no significant difference between the two groups (Table 2). Similar results were found when we compared the change in wing-feather length and tail-feather length between the two years, i.e. following the experimental manipulation (Table 1). The survival rates of the birds in the experimental and control groups were similar (males: $\chi^2_{[21,21]} = 0.10$, $P = 0.76$; females: $\chi^2_{[23,20]} = 0.17$, $P = 0.28$), again indicating that feather mites are harmless.

Discussion

Correlative studies on the relationship between the intensity of infestation by feather mites and the condition of the host have generated antagonistic results (Blanco et al. 1997, 1999; Thompson et al. 1997; Harper 1999; Dowling et al. 2001; Møller et al. 2004). These contradictory results may be the drawback of correlative studies; for example, in a host–parasite association, positive and negative associations, and even no association, between the size of the parasite population and the condition of the host are expected. However, Figuerola et al.'s (2003) experimental study, which supports the parasitic life of feather mites, and our results supporting the commensal nature of feather mites suggest that this interaction may vary among host–symbiont associations. Our experimental results support the commensal life of feather mites, as we found no difference between the fumigated and control groups in the morphological variables and breeding performance of the birds, or in the change in wing- and tail-feather lengths following the experimental year. Furthermore, it is worth mentioning that the difference in the number of mites between the experimental and control groups persisted even 1 year following the manipulation. We consider this finding to be important, since some authors attribute the absence of a relationship between the number of feather mites and the condition of the host to methodological drawbacks. That is, most studies followed the host–symbiont association during the nonmolting period, but the effect of symbionts on condition-dependent feather characters can be expressed only during the period of development of the character in question (e.g., during the molt in the case of periodically replaced characters) (Thompson et al. 1997; Pérez-Tris et al. 2002; Figuerola et al. 2003). Blanco et al.'s (2001) preliminary data about the composition of the diet of another mite species (*Pterodectes rutilus* Mégnin in Robin & Mégnin, 1877) living on barn swallows is in accordance with our results, considering the absence of effects of *Trouessartia* spp. on barn swallows. It has been hypothesized that the host may even benefit from the interaction with feather mites, because the mites feed on pathogenic microorganisms such as fungi and bacteria accumulated on the feathers (Blanco et al. 1997). In this respect we would expect that by eliminating the population of mutualistic symbionts, the fitness of the host would decrease. Our experimental results do not support the beneficial effect of feather mites on the fitness of barn swallows, as we did not find any effect of the fumigation on the breeding performance and morphological variables of the birds relative to the control group. As our data support the commensal nature of feather mites, features

Fig. 1. Differences in numbers of feather mites between juvenile and adult postbreeding barn swallows (*Hirundo rustica*) in Romania (a) and between 1-, 2-, 3-, and 4-year-old breeding barn swallows in Hungary (b). For the postbreeding birds the number of feather mites is the total number on the wing and tail feathers, while for the breeding birds, infestation of only the three outermost primaries was used. The numbers within the bars show the sample size for each group. Values are shown as the mean $\pm$ SE.



other than variation in host defenses should explain the difference in the numbers of mites among individual barn swallows. It is worth mentioning that the insecticide used may kill or harm other microorganisms living on the feathers, such as the bacterial assemblage on the plumage (Lucas et al. 2005), which can affect the results and conclusions drawn. Unfortunately, we have information neither about the occurrence and abundance of microorganisms of the barn swallow nor about the effect of insecticides on the abun-

dance of these symbionts of the birds. We emphasize that our results should be considered with this defect of the experimental design in mind.

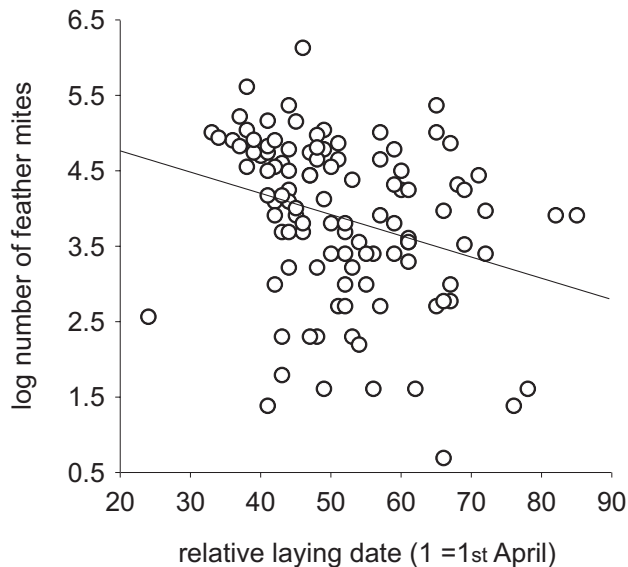
Our results on the difference between the numbers of feather mites on juvenile and adult barn swallows during the postbreeding period are in accordance with previous findings on several different host species, namely that birds in their first year of life have fewer mites than adults (Blanco et al. 1997, 1999; Jovani and Blanco 2000; Blanco and Frías

Table 1. Results of stepwise GLMs of the relationship between number of feather mites (*Trouessartia* spp.) (dependent variable), age (categorical predictor), and condition indices and breeding performance (continuous predictor) in male and female barn swallows (*Hirundo rustica*).

Variable	MS	df	<i>F</i>	<i>P</i>
Breeding barn swallows in Hungary				
Males				
Capture time	14 077.7	1	5.47	0.02
Age	18 865.5	1	7.33	0.008
Model	$F_{[1,99]} = 6.68, r^2 = 0.12, P = 0.002$			
Females				
Laying date	10.93	1	10.33	0.002
Model	$F_{[1,106]} = 10.33, r^2 = 0.09, P = 0.002$			
Postbreeding barn swallows in Romania				
Day of capture	35786.2	1	9.73	0.002
Time of capture	17305.0	1	4.70	0.03
Age	445537.1	1	121.10	<0.0001
Model	$F_{[3,92]} = 46.29, r^2 = 0.60, P < 0.0001$			

Note: For the confounding variables included in the model see Methods.

Fig. 2. Laying dates for Hungarian female barn swallows in relation to the intensity of infestation by feather mites between 2002 and 2004. The line is a linear regression line with the equation $Y = 0.53 - 0.03X$.



2001). This difference between age classes can be explained by the fact that after juvenile birds are colonized by mites, probably by their parents in the nest (Proctor 2003) or during the social life of the birds (Blanco and Frías 2001), the time available for the population of mites to build up is short. However, the difference between age classes persisted even 1 year after hatching, since 1-year-old breeding barn swallows had fewer mites than birds at least 2 years of age. This difference could be explained by the low reproductive rate of feather mites, since only one egg matures per reproductive event (Proctor 2003). The lack of difference in the numbers of mites between 2-year-old barn swallows and those that were more than 2 years old suggests that after the

second year of life of the host, the number of mites reaches an upper limit. Above this limit their population size is probably limited by factors other than their reproductive potential. One year after the experimental treatment, the number of mites was significantly lower in the case of birds fumigated with an insecticide. This difference could be explained also by the low population growth rate of feather mites. The insecticide used has a long-term effect, but barn swallows undergo a complete annual molt on the wintering grounds, which can terminate the effect of the insecticide, and birds are then exposed to infestation with mites from other group members during the migratory and wintering periods (Jovani and Blanco 2000; Blanco and Frías 2001; Proctor 2003). An alternative explanation for the pattern of differences between the age classes is that mites obtain fewer resources from young swallows than from older birds, resulting in smaller mite populations on young birds. Indirect evidence for this explanation is that condition indices and breeding performance of the barn swallows increase during the first 2 years of life, but afterwards their performance remains unchanged at least until they are 4 years old (Møller and deLope 1999). However, a direct test in this respect is required, such as analyzing the difference between age classes in the quantity and quality of the food supply of feather mites. The positive relationship between the laying date of female barn swallows and the number of feather mites apparently supports the condition-dependent abundance of mites on the host, since laying date in birds generally is regarded as a good index of condition (e.g., Møller et al. 2004). But it is important to mention that none of the other variables related to the condition indices of males and females showed a significant association with the number of mites. This can be explained by the assumption that morphological variables of the barn swallows are weakly related to the abundance of preening oil and microorganisms on the feathers. Unfortunately, we have no data on birds concerning this association that would allow us to speculate about the mechanism responsible for the pattern of abundance of feather mites among hosts.

Table 2. ANOVA results of a comparison of morphological variables and breeding performance of barn swallows in fumigated and control groups in the year following the experimental year, and the difference in the change in wing-feather length and tail-feather length between the two years in the two groups of birds.

	MS	$F_{[df]}$	P
Wing-feather length			
Fumigation treatment	9.00	1.11 _[1,58]	0.30
Sex	38.58	4.77 _[1,58]	0.033
Tail-feather length			
Fumigation treatment	30.45	0.64 _[1,58]	0.43
Sex	4614.69	96.55 _[1,58]	<0.0001
Fluctuating asymmetry in tail-feather length			
Fumigation treatment	0.87	0.28 _[1,50]	0.60
Sex	14.77	4.77 _[1,50]	0.34
Δ wing-feather length (2003–2004)			
Fumigation treatment	0.36	0.44 _[1,57]	0.51
Sex	3.92	4.86 _[1,57]	0.031
Δ tail-feather length (2003–2004)			
Fumigation treatment	10.22	1.26 _[1,57]	0.27
Sex	66.46	8.16 _[1,57]	<0.01
Laying date in 2004			
Fumigation treatment	165.97	1.86 _[1,49]	0.18
Sex	80.98	0.91 _[1,49]	0.35
Clutch size in 2004			
Fumigation treatment	0.47	0.52 _[1,50]	0.47
Sex	0.94	1.03	0.31

Note: None of the interactions between the variables in treatment and sex were significant.

In conclusion, our results indicate that two *Trouessartia* species of feather mites have neither deleterious nor beneficial effects on the fitness of barn swallows, supporting previous suggestions concerning the commensal nature of feather mites. Juvenile barn swallows had fewer mites than adults, and this difference between age classes persisted until the second year of life of the birds. The difference in size of mite populations between age classes could be attributed to the low reproductive potential of mites. Alternatively, the difference in food supply for feather mites could be responsible for the smaller population of mites on 1-year-old hosts. The positive relationship between the abundance of feather mites and the laying date of female barn swallows suggests that the abundance of mites among hosts is condition-dependent.

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