

Habitat preference, escape behavior, and cues used by feather mites to avoid molting wing feathers

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We analyzed the pattern of distribution and the effect of molting on the escape behavior of feather mites on the wing feathers during the nonmolting and molting season of the barn swallow *Hirundo rustica*. Feather mites showed consistent preference for the second outermost primary, with a steady decrease in proximal distance and avoidance of the outermost primary. Several explanations are suggested to explain this unusual distribution. Further, analyzing the escape behavior of feather mites on molting primaries, we show that mites avoid the feathers destined to be dropped next on molting barn swallows, and in the case of the outermost primary, mites use the “last moment” strategy, namely, leaving feathers shortly before it is dropped. Next, we performed an experiment in which we simulated shedding feathers or feathers about to be shed on nonmolting barn swallows, in order to test cues used by feather mites in avoiding molting primaries. Both the vibration of the incised feather and the gap of the pulled feather induced mites to leave primaries situated distally, at two-feathers distance from the manipulated primary, related to the control group. Our results show that feather mites have the ability to perceive the signal produced by the feather that will drop next and by the gap of the missing feather. It remains to be demonstrated, whether feather mites have the ability to perceive the vibration of the feather per se or they perceive the altered airflow caused by the vibrating feathers. **Key words:** barn swallow, distribution, *Hirundo rustica*, symbionts, vibration hypothesis, window hypothesis. [*Behav Ecol* 17:277–284 (2006)]

Birds host a rich diversity of arthropod symbionts, of which the greatest diversity is made up of feather mites, Acari: Astigmata, a small-bodied symbiotic acarine group dwelling in/on the skin and feathers (Proctor and Owens, 2000). Little is known about the relationships of birds and their feather mites (O'Connor, 1982; Proctor and Owens, 2000), these being considered as parasites, commensals, or mutualistic symbionts (Figueroa et al., 2003; Proctor and Owens, 2000). Data available for the barn swallow *Hirundo rustica* indicate that the feather mites of this host are commensals with no harmful effects on the fitness of the birds (Blanco and Frías, 2001; Blanco et al., 2001; Møller et al., 2004; Pap et al., 2005). Feather mites live primarily on the ventral surface of the wing and tail feathers, between the barbs of feathers. Their distribution seems to be affected by the morphology and structure of the feathers, the life history and social behavior of the host, and several external environmental factors such as humidity, air temperature, and possibly the airflow on the surface of the feathers (Blanco et al., 1997; Bridge, 2003; Choe and Kim, 1989; Figuerola, 2000; Jovani and Blanco, 2000; Rózsa, 1997). Despite the limiting locomotor capacity of feather mites due to the adaptation to symbiotic life, seasonal and daily movement of mites has been observed (e.g., Wiles et al., 2000). This probably reflects the response of mites to

the changing environment or in case of molting birds, an adaptive behavior to avoid molting feathers.

The periodic shedding of feathers, fur (known as molting), and the external epidermal layer was considered an important factor in disrupting the life cycle of ectosymbionts (see Moyer et al., 2002). Studies on lice, quill mites, and feather mites indicate that these symbionts have the ability to escape from the shedding parts of the host by modifying their behavior during the molting period. For example, quill mites abandon old feathers and enter the quills of new ones (Casto, 1974; Kethley, 1971), and lice actively seek refuge inside the sheath of the developing feather during the molt, where they are safe (Moyer et al., 2002). Feather mites of several passerines abandon wing feathers next, and also the second one, to be molted (Jovani and Serrano, 2001). But, despite the importance of molt in disrupting the life cycle of mites, little is known about the behavior of feather mites and the way they deviate from their normal pattern of distribution on the molting feathers. The response of feather mites to the molting feather has been investigated in only two studies (Dubinin, 1951; Jovani and Serrano, 2001). The aforementioned study has the problem of low sample size. In the second study, different species with generally small sample sizes were pooled together without controlling, for example, for the different patterns of distribution of feather mites on the wing feathers of different bird species. Apparently, nothing is known about the mechanisms by which these organisms detect the shedding external parts of the host (e.g., Proctor, 2003). Dubinin (1951; cited in Jovani and Serrano, 2001) and others (e.g., Blanco and Frías, 2001) proposed several hypotheses explaining the capacity of feather mites to perceive molting wing feathers. However,

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except for Dubinin's pioneering study, to the best of our knowledge, the mechanisms responsible for the escape behavior have never been tested. Dubinin (1951) proposed that the vibration of loosening feathers prior to molt provides a cue to feather mites to leave the shedding part of the wing (vibration hypothesis). Alternatively, feather mites detect the altered airflow produced by the gap of the missing adjacent feather (window hypothesis; Jovani and Serrano, 2001) and leave the feather.

In this study, we first describe the distribution patterns of feather mites on the primary wing feathers of the barn swallow during their nonmolting breeding season in Hungary, which presumably reflects their adaptive microhabitat preferences. Second, we analyze the distribution of feather mites on different wing feathers of molting birds in South Africa in relation to the molting stage of different primary feathers, in order to analyze the escape behavior of feather mites. Third, in an experimental study on a breeding barn swallow population in Hungary, we tested the efficacy of the "window and vibration hypotheses" as cues used by feather mites in avoiding the molting feathers. That is, we mimicked a loosening feather by incising the base of the rachis of the sixth primary (e.g., the fifth primary from the distal part of the wing) (first experiment) in order to imitate the vibrating feather shortly before it was molted. By pulling out the same primary (second experiment), we mimicked the gap caused by the missing feather during molt. The change in the number of feather mites on each primary feather was calculated as the difference between the number counted on first capture and that counted on the second capture approximately 3 weeks later. Our prediction was that feather mites use the vibrating feather or the altered airflow on gap of the fallen feather as cues during escape, they should leave at least the next distal (normally the next to be molted) feather from the manipulated primary in the first or/and the second experimental group.

METHODS

Study areas and species

The barn swallow is a long-distance migratory species, with the central-eastern European breeding populations probably wintering south of the equator, in the central and southern part of Africa (Cramp, 1988). Birds have a complete molt once a year during their Austral migration, when both adults and juveniles replace old wing and tail feathers. This study was carried on in a breeding barn swallow population in eastern Hungary, near Balmazújváros (47° 37' N, 21° 21' E) between 24th of May and 30th of June 2004, and in three different wintering populations in South Africa, namely, near Bloemfontein, Free State (29° 2' S, 26° 24' E), at Creighton, Kwazulu-Natal (29° 58' S, 29° 49' E), and near Durban, Kwazulu-Natal (29° 38' S, 31° 5' E), between 25th and 30th of January 2004. The breeding area is characterized by scattered farms, where the birds breed alone or in loose colonies of up to 15 pairs. During the wintering period in Africa, hundreds or thousands of birds roost in reed beds, where the birds were captured randomly in mist nets at dusk. After capturing and ringing the birds, one of us (P.L.P.) measured a number of morphological characters on the barn swallows, and on the birds in South Africa the molt of wing and tail feathers was recorded according to the scheme of Newton (1966). A dropped feather was scored as 1, quarter-, half-, and three-quarters-regrown feathers were scored 2, 3, and 4, respectively, and a full-regrown feather was scored 5. The molting pattern of barn swallow is similar to that of most passerines in that it sheds primary (P) flight feathers from the wing in sequential order (Jenni and Winkler, 1994), from

the innermost P1 to the outermost P9 (P10 is rudimentary in swallows). Barn swallows were about half way through their molt during our fieldtrip season in South Africa, presenting a high degree of synchronization in molt (e.g., all captured birds were in active molt, and 98% of them molted the fifth, sixth, seventh, or eighth primaries).

Examination of birds for mites

Feather mites are present on the vanes of wing and tail feathers and are individually visible without magnification. On completion of morphometric measurements, the number of feather mites on the whole vane of primaries, secondaries, and tertials of the left and right wings and on the tail feathers were examined by the same person (P.L.P.) after the following procedure. The wing and the tail feathers were extended and held up to ambient or artificial light, and the feather mites attached to the feathers were counted until 10 on each feather and above this number their intensity of infestation was assessed by scoring the mite clusters on a five-grade scale (e.g., 15, 20, 25). The use of semiquantitative assessment was necessary because barn swallows are heavily infested, some of them holding hundreds of feather mites. The use of this visually inspecting semiquantitative method holds measurement errors due to the difficulties in distinguishing live mites and skin casts (Proctor and Owens, 2000) and due to the general problem with the repeatability of estimates. We verified the efficacy of this method in two ways. First, in some 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 dust-ruffling method (Clayton and Drown, 2001). To remove the feather mites, we used a common insecticide developed for veterinary use, containing 0.17% permethrin and 0.07% bioresmethrin (Insecticide 2000, Waldner GmbH Wien, Austria). The intensity of infestation by feather mites based on visual inspection of the three outermost primaries (the most heavily infested feathers; see Results) correlated significantly with the number of feather mites counted on the collecting plate (Spearman rank correlation: $r = .65$, $n = 48$, $p < .0001$), supporting the accuracy of the counting method used. Second, on a subset of breeding birds in Hungary in 2004, we recounted the number of feather mites on the flight feathers of the same birds several days later after initial measurements, in order to calculate the repeatability of our assessment. The high repeatability indicates again the accuracy of the method used ($R = .97$, $F_{10,11} = 75.3$, $p < .0001$).

Two species of feather mite, *Trouessartia crucifera* and *Trouessartia appendiculata*, collected from the Hungarian birds were identified. *T. crucifera* also was present in all three South African populations, and at Creighton and Bloemfontein another species, *Scutulanysus* sp. (probably *Scutulanysus hircundicola* or *Scutulanysus obscurus*), was identified by Ronald Schmäschke (University of Leipzig, Germany). Because the identity of different mite species could not be visually identified during counting, the relative frequency of the different feather mite species was not possible to calculate. Thus, we pooled the abundance data (for the drawback of pooling data, see Discussion). We did not find any data in the literature about the biology of these feather mite species, so we assume that the life history of the feather mite species do not differ in the manner which can cause differences in results between different populations.

Experimental manipulation

Adult male and female breeding barn swallows from the Hungarian population were selected randomly to be in one of

the three experimental groups. In the first experimental group, we mimicked the vibration of the feathers shortly before molt by laterally incising half of the rachis at the base of the left and right sixth primary. Our experiment most probably had an effect on the vibration of the feathers because from the 26 experimental birds, 15 had broken their incised feathers on at least one side of the wing 3 weeks after the first capture. In the second experimental group, we pulled out the sixth primary on both sides of the wing, imitating in this way the gap produced by the missing feather during the molt. The third group was held as a control, where except for feather manipulation, we followed the same procedure in capturing and measuring birds as in the two other groups. The number of feather mites was counted on both capture sessions, and the change in number of mites between the first and second measure was used in the analyses (see below). The time elapsed during capture-recapture did not differ between the control, first, and second experimental groups (20.1, 21.5, and 20.3 days, respectively; $F_{2,62} = 0.44$, $p = .65$).

Data analysis

The mean intensity of infestation of barn swallows by feather mites differed among the three South African sites ($F_{2,110} = 42.98$, $p < .0001$), while juveniles did not differ from adults in this respect ($F_{1,110} = 1.41$, $p = .24$). The determination of sexes with accuracy was difficult because most birds had broken or molting outermost tail feathers, a highly sexually dimorphic character. Hence, we pooled the data of males and females. Because we did not find significant effect of the intensity of infestation on the pattern of distribution of feather mites on wing feathers, we pooled the data of birds captured in South Africa. The data pooling was appropriate because after controlling for the place of collection none of the results changed. The pooling procedure was also followed in the Hungarian breeding population, but in this case we used only the data of adult birds, and the sexes did not differ significantly in their numbers of feather mites ($F_{1,152} = 0.49$, $p = .49$).

We included only data from infected birds in the analysis. Because the prevalence was high in each population studied (e.g., 97% of the Hungarian population), we had to exclude the data of only a few birds. Feather mites show a strong preference for the primaries. Of the total number of feather mites counted on the wing and tail feathers of 151 nonmolting adult infected birds in Hungary, 90% were on primaries, 3% on secondaries, 2% on tertials, and 5% on tail feathers. Therefore, the distribution and movement of mites on secondaries, tertials, and tail feathers were not analyzed, except when we followed the redistribution of the mites on flight feathers after the experimental manipulation. For the experiment, we included birds with at least 10 feather mites on the most preferred primary 8 (~5% of the mean intensity of infection). We used this arbitrary selection of birds for the experiment because below this infection intensity the movement of mites is hard to follow due to the problem of statistical perceivability on low infestation level (Jovani and Serrano, 2004). In the data analyses of Hungarian birds, we used the average values of the left and right wings in order to increase the robustness of the data, while for the South African birds, we used the data obtained only for the left wing (the average value for this data set could not be calculated due to the asymmetry observed in molting for some birds). The correlation in the number of feather mites between the left and right wings is highly significant (Behnke et al., 1999; Jovani and Serrano, 2004; Pap PL and Tökölly J, personal observation), therefore it was appropriate to use the data of only one wing for the molting birds.

The data for eight out of 25 birds from the first experimental group (incised primaries) with broken primary 6 on one side of the wing was excluded initially from the analyses. Similarly, data for seven birds from the same group recaptured after several days after the manipulation with both primaries broken were excluded from the analyses. First, we analyzed the effect of manipulation on the distribution of feather mites on the wing feathers on the subset sample excluding these birds with broken primaries. In the following, we repeated all analyses on the large data set including birds with one primary 6 broken in the first experimental group (using the data of feather mites for the same side of the wing) and including birds with primaries broken on both wings in the second experimental group. This transfer was done by pulling out the calamus of the broken feathers of the birds recaptured within a few days after the initial measurements. Because none of the results differed between the two analyses on small and large data sets, we kept the data of these birds, increasing the samples size in the control, first, and second experimental groups to 19, 18, and 28, respectively.

Due to the nature of dispersion of symbionts, feather mites from the Hungarian population showed a negative binomial distribution (skewness = 0.73, Kolmogorov-Smirnov test, $d = 0.09$, $n = 157$, $p < .15$), while the South African population fitted to normal distribution (skewness = 0.51, Kolmogorov-Smirnov test, $d = 0.08$, $n = 116$, $p < .30$). Hence, we used nonparametric statistical analyses whenever it was necessary. Parametric tests were used for analyzing the results of the experiment, where because of excluding birds with no or very low level of infestation the data were normally distributed. Medians and lower quartile ranges or means and SE (for parametric tests) are given for the data presented.

RESULTS

Distribution of feather mites on nonmolting barn swallows in Hungary

The distribution of the number of feather mites on the primary feathers was far from random (Figure 1), with primaries differing significantly among each other in the intensity of their infestations (Friedman ANOVA test: $\chi^2_{8,151} = 702.5$, $p < .0001$). The Wilcoxon matched-pairs signed-rank test indicates that mites showed a high consistency in their preference for the primary 8, and interestingly they consistently avoided the

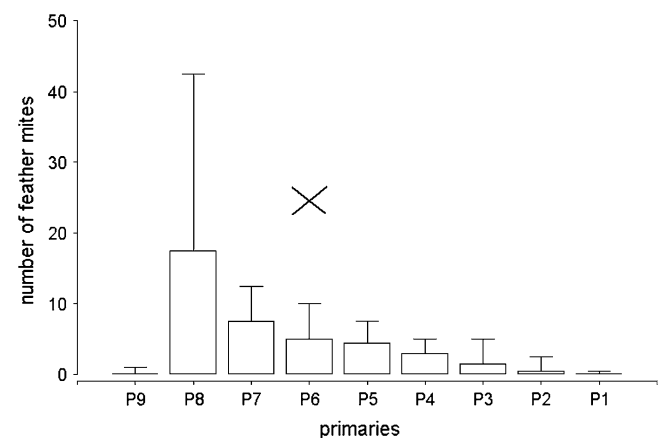


Figure 1

The distribution of feather mites on primary feathers of the nonmolting barn swallows in Hungary (median and lower quartile range). Cross indicates the primary which was experimentally incised or pulled out ($n = 151$).

Table 1
Wilcoxon matched-pairs signed-rank test of the consistency among nonmolting birds in the difference in the number of feather mites between neighboring primaries ($n = 151$)

Primary	Neighbor proximal feather of the target primary	
	<i>Z</i>	<i>p</i>
9	−10.41	<.0001
8	8.96	<.0001
7	6.31	<.0001
6	6.14	<.0001
5	5.60	<.0001
4	6.89	<.0001
3	7.48	<.0001
2	7.06	<.0001
1	—	—

Primary 9 = outermost primary.

outermost primary (Table 1). The consistency in preference of feather mites for the primaries 7–1 was also high, with a gradual decrease in their number from distal to proximal.

Distribution of feather mites on molting barn swallows in South Africa

The distribution of feather mites on molting wing feathers apparently differed from the pattern on the nonmolting birds

(Figure 2); feathers unoccupied by mites or with low infestation in the case of nonmolting birds can be highly infected in molting birds (e.g., primary 9). In order to test the effect of molt on the distribution of feather mites on primaries, we performed separate analyses for the primaries 7, 8, and 9, where we included the data of those birds which had a dropped or growing feather neighbor, second proximal, and in the case where we had sufficient data the third proximal from the target (7, 8, and 9) primaries. For the primary 7, we had enough data to test the effect of only the neighbor and second proximal primary on the number of feather mites of the target feather (see Figure 3a). The number of mites on primary 7 decreased significantly when the neighboring primary was dropped related to when the second proximal feather was in molt (Mann-Whitney *U* test: $Z = -2.68$, $n_1 = 43$, $n_2 = 21$, $p < .01$, Figure 3a). We found a similar effect of the molt of the neighbor and second or third proximal feather on the intensity of mites on primary 8, namely, only the neighbor feather influencing negatively the number of mites on the target primary ($F_{2,88} = 9.06$, $p < .001$, Figure 3b), and the abundance of feather mites on primary 8 was not affected by molting of the second and third primaries next to the neighbor primary (Tukey post hoc test: $p = 1.0$). The number of feather mites on the outermost primary (P9) did not change significantly whether the dropped primary was neighbor or second or third proximal from the primary in case ($F_{2,88} = 0.14$, $p = .87$, Figure 3c). However, when we separated the data of birds to feathers in pin (molt category 1) and expanded feather (molt category 2 and 3) of the neighbor primary, we found a significant difference between the

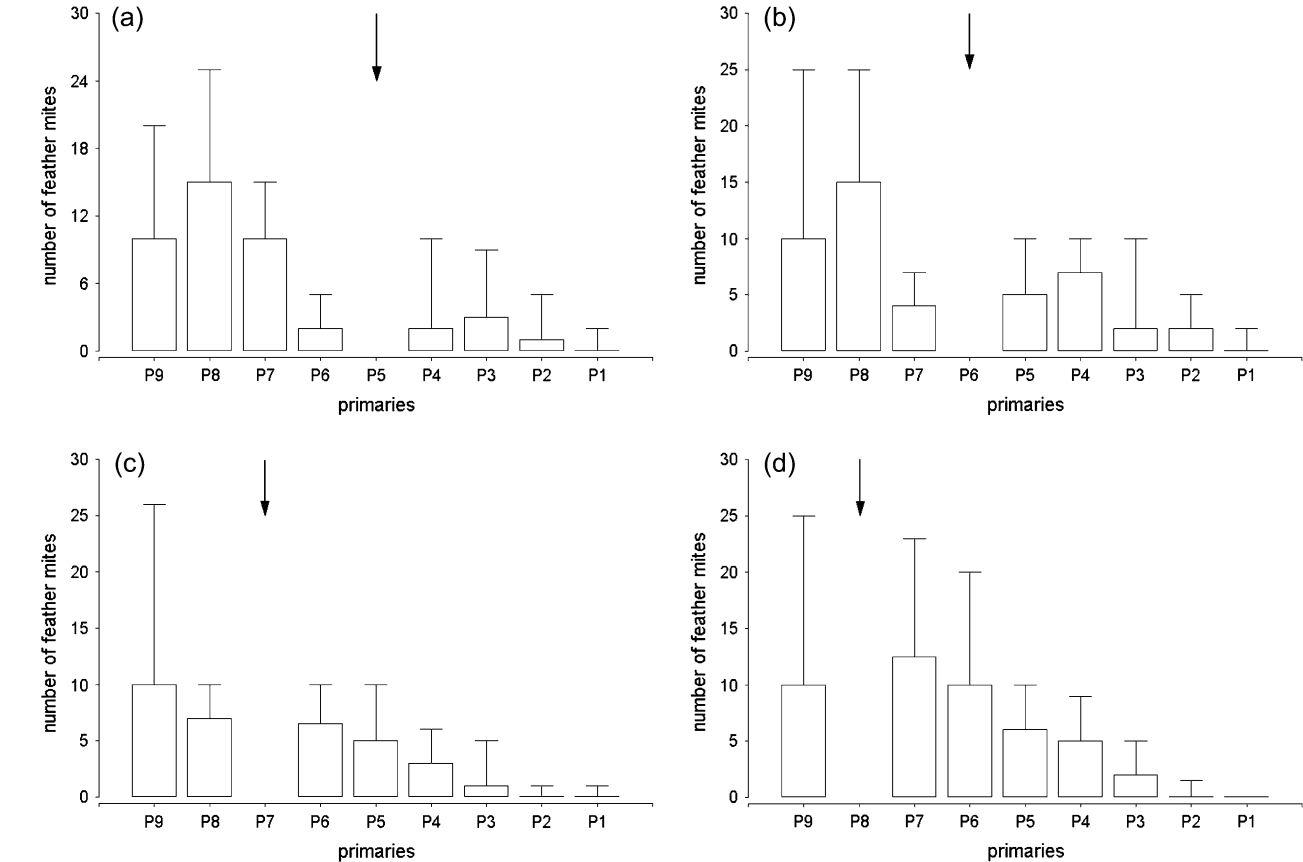
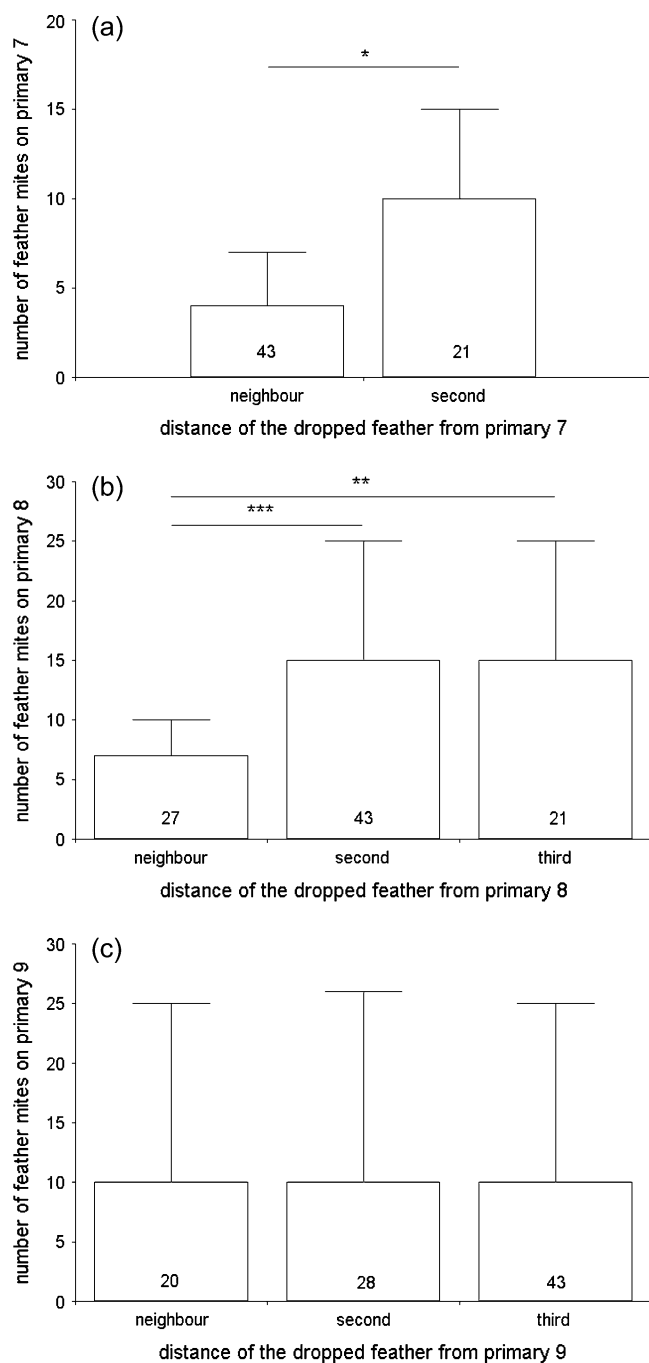


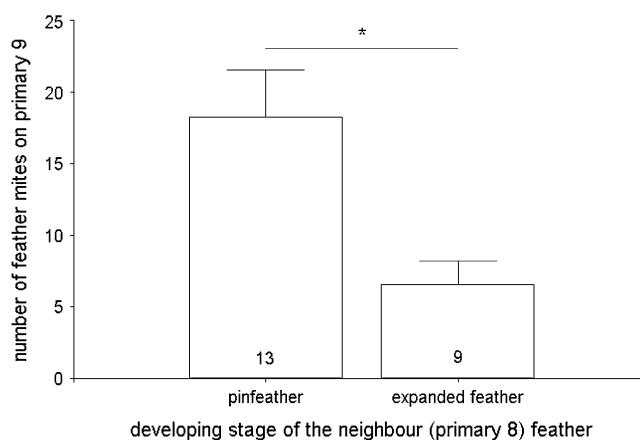
Figure 2
The distribution of feather mites on primary feathers in relation to molting of the fifth, sixth, seventh, and eighth primaries (a, b, c, and d in increasing order) of the barn swallows in South Africa (median and lower quartile range). Arrows indicate the gap of the dropped feather (sample size are 21, 43, 27, and 20, respectively).

**Figure 3**

Number of feather mites on the seventh, eighth, and ninth primaries (a, b, and c) in the case where the dropped feather is a neighbor, the second one and the third one from the target primary (median and lower quartile range). Significance levels for Mann-Whitney *U* test and multiple comparison Tukey post hoc test for unequal sample size are shown above the horizontal bars (** $p < .001$; * $p < .01$).

two groups in the number of mites on the outermost feather ($F_{1,20} = 7.65$, $p = .01$, Figure 4).

We performed separate analyses for the primaries 6 and 7 for which we had sufficient data in order to test the recolonization capacity of mites by analyzing the change in the number of feather mites before molting (i.e., on an old primary) and after molting (i.e., on a new primary) in the same posi-

**Figure 4**

Number of feather mites on the outermost primary in relation to the developing stage of the neighbor proximal feather (mean and SE). Significance level is shown above columns (* $p = .01$).

tion. The results clearly show the rapid recolonization of these two primaries because in both cases the number of mites increased in number on new primaries relative to the old feathers in the same position (ANOVA planned comparison of the number of mites on old and new feathers; primary 6: $F_{1,60} = 13.07$, $p < .001$; primary 7: $F_{1,69} = 8.12$, $p < .01$).

Effect of experiment on the movement of feather mites

We performed separate repeated measure ANOVA analyses for different primaries, in order to test the effect of the experiment on the change in the number of feather mites on primary feathers 7, 8, and 9 when primary 6 was manipulated. We found no difference between the three experimental groups for any of the three primaries in the number of feather mites (Table 2), but in case of primary 8 the significant interaction between the treatment and repeated measure shows the significant difference in the change in number of mites between the groups (Figure 5a). The Tukey post hoc test for unequal sample size indicates that the decrease between the first and second count of the feather mites was significant for both experimental groups but not for the control one ($p < .05$, $p < .001$, and $p = \text{ns}$ for the first and second experimental groups and for the control group, respectively). Surprisingly, the number of feather mites did not change significantly between the groups on the distal neighbor feather (P7) of the manipulated primary, as we would have expected based on the response of mites to the nearest primary feather that had been dropped. However, this could be a problem of statistical perceivability of mites in low number (Jovani and Serrano, 2004) because the change in the number of feather mites on distal primaries during the 3 weeks of the experiment was proportional to the initial abundance of mites (Spearman rank correlation, P7: $r = .50$, $p < .0001$; P8: $r = .60$, $p < .0001$, $n = 65$; P9: $r = .30$, $p < .05$), and primary 7 held significantly less mites than the most preferred primary 8 (see Table 1, Figure 1).

Feather mites leaving the most preferred distal primary 8 due to the experiment raise the question of where these mites disperse to. Accordingly, we performed the same repeated measure ANOVA test on the total number of feather mites counted on all wing and tail feathers, except the manipulated primary (Table 2, Figure 5b). In this analysis, we omitted from all three groups the counting data of the manipulated primary because incising disturbs or may kill the mites and because the mite-laden of the pulled feathers could lower the total number of mites available to colonize other feathers in the

Table 2
Results of repeated measure ANOVA on the change in experimental groups of the number of feather mites on the seventh, eighth, and ninth primaries and on flight feathers (wing—except the primary 6—and tail feathers)

Source	df	sum of squares	F	p
Primary 7				
Treatment	2	134.4	1.28	.29
Subject within groups	62	6531.4	—	—
Repeated measure	1	1024.4	51.13	<.0001
Treatment × repeated measure	2	20.2	1.00	.37
Repeated measure × subjects within groups	62	1242.3	—	—
Primary 8				
Treatment	2	901.0	0.66	.52
Subject within groups	62	42601.4	—	—
Repeated measure	1	1552.1	23.23	<.0001
Treatment × repeated measure	2	653.0	4.89	.01
Repeated measure × subjects within groups	62	4142.4	—	—
Primary 9				
Treatment	2	152.8	1.03	.36
Subject within groups	62	4604.1	—	—
Repeated measure	1	63.2	2.23	.14
Treatment × repeated measure	2	29.2	0.51	.60
Repeated measure × subjects within groups	62	1758.3	—	—
Total number of feather mites				
Treatment	2	23574.3	3.20	.31
Subject within groups	62	610377.7	—	—
Repeated measure	1	37432.8	38.13	<.0001
Treatment × repeated measure	2	6161.4	3.14	.05
Repeated measure × subjects within groups	62	60861.1	—	—

experimental groups. Again, the significant interaction between the treatment and repeated measure indicates that the two experimental groups differed in the degree of decrease in the number of mites from the control group ($p < .01$, $p < .001$, and $p = ns$ for the first and second experimental groups and for the control group, respectively). Furthermore, the significant relationship between the changes in the numbers of mites during the experiment of the outermost primaries of the right and left wings within the same individual indicates that feather mites have a fine-tuned movement to changing environment (Spearman rank correlation, P2: $r = .72$, $p < .001$; P3: $r = .84$, $p < .001$; P4: $r = .56$, $p < .001$, $n = 65$).

DISCUSSION

We have found that feather mites have a fine-tuned distribution on the wing feathers of the nonmolting barn swallows, with a strong preference for the second outermost primary, a consistent avoidance of the outermost wing feather, and with a gradual decrease in their number from distal to proximal primaries. Our results confirm previous data about the ability of feather mites to avoid molting feathers. Feather mites avoided the next to be molted feather during the molting period of the barn swallow, except on the outermost primary, in which case it seems that they use the last moment strategy in order to avoid being dropped. Mimicking the vibration of the feathers shortly before molt and the gap caused by the missing feather during molt, performed on nonmolting barn swallows, we showed that feather mites have the ability to

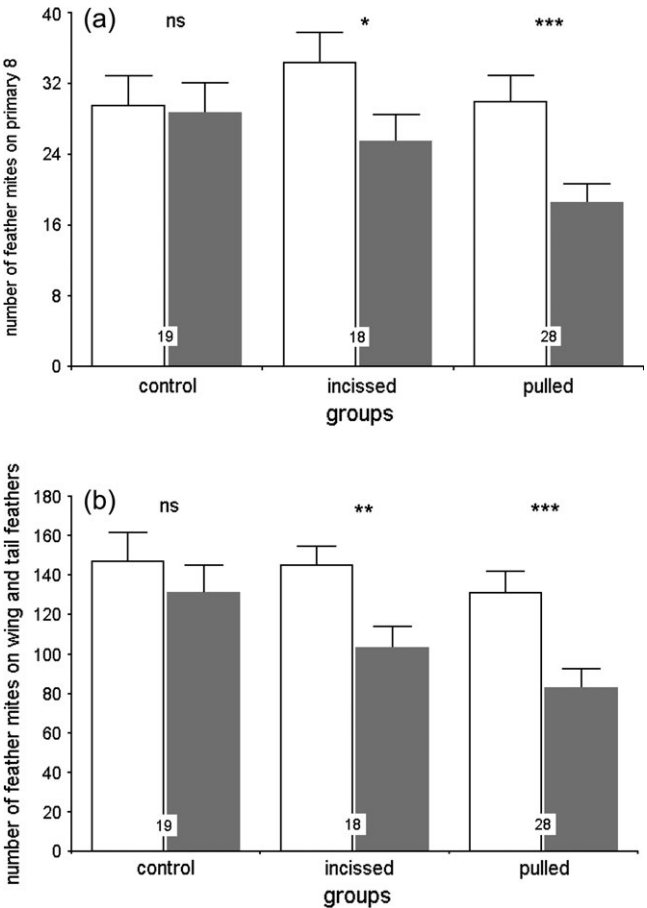


Figure 5
Change in the number of feather mites on the primary 8 (a) and on wing (except the primary 6) and tail feathers (b) between the first (white) and second (gray) measurements in the three experimental groups. The decrease of feather mites was significant for the incised and pulled groups. (For the statistical tests see text. * $p < .05$; ** $p < .01$; *** $p < .001$) (mean and SE).

perceive the signal produced by the feather that will drop and by the gap of the missing feather. Thus, our results support both—the vibration and window—hypotheses, proposed to explain the mechanism used by feather mites in order to avoid molting feathers.

Distribution of feather mites on wing feathers

Studies of the patterns of feather mites distribution have pointed out the importance of external factors (temperature, probably humidity, interspecific competition, social life of the host, etc.) in determining the host species-specific intensity of infestation and distribution of mites on wing feathers (Blanco et al., 1997; Choe and Kim, 1989; Figuerola, 2000; Jovani and Blanco, 2000; Wiles et al., 2000). Our preliminary observations on several different bird species and the few data from the literature we have (e.g., Bridge, 2003; Choe and Kim, 1989; Jovani and Serrano, 2004) suggest that there is a great variability between different host species in their feather mites' distribution on the wing. In addition, feather mites show a high consistency in their fine-tuned distribution on the wing within the same host species, as revealed by the present study and in a recent work by Jovani and Serrano (2004) on the blackcaps *Sylvia atricapilla*. The consistent distribution pattern of feather mites on the nonmolting barn

swallows, with a clear avoidance of the outermost wing feather, their preference for the second outermost primary, and the consistent decrease in their number to proximal primaries, raises the question of why these mites show this pattern of preference for specific feathers. There are probably a number of important factors that influence the microhabitat selection of feather mites, and at least three explanations may account for this distribution pattern. First, the morphological features of the feathers on which mites live differ (e.g., in barb height), as suggested by Bridge (2003) and Choe and Kim (1989). This means that differences in structure between feathers determines the way that mites can attach to the feather, which for example is important to resist air turbulences at the surface of the feather. This is less likely in our case for at least the two distal primaries, however, because the difference between neighbor primaries in barb height is probably more uniform (Bridge, 2003), and this should be reflected in the distribution pattern of mites also. The sharp difference between the outermost and its proximal neighbor primary in their numbers of mites apparently contradicts this explanation. Second, the air turbulence at the level of feather surface could influence the site preference of the mites as aerodynamically more stressful feathers are probably less appropriate for living. The air turbulence decreases from distal to proximal direction of the wing, with probably the greatest turbulence on the outermost primary (Rayner, 1988). This is in accordance with the reduced number of feather mites from the outermost primary but inconsistent with their decreasing number to proximal direction and their almost complete absence from secondaries and tertiaries, where the air turbulence is lowest. Furthermore, feather mites seem to prefer the outer half of the feathers (Bridge, 2003; Pap PL, personal observation), which does not support the prediction of spatial distribution based on aerodynamic considerations. However, the distribution of mites on the wing feathers probably reflects a compromise between the aerodynamically less stressful position and other factors, such as the barb height of the feathers. Third, the observed distribution pattern could be explained by the feathers differing in their nutritional content (e.g., preen gland oil), which ultimately determines the feather-specific distribution of feather mites. This difference can be caused by the preference of the host of preening, for example, the distal part of the wing, leading a greater chance to smear preen oil on feathers of the respective part of the wing. Again, the sharp difference in the number of feather mites between the two outermost primaries is hard to explain by this assumption, thus we consider this explanation to be implausible. The present study was not designed to distinguish between these alternatives. In order to understand the intriguing life of feather mites, we recommend further study.

Escape behavior of feather mites

Our observational data of feather mites on molting barn swallows confirm the previous findings (Dubinin, 1951; Jovani and Serrano, 2001) that mites avoid molting wing feathers. But contrary to Jovani and Serrano (2001), our results show that mites abandon feathers only when the proximal neighbor feather is molted, not when the second primary from the target feather is dropped, as previously reported (ibid.). However, our experimental results show that at least on the non-molting birds, feather mites have the capacity to sense the molting feather when the second proximal feather is dropped or is close to being dropped (see below). But, it is worth to be mentioned that the results of the experimental manipulation may be confounded by the fact that a simulated molt was presented to the mites in a geographic locale far removed from whence the birds normally molt (South Africa), with

its attendant differences in environmental conditions and host behavior and ecology relative to the geographic locale where molting normally takes place. Another factor that can affect the conclusions on the escape behavior of feather mites on molting and nonmolting birds is the at least partly different species composition of wintering and breeding barn swallow populations. In all populations *T. crucifera* was identified, while two other species (*T. appendiculata* and *Scutulanysus* sp.) were detected in the breeding and two wintering populations. Because different feather mite species may differ in their life history and frequency and pattern of distribution, even within the same host species (e.g., Choe and Kim, 1989), we emphasize to value the results with this defect. The ideal situation would be analyzing separately the data obtained from different feather mite species, which is, however, very problematic due to the difficulties in determining different feather mite species on the field. The difference between the findings of Jovani and Serrano (2001) and our results on molting birds can be explained by the difference in hosts and their specific symbionts analyzed. Our detailed analyses of the escape behavior of mites on the three outermost primaries revealed that feather mites abandon the next to be molted feather only in the case of the second outermost and proximal neighbor feathers. This difference in escape behavior of feather mites between primaries suggests that their escape is limited in the case of the outermost primary. The logical assumption for this limited escape behavior of mites on the outermost feather is that in case of mites on inner primaries they have the possibility to redistribute themselves on the next distal primary. However, if this assumption is true, we would expect in case of primary 8 (for which we have sufficient data) a significant difference in the number of feather mites between primary 8 with the second proximal feather dropped and primary 8 with the third proximal feather dropped (Figure 3b), which based at least on this subset of data is not true. Our results on the differences between the three experimental groups in the total number of feather mites on nonmolting flight feathers indicate that mites during molt disperse away from the remiges, finding refuge probably within body feathers. This movement of mites is also supported by the observation on the transfer of mites from parents to fledglings, when initially feather mites are distributed over the body of the fledglings, from where they later redistribute to their typical positions, similar to that of adults (Dubinin, 1951; cited in Kethley, 1971; Proctor, 2003). The difference between the outermost primary with the feather in pin and the expanded proximal neighbor feather in the number of feather mites indicates that feather mites use a last moment strategy, leaving the molting feather shortly before it is dropped. This is based on our observation on molting barn swallows and generally on birds, namely, that after expanding the growing primary, the next to be molted feather is dropped within a short time. Because the neighbor growing feather in pin and expanded feather differ in just a few millimeters, this probably does not significantly modify the air turbulence at this level, excluding the window hypothesis. Thus, it is reasonable to conclude that at least at this level of outermost primary, the vibration hypothesis works. Connected with this, it remains to be demonstrated whether feather mites sense the vibration of the feather per se or the airflow caused by the vibrating feather (see below).

Our experiment supports the observations of the escape behavior of feather mites on molting birds because the number of mites on primary 8 declined after the manipulation of primary 6. Contrary to our expectation, our manipulations had no effect on the number of mites on the distal neighbor feather of the manipulated primary. As mentioned before, this could be caused by a statistical drawback to detect the change of the number of mites in case of low intensity of infestation,

because on this primary the number of mites is low, and the magnitude of change of mites is proportional with their initial number (see also Jovani and Serrano, 2004). The experimentally vibrating feather and the gap of the pulled primary both induced the movement of mites on primary 8, which resulted after a 3-week experiment in a significant decrease in their number related to the control group. Our results support both hypotheses suggested by Jovani and Serrano (2004), namely, the vibration and window hypotheses. This would allow us to suppose that feather mites have a developed “sense system” of detecting the altered vibration of the feather and the altered airflow produced by the gap of the molted feather. But, considering the fact that feather mites changed their behavior two feathers distal from the manipulated one, it is tempting to accept that in both situations mites sense the altered airflow caused by the vibrating feather or by the gap of the dropped feather. However, further research is required to understand the mechanisms used by feather mites.

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