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Seasonality in the uropygial gland size and feather mite abundance in house sparrows *Passer domesticus*: natural covariation and an experiment

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The seasonal change, i.e. the marked differences between seasons of low and high productivity, in the abundance of ectosymbionts and the defence intensity of the host against pathogens is a well defined characteristic of temperate zone organisms. Here we investigate the seasonal variation in the uropygial gland size and the abundance of *Proctophyllodes* feather mites on the wing feathers of house sparrows *Passer domesticus* in two breeding populations. The size of the uropygial gland varied significantly in male and female house sparrows over the annual cycle. The gland was small during the non-breeding and mating season, after that it started to grow sharply, reaching its maximum size during breeding. Females had larger gland volumes than males during breeding, and the increase in gland size during breeding was more pronounced in females than in males. The number of feather mites was the lowest during breeding, followed by an increase during moult and reaching its maximum between the wintering and mating seasons. The absence of a significant relationship between the uropygial gland size and the abundance of feather mites, after controlling for potential confounding variables, supports the view that gland oils do not regulate the number of mites. To investigate further this hypothesis, through a full factorial experimental design we tested the effect of uropygial gland and photoperiod manipulation on the population size and population dynamics of feather mites. The manipulation of uropygial gland had no effect on mites, supporting our observational results. As a result of the experimentally increased day-length, the abundance of feather mites on wing feathers decreased significantly and more sharply than in the control group, supporting the previous anecdotal evidence about the photosensitivity of these organisms. Using photoperiodic cues, feather mites may respond to seasonal changes that affect their life-history and population dynamics.

Abundance of feather mites, one of the most common ectosymbionts of birds (Proctor 2003), varies greatly among individual hosts and species (Rózsa 1997, Figuerola 2000, Jovani and Blanco 2000, Pap et al. 2005, Galván et al. 2008). Several factors, like the increased temperature, the exposure to saline-free environments and the high quantity of oils secreted by the uropygial gland and dispersed on the plumage surface are suggested to explain the increased population size of feather mites (Wiles et al. 2000, Dowling et al. 2001a, Galván and Sanz 2006, Galván et al. 2008). For example, Galván and Sanz (2006) and Galván et al. (2008) have shown that a significant part of the variation in the abundance of feather mites on the great tit *Parus major* as well as among passerine species can be explained by the size of the uropygial gland: more mites are harboured by hosts with larger gland volumes. As the authors argued, this might arise because oil serves as food for feather mites (Blanco et al. 2001, Proctor 2003) and gland size correlates positively with the quantity of oil secreted (Bhattacharyya and Chowdhury 1995, Martín-Vivaldi et al. 2009, Møller et al. 2009). Based on anecdotal evidence, several other factors may also affect the abundance of feather mites, among which the light intensity may be an important proximate cue that can govern the response to environmental changes (Dubinin 1951). All the variables considered so far can change during the annual cycle, which may explain the seasonality found in the abundance and distribution pattern of feather mites (Mironov 2000, Wiles et al. 2000, Hamstra and Badyaev 2009). The variation in the abundance of feather mites between seasons can be explained by the adaptive response of mites to the changing environmental conditions, and/or by the change in defence intensity and/or resources provided by the host for these ectosymbionts (see below).

Feather mites are considered to be commensals, mutualistic organisms, or parasites (Blanco et al. 1997, Blanco et al. 1999, Dowling et al. 2001b, Pérez-Tris et al. 2002, Figuerola et al. 2003, Møller et al. 2004, Pap et al. 2005),

and their influence on the host is expected to be minimal. Considering the nature of the host–symbiont relationship, the effect of feather mites on the fitness of the host is crucial in the evolution and maintenance of defence 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). In this case hosts with strong defensive response will have low number of parasites related to individuals with reduced protection. On the other hand, if the symbionts have little or no effect on the fitness of the host, the evolution of defence 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, Blanco et al. 1999, Dowling et al. 2001b, Møller et al. 2004, Pap et al. 2005). In this case, the variation in the number of feather mites among hosts may be determined by factors other than host defence, like the availability of resources, e.g. oil from the uropygial gland (Blanco and Frías 2001, Galván and Sanz 2006, Galván et al. 2008). However, one of two studies (Figuerola et al. 2003, Pap et al. 2005), where the abundance of feather mites on the hosts was manipulated, found a significant negative effect of these ectosymbionts on plumage colouration (Figuerola et al. 2003), indicating a parasitism-like fitness cost at least in some host–feather mite systems.

The oil secreted by the uropygial gland of the birds is supposed to serve as food for feather mites (Blanco et al. 2001, Proctor 2003). In line with this expectation, a significant positive association was found between the size of the gland and the abundance of feather mites (Galván and Sanz 2006, Galván et al. 2008). On the other hand, the secretion of the uropygial gland may have an insecticidal property acting as a defence against ectoparasites and micro-organisms (Moyer et al. 2003, Shawkey et al. 2003, Martín-Vivaldi et al. 2009, Møller et al. 2009, Martín-Vivaldi et al. 2010, Moreno-Rueda 2010), and may reduce the population growth of feather mites. Therefore, in this second case one might expect a negative relationship between the uropygial gland size and the abundance of feather mites. Third, if the secretion of the uropygial gland plays no role in the life of feather mites, an absence of association can be expected between the intensity of infestation by mites and the size of the gland. The seasonal variation in the size of the uropygial gland, with a greater volume during the breeding than the non-breeding period (Jacob and Ziswiler 1982, Bhattacharyya and Chowdhury 1995, Martín-Vivaldi et al. 2009), offers a natural opportunity to investigate its effect on mites. One might expect a seasonal change in the abundance of mites in the same or opposite phase as that of the uropygial gland, corresponding the first two cases above. In the case where there is no association between the size of the gland and the abundance of feather mites, the number of mites may vary independently from the gland size.

Feather mites are supposed to be photosensitive organisms (Proctor 2003), supported by anecdotal evidence about their rapid avoidance of feathers exposed to intensive light (Proctor 2003, pers. obs.). Therefore, one might predict that the seasonal fluctuation in the abundance and distribution of feather mites living on the surface of the wing feathers is mediated by the variation in day-length, in other words, mites respond to seasonal changes through using the photoperiodic cue. Here we first investigate seasonality in the abundance of *Proctophyllodes* feather mites and uropygial gland volume and study the possible correlation between them in two wild house sparrow *Passer domesticus* populations over the annual cycle. To tease apart the possible confounding effects of photoperiod and uropygial gland volume we perform a two way full factorial experiment by removing uropygial gland and manipulating day-length in indoor aviaries.

Material and methods

Study areas and field measurements

The field study was performed between May 2007 and December 2008 on two house sparrow populations situated near Cluj Napoca (46° 46′N, 23° 33′E), and Cojocna village (46° 44′N, 23° 50′E), Transylvania, central Romania, where the birds were breeding in barns. The distance between the two populations is 22 km, which seems to be sufficient to prevent the birds to migrate between the two breeding sites as no house sparrow ringed at one farm was ever recaptured at the other. During the study period, we monthly captured approximately 15 male and 15 female house sparrows at both sites with mist nets (Ecotone, Poland), resulting in 1273 birds captured (897 first captures and 376 recaptures). Sampling was done generally on the same day or on two consecutive days at the two study sites (mean $\pm$ SD: 1.3 ± 1.4 days) in order to reduce the confounding effect of the date (see Results) on the difference in feather mite abundance and gland size between populations.

House sparrows have an annual cycle typical for most European non-migratory passerines. They start breeding in April and nestlings fledge mainly between May and July. Adults and fledglings moult during late summer, which may last several months from July to November (Pap et al. 2008). Following their first moult, the age of the house sparrows cannot be determined on the basis of external morphological characters (Svensson 1992). Therefore, in the present study we use the data of adult birds collected during the breeding and moulting periods, when the age of birds could be determined, and after moult the data of all captured birds were included in the analyses. We marked all birds with a uniquely numbered aluminium ring, and measured the tarsus length, wing length, body mass, and the maximum length, width and height of the uropygial gland with a digital calliper (0.01 mm precision). We calculated the gland size as $L \times W \times H$, which is a good surrogate of gland volume (see Galván and Sanz 2006, Galván et al. 2008). The number of feather mites was assessed by a semi-quantitative method described in detail elsewhere (Pap et al. 2005, Pap et al. 2006). In short, we counted feather mites separately on individual primaries, secondaries and tertials on both wings for up to 10 mites per feather; 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 and so on). The sum of the numbers of feather mites

counted on individual flight feathers was used in all analyses. Only one feather mite species, *Proctophyllodes troncatus* (robin), was identified from the specimens collected from these two populations. All measurements and the estimate of feather mite numbers were done by PLP. We tested for the relationship between the uropygial gland size and oil abundance on a sample of 14 males and 15 females captured on the Cojocna farm on 9th and 10th July 2010. The gland size was measured by PLP as described before, after then it was gently touched repeatedly with the finger until no more excretions emerged. The amount excreted was collected into a capillary tube which was subsequently measured with a digital calliper to the nearest 0.01 mm.

Experimental protocol

On 29 January and 1 February 2009 we captured 37 adult female house sparrows with at least 25 mites on the left and right wings from the Cojocna farm. The birds were then introduced randomly in one of the two indoor aviaries of $4 \times 3.5 \times 4$ m (L × W × H) situated at the Campus of the Babeş-Bolyai University, Cluj Napoca. At capture we recorded the wing and tarsus length, uropygial gland size, body mass and the number of feather mites. Similar housing conditions were described in detail elsewhere (Pap et al. 2008). Briefly, bushes, perch sites and nest boxes were installed to enhance the comfort of birds. A seed mixture with crumbled eggshells, grated boiled eggs and mealworms, sand and drinking water supplemented with vitamins was provided *ad libitum* throughout the experiment. To prevent Isosporan infection that emerges spontaneously in captive birds (Pap et al. 2009), we administered an anticoccidial cure by adding toltrazuril, 1 ml Baycox 2.5% (Bayer HealthCare, Germany) in 1l water to the drinking water for two consecutive days following the introduction of birds into the aviaries. After 4 to 6 days of accommodation, we started the experiment on 5 February 2009.

We used a 2×2 experimental design by maintaining 20 birds in one aviary at a constant natural-like light regime throughout the experiment, which is characteristic for February at the latitude of the population (short-day length, hereafter 'SD' group; 12L:12D), while in the other aviary (17 birds) we experimentally simulated the photoperiod characteristic for the summer period (long-day length, hereafter 'LD' group; 18L:6D). Aviaries were lightened with 36 W white fluorescent tubes. Within each aviary, half of the birds was glandectomized (LD/UG–, $n = 9$; SD/UG–, $n = 10$), while in the case of the other group a short incision was performed on the skin above the uropygial gland in order to control for the surgical gland removal (LD/UG+, $n = 8$; SD/UG+, $n = 10$). Following capture and measurements, all birds were anaesthetised with a combination of 100 mg mL^{-1} ketamine (Ketaminol 10, Intervet, The Netherlands) and 20 mg mL^{-1} xylazine (Narcoxyl 2, Intervet, The Netherlands) diluted in 0.9% saline solution. During surgery, which took approximately 10 minutes per bird, sparrows were monitored for cardiac and respiratory parameters, as well as for the colour of the mucous membranes. After surgery the birds were kept, until complete recovery from anaesthesia, in warmed individual textile bags in order to prevent hypothermia. All birds were then released in the aviaries where we administered antibiotics (2 ml Enrofloxacin in L^{-1} water, Krka, Slovenia) into the drinking water for 10 days in order to prevent infection. None of the house sparrows died as a result of surgery. In the course of the experiment, the body mass of the birds and the abundance of feather mites were measured on 15 and 22 February and on 1 March. At the start of the experiment, there was no difference between treatment groups in wing length (photoperiod: $F_{1,33} = 0.1$, $p = 0.75$; gland: $F_{1,33} = 0.1$, $p = 0.80$; interaction: $F_{1,33} = 0.2$, $p = 0.62$), tarsus length (photoperiod: $F_{1,33} = 0.7$, $p = 0.42$; gland: $F_{1,33} = 1.4$, $p = 0.25$; interaction: $F_{1,33} = 0.0$, $p = 0.94$), body mass (photoperiod: $F_{1,33} = 0.2$, $p = 0.64$; gland: $F_{1,33} = 1.7$, $p = 0.20$; interaction: $F_{1,33} = 0.3$, $p = 0.56$), uropygial gland volume (photoperiod: $F_{1,33} = 0.4$, $p = 0.54$; gland: $F_{1,33} = 0.3$, $p = 0.62$; interaction: $F_{1,33} = 0.1$, $p = 0.80$), and the abundance of feather mites (photoperiod: $F_{1,33} = 3.0$, $p = 0.09$; gland: $F_{1,33} = 1.4$, $p = 0.25$; interaction: $F_{1,33} = 2.5$, $p = 0.12$). During the experiment, one bird died (from the LD/UG– group) on 15 February due to unknown reason. At the end of the experiment the birds were released at their place of origin, when no difference was observed in body mass between the glandectomized and control groups (photoperiod: $F_{1,32} = 7.4$, $p = 0.01$; gland: $F_{1,32} = 1.8$, $p = 0.19$; interaction: $F_{1,32} = 0.0$, $p = 0.88$). We decided to release the glandectomized birds because in our house sparrow populations ~1% of the birds have deformed and probably non-functional uropygial gland without any apparent illness (see also Moyer et al. 2003 for similar observations on rock pigeon *Columba livia*). Several experimental birds (3 UG+ and 2 UG–) were recaptured after few months of their release in good condition, which may suggests the minor effect of the surgery on the health status and survival of the birds. The experimental procedures were licensed by the Romanian Academy of Sciences (license no. 2257).

Statistical analyses

The seasonal variation in the size of the uropygial gland and the number of feather mites was analysed by fitting mixed effect linear models (GLMs with the 'lme' function of the R statistical environment; R Development Core Team 2008). In these analyses the identity of birds was introduced as random factor, to control for the effect of pseudoreplication caused by the recaptures. Year, population, sex and months were introduced as explanatory factors and their effects were analysed, while the size of the uropygial gland and the logarithmic value of the abundance of feather mites were introduced as dependent variables in separate analyses. In mixed effect linear models the denominator df is calculated as the sample size – (number of groups – 1) – sum(numerator df), therefore the df is much smaller than expected from sample size and in general linear models. The relationship between the number of feather mites, uropygial gland size and the body condition, calculated as the body $mass^{1/3}$/tarsus length, was analysed by entering the gland and morphological variables as covariates into the model, while the effect of the above explanatory factors was controlled. Due to the large number of variables we

calculated all two-level interactions, after then we eliminated all non-significant interactions by using backward procedure, while the main effects were kept fixed in the models (see Table 2). Because the farm near Cluj Napoca had closed definitively in January 2009, and the house sparrows quickly abandoned the area, we could not finish the data collection until the end of the second annual cycle (May 2009). The relationship between the quantity of oil secreted and the size of the uropygial gland, based on the sample of birds captured on 9th and 10th July 2010 was analysed by using GLM, where oil quantity was entered as the dependent factor, gland size as covariate and sex was controlled as factor. The logarithmic values of the gland size and oil quantity were used because of the non-normal error distributions. The effect of experimental manipulation was tested using repeated measures ANOVA, where the body mass and the number of feather mites were introduced separately as dependent variables, while the photoperiod and the uropygial gland manipulation were introduced as explanatory factors. The abundance of feather mites estimated on birds captured on the field and from the experiment was log(x+1)-transformed in order to normalize its skewed distribution. Mean ± SD are shown throughout the text.

Table 1. Results of mixed effect linear models on the variation of the uropygial gland size and the abundance of feather mites in male and female adult house sparrows breeding in two populations.

Variable	DF	F	p
Uropygial gland size			
Intercept	1,895	601.3	<0.001
Population	1,336	0.3	0.61
Year	1,336	22.3	<0.001
Sex	1,336	0.9	0.34
Month	11,336	29.1	<0.001
Sex × Population	1,336	1.5	0.23
Sex × Year	1,336	3.7	0.05
Sex × Month	11,336	14.2	<0.001
Year × Population	1,336	0.2	0.65
Month × Population	11,336	2.0	0.03
Log (number of feather mites +1)			
Intercept	1,896	277.8	<0.001
Population	1,339	9.3	0.002
Year	1,339	22.3	<0.001
Sex	1,339	0.2	0.65
Month	11,339	50.3	<0.001
Sex × Population	1,339	0.2	0.70
Sex × Year	1,339	0.3	0.62
Sex × Month	11,339	0.6	0.83
Year × Population	1,339	9.9	0.002
Month × Population	11,339	3.9	<0.001

Results

Natural covariation

On the sample of house sparrows captured for measuring the oil content of the gland, females had significantly larger uropygial gland related to males ($F_{1,28} = 5.6$, $p = 0.03$), while the quantity of oil excreted was similar between sexes ($F_{1,28} = 0.0$, $p = 0.98$). The amount of oil excreted was significantly related to the size of the uropygial gland (uropygial gland: $F_{1,26} = 17.7$, $p < 0.001$; sex: $F_{1,26} = 1.1$, $p = 0.30$; uropygial gland × sex: $F_{1,26} = 0.9$, $p = 0.36$).

The volume of the uropygial gland was significantly explained by year, month and sex×month interaction, and we found a slight but significant month × population and sex × year interactions (Table 1). Uropygial gland was larger during the first annual cycle (May 2007 to May 2008) related to the second (June 2008 to December 2008) and varied significantly over the annual cycle in male and female house sparrows (Table 1; Fig. 1a). The volume of the uropygial gland was low during the non-breeding and mating season, after that it started to increase sharply, reaching its maximum value between May and August, when the house sparrows breed and start to moult in our populations. The increase in the size of the uropygial gland during breeding was more pronounced in females than in males, resulting in a significant sex × month interaction (Table 1; Fig. 1a). The abundance of feather mites was significantly explained by population, year, month, year × population and month × population interactions (Table 1). The seasonal variation in the abundance of feather mites on wing feathers was opposite to that of the volume of the uropygial gland, as their number was the lowest from May to August when the house sparrows are in the middle of the breeding season and beginning of moulting. Following breeding and during moult, from September to November, the number of feather mites increased, reaching its maximum during the non-breeding and mating seasons (Table 1; Fig. 1b). Feather mites were more abundant in the Cojocna farm and during the first annual cycle related to the second. The significant year × population interaction was caused by the difference in the number of feather mites between the two populations during the second annual cycle, while the population size of mites was more similar during the first annual cycle. Feather mites were more abundant during mating and breeding in the Cojocna related to the Cluj Napoca farm, while during the rest of the year the population size was more similar, as indicated by the significant month × population interaction. No difference was observed between the sexes, and the seasonal variation was similar between males and females, as indicated by the non-significant interactions of sex × month.

We found no significant association between the number of mites and the volume of the gland, after controlling for the effect of sex, population, year and month (Table 2; Fig. 2). The effect of the uropygial gland on the abundance of feather mites was similar in male and female house sparrows and between seasons, as indicated by the non-significant uropygical gland size × sex ($F_{1,321} = 0.4$, $p = 0.51$) and uropygical gland size × month ($F_{11,321} = 0.8$, $p = 0.60$) interactions excluded by the backward procedure (Table 2). The abundance of feather mites was not significantly explained by body condition (Table 2). The non-significant relationship between the size of the gland and the abundance of feather mites remained unchanged even after controlling for the body condition of the hosts ($F_{1,275} = 0.2$, $p = 0.65$).

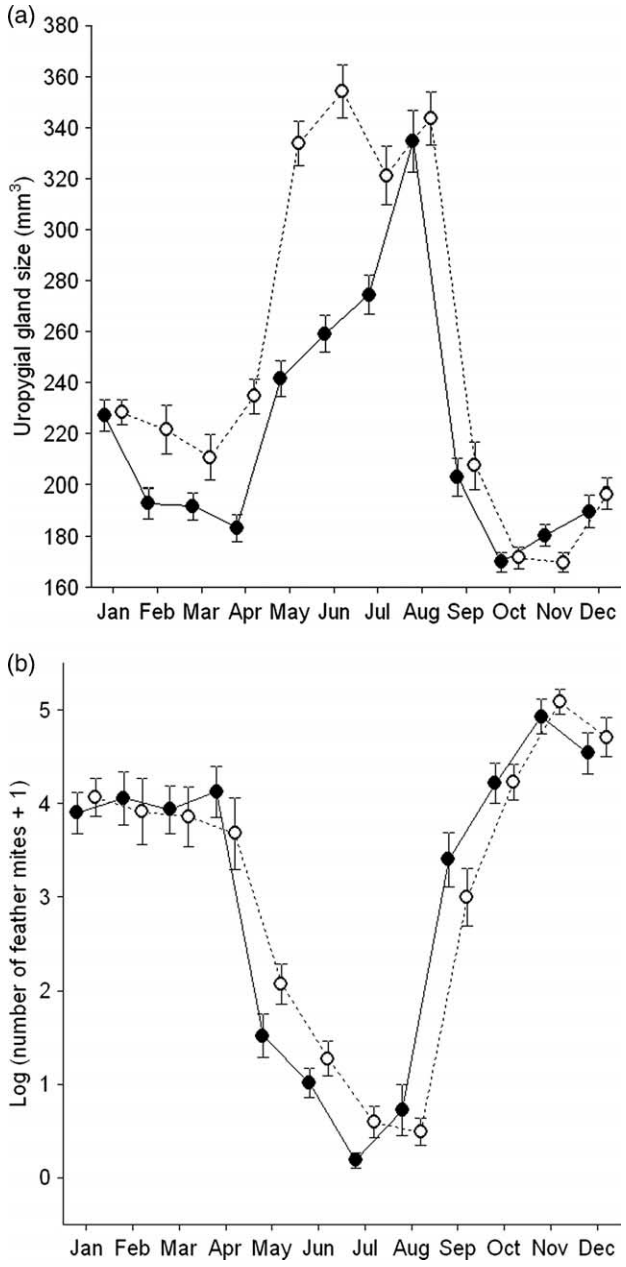

Figure 1. Seasonal variation in the uropygial gland size (a) and the abundance of feather mites (b) in male (filled symbols), and female (open symbols) house sparrows. Mean ± SE are shown.

The experiment

The surgical removal of the uropygial gland had no significant effect on the body mass of the birds during the experiment, while photoperiod treatment had: female house sparrows from the LD group increased their body mass related to the SD group (Table 3). At the end of the experiment the mean body mass was 27.1 ± 1.6 g (n = 20) and 28.6 ± 1.7 g (n = 16) in the SD and LD groups, respectively. The abundance of feather mites decreased in the course of the experiment, and the photoperiod manipulation affected the rate of decreasing of the number of mites, as indicated by the significant photoperiod and photoperiod × repeated measures effect (Table 3, Fig. 3). Glandectomization had no significant effect on the abundance of feather mites on birds (Table 3).

Table 2. Results of mixed effect linear models after backward elimination of non-significant terms on the effect of the uropygial gland size, body condition and confounding variables (population, year, sex, month) on the abundance of feather mites on house sparrows. Note that all main factors and the significant interactions are included in the models.

Variable	DF	F	p
The effect of uropygial gland size			
Intercept	1,895	244.6	<0.001
Population	1,348	8.8	0.003
Year	1,348	31.5	<0.001
Sex	1,348	0.8	0.36
Month	11,348	53.7	<0.001
Uropygial gland size	1,348	0.7	0.40
Year × Population	1,348	8.5	0.004
Month × Population	11,348	3.9	<0.001
The effect of body condition			
Intercept	1,878	6.0	0.01
Population	1,318	8.2	0.004
Year	1,318	32.5	<0.001
Sex	1,318	1.6	0.21
Month	11,318	62.3	<0.001
Body condition	1,318	2.1	0.15
Year × Population	1,318	7.4	0.007
Month × Population	11,318	4.4	<0.001

Discussion

In the present study we have shown that the size of the uropygial gland varies significantly over the annual cycle in male and female house sparrows. The volume of the gland was the largest during the breeding periods, and females had significantly larger glands than males during breeding. These results are in line with Kennedy's (1971), Bhattacharyya and Chowdhury's (1995), Martín-Vivaldi et al.'s (2009), and Moreno-Rueda's (2010) studies, but contradict the results of Møller et al. (2009) about the increased uropygial gland size during breeding in male related to female barn swallows *Hirundo rustica*. We assumed a positive relationship between the size of the gland and the amount of oil secreted, because the lobes, which are the most voluminous part of the gland, are made up of tubules, where secretion occurs, and of various-sized cavities, which store the secretion (Jacob and Ziswiler 1982). The significant positive correlation between the gland size and the volume of secretion produced supports our assumption (see also Bhattacharyya and Chowdhury 1995, Martín-Vivaldi et al. 2009, Møller et al. 2009) which further suggests that house sparrows produce more gland oil during breeding than they do during the non-breeding and mating periods. Several hypotheses were suggested to explain the variation of the uropygial gland volume in birds, among which the predator avoidance and antimicrobial defence (e.g. against feather-degrading bacteria) received experimental support (Shawkey et al. 2003, Reneerkens et al. 2005, Martín-Vivaldi et al.

Table 3. Results of the repeated measures ANOVA on the effect of photoperiod- and uropygial gland manipulation on the change in body mass and abundance of feather mites of female house sparrows during the course of the experiment.

Source of variation	DF	MS	F	P
Body mass				
Photoperiod manipulation	1	3.0	0.4	0.54
Uropygial gland manipulation	1	14.3	1.9	0.18
Subjects within groups	32	7.5	...	...
Repeated measures	3	30.9	69.3	<0.001
Photoperiod m. × Uropygial gland m.	1	0.9	0.1	0.73
Photoperiod m. × Repeated measures	3	6.5	14.5	<0.001
Uropygial gland m. × Repeated measures	3	0.1	0.1	0.95
Repeated measures × Subjects within groups	96	0.4	...	...
Log (number of feather mites + 1)				
Photoperiod manipulation	1	47.3	9.0	0.005
Uropygial gland manipulation	1	14.9	2.8	0.10
Subjects within groups	32	5.3	...	...
Repeated measures	3	94.4	93.8	<0.001
Photoperiod m. × Uropygial gland m.	1	11.2	2.1	0.15
Photoperiod m. × Repeated measures	3	3.5	3.5	0.02
Uropygial gland m. × Repeated measures	3	1.3	1.3	0.28
Repeated measures × Subjects within groups	96	1.0	...	...

2009, Møller et al. 2009, Martín-Vivaldi et al. 2010). Given that the uropygial gland oil inhibits the growth of micro-organisms, our results are in line with the reduced occurrence of feather degrading bacteria during summer (Burtt and Ichida 1999), when the amount of secreted oil is the highest. The antimicrobial effect hypothesis may also explain the increased gland secretion in females compared to males during the breeding season. The general antimicrobial effect of the gland oil (Shawkey et al. 2003, Martín-Vivaldi et al. 2009, Møller et al. 2009), as well as the role of microbial infections in reducing the viability of the eggs (Cook et al. 2005) are known. It follows that by the increased secretion during breeding birds can protect their eggs against microbes by coating them with gland oil. If this is the case, one would expect the size of the uropygial gland during breeding to be higher in females than in males in those avian species where the relative contribution of females to incubation is higher, because those parents which incubate more the clutch have more contact with the eggs. The house sparrow fits into this script, as most of the incubation is done by the females (Anderson 2006).

Another possible explanation for the annual change in the size of the uropygial gland can be related to the defence provided by the gland oil against the seasonally emerging feather mites. However, feather mites seem to have no effect on the fitness and condition of the host (Blanco et al. 1997, Blanco et al. 1999, Dowling et al. 2001b, Møller et al. 2004, Pap et al. 2005; but see Figuerola et al. 2003), limiting their evolutionary pressure that would select for the increased uropygial gland size. It is worth to mention that

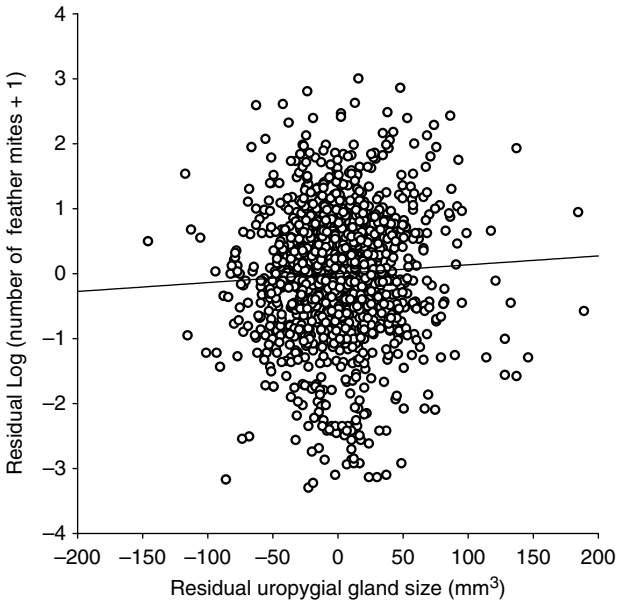

Figure 2. The relationship between the uropygial gland size and the number of feather mites in house sparrows after controlling for the confounding effect of year, population, sex and season.

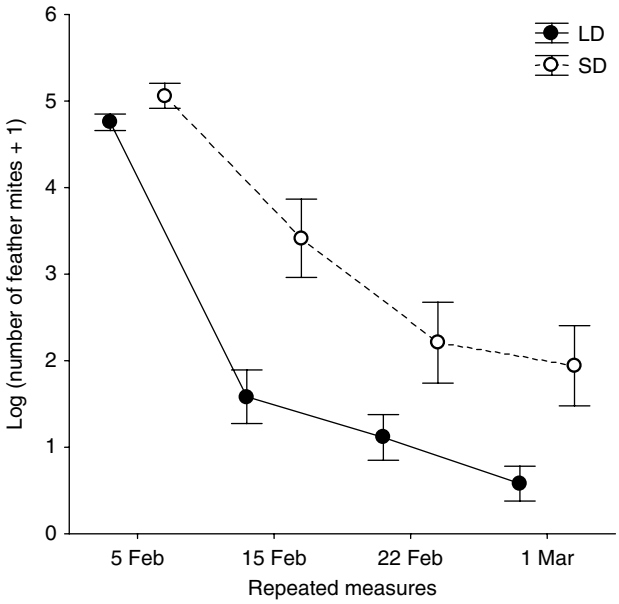

Figure 3. The effect of photoperiod manipulation on the change in the number of feather mites of female house sparrows. LD: long day, SD: short day. Mean ± SE are shown.

most of the studies about the host–feather mite interaction are observational, making difficult to discern the direction of causation. In fact, one out of two experimental studies (Figuerola et al. 2003, Pap et al. 2005) found a significant negative effect of feather mites on plumage colouration of the host (Figuerola et al. 2003), suggesting some possible negative effects of these ectosymbionts on birds. Our results, about the absence of relationship between the abundance of feather mites, the size of the uropygial gland and body condition of the host, support the commensal and/or mutualistic nature of feather mites (Blanco et al. 1997, Blanco et al. 1999, Dowling et al. 2001b, Møller et al. 2004, Pap et al. 2005). Therefore, we consider that the gland secretion in house sparrows is probably not directed primarily against feather mites. On the other hand, the uropygial secretions could, however, influence the abundance of symbiotic feather mites as a side effect. The opposing pattern of seasonal variation of the abundance of feather mites and uropygial gland size suggests an inhibitory effect of the gland secretion on mites. But, the absence of relationship between the gland size and feather mites' abundance suggests that in our house sparrow populations the annual population dynamics of feather mites is not affected by the secretion of the gland. This absence of relationship, however, should be treated with caution because in descriptive analysis the direction of causality cannot be discerned. The non-significant effect of gland size on the abundance of feather mites is in line with the absence of effect of glandectomization on the population size of feather mites. On the other hand, the absence of relationship between uropygial gland manipulation and the abundance of feather mites can be related to the short experimentation period during which the gland oil persisted abundantly on the plumage of the glandectomized birds (see also Moyer et al. 2003), or by the reduced detectability of the effect due to the limited sample size. One may argue that the non-significant effect of the uropygial gland manipulation on the number of feather mites is related to the horizontal dispersion of mites between individual host birds belonging to the glandectomized and control groups. However, this effect is probably minimal, because in case of horizontal infection of birds with differential feather mite abundance we would expect the infestation rate to increase, at least transiently, in case of birds with initially low abundance of mites. Our observation supports the high host fidelity of feather mites, at least during the experiment, as in none of the cases we observed an increase in the number of mites on individual house sparrows. It is worth mentioning, that our experimental study was performed during winter, when the uropygial gland reach the lowest size. Hence the effect of glandectomization on the difference in oil quantity on feathers between experimental groups is probably less than during breeding. On the other hand, the abundance of feather mites on the feathers during breeding is low, reducing the probability to detect changes in population size. Finally, our experiment was performed only on female house sparrows which may limit the generalization of the results for males. Our results contradicts Galván and Sanz's (2006) correlative study on the great tit and the comparative study by Galván et al. (2008) about the positive relationship between the uropygial gland size and the abundance of feather mites on different passerine birds. These results may suggest, that the uropygial gland secretion has a divergent effect on the abundance of feather mites in different avian species, supported also by the study of Galván et al. (2008), where the relationship between the two variables was more pronounced in migratory than in sedentary avian species. It is interesting to note, that the seasonal variation in the abundance of feather mites seems to be variable between different species, as in the present study the number of mites on wing feathers was highest during winter, while Wiles et al. (2000) and Hamstra and Badyaev (2009) found different pattern on other host species. This suggests that different environmental and host-related morphological, ecological, physiological or social factors are responsible for shaping the seasonality in the population size of feather mites. These caveats need future investigations.

The photoperiod manipulation significantly affected the abundance of feather mites on the wing feathers of female house sparrows, indicating that mites use the changing day-length as a cue in their response to environmental changes related to the annual cycle. The negative effect of long days on the abundance of feather mites is in line with the seasonality in the number of mites on house sparrows, as during spring, when the day-length increases, the number of feather mites falls. It is interesting to note, that the number of feather mites decreased in both photoperiodic experimental groups, while our expectation was that the abundance of mites will be constant in SD groups. This suggests that the change in the number of feather mites was also affected by factors other than the photoperiod. Because of the regular disturbance of birds due to daily feeding and periodic capture, their wings' collision with the wall of the aviary is frequent, increasing the vibration of wing feathers and the distraction of feather mites attached to the wing feathers (see Pap et al. 2006). This may explain the decrease in the abundance of feather mites on captive house sparrows, which is also supported by our observation on the rapid disappearance of feather mites on birds held in small individual cages, where the effect of agile behaviour of the birds on mites is more pronounced than in the case of large aviaries (pers. obs.).

One may ask where feather mites do move when their number is declining so drastically. We consider plausible three non-exclusive possibilities. First, mites move onto the skin of the host between May to August when the house sparrows are in the middle of the breeding season and beginning of moulting, to avoid being lost during the moult (Jovani and Serrano 2001, Pap et al. 2006). Second, they may remain on the feathers but as eggs or larvae, that are too small to be readily counted. Finally, feather mites may move from the parents onto the chicks during breeding, as suggested by the study of Mironov (2000), who monitored changes in feather mite load in chaffinches *Fringilla coelebs* over the breeding season, and found that the majority of mites moved from the brooding females to the fledglings, resulting in a very sharp drop in mean load in female birds. Because in house sparrows both males and females are brooding and take part in rearing nestlings (Anderson 2006), the drop in the number of feather mites is similar between sexes, resulting in a non-significant difference between sexes in their number of feather mites.

In conclusion, we have found that the volume of the uropygial gland varied seasonally during two annual cycles in male and female house sparrows originating from two populations, and the size of the gland was the highest during breeding. Females have larger glands than males during breeding. The change in the abundance of *Proctophyllodes* feather mites was opposite to that of the uropygial gland size, suggesting a negative relationship between the population size of the mites and gland secretion. However, the absence of effect of the uropygial gland size on the abundance of feather mites seems to support the non-regulatory effect of the gland on the abundance of feather mites, which is sustained further by the absence of effect of glandectomization on the population change of mites. Finally, the results of the experimental photoperiod manipulation indicate that feather mites use day-length as a cue of seasonal changes, making possible to calibrate their population size when the day-length increase.

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