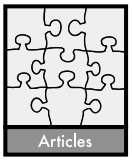

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Uropygial gland size correlates with feather holes, body condition and wingbar size in the house sparrow *Passer domesticus*

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The uropygial gland is an organ exclusive of birds that secretes an oily substance, the uropygial secretion, the functions of which are still debated. One of the proposed hypothesis is its possible action against chewing lice (order Phthiraptera), a group of avian ectoparasites that feed on feathers, causing different types of harm. However, this hypothesis lacks support. The present study analyses the relationship between uropygial gland size and the number of feather holes (which is correlated with the load of chewing lice) in the house sparrow *Passer domesticus*. Moreover, the relationship between the uropygial gland size and different aspects of sparrow health (body condition, immunocompetence and haematocrit), as well as sexually selected traits in males (badge and wingbar size), is tested. The results show a negative correlation between uropygial gland size and number of feather holes, a result found both years of the study. This result supports the hypothesis that uropygial secretion is used against chewing lice. Uropygial gland size also correlated positively with body condition (residuals of body mass relative to tarsus length) and immunocompetence, being therefore related to bird health. After a year in captivity, with resources provided ad libitum, no correlation was found between individual uropygial gland size and body condition or haematocrit, perhaps because the negative effect that chewing lice exert on bird health was offset by captivity conditions. Uropygial gland size was not correlated with badge size, but it was correlated with wingbar size, which furthermore supports the contention that this sexually selected signal acts as an indicator of lice resistance in the house sparrow. In summary, this study supports the idea of a positive relationship between uropygial gland and bird health in the house sparrow, the gland secretion affording resistance against chewing lice.

The uropygial (also called preen) gland is a holocrine complex, exclusive of birds, located in the integument above the posterior free caudal vertebrae (i.e. in the rump; Jacob and Ziswiler 1982). This gland produces an oleaginous secretion that birds spread onto their plumage when preening. Its chemical composition is highly variable at interspecific and intraspecific levels (Reneerkens et al. 2002, Haribal et al. 2005, Montalti et al. 2005).

The function of the uropygial secretion is still disputed, and various non-exclusive hypotheses have been proposed. First, uropygial preen oil has a function in maintaining flexibility and impermeability of plumage, given that feathers deteriorate in many species when the uropygial gland is experimentally extirpated (Elder 1954, Jacob and Ziswiler 1982, Moyer et al. 2003). In addition, the antimicrobial activity of the preen secretion may inhibit the growth of feather-degrading bacteria (Shawkey et al. 2003), while favouring the establishment of feather mites (Acari; Astigmata), which improve feather conditions by feeding on microbes and dirt trapped in the uropygial secretions (Galván et al. 2008). Moreover, the uropygial gland intervenes in processes of sexual communication, through the production of pheromones (Hirao et al. 2009) and affect feather coloration (reviewed by Delhey et al. 2007). A function as predator deterrence (Steyn 1999) or crypsis (Reneerkens et al. 2005) has been also hypothesised.

The uropygial secretion may also have an insecticide function against chewing lice (Jacob and Ziswiler 1982, Dumbacher and Pruett-Jones 1996, Moyer et al. 2003). Chewing lice (also called feather lice; Phthiraptera, formerly Mallophaga) are a paraphyletic group of ectoparasites that develop their complete cycle on birds, feeding mainly on feather keratin (which constitute the 90% of feather composition), on skin debris, and in the case of the suborder Amblycera, on blood (Price et al. 2003). By digesting the keratin, lice deteriorate the plumage, causing small holes in the feathers (Møller 1991, Vas et al. 2008), which in turn, cause a variety of harmful consequences to hosts: diminishing the thermoregulatory capacity (Booth et al. 1993), decreasing body condition (Potti and Merino 1995), facilitating feather breakage (Kose and Møller 1999), affecting flight (Barbosa et al. 2002), delaying arrival dates of migratory birds (Møller et al. 2004a), delaying breeding initiation (Pap et al. 2005), and

even diminishing host survival (Brown et al. 1995, Clayton et al. 1999, Pap et al. 2005).

It has been shown that the oily secretion produced by the uropygial gland has an insecticide effect on chewing lice (Moyer et al. 2003), and the uropygial gland size is positively correlated with the quantity of produced secretion (Martín-Vivaldi et al. 2009). For this reason, a negative correlation between uropygial gland size and lice load is expected. However, to my knowledge, no study has reported such a relationship. In the present work, I examined the relationship between uropygial gland size and the number of feather holes in the house sparrow *Passer domesticus*. Descriptive studies show that the number of feather holes is correlated with the abundance of certain species of chewing lice in different bird species, including the house sparrow (Vas et al. 2008). This suggests that such feather damage is caused by chewing lice, and may be used as an indirect mechanism for quantifying lice load (Møller 1991).

Moreover, I examined whether there was a relationship between uropygial gland size and some parameters of bird health, such as body condition (estimated as the residuals of the regression of body mass on tarsus length), haematocrit, and immune capacity. Finally, I also analysed the relationship between uropygial gland size and the size of two known sexually selected patches of male house sparrows: the badge and the wingbar. The badge is a black patch on the throat and upper breast, which is under sexual selection (reviewed by Anderson 2006), and is indicative of diverse aspects related to parasite resistance, including resistance to chewing lice (Møller et al. 1996). The wingbar is a white patch on wing coverts, which is indicative of resistance to chewing lice, its size being negatively correlated with the number of feather holes (Moreno-Rueda 2005). Therefore, it would be possible that the relationship between wingbar size and feather holes is mediated by the uropygial gland size; males with larger uropygial gland having less chewing lice load, and thus affording a larger wingbar. In addition, female house sparrows prefer males with large wingbars (Moreno-Rueda and Hoi unpubl.).

Material and methods

Study population

At the end of January 2008, 96 house sparrows (61 males and 35 females) were captured on a farm in Padul (southeast Spain, 7°01′28″N, 3°37′36″W). The sparrows were housed in an outdoor aviary of 50 m^3, located in Moraleda de Zafayona, where they were supplied with water and food ad libitum. All work was performed with permissions from the Andalusian government.

Uropygial gland size and feather holes

Shortly after capture of the sparrows (first week of February 2008), I measured length, width and height (from the base of the gland to the base of the papilla) of the uropygial gland (three times each) with a digital calliper (accuracy 0.01 mm). The uropygial volume was estimated by multiplying the three measurements (following Galván et al. 2008). Although this is a gross measurement of uropygial gland size, it has been proven useful (Ruiz-Rodríguez 2007, Galván et al. 2008). Surviving birds (49 males and 30 females) were measured again in February 2009.

I counted the number of holes in the primaries and secondaries of the left wing in 2008, and on both wings in 2009. Descriptive studies suggest that these marks in feathers are caused by chewing lice, because the density of some louse species and feather holes are correlated ($r = 0.62$, $p < 0.01$, $n = 20$; Møller 1991, Vas et al. 2008). Therefore, the number of feather holes can be used as an indicator of lice load in birds (Clayton and Walther 1997).

Body condition, immunocompetence and haematocrit

I estimated condition as the residuals from the regression of mass against tarsus length (log-transformed), measuring mass with a digital balance (accuracy 0.1 g) and tarsus length with a digital calliper. Mass data were lost for four individuals (1 in 2008, 3 in 2009), diminishing sample size in analyses including this variable. Although use of this body-condition index has been controversial, it has been demonstrated to be a good estimator of the individual physical condition (Schulte-Hostedde et al. 2005).

In September 2008, I used a sub-sample of 24 males to measure the relationship between immunocompetence and uropygial gland size. As an indicator variable of the individual's immunocompetence, skin swelling elicited by the injection of phytohemoaglutinine (PHA-P, L-8754) was used. PHA-P is an innocuous protein that provokes an immune response in birds mediated by T-cells (Kennedy and Nager 2006), although other components of the immune system could also be involved in the response (Martin et al. 2006). I injected 0.5 mg of PHA diluted in 0.1 ml of isotonic phosphate buffer, in the patagium of male left wings (following Smits et al. 1999). Previously, I measured (three times) the patagium thickness with a pressure-sensitive micrometer (accuracy: 0.01 mm). I subsequently measured the patagium 24 h (± 2 h) after the injection, calculating the T-cell mediated immune response as the difference between the second and first measurements.

In February 2009, I extracted 20 µl of blood from 66 sparrows (42 males and 24 females) in heparinized capillaries. The blood was immediately centrifuged for 5 min at 12 000 g, separating red cells from plasma (Fair et al. 2007). With a digital calliper, I measured the length of the capillary occupied by red cells and plasma, and estimated the percentage of volume occupied by the erythrocytes (i.e. the haematocrit).

Sexual patches in the house sparrow

In 2008, I measured two sexual signals of male house sparrows: badge size and wingbar size. The two patches were measured by photographing birds properly disposed in a standard way on sectional paper with a digital camera. The camera was emplaced on a tripod, consistently at the same distance from birds. Afterwards, patch surfaces were measured with the program Image J (Figuerola and Senar 2000).

Statistical analyses

I estimated the repeatability of morphological traits used in this study (Table 1) by measuring the traits in the same individuals (randomly selected) two times (following Lessells and Boag 1987, Bailey and Byrnes 1990). The second measurement was performed at least 30 min after of the first one, not to remember the value of the first measurement. For wingbar size and badge size, I estimated the repeatability within photos, and moreover, I estimated the repeatability between photos in 8 individuals that were photographed twice in different days. To estimate the repeatability measuring patagium thickness, I measured it three times in 8 birds and estimated the average value. Thirty min later, I repeated the same operation to examine the repeatability in this trait when three measures were taken. I calculated the repeatability of the haematocrit by taking two capillaries in 12 sparrows and comparing the haematocrit obtained with each capillary. To estimate the repeatability of the uropygial gland size, I calculated the uropygial gland size in 21 individuals as explained above, and 30 min later I repeated the process, achieving a second measurement of uropygial gland size.

All variables followed a normal distribution according to a Lilliefors test ($p > 0.20$), except the number of feather holes and uropygial gland size in 2009, which were log-transformed to adjust to a normal distribution (Quinn and Keough 2002). Parametric statistics were used in all the analyses, performed with the program Statistica 7.1 (StatSoft 2005). Means are given with standard deviation (SD). In figures, raw data are shown, although transformed data were used in some analyses.

Results

Sexual and inter-annual variation in uropygial gland size

In 2008, I found no significant differences between males (83.40 ± 22.06 mm^3, $n = 61$) and females (90.99 ± 23.86 mm^3, $n = 35$) in uropygial gland size (t-test, $t_{94} = 1.57$, $p = 0.12$). However, it should be noted that males are bigger than females (Moreno-Rueda 2006). When controlling for body mass, I found that females had a relatively larger uropygial gland than males ($F_{1,92} = 5.63$, $p = 0.02$). In 2009, by contrast, there was a non-significant trend for males (130.76 ± 46.29 mm^3, $n = 49$) to have larger uropygial glands than females (114.24 ± 28.73 mm^3, $n = 30$; test performed with the log-transformed data: $t_{77} = 1.87$, $p = 0.065$). The inclusion of body mass as covariate did not alter this result ($F_{1,73} = 2.53$, $p = 0.12$). Uropygial gland size was not significantly correlated with tarsus length (2008: $\beta = 0.17$, $F_{1,93} = 0.26$, $p = 0.61$; 2009: $\beta = -0.03$, $F_{1,76} = 0.05$, $p = 0.83$; sex as covariate), suggesting that its size was independent of structural body size.

Table 1. Repeatability of the traits analysed in the study.

Trait	Repeatability	n
Wingbar size (within photos)	>0.99	23
Wingbar size (between photos)	0.98	8
Badge size (within photos)	>0.99	23
Badge size (between photos)	0.99	8
Body mass	>0.99	11
Tarsus length	0.98	15
Patagium thickness	0.98	8
Haematocrit	0.93	12
Uropygial gland size	0.76	21

Of 79 individuals measured in 2009, 53 were of known identity (loss of colour rings, $n = 26$, diminished the sample size). In 2009, the uropygial glands of these individuals were larger than in 2008 (122.86 ± 41.15 mm^3 versus 83.01 ± 23.81 mm^3, respectively; Repeated Measures ANOVA with log-transformed data, $F_{1,51} = 50.39$, $p < 0.001$), while the interaction between year and sex was not significant ($F_{1,51} = 0.95$, $p = 0.33$).

Uropygial gland size and feather holes

I found a significant negative correlation between uropygial gland size and number of feather holes in the two years (2008: $r = -0.23$, $p = 0.026$, $n = 96$; 2009: $r = -0.29$, $p = 0.01$, $n = 79$; Fig. 1). I found no significant differences in number of feather holes between sexes (2008: $t_{94} = 0.32$, $p = 0.75$; 2009: $t_{77} = 1.56$, $p = 0.12$), but, as the uropygial gland size differed between sexes in 2008, and tended to differ in 2009, I repeated the analyses including sex as covariate in an ANCOVA. The negative relationship

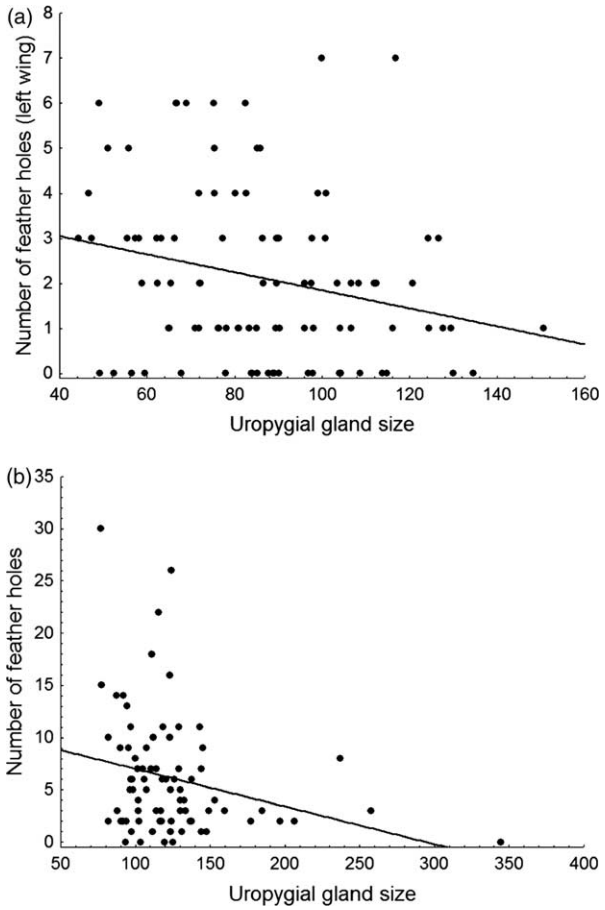

Figure 1. Relationship between uropygial gland size (mm^3) and number of feather holes in the house sparrow during 2008 (a) and 2009 (b). The line indicates the regression fit.

between uropygial gland size and number of feather holes remained significant when controlling for sex and body condition (Table 2). In 2009, findings could have been caused by an outlier (the largest uropygial gland, Fig. 1b). The relationship between uropygial gland size and number of feather holes remained significant when I removed this outlier ($\beta = -0.25$, $F_{1,71} = 4.82$, $p = 0.03$; sex and condition as covariates). Moreover, individuals in which the uropygial gland size increased in 2009 tended to have relatively fewer feather holes than in the previous year ($r = -0.26$, $p = 0.065$, $n = 53$).

Body condition, immunocompetence, haematocrit and uropygial gland size

In 2008, uropygial gland size was positively correlated with body mass in male and female house sparrows (in both, $r = 0.35$, $p < 0.05$, $n = 60$ males and 35 females). However, in 2009, no significant relationship between body mass and uropygial gland size was found (males: $r = -0.08$, $p = 0.59$, $n = 47$; females: $r = 0.31$, $p = 0.11$, $n = 29$). Nonetheless, females, but no males, showed similar correlation coefficients the two years. Individuals with better body condition also had larger uropygial glands ($r = 0.34$, $p = 0.001$, $n = 95$; Fig. 2a). The inclusion of sex as covariate did not alter this result ($\beta = 0.34$, $F_{1,\ 92} = 12.05$, $p < 0.001$; effect of sex: $F_{1,92} = 2.78$, $p = 0.10$). However, in 2009, when birds had spent one year in captivity, no significant relationship between body condition and uropygial gland size was noted ($r = -0.07$, $p = 0.65$, $n = 76$; Fig. 2b). The outlier removal did not alter the result ($r = -0.09$, $p = 0.46$, $n = 75$). For known individuals, body condition trended to be superior in 2009 (0.012 ± 0.071) compared to 2008 (-0.002 ± 0.029; paired t-test, $t_{53} = 1.68$, $p = 0.099$); however, there was no significant relationship between the increase in body mass and the increase in uropygial gland size ($r = 0.10$, $p = 0.50$).

The immune response was positively correlated with uropygial gland size ($r = 0.50$, $p = 0.013$, $n = 24$ males; Fig. 3), although this relationship did not reach significance when controlled for body mass ($\beta = 0.34$, $F_{1,21} = 3.08$, $p = 0.09$; effect of body mass: $\beta = 0.36$, $F_{1,21} = 3.44$, $p = 0.08$). Immune response was correlated with body condition in this sample ($r = 0.51$, $p = 0.01$, $n = 24$). On the contrary, haematocrit did not significantly correlate with uropygial gland size ($r = 0.05$, $p = 0.72$, $n = 66$; Fig. 4), and did not differ significantly between sexes ($t_{64} = 0.52$, $p = 0.61$), although there was a trend for an increase with body condition ($r = 0.22$, $p = 0.09$). The correlation between haematocrit and uropygial gland size was not affected when sex and body condition were included in the analysis ($\beta = 0.04$, $F_{1,59} = 0.09$, $p = 0.77$).

Table 2. Effect of the uropygial gland size on the number of feather holes, after controlling for sex and body condition.

Effect	2008			2009		
	β	$F_{1,91}$	p	β	$F_{1,72}$	p
Uropygial gland size	−0.23	4.40	<0.05	−0.34	9.31	0.003
Body condition	0.02	0.02	0.88	0.09	0.67	0.42
Sex		0.001	0.97		3.55	0.06

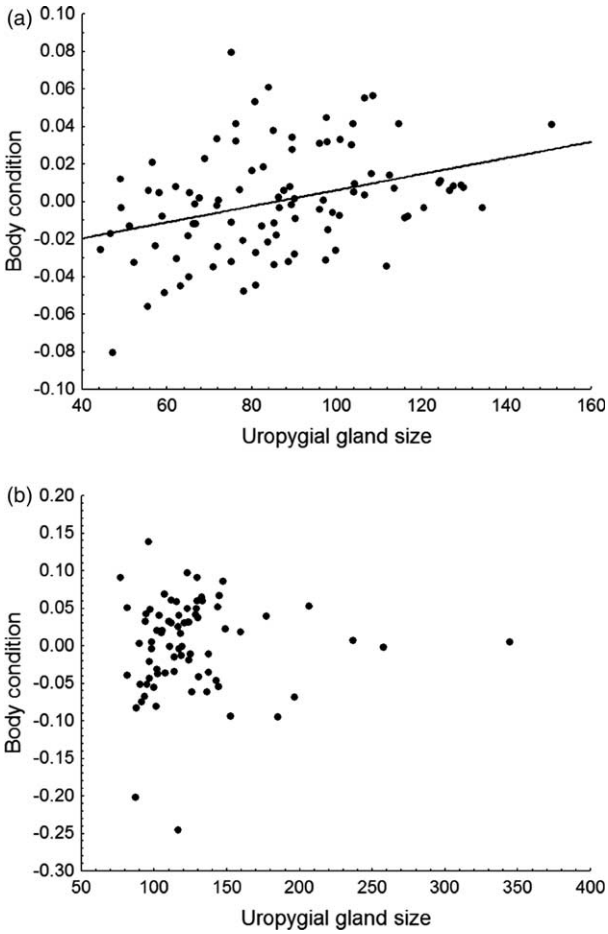

Figure 2. Relationship between uropygial gland size (mm^3) and body condition (residuals) during 2008 (a) and 2009 (b). The line indicates the regression fit.

Uropygial gland size and the size of badge and wingbar in males

Uropygial gland size was positively correlated with wingbar size ($r = 0.29$, $p = 0.024$, $n = 61$; Fig. 5a), but not with badge size ($r = -0.04$, $p = 0.78$, $n = 0.61$; Fig. 5b).

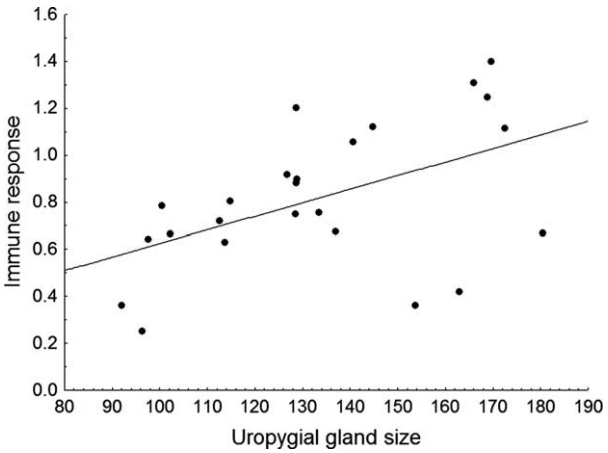

Figure 3. Relationship between uropygial gland size (mm^3) and immune response (mm) in the house sparrow. The line indicates the regression fit.

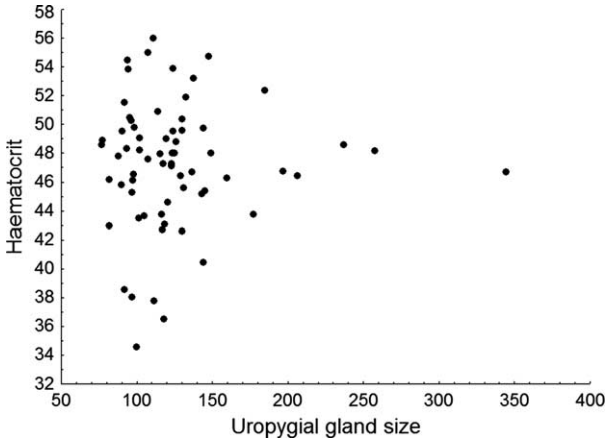

Figure 4. Relationship between uropygial gland size (mm^3) and haematocrit (%).The line indicates the regression fit.

Wingbar size was positively correlated with body condition ($r = 0.27$, $p < 0.05$), but badge size was not ($r = 0.02$, $p = 0.86$). When body condition was controlled for, the correlation between wingbar size and uropygial gland size was not significant ($\beta = 0.24$, $F_{1,57} = 3.79$, $p = 0.056$; effect of body condition: $\beta = 0.31$, $F_{1,57} = 6.31$, $p = 0.01$).

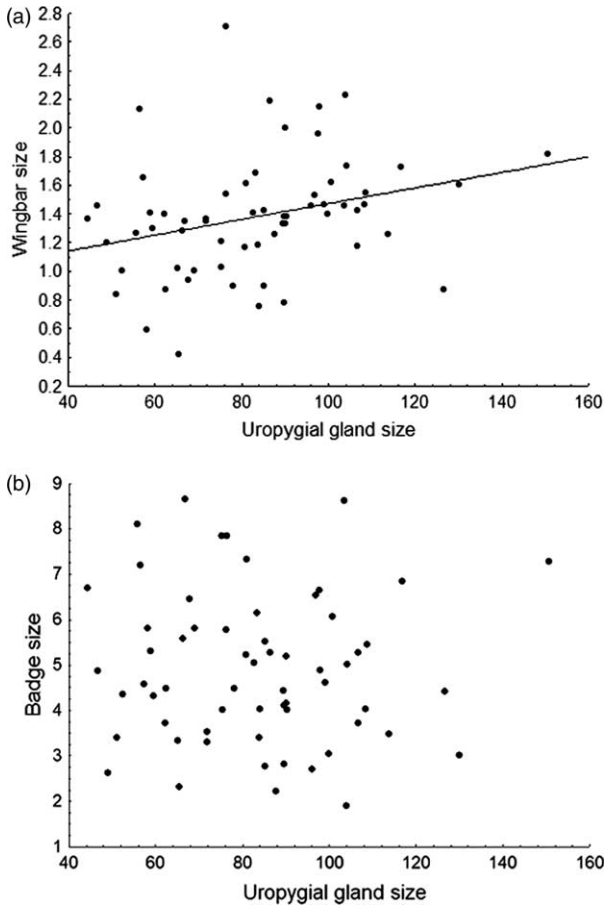

Figure 5. Relationship between uropygial gland size (mm^3) with (a) badge size (cm^2) and (b) wingbar size (cm^2). The line indicates the regression fit.

Discussion

Uropygial gland size and lice load

As predicted, I found a negative correlation between uropygial gland size and the number of feather holes in the house sparrow. This result was found both years of study. In the barn swallow *Hirundo rustica*, feather holes have been shown to have negative effects on migration date (Møller et al. 2004a), laying date, and survival (Pap et al. 2005). Although no experimental test has been performed, descriptive studies suggest that feather holes are produced by chewing lice while feeding on feathers (Møller 1991, Vas et al. 2008), thus, this study suggests a relationship between uropygial gland size (which is related to preen-oil production, Martín-Vivaldi et al. 2009) and resistance to chewing lice. Although a possible anti-parasitic function of the uropygial secretion against chewing lice has been proposed (Jacob and Ziswiler 1982, Dumbacher and Pruett-Jones 1996), as far as I know, no studies have supported this hypothesis until now. Moyer et al. (2003) showed that the uropygial secretion kills chewing lice, probably by occluding their respiratory orifices. Nevertheless, these authors did not find an increase, with respect to control, in the lice load among rock dove individuals *Columba livia* in which the uropygial gland had been extirpated. Probably, in this species, the mechanical use of the beak defends against chewing lice more than the chemical defence of the uropygial gland secretion (Clayton et al. 2005), as suggested by the fact that many doves lack an uropygial gland (Johnston 1988, Moyer et al. 2003). Nonetheless, it should be noted that the findings in the present study are correlative, and manipulative tests would be necessary to confirm them.

Acting against chewing lice, the uropygial gland, through the production of preen oil, helps to maintain the plumage in good condition, which favours bird fitness (Introduction). This mechanism does not preclude other contributions of the uropygial secretion to feather maintenance, such as encouraging the establishment of mutualistic feather mites (Galván et al. 2008), or killing feather-degrading microbes (Shawkey et al. 2003).

Uropygial gland size and health

I found a positive correlation between uropygial gland size and body condition in house sparrows. Given that chewing lice provoke an energetic cost to hosts (Booth et al. 1993), and may affect flight (Barbosa et al. 2002), birds with better defences against lice (e.g. larger uropygial gland), could allocate more energy to increase their body condition. In fact, in the pied flycatcher *Ficedula hypoleuca*, females that are more infested by chewing lice have a worse body condition than less infested females (Potti and Merino 1995). Alternatively, individuals in better condition could develop a larger uropygial gland. For example, immune challenge negatively affects the development of the uropygial gland size in nestlings of tawny owls *Strix aluco*, implying that uropygial gland development is costly (Piault et al. 2008). When more resources are invested in a function (e.g. immune system), less are available for other functions

such as the development of the uropygial gland (principle of allocation, Cody 1966). The latter suggestion would explain why in 2009 sparrows had larger uropygial glands. After a year in captivity, with resources offered ad libitum, sparrows might invest more resources in the development of the uropygial gland. On the other hand, when sparrows had spent a year in an aviary, the correlation between uropygial gland size and body condition disappeared. Presumably, when sparrows had food ad libitum, protection against adverse weather, and an absence of costly flights searching for resources, lice had no appreciable effect on body condition of the sparrows. This could also explain the lack of a relationship between uropygial gland size and haematocrit in 2009.

Given the positive correlation of the uropygial gland size with immune response, the development of the gland in house sparrows could thus be related to immune capacity, as recently found in the hoopoe *Upupa epops* (Ruiz-Rodríguez 2007). Other studies have found that the host immune system is related to the resistance to chewing lice of the suborder Amblycera in the house sparrow and other birds (Møller et al. 1996, Møller and Rózsa 2005, Whiteman et al. 2006). Similarly, populations of house sparrows that invest more resources in the immune system have less chewing lice than do populations with a weaker immune capacity (Martin et al. 2007). Therefore, a relationship could exist between the immune system and resistance to chewing lice mediated by the uropygial gland. However, feather holes in the house sparrow are probably caused by *Brueelia* sp. (Vas et al. 2008), a louse belonging to the suborder Ischnocera, a group of chewing lice not affected by the host immune system (Møller and Rózsa 2005). Another possibility is that the found correlation reflects a relationship between condition and uropygial gland size, as immune capacity is positively correlated with condition in the house sparrow (Navarro et al. 2003; this study). In accordance with this proposal, when controlling for body condition, the correlation between uropygial gland size and immune response did not reach significance.

Uropygial gland size and sexual selection

There was no relationship between the uropygial gland and badge size. However, as predicted, a positive correlation between uropygial gland size and wingbar size was found. This correlation, however, should be taken with caution, given that, when body condition was included as a covariate, the correlation was not (though almost) significant. Chewing lice prefer white feathers (Kose et al. 1999, but see Bush et al. 2006), which are softer (Bonser 1995). For this reason, white patches might indicate lice load, where individuals with more lice have smaller white patches (chewed by lice). In house sparrows, in fact, wingbar size is negatively correlated with feather holes (Moreno-Rueda 2005), a situation also found for the tail white spots in barn swallows (Kose et al. 1999). Similarly, in barn owls *Tyto alba*, individuals with a larger uropygial gland have whiter plumage (Roulin 2007). Females may use the information in these white patches for mating and, in fact, females of some bird species, including the house sparrow, show a preference for males with larger white patches (Pryke 2007, Moreno-Rueda and Hoi unpubl.). By choosing a male with a larger wingbar, female house sparrows may obtain a direct benefit, diminishing the probability of contagion (Able 1996, Møller et al. 1999), but also genetic benefits, given that the resistance to certain chewing lice is heritable (Møller et al. 2004b).

Other studies have found that uropygial secretion affects sexually selected signals by altering microbial activity, brightness, or coloration (reviewed by Delhey et al. 2007). Recently, it has been found that some strains of *Bacillus licheniformis* degrades white feathers at a higher rate than black feathers (Goldstein et al. 2004, Gunderson et al. 2008). Thus, given that the uropygial secretion has antimicrobial activity (Shawkey et al. 2003, Ruiz-Rodríguez 2007), the wingbar size, positively correlated with uropygial gland size, might be an honest indicator of resistance to both chewing lice as well as feather-degrading bacteria. In any case, the findings in this study showed that wingbar size is an indicator of male condition, but the interrelationships among condition, uropygial gland size and wingbar size remains unclear, and hence, more experimental tests are necessary.

Sexual dimorphism in uropygial gland size

In 2008, but not in 2009, I found a sexual dimorphism for uropygial gland size, with females having larger glands. Martín-Vivaldi et al. (2009) found a similar dimorphism in uropygial gland size of the hoopoe during breeding season, but not during the pre-breeding period. This was related to the use of uropygial secretions by females for killing bacteria on eggs. It is possible that, in the house sparrow, when breeding is proximate, females develop a larger uropygial gland for similar reasons. In 2009, preparation for breeding was probably delayed due to a more severe and colder winter (State Agency of Meteorology; <http://www.aemet.es/>). In any case, more studies are necessary to evaluate the reasons for sexual dimorphism in uropygial gland size in this species.

Conclusions

This study gives the first evidence that the uropygial gland, through secretion of preen oil, could act against the formation of feather holes, probably by killing chewing lice. The uropygial gland was also correlated with body condition and immune capacity in house sparrows, suggesting a positive relationship between gland size and bird fitness. Lastly, the wingbar, a sexually selected trait, could be considered as an indicator of uropygial gland size, and thus, an indicator of an individual's resistance to lice.

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References

Able, D. J. 1996. The contagion indicator hypothesis for parasite-mediated sexual selection. – Proc. Nat. Acad. Sci. USA 93: 2229–2233.

Anderson, T. R. 2006. Biology of the ubiquitous house sparrow. From genes to populations. – Oxford Univ. Press.

Bailey, R. C. and Byrnes, J. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. – Syst. Biol. 39: 124–130.

Barbosa, A., Merino, S., de Lope, F. and Møller, A. P. 2002. Effects of feather lice on flight behavior of male barn swallow *Hirundo rustica*. – Auk 119: 213–216.

Bonser, R. H. C. 1995. Melanin and the abrasion resistance of feathers. – Condor 97: 590–591.

Booth, D. T., Clayton, D. H. and Block, B. A. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. – Proc. R. Soc. Lond. B 253: 125–129.

Brown, C. R., Brown, M. B. and Rannala, B. 1995. Ectoparasite reduce long-term survival of their avian host. – Proc. R. Soc. Lond. B 262: 313–319.

Bush, S. E., Kim, D., Moyer, B. R., Lever, J. and Clayton, D. H. 2006. Is melanin a defense against feather-feeding lice? – Auk 123: 153–161.

Clayton, D. H. and Walther, B. A. 1997. Collection and quantification of arthropod parasite of birds. – In: Clayton, D. H. and Moore, J. (eds), Host–parasite evolution: general principles and avian models. Oxford Univ. Press, pp. 419–440.

Clayton, D. H., Lee, P. L. M., Tompkins, D. M. and Brodie III, E. D. 1999. Reciprocal natural selection on host–parasite phenotypes. – Am. Nat. 154: 261–27

Clayton, D. H., Moyer, B. R., Bush, S. E., Jones, T. G., Gardiner, D. W., Rhodes, B. B. and Goller, F. 2005. Adaptive significance of avian beak morphology for ectoparasite control. – Proc. R. Soc. Lond. B 272: 811–817.

Cody, M. L. 1966. A general theory of clutch size. – Evolution 20: 174–184.

Delhey, K., Peters, A. and Kempenaers, B. 2007. Cosmetic coloration in birds: occurrence, function, and evolution. – Am. Nat. 169: S145–S158.

Dumbacher, J. P. and Pruett-Jones, S. 1996. Avian chemical defense. – In: Nolan, V., Jr and Ketterson, E. D. (eds), Current Ornithology. Vol. 13. Plenum Press, pp. 137–174.

Elder, W. H. 1954. The oil gland of birds. – Wilson Bull. 66: 6–31.

Fair, J., Whitaker, S. and Pearson, B. 2007. Sources of variation in haematocrit in birds. – Ibis 149: 535–552.

Figuerola, J. and Senar, J. C. 2000. Measurement of plumage badges: an evaluation of methods used in the great tit *Parus major*. – Ibis 142: 482–484.

Galván, I., Barba, E., Piculo, R., Cantó, J. L., Cortés, V., Monrós, J. S., Atiénzar, F. and Proctor, H. 2008. Feather mites and birds: an interaction mediated by uropygial gland size? – J. Evol. Biol. 21: 133–144.

Goldstein, G., Flory, K. R., Browne, B. A., Majid, S., Ichida, J. M. and Burtt, E. H. 2004. Bacterial degradation of black and white feathers. – Auk 121: 656–659.

Gunderson, A. R., Frame, A. M., Swaddle, J. P. and Forsyth, M. H. 2008. Resistance of melanized feathers to bacterial degradation: is it really so black and white? – J. Avian Biol. 39: 539–545.

Haribal, M., Dhondt, A. A., Rosane, D. and Rodriguez, E. 2005. Chemistry of preen gland secretions of passerines: different pathways to same goal? Why? – Chemoecology 15: 251–260.

Hirao, A., Aoyama, M. and Sugita, S. 2009. The role of uropygial gland on sexual behavior in domestic chicken *Gallus gallus dometicus*. – Behav. Proc. 80: 115–120.

Jacob, J. and Ziswiler, W. 1982. The uropygial gland. – In: Farner, D. S., King, J. R. and Parker, K. C. (eds), Avian biology. Vol. VII. Academic Press, pp. 359–362.

Johnston, D. W. 1988. A morphological atlas of the avian uropygial gland. – Bull. Brit. Mus. Nat. Hist. 54: 1–259.

Kennedy, M. W. and Nager, R. G. 2006. The perils and prospects of using phytohaemagglutinin in evolutionary ecology. – Trends Ecol. Evol. 21: 653–655.

Kose, M. and Møller, A. P. 1999. Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barn swallow *Hirundo rustica*. – Behav. Ecol. Sociobiol. 45: 430–436.

Kose, M., Mänd, R. and Møller, A. P. 1999. Sexual selection for white spots in the barn swallow in relation to habitat choice by feather lice. – Anim. Behav. 58: 1201–1205.

Lessells, C. M. and Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. – Auk 104: 116–121.

Martin II, L. B., Han, P., Lewittes, J., Kuhlman, J. R., Klasing, K. C. and Wikelski, M. 2006. Phytohemagglutinin-induced skin swelling in birds: histological support for a classic immunoecological technique. – Func. Ecol. 20: 290–299.

Martin II, L. B., Pless, M. I. and Wikelski, M. 2007. Greater seasonal variation in blood and ectoparasite infections in a temperate than a tropical population of house sparrows *Passer domesticus* in North America. – Ibis 149: 419–423.

Martín-Vivaldi, M., Ruiz-Rodríguez, M., Soler, J. J., Peralta, J. M., Méndez, M., Valdivia, E., Martín-Platero, A. M. and Martínez-Bueno, M. 2009. Seasonal, sexual and developmental differences in hoopoe preen gland morphology and secretions. Evidence for a role of bacteria. – J. Avian Biol. 40: 191–205.

Møller, A. P. 1991. Parasites, sexual ornaments and mate choice in the barn swallow *Hirundo rustica*. – In: Loye, J. E. and Zuk, M. (eds), Ecology, behavior and evolution of bird–parasite interactions. Oxford Univ. Press, pp. 328–343.

Møller, A. P. and Rózsa, L. 2005. Parasite biodiversity and host defenses: chewing lice and immune response of their avian hosts. – Oecologia 142: 169–176.

Møller, A. P., Kimball, R. T. and Erritzøe, J. 1996. Sexual ornamentation, condition, and immune defence in the house sparrow *Passer domesticus*. – Behav. Ecol. Sociobiol. 39: 317–322.

Møller, A. P., Christe, P. and Lux, E. 1999. Parasitism, host immune function, and sexual selection. – Quart. Rev. Biol. 74: 3–20.

Møller, A. P., de Lope, F. and Saino, N. 2004a. Parasitism, immunity, and arrival date in a migratory bird, the barn swallow. – Ecology 85: 206–219.

Møller, A. P., Martinelli, R. and Saino, N. 2004b. Genetic variation in infestation with a directly transmitted ectoparasite. – J. Evol. Biol. 17: 41–47.

Montalti, D., Gutierrez, A. M., Reboredo, G. and Salibian, A. 2005. The chemical composition of the uropygial gland secretion of rock dove *Columba livia*. – Comp. Biochem. Physiol. A Mol. Integrat. Physiol. 140: 275–279.

Moreno-Rueda, G. 2005. Is the white wing-stripe of male house sparrows *Passer domesticus* an indicator of the load of Mallophaga? – Ardea 93: 109–114.

Moreno-Rueda, G. 2006. Sexual size dimorphism and assortative mating for morphological traits in *Passer domesticus*. – J. Ethol. 24: 227–230.

Moyer, B. R., Rock, A. N. and Clayton, D. H. 2003. Experimental test of the importance of preen oil in rock doves *Columba livia*. – Auk 120: 490–496.
Navarro, C., Marzal, A., de Lope, F. and Møller, A. P. 2003. Dynamics of an immune response in house sparrows *Passer domesticus* in relation to time of day, body condition and blood parasite infection. – Oikos 101: 291–298.
Pap, P. L., Tökölyi, J. and Szép, T. 2005. Frequency and consequences of feather holes in barn swallows *Hirundo rustica*. – Ibis 147: 169–175.
Piault, R., Gasparini, J., Bize, P., Paulet, M., McGraw, K. J. and Roulin, A. 2008. Experimental support for the makeup hypothesis in nestling tawny owls *Strix aluco*. – Behav. Ecol. 19: 703–709.
Potti, J. and Merino, S. 1995. Louse loads of pied flycatchers: effects of host's sex, age, condition and relatedness. – J. Avian Biol. 26: 203–208.
Price, R. D., Hellenthal, R. A., Palma, R. L., Johnson, K. P. and Clayton, D. H. 2003. The chewing lice: world checklist and biological overview. – Illinois Nat. Hist. Surv.
Pryke, S. R. 2007. Sexual selection of ultraviolet and structural color signals. – In: Jamieson, B. G. M. (ed.), Reproductive biology and phylogeny of birds. Part B. Science Publishers, pp. 1–40.
Quinn, G. P. and Keough, M. J. 2002. Experimental design and data analysis for biologists. – Cambridge Univ. Press.
Reneerkens, J., Piersma, T. and Damsté, J. S. S. 2002. Sandpipers (Scolopacidae) switch from monoester to diester preen waxes during courtship and incubation, but why? – Proc. R. Soc. Lond. B 269: 2135–2139.
Reneerkens, J., Piersma, T. and Sinninghe-Damsté, J. S. 2005. Switch to diester waxes may reduce avian nest predation by mammalian predators using olfactory cues. – J. Exp. Biol. 208: 4199–4202.
Roulin, A. 2007. Melanin pigments negatively correlates with plumage preening effort in barn owls. – Funct. Ecol. 21: 264–271.
Ruiz-Rodríguez, M. 2007. Simbiosis entre aves y bacterias. Propiedades y modo de adquisición de la microbiota intestinal de críalos y urracas, y de la existente en la glándula uropigial de abubillas. PhD thesis. – Univ. de Granada, Spain.
Schulte-Hostedde, A. I., Zinner, B., Millar, J. S. and Hickling, G. J. 2005. Restitution of mass-size residuals: validating body condition indices. – Ecology 86: 155–163.
Shawkey, M. D., Pillai, S. R. and Hill, G. E. 2003. Chemical warfare? Effects of uropygial oil on feather-degrading bacteria. – J. Avian Biol. 34: 345–349.
Smits, S. E., Bortolotti, G. R. and Tella, J. L. 1999. Simplifying the phytohaemaglutinin skin-testing technique in studies of avian immunocompetence. – Funct. Ecol. 13: 567–572.
StatSoft Inc. 2005. STATISTICA, ver. 7.1. – StatSoft, Inc.
Steyn, P. 1999. The breeding biology of the scimitar-billed woodhoopoe. – Ostrich 70: 173–178.
Vas, Z., Csörgö, T., Møller, A. P. and Rózsa, L. 2008. The feather holes on the barn swallow *Hirundo rustica* and other small passerines are probably caused by *Brueelia* spp. lice. – J. Parasitol. 94: 1438–1440.
Whiteman, N. K., Matson, K. D., Bollmer, J. L. and Parker, P. G. 2006. Disease ecology in the Galápagos hawk *Buteo galapagoensis*: host genetic diversity, parasite load and natural antibodies. – Proc. R. Soc. Lond. B 273: 797–804.