



# Development of Badges of Status in Captive Male House Sparrows (*Passer domesticus*) in Relation to the Relative Ornamentation of Flock-Mates

Silke Laucht\* & James Dale\*†

\* Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology Seewiesen, Germany

† Institute of Natural Sciences, Massey University Auckland, New Zealand

## Correspondence

Silke Laucht, Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard-Gwinner-Straße, Haus 7/8, D-82319 Seewiesen, Germany.  
E-mail: laucht@orn.mpg.de

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## Abstract

The development of quality signals is expected to be largely influenced by environmental conditions among which the social environment could be an important factor, particularly in gregarious animals. Here, we investigated the role of the presumed social environment on the development of badge size in moulting male House Sparrows (*Passer domesticus*) over a 3-yr time span. House Sparrow badges are testosterone-dependent ornaments that are typically argued to be 'badges of status' –that is, signals of competitive ability and aggression. Immediately prior to moult, we created several groups of males, either with similarly sized badges or with badges of different sizes, and we measured each male's badge size before and after moult. The former groups were presumed to have a less clear social hierarchy than the latter groups because of group members advertising relatively similar competitive ability (and thus were expected to more frequently challenge one another in order to establish dominance). Conversely, the latter groups were presumed to have relatively higher social stability because birds would less frequently encounter rivals advertising similar agonistic threat. We predicted in groups of birds with similarly sized badges, both (1) larger changes (i.e. increases or decreases) in badge sizes and (2) higher increases in between-individual variation within groups. The first prediction was supported in one of the 3 yrs, but there was no support for the second prediction in any year. We conclude that social environment has an effect on the development of badges of status, but that it is highly contingent on the specific nature and timing of group interactions.

## Introduction

Many animals possess distinct patches of skin or pelage (ornaments), which are thought to act as signals of quality that convey information about one or more aspects of their bearer's genetic and/or phenotypic constitution (such as good genes, physical condition, freedom from disease, parental care abilities and social status) (Searcy & Nowicki 2005; Dale 2006). To understand how specific information becomes encoded in a particular signal, it is essential to understand the factors which influence its expression. Signal development may be determined by either genetic or envi-

ronmental factors, or some combination of the two, although environmental factors are thought to be the most influential (Hill 2006). Using plumage colouration of birds as a model, Hill (2006) described four broad, non-mutually exclusive classes of environmental factors that can influence the expression of signals of quality: (1) pigment access (Witmer 1996; Hill et al. 2002), (2) nutritional condition (McGraw et al. 2002; Ohlsson et al. 2003), (3) parasites (Zuk et al. 1990; McGraw & Hill 2000) and (4) social environment (McGraw et al. 2003; Gautier et al. 2008; Safran et al. 2008). While the first three have been extensively studied in a variety of bird species, little is known

about the influence of social environment on ornament development (Hill 2006; Gautier et al. 2008).

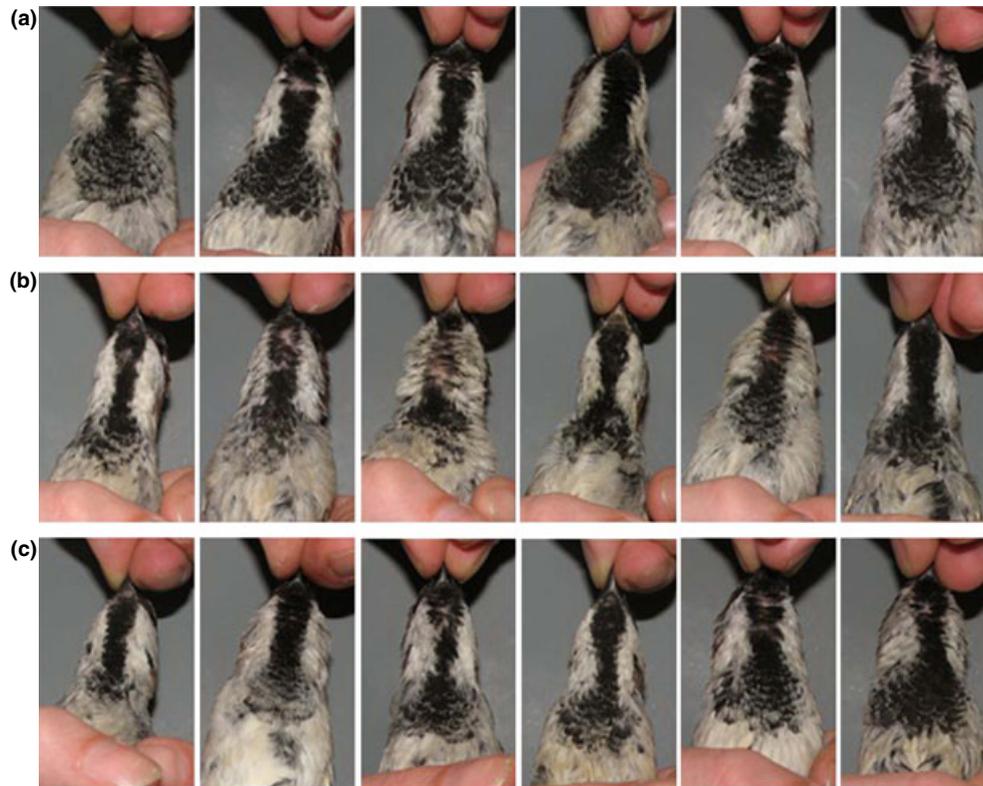
Hill (2006) further reviewed the literature and outlined three major pathways through which the social environment could influence ornamentation: (1) competition for access to food or key limiting nutrients, (2) effects of parasites transferred from other group members and (3) effects of agonistic interactions on hormone levels. So far, most research has focused on the effects of the agonistic behaviour on testosterone levels of group members (Adkins-Regan 2005; Hill 2006). There is a complex interplay between testosterone and aggression, because testosterone is known to affect aggression (Wingfield et al. 1987), while the outcome of aggressive interactions in turn can strongly affect hormone levels {i.e. increase during challenges [‘the Challenge Hypothesis’ (Wingfield et al. 1990)] or increase in winners and decrease in losers via ‘winner–loser’ effects (e.g. Oyegbile & Marler 2005)}. Moreover, testosterone levels are thought to play a role in ornament elaboration (Adkins-Regan 2005; Rubenstein & Hauber 2008). Therefore, aggressive interactions and the stability of dominance hierarchies could indirectly affect ornamentation (McGraw et al. 2003; Rubenstein & Hauber 2008). In agreement with this hypothesis, ornament elaboration was related to both circulating androgen levels and social rank within groups in male Mandrills (*Mandrillus sphinx*) and Red Junglefowl (*Gallus gallus*) (Parker et al. 2002; Setchell et al. 2008). Additionally, a study on captive male House Sparrows (*Passer domesticus*) held in triads during the annual moult suggested that the size of the black breast patch – a male status signal – increased more in middle-ranked males that experienced higher aggression during moult (McGraw et al. 2003).

The above examples involve ‘badges of status’ – traits which are typically testosterone-dependent and generally considered to indicate aspects of fighting ability (Rohwer & Ewald 1981; Jawor & Breitwisch 2003; Tibbetts & Dale 2004; Searcy & Nowicki 2005; Senar 2006). In general, status signals should make good candidates for indicators that are strongly influenced by the social environment because individual status is a *relative* characteristic. That is, an individual’s status is not only determined by its intrinsic ability and quality but is also contingent on the degree of expression of equivalent characteristics in other members of its social group. For example, a male with an average signal of fighting ability would achieve higher status within a subgroup of individuals with below-average signals than he would within a subgroup of individuals with above-average signals. As such, one

could in theory manipulate the relative status of individuals simply by re-organizing the phenotypic variability of the ornaments in the population. To date, no study has manipulated the range of signals possessed by group members and then evaluated how this affects ornament development. Here, we examine how the relative advertised status of flock-mates might influence signal development in a highly social species with a well-established badge of status.

In this study, we experimentally tested whether characteristics of the social environment, as determined by the size range of signals possessed by social rivals, affect badge size in House Sparrows (*Passer domesticus*). House Sparrows are an ideal species in which to examine social effects of plumage development as they are highly gregarious throughout the year, that is, they feed and roost in flocks and breed semicolonally (Anderson 2006). In addition, male House Sparrows possess a range of ornaments of which the size of the black breast bib or badge has been widely studied and is commonly accepted as a badge of status (Møller 1987a,b; Veiga 1995; Hein et al. 2003). Across various studies, badge size has been found to correlate with overall fighting success (Møller 1987b; Liker & Barta 2001; McGraw et al. 2003; Bókony et al. 2006; Morrison et al. 2008), age (Veiga 1993; Morrison et al. 2008) and testosterone levels (Evans et al. 2000; Buchanan et al. 2001; Gonzalez et al. 2001; Laucht et al. 2011). In addition, males possess a second ornament, bill colour, which changes from horn to black between the non-breeding and breeding season and can be used as a dynamic indicator of a ‘running average’ of recent testosterone levels (Keck 1933; Witschi 1936; Pfeiffer et al. 1944; Laucht et al. 2010).

Over 3 yrs, we monitored badge sizes before and after moult in a large captive population of male House Sparrows where we formed flocks according to two treatments: (1) birds of the ‘uniform’ treatment shared an aviary with only individuals with similarly sized badges and (2) birds of the ‘variable’ treatment shared an aviary with individuals with differently sized badges (see Fig. 1). We reasoned that individuals in uniform groups would be competing with individuals advertising similar competitive abilities as themselves and thus would engage in more intense social competition (Maynard Smith & Harper 1988; Jawor & Breitwisch 2003; Tibbetts & Dale 2004; Tibbetts & Safran 2009). On the other hand, birds in variable groups would be competing with individuals advertising dissimilar competitive abilities as themselves and thus would engage in less intense competition. For example, small-badged males in uniform groups



**Fig. 1:** Photographs of male House Sparrows present in representative combinations of treatment and badge size (a) uniform badge size treatment where all males have large badges (b) uniform badge size treatment where all males have small badges (c) variable badge size treatment where males have a range of badge sizes from small to large. Note that not all combinations are illustrated.

would be housed with competitors advertising lower competitive ability (on average) than small-badged males in variable groups (who would be competing mostly with larger-badged individuals). Similarly, large-badged males in uniform groups would be competing with rivals advertising higher competitive ability than large-badged males in the variable groups.

Based on this reasoning, we first predicted that birds in the uniform groups would show larger changes in badge size on average, while those in the variable groups should show smaller changes on average. Second, we predicted that the variance in badge size between individuals should increase among birds in the uniform treatment groups, but there should be no change in the variance among birds in the variable groups. Further, in 1 yr, we evaluated the effect of treatment on male testosterone levels using bill colour as a proxy (see above). Based on the Challenge Hypothesis (Wingfield et al. 1990), we predicted birds in the uniform treatment to have darker bills (i.e. higher testosterone levels) than males in the variable treatment (owing to increased competition with rivals of similar badge sizes). However, based on

winner–loser effects, we expected a significant effect of the interaction between treatment and badge size on bill colour, with more interactions (unstable hierarchies) in the uniform cages causing smaller-badged males to have relatively darker bills (i.e. higher testosterone) than larger-badged males.

## Material and Methods

### Study Population

We studied a population of 169 captive male House Sparrows held at the Max Planck Institute for Ornithology, Seewiesen, Germany. Most ( $n = 139$ ) were captured as adults from rural areas in Bavaria, Germany, and the remainder ( $n = 30$ ) were raised in captivity at the institute. We feel justified in pooling birds with different origins as we have found no phenotypic or behavioural difference between wild- and captive-bred birds. All birds were held in captivity for at least 8 mo before being used in the experiment to allow them to acclimate to captivity and also to minimize age-related differences in competitive ability and

badge size. We housed birds in groups of varying sizes in aviaries (1.2 × 2.0 × 4.0 m) that were equipped with perches, nest boxes and large branches for roosting in. At all times, the birds had *ad libitum* access to food provided in a single dish, drinking and bathing water and sand for dust-bathing. The light–dark cycle and temperatures in the aviaries were close to natural conditions, as the aviaries were semioutdoor with the outdoor-facing side enclosed only by chicken wire. The sides towards neighbouring aviaries were covered with hessian cloth so that birds could not see or interact with those from other groups. Further details about our study population can be found in Laucht et al. (2010). Capture of wild birds and experimental procedures adhere to the animal ethic laws in Germany (license: permit nr. 55.1-8642.3-3-2006 of the ‘Regierung Oberbayern’, with several extensions).

### Experimental Procedures

We performed our experiments during the annual moult periods of 2006, 2007 and 2009 (beginning of August–October). Most of the birds were used in all three experiments, with the exception of a few which died of natural causes during the course of the study or which were born later. This resulted in 139 birds in 2006, 133 birds in 2007 and 118 birds in 2009. At the start of each experiment, we determined the size of each male’s badge from digital photographs and used the size data to assign individuals to one of two treatments: uniform or variable. The uniform treatment consisted of groups of males with similarly sized badges whereas the variable treatment consisted of groups of males with differently sized badges (ranging from small to large) (see Fig. 1). To assign males to groups, male badge scores were ranked, and then individuals were assigned randomly to either the uniform or variable treatment, such that the mean and variance of badge sizes were similar between the two treatments, although not between groups. Males were then randomly assigned into new social groups (i.e. aviaries), and we made sure new groups were comprised of males that had not been housed together at any time during the previous year. The number of birds in each aviary was six in 2006 (24 aviaries), ten in 2007 (14 aviaries) and either seven or eight in 2009 (16 aviaries). In 2006 and 2009, birds were moved into new groups near the start of the moult period (early August). In 2007, however, birds were arranged into new groups about 3 wk before the start of moult (mid-July). The differences between years in the time at which groups were formed and the number of birds per aviary were owing to constraints

imposed by other experiments running concurrently at the institute. In all 3 yr, birds were maintained in their groups until they had all moulted (end of September) at which point we measured the size of their new badge. In 2007, we also captured all males in the beginning of September (mid-moult) to measure bill brightness.

### Measurement of Badge Size

We measured badge size of each male at different seasons before and after each moult from four digital photographs (i.e. in July 06, Nov 06, Jan 07, March 07, June 07, Jan 08, June 08, Jan 09, April 09, July 09, Nov 09, March 10). We held the birds such that the throat and bib were extended and then took a ventral photograph (as in Fig. 1). Between each of the four photographs, the birds were allowed to regain their original posture before being positioned for the camera. Photographs were imported into the program ImageJ 1.36b (Abramoff et al. 2004), and then SL measured the size of each badge by outlining its perimeter and using the program to calculate the area contained within. This was converted from pixels to cm<sup>2</sup> from a size standard included in each photograph. We then calculated badge size for each bird as the average size from the four photographs taken during each season within the same moult year (e.g. Nov 06, Jan 07, March 07, June 07) and used these scores as post-moult scores and the ones from the previous moult year as pre-moult scores. Using the four average scores per individual (i.e. means of pictures 1, 2, 3 and 4 of all seasons within a moult year), these measurements were highly repeatable for pre-moult badge measures ( $R = 0.90$ ,  $p < 0.001$ ;  $n = 390$  birds, each measured four times) and for post-moult badge measures ( $R = 0.91$ ,  $p < 0.001$ ;  $n = 390$  birds, each measured four times), estimated according to Lessells & Boag (1987). Similarly, using individual badge size (calculated as averages of the four photographs), pre- and post-moult badge sizes were also repeatable ( $R = 0.13$ ,  $p = 0.01$ ;  $n = 390$  birds, two averages for each). See Laucht et al. (2010) for additional details.

### Measurement of Bill Brightness

We measured bill brightness of all males during mid-moult (i.e. moult had progressed between the third and fifth primary) in September 2007 from two digital photographs. For photographs, we held the birds with their right side of the head and bill in front of a grey card. Pictures were imported into a processing software

written into R 2.4.0 (R Development Core Team 2006), and SL measured the brightness of individual pixels located at five randomly chosen positions each on the upper bill, lower bill and the grey background around the bill. We standardized brightness measures between photographs by the determination of the deviation of a focal picture's grey card brightness from the overall mean and subtracted this deviation from mean bill brightness for each photograph. For analyses, we used the mean of the standardized measures of upper and lower bill brightness from the two photographs. For more details on the methods, see Laucht et al. (2010). Using the two taken photographs per individual, these measures were highly repeatable ( $R = 0.94$ ,  $p < 0.001$ ;  $n = 133$  birds, each measured twice), estimated according to Lessells & Boag (1987).

### Statistical Analyses

We performed all statistical analyses using R 2.11.0 (R Development Core Team 2010) (packages: nlme, RODBC) at the significance level  $\alpha = 0.05$ . For overall analyses, we used linear mixed effect models (lme), including year as a fixed effect and individual ID as a random factor, to account for the fact that the same individuals were involved in multiple years. For analyses within a given year, where each individual was represented only once, we used linear models (lm). To control for body condition, we included both tarsus length and body mass as covariates in the model where indicated.

Before testing our predictions, we first tested whether there was an effect of treatment (uniform vs. variable) on post-moult badge size at the individual level, after controlling for pre-moult badge size and body condition in each year. Using absolute (i.e. post-minus pre-moult badge) or relative (i.e. post- divided by pre-moult badge) change in badge size instead of post-moult badge size did not qualitatively change the results. Including social-group ID (i.e. aviary ID) as a random factor also did not qualitatively change the results.

To test our predictions, we needed to control for regression towards the mean (Barnett et al. 2005). According to this, we generally expected larger changes in birds at either end of the continuum. Thus, irrespective of treatment, individuals with a small pre-moult badge will tend to increase badge size while individuals with a large pre-moult badge will tend to decrease badge size. However, regression towards the mean does not predict differences in the slopes of these relationships between treatments; thus, we tested for significant interactions

between treatment and pre-moult conditions on post-moult badge.

We tested our first prediction using linear mixed effect models of post-moult badge size in relation to the interaction of pre-moult badge size and treatment after accounting for body condition and with social-group ID as random effect, both overall and in the 3 yr separately. By doing so, we accounted for a high correlation between pre- and post-moult badge size and examined whether the two treatments differed in slopes. To test for an effect of treatment on bill brightness and hence testosterone levels, we performed the same analysis (as described above) using bill brightness instead of post-moult badge size. Note that for graphical presentation, we used centred (i.e. yearly means subtracted from individual badges) and scaled [divided by the yearly standard deviation (SD)] post- and pre-moult badges to exclude confounding year effects.

We tested our second prediction by examining the SD of post-moult badge sizes of different groups in relation to the SD of their pre-moult badge sizes and treatment. By doing so, we tested for an effect of treatment, but not of a significant interaction between treatment and pre-moult SD; hence, we examined whether the slopes between pre- and post-moult SD were parallel in each treatment and differed in intercept. We pooled data from all 3 yr for this analysis as our power to detect within-year differences was low because group values were used. Consequently, each bird is represented up to three times in the analysis. However, the data are not pseudoreplicated because each group contained a unique composition of birds, and data points refer to group values rather than individuals. Because our power was too low (only 1 yr), we could not perform the same analysis with bill brightness SD.

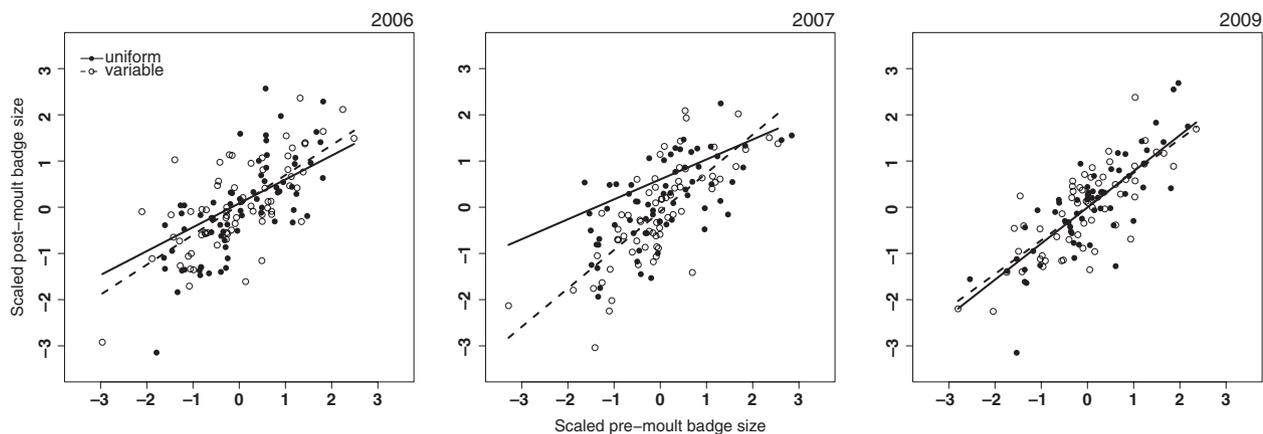
### Results

First, there was no difference in post-moult badge size among birds in the two experimental treatments when pooling all 3 yrs (lme:  $t_{214} = -1.55$ ,  $p = 0.12$ , after controlling for year and body condition, with bird ID as a random effect) or in single years (lm: 2006:  $t_{134} = 0.93$ ,  $p = 0.36$ ; 2007:  $t_{125} = -1.66$ ,  $p = 0.10$ ; 2009:  $t_{96} = 0.17$ ,  $p = 0.86$ ).

Second, when pooling data from all 3 yrs, there was no interaction between pre-moult badge size and treatment on post-moult badge size (Table 1). However, in one of the 3 yrs (2007), there was a significant effect of treatment, with the slope between pre- and post-moult badge size being more shallow among birds in the

**Table 1:** Results of linear mixed effect models of House Sparrow badge size and bill brightness in relation to the interaction of pre-moult badge size and experimental group after accounting for condition (i.e. body mass and tarsus length entered as fixed effects into the model) and with social-group ID (i.e. aviary ID) as a random factor. In the overall model, we also accounted for year and included bird ID as a random factor

Year	Pre-moult badge		Treatment		Interaction		
Overall	$z = 6.33$	$p < 0.001$	$z = -0.80$	$p = 0.42$	$z = 0.81$	$p = 0.42$	$n = 370$ observations
2006	$t_{111} = 6.18$	$p < 0.001$	$t_{22} = 0.95$	$p = 0.35$	$t_{111} = -0.82$	$p = 0.41$	$n = 139$
2007	$t_{112} = 5.61$	$p < 0.001$	$t_{12} = -2.70$	$p = 0.02$	$t_{112} = 2.55$	$p = 0.01$	$n = 130$
2009	$t_{81} = 8.12$	$p < 0.001$	$t_{14} = 1.26$	$p = 0.23$	$t_{81} = -1.23$	$p = 0.22$	$n = 101$
2007 bill	$t_{112} = 2.21$	$p = 0.03$	$t_{12} = 2.36$	$p = 0.04$	$t_{112} = -2.59$	$p = 0.01$	$n = 130$



**Fig. 2:** Scaled post-moult badge size in relation to scaled pre-moult badge size among male House Sparrows from the two experimental treatments in each of 3 yrs. We centred and scaled badge sizes by year to standardize the graphs. For each year separately, we subtracted the mean badge size from an individual's badge size and divided this by the standard deviation. Closed circles and straight lines represent birds in the uniform badges treatment; open circles and dashed lines represent birds in the variable badges treatment.

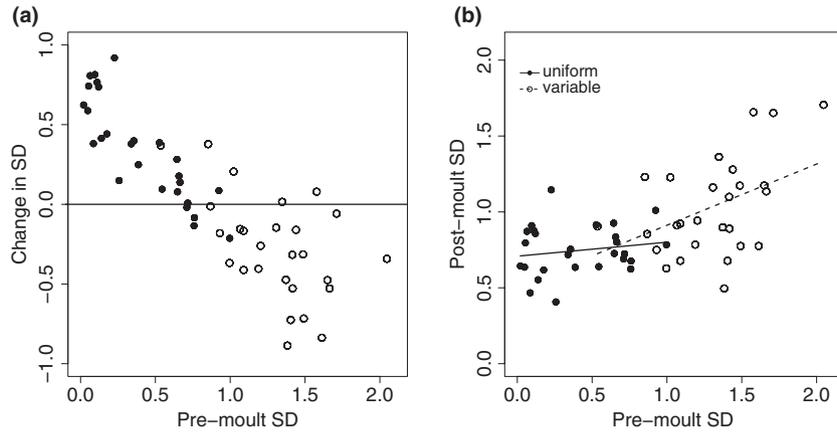
uniform groups (Fig. 2, Table 1), suggesting that males in the uniform treatment moulted into larger badges when they had smaller pre-moult badges.

Third, the SD in post-moult badge size within a group was strongly negatively correlated with pre-moult badge size SD (lm:  $t_{51} = -12.05$ ,  $p < 0.001$ , after accounting for year, Fig. 3a). Thus, post-moult SD within a group tended to decrease if pre-moult SD was high, but tended to increase if pre-moult SD was low (i.e. regression towards the mean). However, experimental treatment had no influence on this relationship. In addition, the slopes of the relationship between pre- and post-moult SD in each group were similar between treatments (lm:  $t_{49} = 0.69$ ,  $p = 0.49$  after accounting for year; Fig. 3b), and there was no overall effect of treatment (lm:  $t_{50} = 0.11$ ,  $p = 0.91$ , after accounting for year). Because the lack of treatment effect could stem from uniform groups that were relatively diverse (i.e.  $SD > 0.5$ ) and from variable groups that were relatively uniform (i.e.  $SD < 1.0$ ), we excluded such groups and re-ran the analysis. However, the results do not qualitatively change.

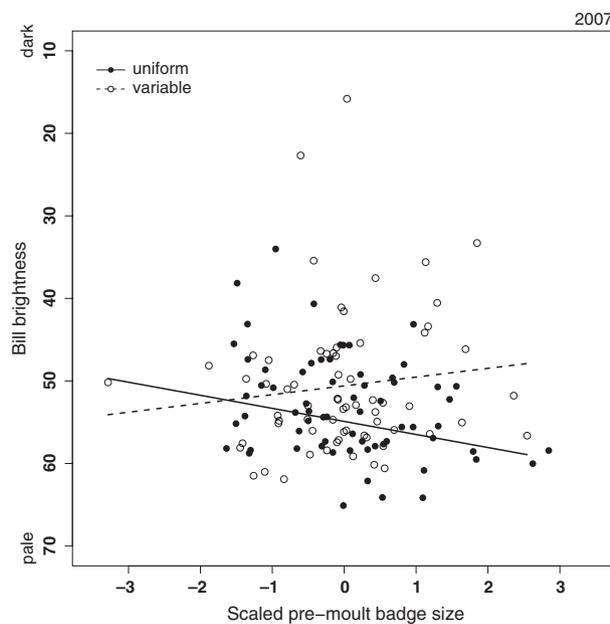
Fourth, in 2007, there was also a significant effect of treatment on bill brightness with the slope between pre-moult badge size and inverted bill brightness (note higher brightness scores mean paler bill, i.e. lower testosterone levels) being negative in the uniform treatment (Fig. 4, Table 1). This means that males in the uniform treatment had generally paler bills and thus lower testosterone levels. In addition, it suggest that males with smaller pre-moult badges in the uniform treatment had darker bills and thus higher testosterone levels than males with larger pre-moult badges that had brighter bills and thus lower testosterone levels. In contrast, bill brightness was not linearly related to pre-moult badge size in males in the variable treatment.

## Discussion

We maintained captive male House Sparrows throughout their moult in groups containing birds with either uniform badge sizes or variable badge sizes to detect if this affected the mean and variance of the



**Fig. 3:** (a) Change in standard deviation (SD) of badge size among groups of House Sparrows pre- and post-moult during three study years. (b) Standard deviation in badge size in groups of House Sparrows post-moult in relation to SD pre-moult. The plot includes data from three study years representing birds from two different experimental treatments. Closed circles and straight lines represent birds in the uniform badges treatment; open circles and dashed lines represent birds in the variable badges treatment.



**Fig. 4:** Bill brightness in relation to scaled pre-moult badge size among male House Sparrows from the two experimental treatments in each of 3 yrs. We centred and scaled badge sizes to standardize the graph the same as the graph of Fig. 2. We subtracted the mean badge size from an individual's badge size and divided this by the standard deviation. Closed circles and straight lines represent birds in the uniform badges treatment; open circles and dashed lines represent birds in the variable badges treatment.

badge sizes produced. We predicted that badge size would show greater average changes in groups with uniform group sizes, because individuals in these flocks would be advertising similar competitive abilities and thus were expected to face more challenges and aggressive interactions. In contrast, individuals in groups with variable badge sizes were expected to form stable dominance hierarchies relatively quickly and thus experience fewer challenges and aggressive

interactions. However, we found that badge sizes changed differently between treatment groups in only one of the 3 yrs, and individual variation in badge size was not affected by treatment. Overall, our results indicate that the relative ornamentation of flock-mates had a smaller effect than we expected on new badges produced by moulting males.

Overall, our finding of a significant treatment effect on badge size in only one of 3 yrs suggests either that our treatment did not influence levels of aggressive interactions strongly enough for an effect on badge size or alternatively that there is no general effect of social-group composition on badge size. Although little is known about how much aggression birds exhibit during moult, it is generally thought to be low (Hahn et al. 1992), and thus, our experimental manipulations may have only increased aggression by a small amount. Nevertheless, we did find a clear significant difference in the predicted direction in 2007 (Fig. 2b), with individuals in the uniform groups showing more changes in badge size. Even though it is possible that this was owing to differences in other environmental conditions in this particular year, it is noteworthy that in 2007 the group size ( $n = 10$ ) was larger than in the other two study years ( $n = 6$  in 2006 and  $n = 7-8$  in 2009), which likely caused a greater number of interactions among flock members. Additionally, in 2007, the birds were moved into their groups at least 3 wks before the onset of moult, whereas in the other 2 yrs they were placed into groups immediately before the beginning of moult. Therefore, in 2007, the birds placed in new groups still had presumably elevated testosterone levels and were more likely to engage in and respond to aggressive interactions because testosterone levels do not drop until the onset of moult (Laucht et al. 2010). Moreover, because it is unknown exactly when and over what period any physiological determination of badge size can or does

occur, it could be that this determination occurred in 2007 after the males were placed in their new groups, but in 2006 and 2009 prior to new group formation. If so, then this suggests that the social environment could indeed have a general effect on ornament development, but that a critical window for this effect to be manifested occurs over a longer period (e.g. via several consecutive days of high or low hormone levels) before moult rather than during moult itself. This idea is supported by other studies in House Sparrows that found badge size to be affected by circumstances/events long before moult, such as yolk hormones (Strasser & Schwabl 2004), body condition as a nestling (Griffith et al. 1999; Jensen et al. 2006) or reproductive effort during the previous season (Griffith 2000). However, more research is needed to examine the exact timing of the determination of the House Sparrow's badge size as well as the potential influence of the social environment on this.

Our results differed from the only other study that examined social effects during moult on House Sparrow badge sizes (McGraw et al. 2003). In this study, McGraw et al. (2003) kept triads of males in relatively small cages throughout their moult and observed the frequency and outcome of aggressive interactions that took place around the cage, mostly over perches. They found that (1) males in triads with the least difference in badge size experienced the most aggression and developed relatively larger badges and (2) that males which occupied the second rank in dominance hierarchies developed larger badges than those at the bottom of the hierarchy. Taken together, this study suggests clear effects of the social environment, while our study suggests rather small carry-over effects from before moult. These different findings could be due to differences in the two experimental set-ups. First, the birds in McGraw et al.'s (2003) study were held in small cages, and thus, aggressive encounters were likely very common and also more stressful as birds could not escape from one another, whereas in our study, birds were held in large aviaries with many refuges and alternative perches. Second and most importantly, McGraw et al. (2003) arranged groups of birds several months before the onset of moult, and thus, they had a long exposure to aggressive interactions and their consequences, such as an increase or decrease in the levels of hormones such as testosterone. Therefore, the observed effect in their study could have easily resulted from social interactions occurring during a badge size determination window that occurs prior to moult rather than during moult.

To indirectly examine the predicted effect of treatment on hormone levels and thus provide a mecha-

nistic explanation for the changes in badge size, in 1 yr, we measured bill colour once during moult as an indicator of average testosterone levels (Keck 1933; Witschi 1936; Pfeiffer et al. 1944; Laucht et al. 2010). We found that males with smaller badges in the uniform treatment had darker bills, suggesting they had higher testosterone levels, and males with larger badges had paler bills and thus lower testosterone levels. This treatment effect provides indirect support for our hypothesis that the uniform treatment causes more interactions and changes in testosterone levels according to winner–loser effects (Oyegbile & Marler 2005) such that large-badged males presumably decreased their testosterone levels because of lost fights. However it is surprising that this decrease in testosterone levels then did not lead to a decrease in badge size. This could suggest that badge size determination is not directly dependent on testosterone levels during moult, but the exact timing of badge size determination and the influence of testosterone need to be examined in more detail.

We predicted that the relative ornamentation of flock-mates alone would be a significant predictor of badge size changes during moult, especially when monitored and averaged over a fairly large population. This is because badge size in House Sparrows is a well-known predictor of dominance and fighting ability (Møller 1987b; Liker & Barta 2001; McGraw et al. 2003; Bókonyi et al. 2006; Morrison et al. 2008). Nevertheless, an important drawback of our experiment was that we did not monitor the frequency or nature of aggressive interactions and thus have no data on the dominance rank of each individual, nor did we measure testosterone levels. Although such data would have been insightful, we did not have the resources required to collect them owing to the large overall size of the population and to other competing activities. Moreover, in a previous study, we have found that testosterone samples collected at a single point in time are only a weak correlate of baseline testosterone levels (Laucht et al. 2010), and thus, we decided not to subject captured birds to additional stress of bleeding.

To conclude, our results suggest that the social environment has an effect on the development of a badge of status signal in male House Sparrows. However, this effect was less clear and straightforward than expected by theory, and we speculate that it depended on the specific nature and timing of group interactions. Taken together with other studies that found specific, rather than general, influences of the social environment on ornament elaboration [e.g. bill colour in male Zebra Finches (*Taeniopygia guttata*) (Gautier et al. 2008),

badge size in male House Sparrows (McGraw et al. 2003)] or on willingness to breed [in male Song Sparrows (*Melospiza melodia*) (Runfeldt & Wingfield 1985)], our results demonstrate the importance of taking the social environment into account when studying animal ornamentation, but also call for further studies addressing social effects and their potential underlying mechanisms on signal development.

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