

## ORIGINAL ARTICLE

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**Seasonal variation in the relationship between cellular immune response and badge size in male house sparrows (*Passer domesticus*)**

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**Abstract** The immunocompetence handicap hypothesis postulates that secondary sexual traits are honest signals of male quality because steroid hormones (such as corticosteroids and sex steroids), which are supposed to favor the development of secondary sexual traits, may also have immunosuppressive effects. Certain secondary sexual traits are not only used as mate choice signals but also play a role as badges of status. In the house sparrow (*Passer domesticus*), males have a bib of black feathers which is used both as a signal of social status in male-male interactions and by females when choosing a mate. We investigated the relationships between bib size and cellular immune response in male house sparrows during and outside the reproductive season. Males with large badges were found to have lower levels of immunocompetence, as assessed using a T-cell-mediated immunity assay, during the reproductive season, as predicted by the immunocompetence handicap hypothesis. Conversely, in November, the correlation between badge size and cellular immune response was positive, possibly reflecting the better access to trophic resources of large-badged dominant males in winter flocks.

**Key words** Dominance · Hormones · Sexual selection · T-lymphocytes · Birds

**Introduction**

Since Darwin (1871), secondary sexual traits have been thought to be involved in two possible mechanisms of sexual selection: male-male competition and female choice. However, the distinction between these two roles is not always clear cut. For instance, male horns and antlers in several mammal species are used as weapons against rival males during contests, but horn size could also be involved in mate choice if females receive direct or indirect benefits from mating with large-horned males (Andersson 1994).

In birds, some plumage characteristics (i.e., badges of status) correlate with dominance (Rohwer 1975). In passerines which form large winter flocks, badges of status are advantageous to both subordinate and dominant birds, being used by subordinates to avoid fights with dominants, and by dominants to save energy from needless agonistic interactions. The house sparrow (*Passer domesticus*) is a small dimorphic passerine; males have a bib of black feathers on the throat and the chest, whereas females are uniformly brown. Males with larger bibs often have higher social rank than males with small bibs and may have better access to food resources in flocks (Barnard and Sibly 1981; Møller 1987a, 1987b). In addition, females in some populations appear to prefer large-bibbed males (Møller 1988), but to prefer small-badged males in others (Griffith et al. 1999). The absence of an association between badge size and female choice has also been reported (Kimball 1996). Bib size is likely, therefore, to have a double function, serving as a signal of social status and as a mate choice trait.

The immunocompetence handicap hypothesis postulates that secondary sexual characters which have a hormonal basis are honest traits, because steroid hormones may have an immunosuppressive effect (Folstad and Karter 1992). Therefore, only males of high phenotypic and/or genetic quality can develop exaggerated sexual signals and afford to pay the cost of immunosuppression. This version of the immunocompetence

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handicap hypothesis has been criticized on the grounds that many secondary sexual traits in birds may not be testosterone dependent (Owens and Short 1995). Castrated male house sparrows, for instance, have black badges but paler bill color than control males (references in Owens and Short 1995). Other observations, however, suggest that testosterone might be positively associated with badge size during the reproductive season. Large-badged males have larger testes and higher sperm production rates than other males (Møller and Erritzøe 1988; Birkhead et al. 1994), they perform within- and extra-pair copulations at a higher rate (Møller 1990), and they are involved in more communal displays and aggressively defend their mate more often against other males (Møller 1987a). Recent experimental work has confirmed that testosterone influences bib size in the house sparrow (M.R. Evans, A.R. Goldsmith, S.R.A. Norris, unpublished data): castrated males still molt in their typical male plumage but the size of their signal is smaller than in birds with experimentally increased testosterone. Interestingly, birds in the high-testosterone group also showed an increase in corticosterone titers, and corticosterone is also known to be a potential immunosuppressive agent (M.R. Evans, A.R. Goldsmith, S.R.A. Norris, unpublished data). If large-badged males also have high testosterone and/or corticosterone titers at the onset of the reproductive season, the immunocompetence handicap hypothesis predicts, then, a negative correlation between bib size and immunocompetence. A negative correlation between badge size and immune response could also be predicted without invoking the immunosuppression by hormones. As noted before, large-badged males are more actively involved in communal displays and sexual behaviors than other males. This might be achieved through reallocation of resources to mating behaviors at the expense of immune function (Wedekind and Folstad 1994). However, the view that immune defenses are costly to produce and maintain is currently under debate, since some authors have failed to find substantial energetic costs of immune defenses (see Råberg et al. 1998; Westneat and Birkhead 1998 for recent reviews).

Outside the reproductive season, house sparrows form large mixed-sex flocks where large-badged males are dominant over other individuals (Møller 1987a, 1987b). Dominance is supposed to confer an advantage in terms of access to trophic resources. Food quality and quantity are known to affect the development of the immune system and the intensity of the immune response (Chandra and Newberne 1977; Gershwin et al. 1985; Lochmiller et al. 1993; Gonzalez et al. 1999). If dominance (bib size) in winter flocks allows better access to food resources, we expect a positive correlation between immune response and bib size in winter.

This study investigated the relationship between immunocompetence, as assessed using a correlate of T-lymphocyte proliferation, and bib size in male house sparrows during and outside the reproductive season.

## Methods

The experiment was carried out on a house sparrow population at Badajoz (Extremadura, south-west Spain). During November 1997 and March–April 1998, we captured male house sparrows in mist nets. The spring sample involved birds which had not yet started to lay, since none of the females captured at the same time and place had incubation patches. We ringed birds, measured tarsus length to the nearest millimeter with a digital caliper (accuracy 0.01 mm), and measured body mass on a Pesola spring balance (accuracy 1 g). Badge length and width were measured with a ruler (accuracy 1 mm). After molt, the black feathers of the badge have white tips which partially cover the underlying feathers. Our measurements refer to the total area covered by black feathers (total and visible area are positively correlated; Møller and Erritzøe 1992). Badge area was estimated using a regression equation derived by Møller (1987a): badge size ( $\text{mm}^2$ ) =  $166.7 + [0.45 \times \text{badge length (mm)} \times \text{badge width (mm)}]$ , and was log transformed.

Cellular immune response was assessed using a T-cell-mediated immunity assay (McCorkle et al. 1980; Sorci et al. 1997). Each bird was injected intradermally in the center of the right wing web (after having marked the injection site with a pen) with 0.025 mg of phytohemagglutinin (PHA; Sigma, St. Louis, Mo.) in 0.04 ml of physiological saline solution (PBS). The left wing web was used as a control by injecting 0.04 ml of PBS. The thickness of each wing web was measured with a pressure-sensitive spessimeter (to the nearest 0.01 mm) at the injection site before and 24 h ( $\pm 15$  min) after injection (birds were held in outdoor aviaries located on the campus of the University of Extremadura, Badajoz, between the two measurements). The wing web swelling (WWS) was estimated as the change in thickness of the right wing web from the day of injection with PHA until the following day minus the change in thickness of the left wing web during the same period.

### Statistical analyses

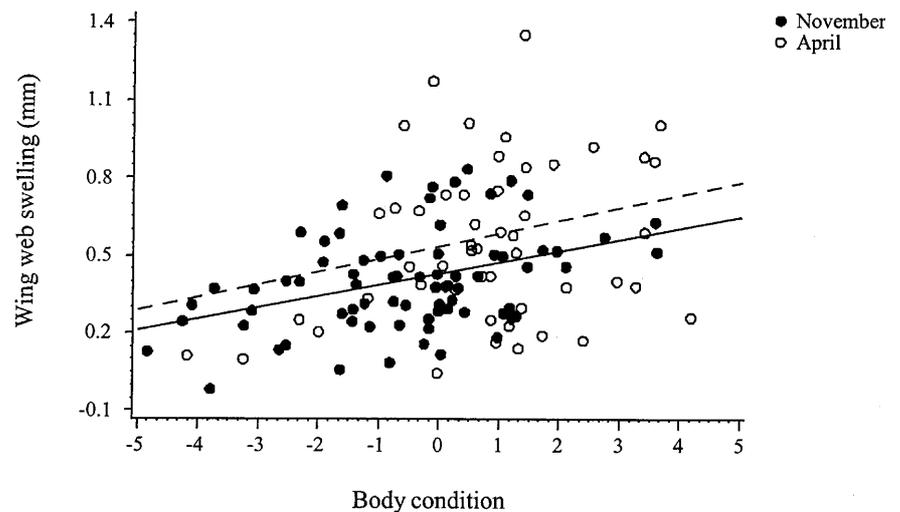
WWS, which reflects T-lymphocyte proliferation after injection of a mitogen might depend on individual condition. For this reason, we first regressed body mass on tarsus length (slope  $\pm$  SE =  $0.317 \pm 0.084$ ,  $n = 128$ ,  $P = 0.0002$ ) and used the residuals of this regression as covariates in the statistical analyses. Different individuals were measured in the two sampling periods, which allowed us to consider them as independent observations. The effect of badge size on WWS was estimated using an ANCOVA model. Linear regression was used to investigate the sign of the relationships between WWS and badge size in the two seasons. All analyses were performed using SAS Release 6.12 (SAS 1996).

## Results

WWS was positively and significantly correlated with body condition both in November and April, as illustrated by a significant effect of body condition and a non-significant interaction between body condition and season (ANCOVA: body condition,  $F_{1,122} = 14.76$ ,  $P = 0.0002$ ; season,  $F_{1,122} = 2.28$ ,  $P = 0.134$ ; body condition  $\times$  season,  $F_{1,122} = 0.0$ ,  $P = 0.961$ ,  $r^2 = 0.17$ ; Fig. 1). Conversely, badge size was not correlated with body condition (ANCOVA: body condition,  $F_{1,112} = 2.11$ ,  $P = 0.149$ ; season,  $F_{1,112} = 0.27$ ,  $P = 0.608$ ; body condition  $\times$  season,  $F_{1,112} = 0.59$ ,  $P = 0.444$ ,  $r^2 = 0.03$ ).

An ANCOVA model with WWS as the dependent variable, season as a factor, and badge size as a covariate

**Fig. 1** Positive correlation between wing web swelling and body condition in male house sparrows caught in November (filled symbols) and in April (open symbols). Body condition from the residuals of the regression of body mass on tarsus length



indicated that the slopes between WWS and badge size were significantly different for the two time periods, as illustrated by a significant time  $\times$  badge interaction (Table 1). A local test of the slopes relating WWS and badge size showed that the relationship was positive and significant in November (slope  $\pm$  SE =  $0.338 \pm 0.159$ ,  $n = 65$ ,  $P = 0.017$ ,  $r^2 = 0.09$ ; Fig. 2a), and negative and significant in April (slope  $\pm$  SE =  $-0.427 \pm 0.183$ ,  $n = 49$ ,  $P = 0.024$ ,  $r^2 = 0.1$ ; Fig. 2b).

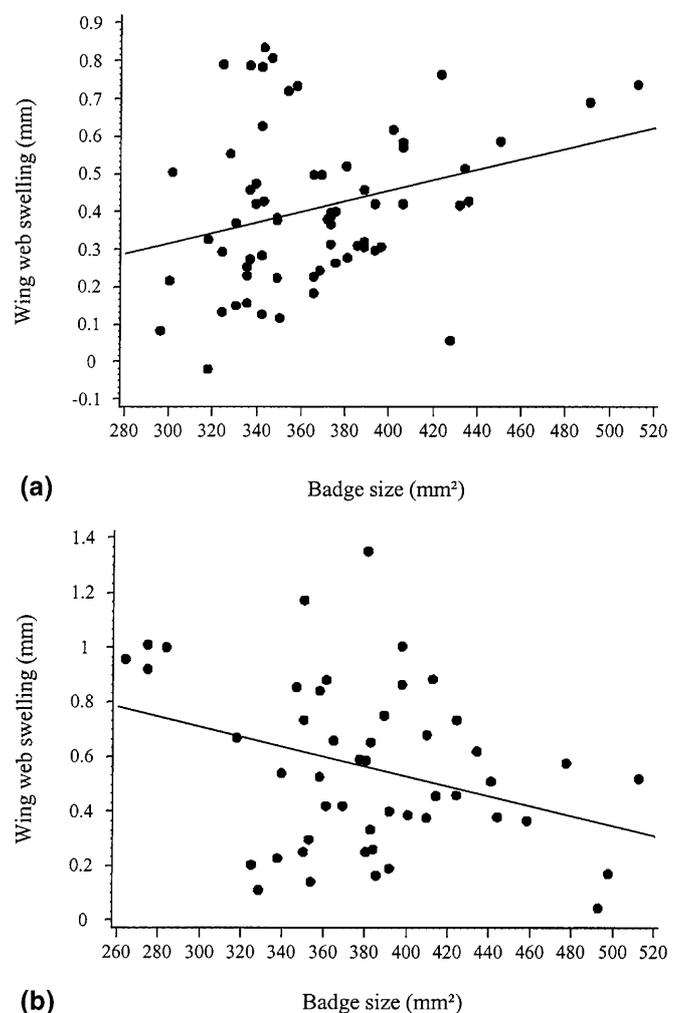
As already mentioned, WWS was positively correlated with body condition, and this correlation could have affected the relationship between badge size and WWS. To take into account the potential confounding effect of body condition, we introduced it in the ANCOVA and regression models. After correcting for body condition, we still found a significant interaction between badge size and time (Table 2). Similarly, multiple-regression analyses showed that WWS and badge size were positively correlated in November and negatively correlated in April, independently of body condition (November: badge size, slope  $\pm$  SE =  $0.343 \pm 0.147$ ,  $p = 0.023$ ; body condition, slope  $\pm$  SE =  $0.031 \pm 0.009$ ,  $p = 0.001$ ,  $n = 65$ ; April: badge size, slope  $\pm$  SE =  $-0.493 \pm 0.180$ ,  $P = 0.009$ ; body condition, slope  $\pm$  SE =  $0.034 \pm 0.016$ ,  $P = 0.043$ ,  $n = 49$ ).

## Discussion

The immunocompetence handicap hypothesis postulates that secondary sexual traits which have a hormonal basis

**Table 1** Analysis of covariance of wing web swelling with season as a factor and badge size as a covariate. Body condition from the residuals of the regression of body mass on tarsus length. Sample size 114 individuals.  $R^2$  of the model 0.16

Source	Type III MS	df	F-value	P
Season	0.3065	1	11.78	0.0008
Badge size	0.0007	1	0.03	0.8740
Season $\times$ badge size	0.3050	1	11.34	0.0010



**Fig. 2** Relationship between wing web swelling (mm) and badge size (mm<sup>2</sup>) in male house sparrows caught in November (a) and April (b)

honestly signal male quality because steroid hormones might have an immunosuppressive action (Folstad and Karter 1992). Cheating could then be prevented because the cost of sexual advertisement for low-quality males

**Table 2** Analysis of covariance of wing web swelling with season as factor, badge size and body condition as covariates. Body condition from the residuals of the regression of body mass on tarsus length. Sample size 114 individuals.  $R^2$  of the model 0.26

Source	Type III MS	df	F-value	P
Season	0.3116	1	13.35	0.0004
Badge size	0.0096	1	0.41	0.5212
Body condition	0.3239	1	13.88	0.0003
Season $\times$ badge size	0.3050	1	13.07	0.0005
Season $\times$ body condition	0.0004	1	0.02	0.8851

would be prohibitively high. The black bib of male house sparrows likely has a double function. It plays a role in female choice, females preferring males with larger badges in some populations (Møller 1988) but males with smaller badges in other populations (Griffith et al. 1999), and it is also used as a badge of status (Møller 1987a, 1987b; G. Gonzalez, personal observation). Our study suggests that secondary sexual traits which are used throughout the year either as signals of dominance status or mate quality during sexual selection have the potential to show different relationships with immunocompetence. We found a negative correlation between badge size and an index of T-lymphocyte proliferation, after injection of a mitogen, among reproductive males in April, and a positive correlation among non-reproductive males in November. We also showed that the slopes of the two regressions were significantly different.

The negative correlation between cellular immune response and badge size in reproductive males was predicted by the immunocompetence handicap hypothesis. Since we captured birds before they started to lay eggs (as assessed by the lack of incubation patches in females captured at the same time and place), we can reject the possibility that interindividual differences in WWS were due to variable reproductive effort (i.e., parental care; Deerenberg et al. 1997).

Steroid hormones exhibit clear seasonal variation in birds (Nelson 1995). Testosterone levels increase sharply during the period when mating occurs, and decrease in the post-breeding period (Wingfield et al. 1987). Experimental studies where testosterone has been implanted in males have revealed that T-implanted birds have higher aggression, higher mating rates, and reduced parental care (Watson and Parr 1981; Wingfield 1984; Wingfield et al. 1987, 1990; Ketterson et al. 1992). Since male house sparrows with larger bibs also show high within- and extra-pair mating rates (Møller 1990), it is likely that they experience higher testosterone levels during the reproductive period. Moreover, males with large badges also have larger testes, where testosterone is produced. Corticosterone could also play a role in the observed negative correlation between bib size and cellular immune responsiveness, if corticosterone directly or indirectly regulates the expression of secondary sexual traits (Hillgarth and Wingfield 1997). In agreement with this view, recent work has shown that house sparrows experimentally implanted with testosterone molted with

larger bibs and also had increased corticosterone titers compared to controls, resulting in reduced humoral immune responsiveness (M.R. Evans, A.R. Goldsmith, S.R.A. Norris, unpublished data). However, it is important to note that, although hormones might have an immunosuppressive effect, responsible for the observed correlation, they only represent a possible mechanism underlying this relationship. The negative correlation between badge size and WWS, observed at the onset of the reproductive season, could be seen as an adaptive allocation of resources to mating behaviors, at the expense of immune function (Wedekind and Folstad 1994). Only large-badged males of high phenotypic/genotypic quality would, then, be able to afford the cost of an impaired immune response.

Behavioral studies have shown that house sparrow flocks have stable hierarchies where large-badged males consistently win contests against small-badged males. When the reproductive season is over, house sparrows form large flocks and most of the foraging activity occurs in groups. Dominant males are likely to have better access to food resources (Barnard and Sibly 1981; Møller 1987b). Higher cellular immune responsiveness of large-badged males is then expected, since previous work has shown that food intake might affect cellular immunity (Chandra and Newberne 1977; Gershwin et al. 1985; Lochmiller et al. 1993; Gonzalez et al. 1999). Our finding of a positive correlation between WWS and badge size, after controlling for body mass, suggests that some environmental variables which do not have obvious effects on growth may influence other physiological functions, such as the immune response. In agreement with this argument, a marginal deficiency in methionine that did not adversely affect growth decreased the lymphocyte response to PHA in young rats (Nauss et al. 1982). Similarly, Lochmiller et al. (1993) reported increased relative (mg/g body mass) masses of spleen and bursa of Fabricius in northern bobwhite chicks fed a protein-rich diet. In another study (Gonzalez et al. 1999) two food regimes (protein poor and protein rich) were offered to juvenile house sparrows; birds in the protein-rich group had higher cellular immune responsiveness, even though body mass was similar in the two groups. Jointly, these observations suggest that body mass should not be considered as a perfect measure of body condition.

In this study we only assessed one component of the immune system: the cellular response. A full-scale estimate of immunocompetence would require information on all components of immune function, such as the relative mass of lymphoid organs (spleen and thymus), in vivo measures of B- and T-cell activity, the in vivo response of B-cells independent of T-cells, and in vitro assay of nitrous oxide production by macrophages from spleen cells (e.g., National Research Council 1992). Obviously, these components are not necessarily positively correlated with each other and some might show consistent relationships with badge size across seasons. However, our study has shown that at least one com-

ponent of immune defense, the cell-mediated response, does show seasonal variation in relation to badge size. Another study has investigated the correlation between badge size and another correlate of immunity in the house sparrow. The bursa of Fabricius is an exclusively avian organ which produces B-lymphocytes responsible for immunoglobulin synthesis (i.e., humoral immune response), and which regresses before sexual maturity is attained. Møller et al. (1996) measured badge size and the volume of the bursa of Fabricius in male house sparrows and found a negative correlation between the two variables, after correcting for the effect of potential confounding variables.

Most work on the relationship between sexual advertisement and immunity has focused on reproductive individuals (e.g., Saino and Møller 1996; Skarstein and Folstad 1996; Saino et al. 1997). Recently, Zuk and Johnsen (1998) studied the relationship between immunity and comb size in red jungle fowl (*Gallus gallus*), before and during the reproductive season. As in this study, they found that one component of the immune response, the relative number of circulating lymphocytes in the blood, was positively correlated with comb size before the breeding season, but negatively correlated during the breeding season (Zuk and Johnsen 1998). Interestingly, these authors used the same immunological assay as this study to assess cell-mediated immunity. Contrary to our results, they found positive correlations between comb size and cell-mediated immunity, irrespective of the sampling period (Zuk and Johnsen 1998), indicating that it could be too simplistic to expect consistent relationships between all aspects of immune function and all aspects of sexual signaling.

Our findings raise the question of the costs and benefits of sexual signals in male house sparrows. Immunosuppression might not be an inevitable consequence of sexual advertisement, and large-badged males can actually show better cell-mediated immunity than small-badged males in winter, as shown in this study. On the other hand, large-badged males should pay some costs, if badge size reliably reflects male quality. Maintaining large badges might be stressful due to social interactions and sexual behaviors. Manipulation of badge size has provided evidence for both the view of social control of dominance status (Møller 1987b) and for survival costs of experimentally enlarged badges (Veiga 1995). We suggest that the currency of such maintenance costs may be the immune status of an individual, as shown by the negative correlation between cell-mediated immunity and badge size in spring.

In conclusion, our study shows that the relationship between immunocompetence and secondary sexual traits may not be constant throughout the year, especially when secondary sexual traits are used as both a mate choice signal and an intrasexual badge of status.

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