

Correspondences

Sexual signal exaggeration affects physiological state in male barn swallows

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A prevailing view in sexual selection theory is that costly physiological processes underlie the development, maintenance and expression of sexual signals, and that the costs of these signals enforce their honesty [1,2]. However, this unidirectional view of how physiology governs signal expression is narrow, because many of the putative physiological underpinnings of signals, such as health status, are themselves dynamic [3]. As such, we predicted that physiological parameters should be affected by sexual signal expression. We therefore manipulated a known sexual signal — plumage coloration — in male barn swallows (*Hirundo rustica erythrogaster*) and measured circulating androgen levels and body mass before and after the manipulation. We found that androgen concentrations increased in color-enhanced males, but decreased in control males, as expected due to typical seasonal androgen declines [4,5]. Color-enhanced males also lost body mass, whereas control males gained weight between successive captures one week apart. These results indicate the existence of feedbacks between an individual's morphological signals and physiology — a finding that is not currently explained by honest signaling theory.

Androgens, such as testosterone, are likely candidates for mediating bidirectional feedbacks between sexual signals and physiological condition, as they can play a role in promoting the development, expression and honest maintenance of ornamental traits in male vertebrates [2,5–8]. In

addition, they also can respond to an individual's social experiences [4]. To understand whether signal expression alters the physiological state of individuals, we targeted androgens as plausible physiological respondents to sexual signal exaggeration in male barn swallows.

To explicitly test the effect of signal expression on circulating sex-steroid levels, we conducted a two-year study in which we examined a male's plasma androgen concentrations both before and after the experimental enhancement of ventral feather coloration, a known sexual signal in North American populations of this species [9]. For comparison, we used a randomly selected group of control males the plumage color of which was not manipulated but which were otherwise treated identically as males assigned the experimental treatment. All males were captured in the wild using mist nets placed around areas of high activity at breeding sites and randomly assigned to one of the two treatments.

Following a well known seasonal decline in circulating concentrations of sex steroids, males captured later in the breeding season showed lower androgen concentrations than males caught only a week earlier (estimate = -0.03 ; $F_{1,4.62} = 34.96$; $P = 0.003$; $R^2 = 0.10$; $n = 130$). Before experimental manipulation, darker males had higher androgen concentrations (estimate = -0.24 ; $F_{1,93} = 11.32$; $P = 0.001$; $R^2 = 0.22$; $n = 97$; lower color scores indicate darker feather color), and heavier males had lower concentrations of androgens (estimate = -0.26 ; $F_{1,57} = 5.15$; $P = 0.03$; $R^2 = 0.14$; $n = 60$).

Prior to experimental manipulation, treatment groups did not differ significantly in plumage color ($F_{1,55.66} = 0.13$; $P = 0.71$; $n = 63$), androgen concentrations ($F_{1,59.18} = 0.66$; $P = 0.41$; $n = 63$), or body mass ($F_{1,55.47} = 0.14$; $P = 0.70$; $n = 63$). The color-enhancement treatment was successful in that males in the color-enhanced group had significantly darker color throughout the ventral region after the experimental manipulation (Unequal Variance t-test: $t = -10.53$; $P < 0.0001$; $df = 48.74$; $n = 52$).

After one week, males from the color-enhanced group showed increased concentrations of circulating androgens, whereas

males in the control group showed decreased androgen concentrations ($F_{1,27} = 6.12$; $P = 0.02$; $n = 30$; Figure 1A). Additionally, males in the color-enhanced treatment group lost body mass, whereas males in the control groups gained weight between the two sampling periods ($F_{1,24.29} = 13.03$, $P = 0.001$, $n = 30$; Figure 1B).

In this study, we found that the usual seasonal trajectory of androgen decline observed in male barn swallows was reversed by changing a male's visual appearance, an observation that counters the view of a one-way relationship between androgens and sexual signals. Males with experimentally enhanced color and, accordingly, increased androgen concentrations also lost body mass. That androgen concentrations and mass were coupled is not surprising, given

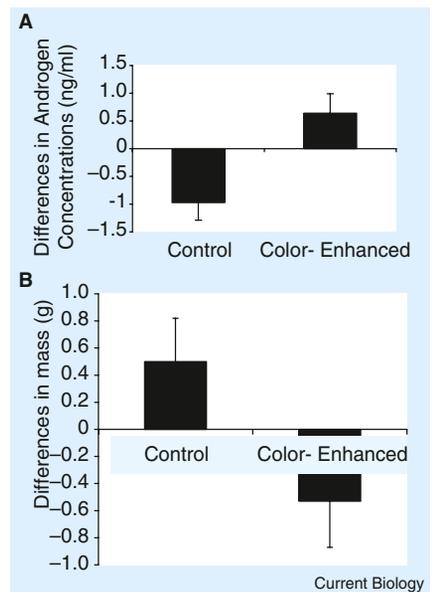


Figure 1. Color enhancement alters androgen levels and body mass of male barn swallows.

Least square mean (\pm s.e.m.) within-individual differences in androgen concentrations, in ng/ml, (A) and in body mass, in grams, (B) are portrayed as a function of plumage treatment. Least square means control for variation of random effects used in mixed linear models (site and year differences, in addition to date of sample collection). (A) Increases in circulating androgen concentrations of color-enhanced males opposes the typical seasonal decline of sex steroids observed in control males. (B) Male barn swallows lost mass after their plumage was experimentally darkened.

previous experimental evidence of a link between these two traits in birds [10] and our finding in pre-manipulated males that heavier individuals had lower concentrations of androgens. The implication of these results is that androgen concentrations change as a function of an individual's signal expression within a social and reproductive context. Furthermore, such a response might be costly, as darkened males lost mass at a time in the reproductive cycle where individuals typically gain weight after having completed their migration to breeding grounds. The hormonal feedback between signal and physiological traits is a likely mechanism for linking signals appropriately to the expression of sexual or aggressive behavior as both signals and the social environment change.

The existing unidirectional view of how physiology and signals are mechanistically related is not sufficient to explain the bidirectional relationship we uncovered between ventral coloration, androgen concentrations and body mass in male barn swallows. The interactions between the expression of signals, their production processes, and the dynamic qualities (e.g., aspects of health and condition) add important complexity to our understanding of sexual signals. For example, if an animal's androgens change due to social stimuli induced by its own signal, that individual will be more or less likely to perform androgen-associated behaviors, such as mating or aggression. Because physiological parameters in addition to the ones we studied here are temporally variable, we expect our results to apply generally to other animal signals. Signals that are flexible and dynamic themselves (i.e. courtship behavior, vocalizations) may even more strongly affect and respond to an individual's current physiological state. The aim in future studies of the signal-physiology nexus should be to determine the suite of social responses to these flexible signals, including traits that advertise resource defense and parental investment, and their effects on specific physiological processes, such as immune function and stress.

Supplemental data

Supplemental data including experimental procedures are available at <http://www.current-biology.com/cgi/content/full/18/11/R461/DC1>

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Crayfish females eavesdrop on fighting males before choosing the dominant mate

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Identifying the traits that influence mate choice is a major challenge in behavioral ecology and evolutionary biology. Male dominance often conditions mating decisions by females, but how the hierarchical status of potential mates is assessed remains poorly understood. In crustacean decapods, chemical signals convey information about male sexual responsiveness and quality. At least in the red swamp crayfish *Procambarus clarkii*, however, females appeared unable to recognize dominant mates using smell only. Here, we report the first evidence that a form of social eavesdropping may occur in an invertebrate species.

Since its first formulation in the 1990s [1], social eavesdropping has attracted increasing attention by researchers interested in animal behavior and communication networks. The ability of animals to extract information from signaling interactions between conspecifics [1] and the benefits gained from attending to the behavior of others — instead of gathering the same information on one's own — have stimulated a plethora of studies focused on fish [2], birds [1], and primates [3]. By witnessing interactions between two or more individuals (for example, male-male fights or male-female courtships), bystanders assess the relative or absolute quality of the interactants; such information can be later used in an adaptive fashion when the same individuals are encountered in a social context (for example, territorial aggression or mate choice). The costs of mate choice, for example, may be reduced in female guppies by copying the mating decision of other females [4].

Because of the apparent complexity of the neural machinery involved, social eavesdropping has been assumed until now to be a prerogative of vertebrates. As recently reported [5], the behavior