Research Focus

Dynamic feedback between phenotype and physiology in sexually selected traits

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Theory predicts that physiological costs of producing elaborate phenotypes assure the honesty of sexually selected traits. It is generally assumed that these physiological processes drive sexually selected displays. However, a recent study by Safran and colleagues demonstrates that the manipulation of plumage ornaments in barn swallows alters the temporal course of circulating androgens, thus rejecting the scenario of a static, unidirectional relationship between physiology and sexual displays. Instead, these results suggest that dynamic feedbacks between physiological, morphological and behavioural costs underlie the development and maintenance of sexually selected ornaments.

Physiology of sexually selected traits

Animals use elaborate displays in mate attraction and territorial defence. Honesty of these signals is often enforced by costly physiological processes that underlie the production and maintenance of sexually selected traits [1–3]. The proximate control of many such ornaments relies on hormones to regulate signal production [4]. Specifically, androgens, including testosterone, influence the expression of many ornamental traits in birds, particularly the melanin-based rusty, brown and black colours that commonly underlie avian plumage. Melanins are the most common avian pigment, and experimental androgen elevations can enhance melanin-based plumage signals used in mate attraction and social dominance [5]. These patterns support the theoretical framework that physiological traits unidirectionally drive sexually selected displays (Figure 1a) [6].

Morphology–hormone feedback in barn swallows

In a recent paper, Safran and colleagues [7] challenge the prevailing view that the relationship between hormones and morphological traits is static and unidirectional. The authors demonstrate that experimentally enhancing male plumage coloration in North American barn swallows *Hirundo rustica erythrogaster* (Figure 2) alters seasonal patterns of circulating androgens and body mass during the breeding season. Rusty ventral plumage in barn swallows is a melanin-based [8] sexually selected trait that influences female mate choice, reproductive timing and paternity allocation [9]. Darker males breed earlier in the season, have greater paternity and circulate more androgens than paler males [7,9]. One week after enhancing the ventral coloration of half of the males, experimental males had elevated androgens but decreased body mass, whereas control males showed the typical seasonal decline in androgens and increase in body mass.

The positive correlation between circulating androgens and coloration in premanipulation males [7] suggests that androgens are mechanistically linked to melanogenesis and pigmentation, or that there is an ongoing behavioural feedback on androgens related to ventral coloration as a social cue. Given that the colour manipulations in this study were done outside of the natural moulting period of barn swallows, it is likely that the increases in androgens were the result of behavioural interactions resulting from the manipulations. The real surprise of this study, however, is that a phenotypic enhancement led to such rapid changes in circulating sex steroids of males. These results demonstrate that the relationship between androgens and ornaments is not fixed (Figure 1a), but rather a dynamic process involving feedback between

Glossary

Androgen: steroid hormones most often associated with masculinisation. The most common androgen in vertebrates is testosterone.
Challenge Hypothesis: hypothesis proposed to explain the social modulation of androgens in males in a seasonal context. It describes how social interactions can lead to increased circulating androgens in animals, helps explain why androgens in males vary seasonally and predicts how male androgen levels relate to social systems.
Corticosterone: the primary glucocorticoid in most non-mammalian vertebrates. It is released from the adrenals in response to a variety of social and environmental stressors.
Glucocorticoid: steroid hormones produced in the adrenals in response to stimulation along the hypothalamic-pituitary-adrenal (HPA) axis. The most common glucocorticoids in vertebrates are corticosterone and cortisol. Glucocorticoids affect many aspects of vertebrate physiology and behaviour and predominantly regulate energy balance.
Hypothalamic-pituitary-adrenal (HPA) axis: describes the hormonal cascade resulting in glucocorticoid release. Corticotropin-releasing hormone (CFH) secreted from the hypothalamus stimulates the pituitary to secret adrenocorticotropic hormone (ACTH), which in turn stimulates glucocorticoid production in the adrenals.
Melanin: the most widespread group of pigments in animals that yield many of the black, brown and buff shades seen in plants, fungi and animals.
Melanogenesis: the formation of melanin in melanocyte cells.
Testosterone: an androgenic steroid primarily secreted from the gonads of vertebrates. It stimulates seasonal reproductive behaviours such as courtship, sexual behaviours, territorial aggression and song, and plays an important role in the production of sperm and a variety of secondary sexual characters.

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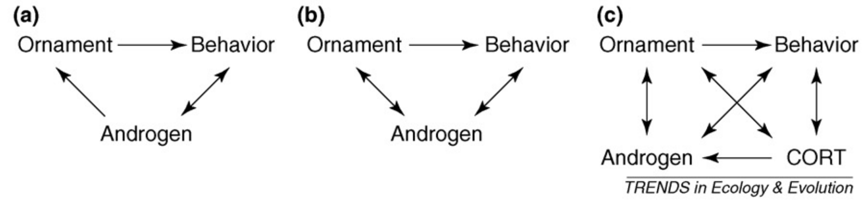

Figure 1. Relationships between melanin-based ornaments, reproductive behaviours and steroid hormones. **(a)** Historically, the relationship between androgens and ornaments has been seen as static and unidirectional, whereas the relationship between reproductive androgens and behavioural displays has been viewed as more dynamic. **(b)** The study by Safran and colleagues [7] demonstrates that the relationship between androgens and morphological traits might be as fluid as that between androgens and behavioural traits. **(c)** Future studies must examine simultaneously the relationships between other hormones, including glucocorticoid stress steroids (CORT), and behavioural and morphological sexually selected traits. Other steroids such as estrogens could also play an important role in trait development, expression and maintenance [5].

morphological signals and physiological traits, likely indirectly via social interactions (Figure 1b).

Androgen–morphology interactions: a complex and changing system

Androgens have long been known to seasonally modulate vertebrate reproductive behaviours. The Challenge Hypothesis formalised the relationship between circulating androgen concentrations in male vertebrates and seasonal patterns of intrasexual aggression [10]; in essence, it was the first model of dynamic feedback between androgens and sexually selected traits. It sought to not only explain seasonal androgen patterns and their relationship with paternal care and mating systems (i.e. hormonal regulation of behavioural traits) but also to predict how males would hormonally respond to intraspecific social challenges (i.e. behavioural feedback upon hormones) (Figure 3).

Despite the known bidirectional relationship between androgens and reproductive behaviours, it is nonetheless surprising that androgens have a similarly dynamic role with sexually selected morphological traits, including plumage coloration. The enhancement of plumage ornamentation in barn swallows reversed a seasonal decline in androgens (Figure 3), suggesting that differences in the timing of seasonal androgen declines among males could be related to temporal variation in the brightness of ventral coloration, rather than the other way around. Such a hypothesis predicts that darker males continue to show androgen-related reproductive behaviours longer into the breeding season, and thereby increase their fitness. Moreover, dynamic hormone–trait feedbacks could be an adaptive mechanism to help fine-tune the link between behaviour and ornament expression in complex social societies where phenotype and fitness vary greatly among males.

Figure 2. North American barn swallow *Hirundo rustica erythrogaster*. Photograph by Marie Reid.

Future directions

These novel results on hormone–morphology relationships in barn swallows suggest a more complicated view of the physiological causes and consequences of vertebrate sexually selected ornaments than is generally theorised [3–5]. To help elucidate these issues, future studies must examine (i) the behavioural and physiological mechanisms by which androgen–ornament feedbacks are maintained, and (ii) the role that other hormones, including glucocorticoid stress steroids, play in dynamic feedbacks of melanin-based signals. We briefly discuss these aspects below.

Androgens and the maintenance of honesty

Although behavioural observations were not conducted in the barn swallow study, it is possible that social cues, through the enforcement of honest badges of status by other males [11] or increased sexual interest by females [9], mediated the interaction of experimental changes in colour, androgens and body mass in barn swallows. Whereas androgen-based traits are typically considered costly because of the tradeoffs of high circulating steroid levels on other physiological functions [6], in some species melanin-based ornaments might be relatively cheap to produce but have high social maintenance costs [11]. Indeed, body mass rapidly decreased in enhanced compared to control males, suggesting that physiological costs enforced by behavioural interactions maintain the honesty of ventral coloration in barn swallows. Thus, ornaments might be more costly to express and maintain than was previously assumed because physiological costs are not just incurred during signal development, but also throughout the season or lifetime owing to social feedbacks.

Glucocorticoids, androgens and honest ornaments

Although androgens are most often studied in relation to honest signalling of avian plumage, glucocorticoids (corti-

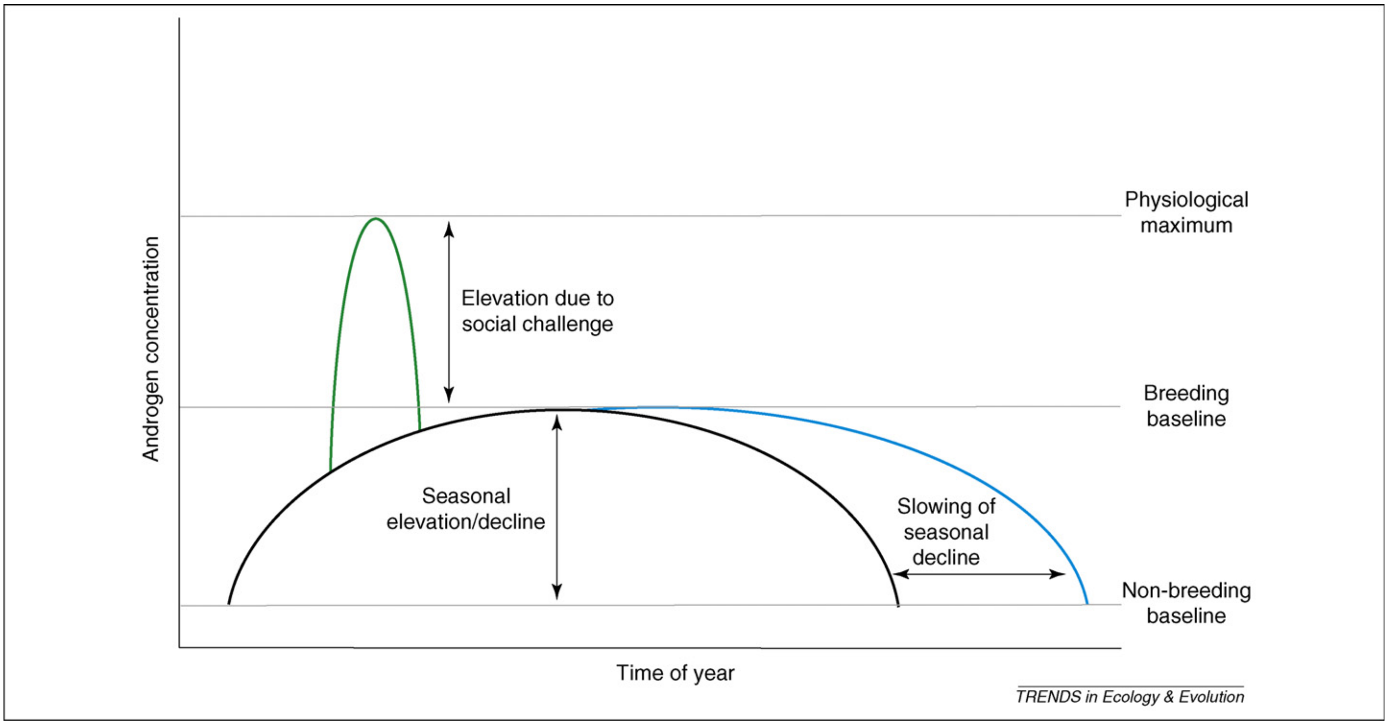

Figure 3. Seasonal and social modulation of androgens in male birds. In many male birds, androgens increase seasonally until the onset of breeding, at which time they often begin to decline steadily (black line). Social stimulation via behavioural challenges can lead to rapid, shorter-term increases in androgens within the breeding or non-breeding seasons (green line). The study by Safran and colleagues [7] suggests that enhancement of plumage ornamentation could lead to a rise, or at least a slowing in the seasonal decline, of androgens (blue line). Figure modified with permission from Goymann and colleagues [15].

costerone in birds) can also be important in regulating behavioural and morphological traits under sexual selection (Figure 1c). Glucocorticoids are related to vocal displays in a variety of vertebrates, and increased glucocorticoids can decrease melanogenesis in avian plumage [12]. Melanocortin receptors, critical for melanogenesis, play an equally important role in stress physiology by initiating the hormonal cascade along the hypothalamic-pituitary-adrenal axis [13]. Moreover, chronic stress and corticosterone elevation inhibit testosterone production in many birds [4]. Future work should examine androgens and glucocorticoids simultaneously to determine whether glucocorticoids exhibit similar dynamic feedbacks as androgens with sexually selected traits (Figure 1c).

Conclusion

Simple models of fixed pathways between hormones and traits clearly do not encompass the full range of complexity surrounding the causes and consequences of sexually selected signals. Dynamic feedbacks from hormones are not only important for influencing behavioural traits, but could also be important in driving the production and maintenance of morphological traits. Moreover, within-population variation in male quality might not only lead to variation in ornament production and maintenance that honestly advertises differences in male quality but the ornaments themselves might further influence seasonal patterns of androgens and local adaptations to honestly signal quality, leading to intra- and interpopulation differences in sexually selected displays and signals [9,14]. Thus, dynamic hormone–trait feedback might be an adaptive mechanism to help fine-tune the link between behaviour and ornament expression in complex social societies where phenotypes and fitnesses vary greatly among males. Further studies with additional hormones (glucocorticoids, estrogens) in avian species that use different mechanisms for plumage production (carotenoids, structural colours, iridescence) and in taxa that use other types of morphological signals (horns, antlers, eyestalks) will help determine whether dynamic feedbacks between endocrine physiology and morphological signals are as common in vertebrates as are the feedbacks between hormones and behavioural displays.

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Research Focus

Birds gone wild: same-sex parenting in albatross

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Same-sex behavior in animals fascinates scientists as well as laypeople, partly because of implications about sexual orientation in humans. After all, if animals engage in homosexuality, can it be dismissed as 'unnatural'? A recent paper by Young and colleagues documents long-term female pairs in >30% of Laysan albatross on the Hawaiian island of Oahu. The unrelated females bred successfully, challenging ideas about cooperative breeding, alternative reproductive strategies and perhaps even the evolution of sexual orientation.

Same-sex behavior in wild birds

Sexual behavior directed toward the same sex has been noted in a variety of animals, including dolphins, sheep, penguins and bonobos [1]. Many of these instances have occurred in captivity, although in at least some cases members of the opposite sex were available as potential mates. By contrast, exclusively homosexual behavior has not been as well documented in wild animal populations, raising the question of its evolutionary relevance. A recent study by Young and colleagues [2] suggests that same-sex behavior in wild albatross colonies could have powerful and long-term effects on population dynamics. Of the 125 nests of Laysan albatross, *Phoebastria immutabilis,* examined by Young and colleagues on the Hawaiian island of Oahu, 31% were attended by a pair of females. This is more than twice the proportion of female pairs ever noted in any other bird species [2]. Two eggs were observed in half of those nests, but only one of them was ever incubated (albatross clutch size is one). Male–female pairs had higher reproductive success than the female pairs, but this was a result of lower hatching success in the same-sex nests rather than reduced fledging success. The males fathering the chicks in female–female nests were paired to other females in the colony, but were not necessarily the nearest neighbor. Partnered females were pair bonded, engaging in such intimate behaviors as mutual preening and mate guarding (Figure 1). The female pairs were remarkably stable, with nearly half remaining together for the 4 years of the study; a female pair on the nearby island of Kauai has been together for 19 years. The population on Oahu has 59% females, probably as a result of female-biased recruitment to this relatively recently formed colony, and Young *et al.* suggest that the skewed sex ratio has driven the same-sex behavior, with a tendency toward social monogamy fostering its persistence.

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Cooperation and alternative reproductive strategies

The behavior of the albatross has elements of both cooperative breeding, where individuals other than the parents help with offspring, and alternative reproductive strategies, where some members of one sex, usually males, exhibit a different path toward achieving mating success than the 'standard' strategy. The differences between the albatross and more traditional cooperative breeding or alternative reproduction, however, are instructive, and suggest that flexibility in social organization and mating systems might need to be viewed more broadly than is currently the case.

In conventional cooperative breeding, helpers can be constrained in their ability to breed on their own, so staying on their natal territory is a viable alternative [3]. Once the decision not to breed is made, helpers can increase their inclusive fitness by helping relatives, or they can gain valuable experience rearing offspring. Similarly, for some of the female albatross, the female-biased sex ratio might have meant that finding a male mate was impossible, but that the females were able to avoid complete loss of reproductive success by joining forces with another female. Whether one or both of the females mate, and which egg is incubated when two are laid, are open questions. Young and colleagues suggest that one egg is shunted aside at random during incubation. Although all social animals show elements of competition, the females do not appear to be competing overtly, making their situation at least superficially more similar to cooperative breeding than, for example, the communal nests of groove-billed anis, neotropical birds in which females throw each others' eggs out of the nest depending on dominance status and the order in which they are laid [4].