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Essay

The stress of elaborate male traits: integrating glucocorticoids with androgen-based models of sexual selection

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Stress hormones are emerging as major factors regulating the expression of elaborate male traits. Surprisingly, however, the effects of glucocorticoids on such traits have not been formally integrated with androgen-based models of sexual selection. Here we point out that consideration of glucocorticoid-mediated effects on the phenotype provides new insight into long-standing hypotheses and controversies associated with such models. In particular, androgen-based 'handicap' models of sexual selection characteristically hinge on graded effects of androgens on male traits, but few studies have found support for such a relationship, suggesting that androgens may not be a primary target of selection. We propose, however, that in many instances, androgens may not appear to have a graded effect on the phenotype because elevated glucocorticoids mask the effects of androgens. Glucocorticoids may be inextricably linked to elaborate traits because the energetic demands associated with such traits promote glucocorticoid production. We thus propose that glucocorticoid-mediated effects on male traits warrant re-evaluation of androgen-based models of sexual selection. In particular, we argue that androgen-based handicap models cannot be dismissed based on the lack of evidence for a graded relationship between androgen level and the extent or magnitude of the trait. Our review of the literature indicates that most studies have examined either the effects of androgens or the effects of glucocorticoids, but not both. A more integrated approach involving the effects of both steroids is necessary to fully understand the role of androgens and the endocrine targets of selection associated with the expression of elaborate male traits.

Hormones often give rise to variable phenotypes that are screened by selection (Adkins-Regan, 2005; Ketterson, Nolan, Cawthorn, Parker, & Ziegenfus, 1996; Ketterson et al., 2001; Moore, Hews, & Knapp, 1998; West-Eberhard, 2003). Androgens, for example, often have a dramatic effect on male secondary sex characteristics and reproductive behaviour and have thus become integral components of current models linking proximate physiological mechanisms and the evolution of elaborate male courtship displays (Adkins-Regan, 2005; Emerson, 2001; Folstad & Karter, 1992; Hau, 2007; John-Alder, Cox, Haenel, & Smith, 2009; Ketterson, Atwell, & McGlothlin, 2009; McGlothlin et al., 2008; Moore & Hopkins, 2009). Despite the historical emphasis on androgens in behavioural endocrinology (Berthold, 1849; Nelson, 2011) and continued interest in androgen-dependent sexually selected male traits, we still have a relatively poor understanding of the nature of the relationship between androgen level and the extent or magnitude of trait expression (Adkins-Regan, 2005; Ball & Balthazart, 2008; Fusani, 2008; Hews & Moore, 1997; Rubenstein & Hauber, 2008). An understanding of this relationship, however, is a central consideration for many androgen-based models of sexual selection. A graded or dose-dependent relationship, for example, emerges as a critical factor in maintaining the honesty of androgen-mediated traits, yet in most cases androgens appear to affect trait expression in a threshold or nonlinear manner (Adkins-Regan, 2005; Hews & Moore, 1997). The preponderance of threshold androgenic effects has stimulated considerable debate and even the dismissal of androgen-based models of sexual selection. Below, we describe an alternative explanation for this hormone–trait relationship that incorporates recent findings associated with glucocorticoid-mediated effects on the phenotype. The traits of interest here are male reproductive behaviours and/or traits associated with courtship. Specifically, we describe how glucocorticoids could mask graded androgenic effects on the phenotype and give rise to a nonlinear association between androgen level and the extent or magnitude of sexually selected male traits. This perspective provides new avenues for continued research aimed at understanding the evolution of the endocrine system as a determinant of male phenotype.

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ANDROGEN LEVEL AS A MEDIATOR OF HONEST SIGNALS

The immunocompetence handicap hypothesis (ICHH) (Folstad & Karter, 1992) has been particularly pivotal in bringing androgens to the forefront of models of sexual selection. The ICHH describes a trade-off associated with androgen level wherein elevations in testosterone level promote the development and expression of elaborate male traits but simultaneously compromise the immune system. Androgen-mediated courtship displays are thus expected to provide females with 'honest signals' when choosing mates because only males that are resistant to pathogens (i.e. males that possess 'good genes') would be able to afford the immunosuppressive costs associated with elevated androgen level (see Greives, McGlothlin, Jawor, Demas, & Ketterson, 2006; Mills et al., 2009; Roberts, Buchanan, & Evans, 2004). Androgen-mediated trade-offs, however, are not necessarily limited to potential immunosuppressive effects; the costs could be associated with other androgen-mediated effects as well (e.g. decreased parental care and/or survivorship; Ketterson et al., 2001; Ketterson et al., 2009; Marler & Moore, 1998; McGlothlin et al., 2010; Reed et al., 2006).

A central criticism associated with the ICHH involves the presumed graded dose-dependent relationship between androgen level and the magnitude and/or intensity of elaborate male traits (Adkins-Regan, 2005; Evans, Goldsmith, & Norris, 2000; Hews & Moore, 1997; Hillgarth & Wingfield, 1997; Poulin & Vickery, 1994; Roberts et al., 2004). Specifically, individuals must show a graded dose-dependent relationship between androgen level and the magnitude or intensity of the trait (Fig. 1a) for androgens to maintain the honesty of the signal (Adkins-Regan, 2005; Hews & Moore, 1997). If the extent or magnitude of the trait does not reliably track intraindividual variation in androgen level, as with a threshold scenario (Fig. 1b), then males could down-regulate circulating androgens to the threshold level to circumvent the potential negative fitness consequences associated with higher androgen levels (e.g. immunosuppression) without negatively affecting the quality of the trait (Fig. 1b). In such circumstances, androgen level does not reliably maintain the honesty of the signal (see also Roberts et al., 2004).

Studies examining the relationship between androgen level and the expression of secondary sexual traits are often inadequate to address whether androgens have graded or threshold effects on traits (Adkins-Regan, 2005; Ball & Balthazart, 2008; Hews & Moore, 1997; Roberts et al., 2004). Relatively few studies, for instance, demonstrate that incremental changes in androgen level, above the level required for development or expression of the trait, result in concordant incremental changes in the magnitude or extent of the trait (reviewed by Adkins-Regan, 2005; Hews & Moore, 1997). There is, however, no reason that hormones cannot affect target tissues in a graded fashion (Ball & Balthazart, 2008) and, indeed, there are many cases in which hormones do appear to alter behaviour or trait expression in such a manner (Adkins-Regan, 2005; Balthazart & Ball, 2006; Emlen, Warren, Johns, Dworkin, & Lavine, 2012; Enstrom, Ketterson, & Nolan, 1997; Hill, Enstrom, Ketterson, Nolan, & Ziegenfus, 1999; Ketterson, Nolan, Wolf, & Ziegenfus, 1992; Ketterson et al., 2001; Ketterson & Nolan, 1994; Lewis & Rose 2003; Moore & Miller, 1984; Roberts et al., 2004; Zuk, Johnsen, & Maclarty, 1995). Hence, the apparent prevalence of threshold androgenic effects in the literature is puzzling. Below, we describe how androgen-dependent effects on male phenotype are likely to increase circulating glucocorticoid levels. We then provide an overview of the evidence suggesting that glucocorticoids obscure graded relationships between androgens and sexually selected male traits.

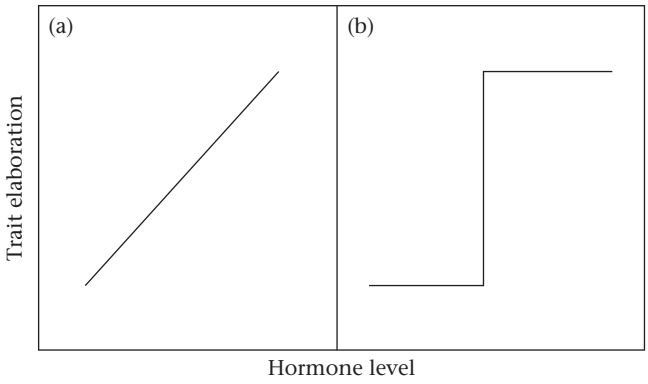

Figure 1. (a) Graded or dose-dependent effects versus (b) threshold effects of hormones on trait elaboration (modified from Hews & Moore, 1997).

GLUCOCORTICOID EFFECTS ON SEXUALLY SELECTED MALE TRAITS

Evidence that Glucocorticoids Promote the Expression of Sexually Selected Male Traits

Sexually selected male traits are often energetically taxing (Andersson, 1994) and glucocorticoids play a prominent role in energy balance and liberating stored energy (Laugero, 2001; McEwen & Wingfield, 2003; Sapolsky, 1992; Sapolsky, Romero, & Munck, 2000; Wingfield & Sapolsky, 2003). Thus, a number of researchers have linked the well-known metabolic effects of glucocorticoids to sexually selected male traits (Bonier, Martin, Moore, & Wingfield, 2009; Bonier, Moore, Martin, & Robertson, 2009; Buchanan, 2000; Eikenaar, Husak, Escallón, & Moore, 2012; Emerson, 2001; Hau, Ricklefs, Wikelski, Lee, & Brawn, 2010; Husak & Moore, 2008; Leary, 2009; Leary, Garcia, Knapp, & Hawkins, 2008; Moore & Jessop, 2003; Romero, 2002; Rubenstein & Hauber, 2008; Wada et al., 2008). The general concept is that moderate elevations in circulating glucocorticoids may be required to meet the metabolic demands associated with an increase in the magnitude or intensity of such traits (e.g. concepts of the 'energy mobilization hypothesis'; Romero, 2002).

Seasonal patterns of glucocorticoid production (e.g. high glucocorticoid levels during the reproductive period) are consistent with this hypothesis (Romero, 2002). Moreover, interspecies differences in baseline glucocorticoid levels have recently been linked to the intensity, and thus metabolic demands, of reproduction. Species where individuals invest more in reproduction, although not necessarily related to the extent or magnitude of elaborate male traits, tend to have higher baseline glucocorticoid levels (Hau et al., 2010).

Considerable correlative evidence suggests that moderate elevations in circulating levels of glucocorticoids are required to channel energy to support costly courtship displays (Buchanan, 2000; Emerson, 2001; Hau et al., 2010; McEwen & Wingfield, 2003; Moore & Jessop, 2003; Romero, 2002). Moreover, the administration of small amounts of glucocorticoids can increase the investment in reproductive behaviours (e.g. parental care in birds), indicating that increased glucocorticoid levels are not merely a consequence of increased reproductive investment but can also promote reproductive behaviour (Ouyang, Muturi, Quetting, & Hau, 2013).

Evidence that Glucocorticoids Negatively Affect the Expression of Sexually Selected Male Traits

While moderate elevations in circulating glucocorticoids potentially promote the elaboration of courtship displays by