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# Do androgens link morphology and behaviour to produce phenotype-specific behavioural strategies?

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Morphological and behavioural traits often covary with each other, and the links between them may arise from shared physiological mechanisms. In particular, androgens such as testosterone have emerged as prime candidates for linking behaviour and morphology due to the environmental sensitivity and pleiotropic effects of these hormones. In this study we investigated the hypothesis that androgens simultaneously relate to morphological and behavioural variation, thereby producing the integrated reproductive phenotypes of male red-backed fairy-wrens, *Malurus melanocephalus*. Males of this species can adopt one of three discrete breeding phenotypes: breeding in red/black plumage, breeding in brown plumage, or remaining as nonbreeding brown natal auxiliaries. Although the expression of morphological traits in this species is regulated by androgens and phenotypes differ in baseline androgen levels (red/black breeder > brown breeder > auxiliary), injection with GnRH failed to expose phenotype-specific constraints on androgen production. Observations of territoriality, nestling feeding and extra-territorial forays revealed phenotype-specific patterns of mating and parental effort, yet these were largely related to age and were not correlated with baseline or GnRH-induced androgen levels, or the androgen change between these points. While these findings support the idea that morphological and behavioural traits are linked via phenotypic correlations, they do not support the hypothesis that behavioural differences arise from variation in circulating androgens or the capacity to produce them.
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Individuals of most species show variation across morphological and behavioural traits, with selection on the collective phenotype often linking suites of related traits (Lande & Arnold, 1983; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004) and even producing morph-specific behavioural strategies (Dammhahn, 2012; Nicolaus et al., 2012; Wolf, van Doorn, Leimar, & Weissing, 2007). Because inherent genetic, energetic and time constraints can limit phenotypic expression, however, suites of traits often fall along life-history continua determined by trade-offs between mating versus parental investment (Magrath & Komdeur, 2003) and current versus future reproduction (Reznick, 1992; Santos & Nakagawa, 2012; Stearns, 1992). Sexual signals represent a unique case of phenotypic variation in which exaggerated morphological and/or behavioural traits expressed by a potential mate convey information about the direct (e.g. resources, parental care) or indirect (genetic) benefits of mating with the sender (Andersson, 1994). Males often advertise their reproductive phenotype (e.g. social status, nutritional state, investment in sexual versus parental behaviour) with morphological and behavioural signals such as bright coloration and elaborate mating displays. The evolution and maintenance of such signalling systems requires that those signals honestly indicate mate quality (e.g. Hill, 1990; Jennions, Møller, & Petrie, 2001; Zahavi, 1975), and morphological and behavioural signals are hypothesized to be honestly linked and constrained via regulation by shared underlying mechanisms that result from physiological trade-offs and antagonistic pleiotropy (Cox, Stenquist, Henningsen, & Calsbeek, 2009; Hau, 2007; Lande, 1980).

Androgens such as testosterone have gained particular attention as regulators of honest signal elaboration because they transduce environmental information and their pleiotropic actions link suites of traits (Ketterson & Nolan, 1999; McGlothlin & Ketterson, 2008), plus they can carry physiological costs (e.g. immunosuppression; Folstad & Karter, 1992; Saino & Møller, 1994). Specifically, androgens are thought to promote the exaggeration of morphological signals (e.g. Gonzalez, Sorci, Smith, & de Lope, 2001; Zuk, Johnsen, & Maclarty, 1995) while shifting behaviour to increase mating effort at the expense of parental investment (reviewed in Ketterson &

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Nolan, 1999). While our understanding of these patterns has benefited greatly from studies of captive populations and hormone manipulations (e.g. Ketterson & Nolan, 1999; Lynn, Prince, Schook, & Moore, 2009; Roberts, Ras, & Peters, 2009; Van Roo, 2004), a more complete picture also requires that individual variation in androgen levels be examined in unmanipulated wild animals (Kempenaers, Peters, & Foerster, 2008; Williams, 2008); such studies often detect no relationship between androgens and phenotype, or even report patterns opposite these predictions (Adkins-Regan, 2005; Lynn, 2008).

The high variability of baseline androgen concentrations across short timescales has created hesitation regarding their usefulness in predicting individual behaviour (Adkins-Regan, 2005; Ball & Balthazart, 2008). McGlothlin et al. (2008; McGlothlin, Jawor, & Ketterson, 2007) suggested that transient increases in testosterone should be more relevant to trade-offs between mating and parental investment because these short-term ‘spikes’ are generated by social exchanges inherent to territorial interactions or courtship (e.g. M. C. Moore, 1983; Oliveira, 2004; Pinxten, de Ridder, & Eens, 2003; Wingfield, Hegner, Dufty, & Ball, 1990) and could allow males to minimize the costs of high testosterone without sacrificing expression of testosterone-mediated behaviour (Wingfield, Lynn, & Soma, 2001). Their research demonstrated that variation in responsiveness to a given dose of gonadotropin-releasing-hormone (GnRH), which regulates gonadal androgen production, predicts the sexual phenotype of male dark-eyed juncos, *Junco hyemalis*; birds with higher GnRH-induced testosterone concentrations were more territorial (McGlothlin et al., 2007), and birds that increased testosterone more in response to GnRH (compared to baseline) exhibited less parental care (McGlothlin et al., 2007) and more sexually selected white coloration of tail feathers (McGlothlin et al., 2008). Similarly, alternative behavioural/morphological phenotypes of male white-throated sparrows, *Zonotrichia albicollis*, also differed in their testosterone response to GnRH challenge (Spinney, Bentley, & Hau, 2006), further suggesting that activity of the hypothalamic–pituitary–gonadal (HPG) axis might integrate morphological and behavioural expression.

Here we investigate whether activity of the HPG axis relates to individual and phenotype-specific differences in morphology and behaviour through action on both phenotype components in a wild songbird, the red-backed fairy-wren, *Malurus melanocephalus*. This Australian species is particularly well suited for studies of the endocrine basis of sexual signal expression and behaviour, as males express three discrete breeding phenotypes that differ in morphology, behaviour and circulating androgen levels (Karubian, 2002; Varian-Ramos, Lindsay, Karubian, & Webster, 2012; Webster, Varian, & Karubian, 2008). During the first year of reproduction males can breed in sexually preferred red/black nuptial plumage and display frequent extraterritorial forays and low nestling feeding rates (‘red/black breeders’), breed in brown female-like plumage with infrequent extraterritorial forays and high nestling feeding rates (‘brown breeders’), or remain on their natal territory as a brown helper with unknown foray frequency and intermediate nestling feeding rates (‘auxiliaries’). Nearly all males are red/black breeders in subsequent breeding seasons, meaning this species shows phenotypic variation within an age class (1-year-old) and age variation within a phenotypic class (red/black breeders); age differences could therefore underlie some phenotypic differences. Baseline androgen concentrations during prenuptial moult and all breeding stages vary across phenotypes with high concentrations in red/black breeders, intermediate concentrations in brown breeders and low concentrations in auxiliaries (Lindsay, Webster, Varian, & Schwabl, 2009). When males shift from an auxiliary role to a breeding role their androgen concentrations increase, accompanied by a darkening of the bill and a capacity to produce red/black plumage (Karubian, 2008; Karubian, Lindsay, Schwabl, & Webster, 2011). Furthermore, testosterone implants prior to and during the prenuptial moult stimulated production of red/black plumage and darkening of the bill (Lindsay, Webster, & Schwabl, 2011). In support of the idea that sexual signal expression should honestly indicate mate quality, males in better condition produced more red/black plumage, although this pattern surprisingly did not appear to arise from condition-dependent androgen regulation (Barron, Webster, & Schwabl, 2013).

In this study we tested the hypotheses that circulating androgen levels, and/or the capacity for androgen production, correlate with integrated male breeding phenotypes in this species. We first aimed to determine whether foray behaviour, nestling feeding and territoriality covary across male phenotypes (Karubian, 2002), as would be expected if male behaviour is constrained by a trade-off between mating and parental investment. For this we predicted that male mating and parental behaviour would vary by phenotype, with red/black males investing more heavily in mating (territoriality and extraterritorial forays) and less in parental care (nestling feeding). Second, we sought to establish whether phenotypes differ in their physiological capacity to produce androgens, which could explain why brown breeders and auxiliary males maintain lower circulating concentrations than red/black breeders. We predicted that males with red/black plumage and/or a breeding role would have a greater capacity to increase androgens (as indicated by their response to a GnRH challenge). Finally, we investigated whether variation in androgen secretion is correlated with behavioural variation and could therefore provide a mechanistic link between morphology and behaviour to produce a correlated phenotype, predicting that males with higher baseline or GnRH-induced androgens would invest more in mating behaviour at the expense of parental care.

## METHODS

### Study Species and Basic Field Methods

This study was conducted in a population of colour-banded red-backed fairy-wrens near Herberton, Queensland, Australia (145°25′E, 17°23′S). Males of this species are phenotypically plastic in their first year, with discrete variation in breeding role (breeder versus auxiliary) and plumage colour (red/black versus brown), although almost all males become red/black breeders in following breeding seasons. These phenotypic differences also extend to other morphological and behavioural traits, as red/black males have shorter tails (Karubian, 2002) and darker bills (Lindsay et al., 2009) and invest in extrapair mating at the expense of parental care by foraging off their territory more frequently and feeding nestlings less than brown breeders (Karubian, 2002). The elevated mating investment of red/black males is mirrored by a female preference for red/black plumage (Karubian, 2002), resulting in higher reproductive success for red/black males through greater production of extrapair young (Webster et al., 2008). While we know that red/black males are more aggressive towards red/black intruders than they are towards brown intruders (Karubian, Sillett, & Webster, 2008), we lack an understanding of whether phenotypes differ in their territorial response to intruders.

We target-trapped birds during the breeding season between 9 October and 6 December, 2011 using mist nets by slowly walking towards the birds to push them towards the nets and/or briefly (<2 min) playing conspecific vocalizations. We collected basic morphological measurements (e.g. mass, tarsus) and determined age of unbanded birds (second year versus after-second year) using

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