Hormones and Behavior 93 (2017) 118–127

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Endocrine differences among colour morphs in a lizard with alternative behavioural strategies

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ARTICLE INFO

Article history:
Received 14 August 2016
Revised 18 March 2017
Accepted 2 May 2017
Available online xxxx

Keywords:
Aggression
Androgen
Bite force
Colour polymorphism
Ctenophorus decresii
Dominance
Corticosterone
Phenotypic organisation
Tawny dragon lizard

ABSTRACT

Alternative behavioural strategies of colour morphs are expected to associate with endocrine differences and to correspond to differences in physical performance (e.g. movement speed, bite force in lizards); yet the nature of correlated physiological and performance traits in colour polymorphic species varies widely. Colour morphs of male tawny dragon lizards *Ctenophorus decresii* have previously been found to differ in aggressive and anti-predator behaviours. We tested whether known behavioural differences correspond to differences in circulating baseline and post-capture stress levels of androgen and corticosterone, as well as bite force (an indicator of aggressive performance) and field body temperature. Immediately after capture, the aggressive orange morph had higher circulating androgen than the grey morph or the yellow morph. Furthermore, the orange morph maintained high androgen following acute stress (30 min of capture); whereas androgen increased in the grey and yellow morphs. This may reflect the previously defined behavioural differences among morphs as the aggressive response of the yellow morph is conditional on the colour of the competitor and the grey morph shows consistently low aggression. In contrast, all morphs showed an increase in corticosterone concentration after capture stress and morphs did not differ in levels of corticosterone stress magnitude (CSM). Morphs did not differ in size- and temperature-corrected bite force but did in body temperature at capture. Differences in circulating androgen and body temperature are consistent with morph-specific behavioural strategies in *C. decresii* but our results indicate a complex relationship between hormones, behaviour, temperature and bite force within and between colour morphs.

The actions and responses of steroid hormones, particularly androgens and glucocorticoids during early development and in breeding adults, appear instrumental in mediating alternative behavioural strategies and their associated life history trade-offs in many colour polymorphic species (e.g. Hayssen et al., 2002; Knapp and Moore, 1996; Pryke et al., 2007; Sinervo et al., 2000a). Organisational effects of hormones during development are thought key to "fixing" discrete phenotypic differences among colour morphs (Hews et al., 1994; Hews and Moore, 1996). However, activational roles of androgens during reproduction are known to further reinforce or potentially modulate behavioural phenotypes (Hau, 2007; Oliveira, 2004) and skeletal muscular hypertrophy (Herbst and Bhasin, 2004) with the dominant morph often showing higher levels of testosterone (Horton et al., 2014b; Küpper et al., 2016; Sinervo et al., 2000a; Swett and Breuner, 2008), larger body size (Barlow, 1976), and greater muscle volume leading to increased aggressive performance (e.g. bite force in lizards; Huyghe et al., 2009a). By contrast, in male white-throated sparrows, behavioural differences between genetic colour morphs can persist in the absence of differences in androgen (Maney et al., 2009). In this species, expression of a hormone receptor better predicted aggression than androgen levels (Horton et al., 2014a).

Initial and stress-induced levels of glucocorticoids can also differ between colour morphs with alternative strategies (Horton and Holberton, 2009; Huyghe et al., 2009b). Furthermore, glucocorticoids can often, but not always, suppress androgen levels in many vertebrates, most often through inhibition of the hypothalamic-pituitary-gonadal (HPG) axis (Greenberg and Wingfield, 1987; Rivier and Rivest, 1991). Indeed, in many colour polymorphic species, morphs may have different relationships between glucocorticoids and levels of androgen in response to stress (Knapp et al., 2003; Knapp and Moore, 1997). For example, the red and black head colour morphs of the Gouldian Finch, *Erythrura gouldiae*, differ in their hormonal response to stress in the social environment. With increased relative density of the dominant, aggressive red morph in a confined captive space, the red morph shows a simultaneous increase in the concentration of testosterone and corticosterone while the black morph shows reduced testosterone levels and unaffected corticosterone levels in response to the greater frequency of red competitors. Therefore, although red-headed males have a

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http://dx.doi.org/10.1016/j.yhbeh.2017.05.001
0018-506X/

dominance advantage over black-headed males, they also show high physiological sensitivity which has potential to reduce lifespan (Pryke et al., 2007) through the costs of elevated testosterone and corticosterone (Korte et al., 2005; Wingfield et al., 2001). As this example highlights, examination of the response of corticosterone and androgens in response to stress may reveal differing life-history trade-offs (between survival and reproductive output), associated with the discrete phenotypic differences of morphs.

In this study, we investigate the endocrinology of male colour morphs of the tawny dragon lizard *Ctenophorus decresii*, to test whether previously established behavioural differences between colour morphs correspond to predicted differences in initial and stress-induced levels of plasma androgen and corticosterone concentrations, as well as bite force (an indicator of aggressive performance). *C. decresii* is a small, agamid species in which males exhibit four discrete colour morphs which can be reliably classified into orange, yellow, grey or orange-yellow (distinct orange centre surrounded by yellow) throat colouration (Teasdale et al., 2013; Fig. 1). Previous field studies have shown that colour morphs do not differ in morphology but do differ in their behavioural response to simulated conspecific intruders and predators (Teasdale et al., 2013; Yewers et al., 2016). The orange morph shows consistent high aggression to conspecifics and the grey morph shows low aggression, whereas the aggression of the yellow and orange-yellow morph is dependent on the colour of its competitor. The grey morph is also less bold towards a simulated predator than the other three morphs, which all have similar boldness. The high aggression of the orange morph implies a dominant strategy while the behaviour of the grey morph suggests a cautious strategy (Yewers et al., 2016; Fig. 1). Although the orange-yellow morph is phenotypically distinct, it remains unclear whether this morph employs a strategy similar to the pure orange or pure yellow morph or employs a unique strategy. More generally, it is important to qualify whether and how human-defined colour morph categories correspond to behavioural strategies and correlated traits, yet this is rarely done. In this study, we compared androgen, corticosterone and bite force between colour morphs and compared statistical support for models with four or three morph categories (orange-yellow grouped with either the orange or yellow morph).

We predicted that relative to other morphs, the aggressive and likely dominant orange morph should maintain higher levels of plasma androgen throughout reproduction, and potentially even during exposure to stressors. In lizards, including the closely related polymorphic species *Ctenophorus pictus*, androgen is likely to mediate aggression and therefore dominance (Olsson et al., 2007). Furthermore, in other polymorphic lizard species, males of aggressive territorial morphs appear less sensitive than less aggressive non-territorial morphs to the suppressive effects of stressors on plasma testosterone levels (Knapp and Moore, 1996; Knapp and Moore, 1997). Here, relatively modest stress-induced levels of corticosterone are thought to facilitate aggression, via direct actions on the central nervous system, or aid metabolic recovery from, or preparation for, aggressive encounters (Knapp and Moore, 1995; Moore and Jessop, 2003; van Duyse et al., 2004). We also predicted that the orange morph would have a greater aggressive performance measured as bite force. Higher levels of androgen can increase muscle volume thereby leading to increased strength, which often indicates fighting ability in lizards (Herbst and Bhasin, 2004; Lailvaux et al., 2004; Lappin and Husak, 2005; Tokarz, 1985). By contrast, we expected the cautious behavioural strategy of the grey morph to be reflected in lower initial androgen, and a greater decrease in androgen following capture stress but lower initial and higher capture stress-induced levels of circulating corticosterone due to lower metabolic demands involved with territory defence, as well as lower bite force.

1. Methods

1.1. Study species

The tawny dragon lizard, *C. decresii*, is a small, sexually dimorphic agamid lizard found on rocky outcrops of Kangaroo Island, Mt. Lofty Ranges and southern Flinders Ranges of South Australia (Houston, 1974). Males exhibit striking throat colour variation both within and between populations (Houston, 1998). In populations in the Flinders Ranges, males occur in four distinct throat colour morphs: orange, yellow, grey and orange-yellow, which can be objectively classified, independently of the human visual system (Teasdale et al., 2013; Fig. 1). Orange males have a variably sized orange patch on a grey/cream reticulated background, yellow males have a variably sized yellow patch on a grey/cream reticulated background, orange-yellow males have a

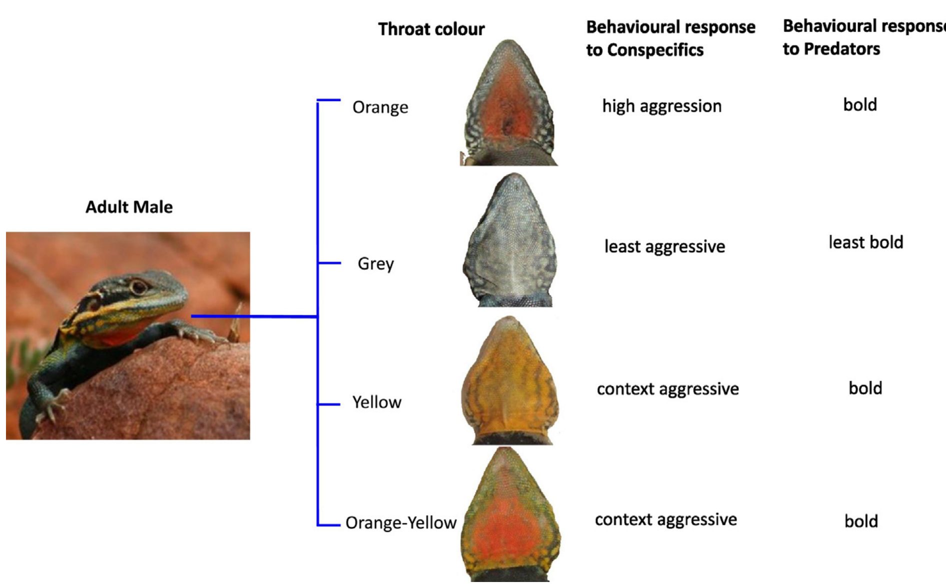

Fig. 1. Examples of *Ctenophorus decresii* throat colour morphs. From top: orange, grey, yellow and orange-yellow. Morphs have alternative behavioural strategies (Yewers et al., 2016). The orange morph is consistently aggressive to all competitors and the grey morph shows low aggression; whereas the aggression of the yellow and orange-yellow morph is dependent on the colour of its competitor, with both showing the highest aggression to like-morphs. The grey morph is also less bold towards a simulated predator than all other morphs which all have similar boldness. The high aggression of the orange morph implies a dominant strategy while the behaviour of the grey morph suggests a cautious strategy. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)