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Does adrenal responsiveness vary with sex and reproductive status in *Egernia whitii*, a viviparous skink?

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Abstract

In mammals, oestrogens generally stimulate adrenal function whilst androgens are inhibitory, and gestating females down-regulate their acute response to stressors in order to protect current reproductive investment. This study aimed to determine if adrenocortical function is similarly modulated by sex and reproductive status in the viviparous lizard, *Egernia whitii*. We compared the adrenocortical response to acute capture stress in female *E. whitii* during active (post-ovulatory and gestating) and quiescent (post-partum) phases of their reproductive cycle. We also compared the responses of reproductively quiescent males and females to acute stress and ACTH challenge to determine if there are sex-related differences in HPA axis activity when the influence of reproductive hormones is minimal. The females' responses to acute capture stress varied significantly with reproductive stage, and quiescent females displayed the strongest immediate response, with a rapid and sustained increase in plasma corticosterone (CORT) concentrations. Post-ovulatory females showed the most conservative adrenocortical response and while gestating females showed a large immediate response, this was not as prolonged as in quiescent females. Reproductively quiescent males and females exhibited similar responses to acute stress, and also responded similarly to ACTH injection, with plasma CORT reaching maximal concentrations of 52.1 and 59.4 ng/mL, respectively. Reproductively quiescent females treated with oestrogen exhibited greater responsiveness to ACTH than control females, although basal plasma CORT concentrations were unaltered: these results suggest that the attenuation of the acute stress response observed in reproductively active females of *E. whitii* may be regulated upstream of ACTH secretion. Our results demonstrate that the activity of the HPA axis is modulated by reproductive status in this viviparous reptile, and that gestating females are able to buffer their embryos from the potentially adverse effects of elevated plasma corticosteroids.

Keywords: ACTH; Capture; Corticosterone; Oestrogen; Reptile; Stress; Viviparity

1. Introduction

In vertebrates, the hypothalamo–pituitary–adrenal (HPA) axis is central to promoting survival by allowing the animal to respond behaviourally and physiologically to environmental stressors. Such responses may, however, include suppression of reproductive activity via inhibition of the hypothalamo–pituitary–gonadal (HPG) axis: current survival is then traded off against future reproductive success (Klose et al., 2006; Wingfield, 2003). Modulation of adrenocortical activity during particular stages of life history may therefore be an important factor in determining an animal's overall fitness (Moore and Jessop, 2003). For example, in arctic (Astheimer et al., 1995; Wingfield et al., 1995) and in desert (Wingfield et al., 1992) birds with limited time for breeding, the stress response is suppressed during the reproductive phase and breeding appears to be prioritised, albeit at the risk of increased mortality due to decreased responses to immediate stressors.

The anti-gonadal effects of stress in reptiles have been well documented (e.g. Lance and Elsey, 1986; Greenberg and Wingfield, 1987; Mahmoud et al., 1989; Elsey et al., 1991; Moore et al., 1991), but reciprocal influences of

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reproductive status on the function of the HPA axis have received much less attention. Marine turtles have been the most comprehensively studied group, with the consistent finding that females exhibit a depressed adrenocortical response to stress when breeding (*Lepidochelys mydas*: Valverde et al., 1999; *Chelonia mydas* and *Eretmochelys imbricata*: Jessop, 2001). This appears to represent a mechanism to ensure that the large energetic reserves accumulated by these capital (oviparous) breeders are not wasted through CORT-mediated stress responses (Jessop, 2001). Similarly in female tree lizards, *Urosaurus ornatus*, vitellogenic females show a large increase in plasma CORT concentrations in response to an acute stressor, but gravid females do not (Woodley and Moore, 2002). In the garter snake *Thamnophis sirtalis*, breeding males from populations with shorter breeding seasons exhibit reduced adrenocortical responses to stress compared with males from latitudes allowing more extended breeding (Moore et al., 2001), reflecting the greater potential of stressors to affect reproductive success in males with shorter breeding seasons.

In mammals, both basal and stress induced concentrations of glucocorticoids are greater in females than in males (Gaskin and Kitay, 1970; Handa et al., 1994a). Sex differences in stress responses of reptiles remain largely unknown but there is some evidence to suggest that reproductive steroids may influence stress responses, with females exhibiting greater adrenocortical responses to stressors than males. For example, Grassman and Hess (1992a) examined the effect of gonadectomy on the acute stress responses of male and female lizards of the species *Cnemidophorus sexlineatus*: intact females subject to the acute stress of hand-chasing in a pail exhibit higher plasma CORT concentrations than males exposed to the same stressor, while castrated males show more dramatic increases in plasma CORT concentrations following acute stress than intact males. In marine green and hawksbill turtles, differences in the stress responses of females and males of differing reproductive states are evident within the first few hours (Jessop, 2001). It remains unclear, however, whether there are differences in the activation of the HPA axis independent of gonadal hormone effects.

Adrenal function may also vary between reproductive stages. In mammals, there is strong evidence that gestating females down-regulate their acute stress responses to protect their current reproductive investment (Neumann et al., 1998), and the negative effects of high maternal corticosteroids on the development of the foetus have been repeatedly demonstrated (e.g. Hansen et al., 1999; Weinstock, 2001). Do viviparous female reptiles similarly buffer their developing embryos against the potentially detrimental effects of high levels of circulating corticosteroids? The available evidence seems contradictory. Pregnant females of the viviparous gecko *Hoplodactylus maculatus* exhibit no suppression of the stress response to capture compared with vitellogenic females although both groups do exhibit greater stress responses than males (Cree et al., 2003), and there is no observable effect on offspring quality in females of this species challenged with ACTH during gestation (Preest et al., 2005). Gestating and post-partum females of the viviparous skink *Egernia whitii* show very similar adrenocortical responses to chronic captivity with corticosterone concentrations returning to baseline levels one week following capture (Cartledge et al., 2005). However, the acute stress response has not been compared between reproductive states in this species and it may be more adaptive to modulate acute stress responses than chronic ones. Once a stressor becomes chronic in nature the reproductive benefits of curtailing the adrenocortical response are likely to be outweighed by the potential threat to fitness or mortality due to the chronic stressor.

Thus although there appears to be considerable interspecies variation in how, and if, stress responses are modulated with reproductive status, there is evidence of reciprocal relationships between the adrenal and gonadal axes in reptiles. Such results may reflect variations in circulating concentrations of gonadal steroids. Generally, oestrogens are stimulatory to adrenal function and androgens are inhibitory (see Handa et al., 1994a for review). For example, in female rats, increased basal CORT concentrations, as well as increased ACTH and CORT responses to stressors, are correlated with higher oestradiol concentrations (Kitay, 1963; Viau and Meaney, 1991; Burgess and Handa, 1992), but there is only indirect evidence that oestrogens may stimulate adrenal activity in reptiles. In female *Uta stansburiana* lizards, peak CORT concentrations are correlated with increased gonadal mass (Wilson and Wingfield, 1992), and in females of the viviparous *Lacerta vivipara*, plasma CORT varies significantly with reproductive status, while no significant variation is observed for males (Dauphin-Villemant et al., 1990).

Building on previous work on adrenal function in the viviparous skink *E. whitii* (Jones and Bell, 2004; Cartledge et al., 2005), we aim to establish whether reproductive status modulates adrenocortical activity in females of this species, and to investigate the endocrine mechanisms that may potentiate differential secretion of CORT between reproductive stages. We therefore compare the changes in plasma CORT concentration in response to the acute stress of capture in females of *E. whitii* at three reproductive stages: post-ovulatory, gestating and postpartum. We hypothesise that, due to their current reproductive investment, both post-ovulatory and gestating (carrying well-developed embryos) females will down-regulate their acute stress response compared with postpartum females, and that gestating females will show the most marked reduction. We extend the comparison to reproductively quiescent males collected at the same time as the postpartum females (Bell, 1997). A comparison of stress responses in males and females when both are reproductively quiescent is included to determine if there are integral differences in the stress responses of the sexes even when the influence of reproductive steroids should be minimal.