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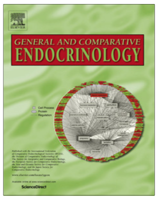

Glucocorticoids in tuatara (*Sphenodon punctatus*): Some influential factors, and applications in conservation management

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ABSTRACT

Glucocorticoid (GC) hormones promote basic life processes, regulate life-history transitions, and help individuals cope with challenges and stressors, thereby playing an important fitness role. Here, we review recent evidence for several factors that influence plasma concentrations of corticosterone (CORT), the main GC in tuatara (*Sphenodon punctatus*), and discuss the application of CORT as a physiological tool to monitor conservation efforts. Observational studies show an association between CORT concentrations and seasonal reproductive activity, ambient temperature, and ecological habitat parameters (including presence of rats/seabird abundance, sex-ratio, and genetic diversity), and experimental studies show a positive influence of acute temperature increase on the CORT response. Recently, CORT physiology has been applied as a monitoring tool in tuatara translocation programmes. No signs of chronic stress in CORT profiles were observed during standard short- and long-term translocation and rat eradication procedures, giving confidence that current conservation efforts are supportive in population recovery. These results provide a foundation for comparative understanding of stress physiology in reptiles, and will be critical for managing future population viability of tuatara in a changing environment.

1. Introduction

The endocrine system in vertebrates produces glucocorticoid (GC) hormones (including corticosterone – CORT) that promote basic life processes, regulate life-history transitions and help individuals cope with intrinsic and extrinsic changes/challenges (i.e. stressors), thereby playing an important fitness role (Crespi et al., 2013; Dufty et al., 2002; Jessop et al., 2013; Schultner et al., 2013). It is generally agreed that baseline GCs serve to meet basic energy regulation, whereas the GC stress response is a reaction to unpredictable and/or challenging events (Wingfield et al., 1998). Human impacts continue to influence ecological change of natural ecosystems; therefore, it is becoming increasingly important to understand how organisms respond and cope with environmental change and unpredicted challenges (Tokarz and Summers, 2011; Wingfield, 2013). Glucocorticoids are the most widely used indicator of physiological stress in vertebrates (Baker et al., 2013; Busch and Hayward, 2009; Dantzer et al., 2014; Wikelski and Cooke, 2006).

Patterns in GC concentrations are not universally consistent; variation is observed among species and within and among populations (Baker et al., 2013; Cockrem, 2013; Creel et al., 2013; Jessop et al., 2013; Love et al., 2013). Variation in GC concentrations can be linked with intrinsic factors such as sex, reproductive status, body condition, and age, and with extrinsic factors such as habitat modification, seasonal or annual changes in food availability, and fluctuating environmental temperature and/or weather (Baker et al., 2013; Cockrem, 2013; Wingfield, 2013). Furthermore, increased energy demands required during reproduction, territorial disputes and migration can influence patterns in GC concentrations (Boonstra, 2013; Creel et al., 2013; Romero, 2002). Prolonged or chronic elevation of plasma GC concentrations in vertebrates has been linked with reduced body condition, depressed immunity, decreased locomotor performance, and changes in behaviour – all of which are performance measures that can have fitness implications (Bonier et al., 2009; Breuner et al., 2008; Busch and Hayward, 2009).

Research investigating GC secretion in vertebrates has focussed primarily on fish, mammals and birds, with reptiles and amphibians constituting only ~10% of studies (Baker et al., 2013). Corticosterone (CORT) is the main GC in reptiles (Greenberg and Wingfield, 1987), including the tuatara (*Sphenodon punctatus*). The tuatara is a protected reptile species endemic to New Zealand and is the sole

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living representative of the order Rhynchocephalia, the sister group to squamates (Cree, 2014). Historically, tuatara were widely distributed throughout New Zealand, but following human settlement, they became extinct on the mainland (North and South Islands). Currently, natural populations occur on 32 isolated offshore islands and translocated populations occur on nine offshore islands and five mainland sanctuaries (Cree, 2014). Tuatara are sexually dimorphic and reach sexual maturity at approximately 13 years of age (∼snout-vent length (SVL) $\geqslant$ 170 mm), whereupon sex can be identified by examining characteristics such as head size and shape, abdomen shape and crest development (Cree, 2014; Cree et al., 1991; Dawbin, 1982). Tuatara have seasonally distinct breeding and nesting seasons. In the best-studied population on Stephens Island, breeding activity (mating and ovulation) occurs in the austral autumn (February–March) and nesting activity occurs in the austral spring (October–December), though not all females ovulate and nest each year (Cree, 2014). Female tuatara exhibit an extended reproductive cycle and produce one clutch of eggs every 2–9 years, depending on population and resources (Cree et al., 1992; Moore et al., 2009; Refsnider et al., 2010). Captive breeding programs, eradication of invasive mammals, and translocations (Cree, 2014; Gaze, 2001) are ongoing conservation efforts for tuatara, all of which have potential to benefit from relevant endocrine data. Here, we review (1) recent work examining several intrinsic and extrinsic factors that are associated with or influence plasma CORT concentrations in the tuatara (*Sphenodon punctatus*), (2) the application of CORT as a conservation physiology tool, and (3) knowledge gaps and directions for future research.

2. Factors that influence CORT concentrations in tuatara

Due to the protected status of tuatara, studies examining factors that influence CORT concentrations are limited, compared to other reptilian orders (Tyrrell and Cree, 1998). In general, baseline CORT concentrations in tuatara are low (about 2–5 ng/ml) in comparison to other vertebrates (Fig. 1a), and there is no evidence of a diel cycle (Cree and Tyrrell, 2001; Tyrrell and Cree, 1998).

A significant elevation in CORT concentration (from baseline CORT) is observed between 10–30 min after capture (Cree and Tyrrell, 2001). Tuatara exhibit a significant CORT response (3 h CORT concentration – 0 h CORT concentration) to capture–restraint (Fig. 1b), with restraint duration ranging from 1.5 h to 66 h (Anderson et al., 2014, 2015; Cree and Tyrrell, 2001). Here we consider recent studies that have further examined patterns of CORT concentrations in tuatara (both baseline and the CORT response), identifying significant associations between plasma CORT concentrations and reproductive activity, temperature, and ecological habitat parameters (Anderson, 2015).

2.1. Reproductive activity

Significant interactions between CORT concentrations and reproduction have been observed in reptiles (Eikenaar et al., 2012; Moore and Jessop, 2003). Commonly, a seasonal elevation in baseline CORT concentration is associated with the breeding season (lasting several weeks), and a more pronounced elevation in CORT usually coincides with energetically demanding reproductive behaviours such as mating and oviposition (lasting hours to days) (Moore and Jessop, 2003; Romero, 2002). Similar patterns have been observed in tuatara.

Nesting (including oviposition) is separated by 6–8 months from mating and ovulation in tuatara (Cree, 1994); therefore, patterns in CORT secretion that are related specifically to reproductive activities (nesting and oviposition, versus mating and ovulation) are much more readily identified than in other reptiles. In general, baseline CORT increases and the CORT response to a standardised (3 h) capture-stress protocol decreases from the non-breeding season to the breeding season (i.e. the period of mating and ovulation) in tuatara ($P < 0.001$, Fig. 1) (Anderson, 2015). Cree and Tyrrell (2001) compared wild and captive adult tuatara to examine associations between poor reproductive output (historically observed in captivity) and baseline CORT concentrations (Cree, 2014); however, no significant difference in baseline CORT was observed between wild and captive individuals.

Sex does not have a significant influence on plasma CORT concentrations (either baseline or the CORT response to capture–restraint) in tuatara (Fig. 2); however, female reproductive condition does (Anderson et al., 2014). Gravid females have significantly higher baseline CORT, and a significantly dampened CORT response, compared to non-gravid females (and also males) during the nesting life-history stage (Anderson et al., 2014). Baseline CORT in gravid females is highest during nest digging and oviposition (Cree and Tyrrell, 2001). Interestingly, a distinct fall (∼5-fold) in baseline CORT is observed after oviposition, even in the case of females that continue to guard their nests. Taken together, these results suggest a potential role of CORT in regulating the metabolic demands of nesting (migration to nesting grounds and nest digging) and/or timing of oviposition (Cree, 2014; Cree and Tyrrell, 2001).

The functional significance of elevated baseline CORT concentrations and a dampened CORT response in gravid female tuatara

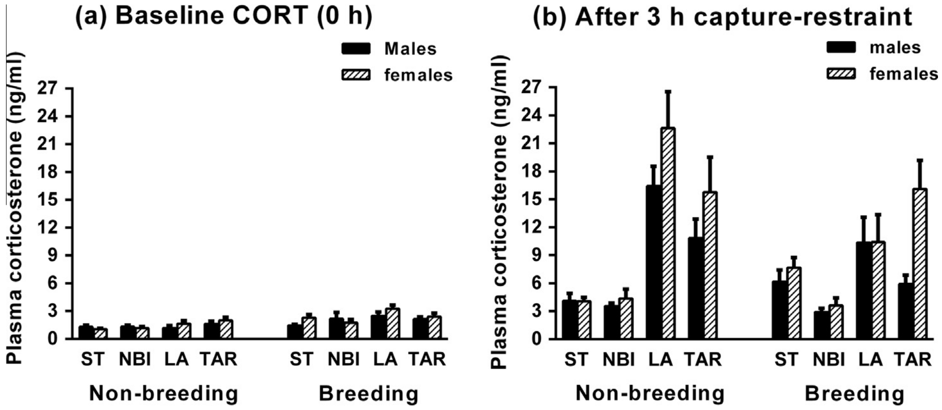

Fig. 1. Plasma corticosterone (CORT) concentrations (ng/ml) in tuatara (*Sphenodon punctatus*) from four island populations during the breeding and non-breeding seasons at (a) capture (baseline CORT) and (b) after 3 h capture–restraint. Sex is not a significant predictor of plasma CORT concentrations (ng/ml, mean ± SE) in adult tuatara ($P > 0.05$). Abbreviations: ST = Stephens Island; NBI = North Brother Island; LA = Lady Alice Island; TAR = Taranga Island.

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