



## Regular article

# Heightened aggression and winning contests increase corticosterone but decrease testosterone in male Australian water dragons



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## ABSTRACT

Water dragons (*Intelegama [Physignathus] lesueurii*) are large (to >1 m) agamid lizards from eastern Australia. Males are fiercely combative; holding a territory requires incessant displays and aggression against other males. If a dominant male is absent, injured or fatigued, another male soon takes over his territory. Our sampling of blood from free-ranging adult males showed that baseline levels of both testosterone and corticosterone were not related to a male's social tactic (territorial versus non-territorial), or his frequency of advertisement display, aggression, or courtship behavior. Even when we elicited intense aggression by non-territorial males (by temporarily removing territory owners), testosterone did not increase with the higher levels of aggression that ensued. Indeed, testosterone levels decreased in males that won contests. In contrast, male corticosterone levels increased with the heightened aggression during unsettled conditions, and were higher in males that won contests. High chronic male–male competition in this dense population may favor high testosterone levels in all adult males to facilitate advertisement and patrol activities required for territory maintenance (by dominant animals), and to maintain readiness for territory take-overs (in non-territorial animals). Corticosterone levels increased in response to intense aggression during socially unstable conditions, and were higher in contest winners than losers. A positive correlation between the two hormones during socially unstable conditions suggests that the high stress of contests decreased androgen production. The persistent intense competition in this population appears to exact a high physiological cost, which together with our observation that males sometimes lose their territories to challengers may indicate cycling between these two tactics to manage long-term energetic costs.

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## Introduction

Vertebrates in which males display two or more alternative reproductive tactics provide robust model systems for the study of interactions between hormones and aggressive behavior (Baird and Hews, 2007). Steroid hormones activate male aggression associated with reproduction in many species (fish: Liley and Stacey, 1983; Ros et al., 2004; birds: Rohwer and Rohwer, 1978; Rohwer and Wingfield, 1981; mammals: Bouissou, 1983; Monaghan and Glickman, 1992), including some lizards (Crews, 1975; Moore and Marler, 1987; Moore et al., 1998; Wikelski et al., 2005). However, causal interactions between hormones and male aggression can operate in the opposite direction also. Aggression with same-sex rivals appears to elicit secretion of androgens (Arlet et al., 2011; Oliveira et al., 2009; Smith and John-Alder, 1999), as well as corticosteroids that may reflect the social stress induced by aggression (Earley and Hsu, 2008; Gilmour et al., 2005; Knapp and

Moore, 1995). Secretion of androgens and corticosteroids might also depend on the outcome of contests with rivals, with both positive and negative associations among secretion of each hormone, social status, and winning or losing being reported (reviewed by Hsu et al., 2006). Moreover, the possibility that testosterone and corticosterone act antagonistically to one another (Moore and Jessop, 2003) may complicate matters further. If aggression prompts secretion of either hormone, levels of the other may be suppressed.

The challenge hypothesis is the leading theoretical framework proposed to explain secretion of androgens in response to aggression (Wingfield et al., 1990). This hypothesis predicts that patterns of androgen secretion will be related to variation in demands on males linked to social structure and their involvement in parental activities. The challenge hypothesis was first developed for and tested in endotherms in which males are generally more aggressive during settlement of reproductive territories, but then aggression diminishes as parental activities commence (Wingfield et al., 1990). Secretion of additional androgens is expected in response to challenges from rivals when hormone levels are below physiological maximum (Wingfield et al., 1990). Because most lizards do not exhibit parental care yet it is common for males to defend territories throughout prolonged reproductive seasons during which

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females produce multiple clutches of eggs (Baird et al., 2001; Fox et al., 2003), they offer interesting opportunities to test the applicability of the challenge hypothesis as a general model. If territory defense requires lizard males to maintain androgen secretion at physiologically maximal levels throughout the season, pulses of androgen secretion are not expected in response to individual challenges by rivals.

Meta-analysis of male vertebrate androgen secretion in response to territorial challenges revealed only moderately strong effects (Hirschenhauser and Oliveira, 2006). Variability in the influence of aggression on androgen levels was likely influenced by differences in the context during which aggression occurred across the diversity of species sampled (Hirschenhauser and Oliveira, 2006), and a number of other ecological and behavioral variables (Goyman et al., 2007). Tests of the influence of aggression on secretion of adrenocorticoids have also generated mixed results, with both positive and negative associations being reported (reviewed by Hsu et al., 2006). Hormone responses by male lizards to contest outcome and heightened aggression are particularly variable. Male green anoles that won contests staged in the laboratory had higher androgen levels than contest-losers or control males (Greenberg and Crews, 1990). However, this response may have been influenced by the presence of females in enclosures, or the low pre-trial androgen levels of male winners. Aggression increased testosterone levels in male marine iguanas (Wikelski et al., 2005), but not in either territorial male tree lizards (Knapp and Moore, 1995) or male mountain spiny lizards (Moore, 1987). The influence of winning on both hormones depended on social status in male tree lizards, with winners having decreased testosterone, but elevated corticosterone (Knapp and Moore, 1995). These mixed results clearly indicate that data from lizard studies are insufficient to evaluate the extent to which patterns of hormone secretion in response to heightened aggression and contest outcome support theoretical predictions, and additional such studies are necessary, especially those that involve manipulations of social conditions in the field.

We studied relationships among aggression, androgens, and corticosterone in the eastern water dragon, *Intellagama [Physignathus] lesueurii*. In our study population, males and females exhibit markedly different levels of aggression, and mature males utilize one of two alternative social tactics (territorial versus non-territorial) that are characterized by territorial males displaying at rates that were over six times that of non-territorial males which usually fled or were repelled by territory owners (Baird et al., 2012, 2013). On three occasions, however, non-territorial males challenged and defeated a territory owner and usurped their territories (Baird et al., 2012, 2013). In the present study, we used this fact to induce social changes in levels of aggression and male social tactics by temporarily removing and later reinstating individual territorial males (Baird et al., 2012). We collected blood samples from free-ranging lizards to test whether testosterone and corticosterone differ with sex, maturity, and male social status. We also examined the extent to which hormone levels were correlated with the frequency of male behavior patterns involved in the advertisement and control of territories, and used temporary removal/reinstatement field experiments to test whether hormone levels changed in response to heightened social stress and winning or losing aggressive encounters.

## Methods

### Study population and general methods

*Intellagama lesueurii* is a large (up to 1 kg) semiaquatic, diurnal agamid that occurs in riparian areas throughout eastern New South Wales and Queensland (Cogger, 1986). They are strong swimmers that enter the water routinely to escape predators, and at night (Courtice, 1981). Water dragons feed primarily on terrestrial insects (Harlow, 2001).

We conducted this study on the grounds of the Flynn's Beach Resort in Port Macquarie, NSW (31° 26' S latitude, 152° 55' E longitude) from

12 Sept to 30 Nov, 2009, during the Austral spring when eastern water dragons are reproductively active (Cuervo and Shine, 2007; Harlow, 2001; Thompson, 1993). Water dragons occur throughout the resort grounds (8980 m<sup>2</sup>) but are most concentrated along 200 m of Wright's Creek which bisects this site (Baird et al., 2012). Microhabitat used by water dragons consisted of naturally vegetated riparian areas as well as lawns, plant beds, sidewalks, and even swimming pool decks. Lizards were habituated enough to humans that they tolerated approach to within 2 m, but retreated when approached more closely. We captured 111 lizards by noose from 15 to 30 Sept 2009. Lizards were marked by painting numbers on each side of the dorsal torso using white water proof nail polish. Worn numbers were retouched during recaptures, but none of the lizards lost their numbers through molting.

### Collection of blood samples

To determine baseline hormone levels, we collected blood samples from 1000 to 1400 h within 5 min of beginning to approach, and within 1 min of capturing lizards (mean pursuit + handling time =  $1.9 \pm 0.18$  min) by inserting a heparinized micro-capillary tube (50  $\mu$ l) beneath the lower eyelid into the orbital sinus (see *Ethics statement*). We collected 100–200  $\mu$ l of whole blood, and then stanchied the blood flow by applying gentle pressure to the closed eye using a clean cloth. Blood samples were kept on ice in the field for a maximum of 3 h, centrifuged, and the plasma was frozen. Frozen plasma samples were transported to the University of Sydney where they were freeze-dried on Dec 10, 2009. Freeze-dried plasma was later transported to Oklahoma State University where all samples were radioimmunoassayed for testosterone and corticosterone (see below). Freeze drying human blood plasma samples did not degrade steroids measured using radioimmunoassay (Das et al., 1983), and freeze dried lizard yolk samples have also been successfully used in quantitative measurements in lizard studies (Warner et al., 2007, 2008).

Baseline samples included 36 females (SVL = 146–223) that we determined were reproductively active by palpation of enlarging ovarian follicles. Fifty-one lizards were males (162–271 mm SVL) as evidenced by their eversible hemipenes, and 38 of these (SVL = 200–271 mm) were secreting seminal fluid. Eight of the reproductively active males moved off our study site after initial marking, whereas the remaining 30 males (SVL = 238–271) were present throughout our behavioral studies (Baird et al., 2012), and most of these were involved in removal experiments (described below). We also collected blood samples from 21 lizards (SVL = 192–214 mm) that we classified as immature because they lacked enlarging follicles or eversible hemipenes.

### Social and spatial behavior of male dragons

We mapped the study site to scale by recording distance and compass measurements among prominent, permanent landmarks (sidewalks, fence and light posts, trees, creek shore-line). The location of each mapping marker was determined using measurements among a minimum of five adjacent markers to yield a composite map accurate to the nearest 2 m.

One of us (TAB) recorded the social behavior of subject lizards on scale-drawn maps during focal observations (*sensu* Altmann, 1974). Focal observations involved recording all of the displays and aggressive encounters with conspecifics of both sexes initiated by subject lizards on scale-drawn maps (see similarly Baird et al., 2007, 2012, Baird, 2013a). Although lizards at this site were not obviously affected by human presence, we recorded focal observations when human disturbance was minimal. Each observation session lasted 20 min, except for a few (<5%) that were terminated earlier because subjects were lost from view in thick vegetation. To quantify behavior during baseline social conditions on 30 mature males, we recorded an average of 9.2 observation sessions/male ( $\pm 0.4$  SE) on separate days, which yielded an average of 204 min of observations/male ( $\pm 17.7$  SE) (Baird et al.,

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