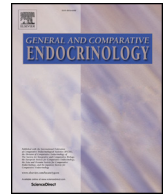




Contents lists available at ScienceDirect

General and Comparative Endocrinology

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

Social coping styles of lizards are reactive and not proactive in urban areas

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ARTICLE INFO

Keywords:

Urbanisation
Corticosterone
Testosterone
Reptile
Courtship
Competition

ABSTRACT

Animals engage in social interactions with changes in their behaviour and physiology. Environmental challenges, however, can influence social interactions by adding additional stressors. Here, we investigated the effects of urbanisation on the behaviour and hormonal responses of a tropical lizard species, *Psammophilus dorsalis*, during social interactions. We recorded behaviour of males from suburban and rural areas during controlled encounters with other males and females. We then measured corticosterone and testosterone levels of individuals at 10 min intervals, from immediately after the social encounter to 30 min later and then at 120 min after the interaction period. We found that differences in social behaviours and subsequent hormone levels were largely driven by habitat, and not social context. Overall, we found that fewer suburban males showed behavioural displays compared to rural males during social encounters. For those that displayed, intensity of aggression was similar across populations, but courtship intensity was lower for suburban males compared to rural males. Suburban males also had significantly elevated levels of corticosterone both under control conditions (no social encounter) and following intra- and intersexual interactions, while rural males retained low levels of corticosterone across contexts. Social interactions were associated with an increase in testosterone levels in all males, but only rural males maintained elevated levels for up to 120 min after interactions with females. Thus, lizards from these suburban and rural populations showed key differences in responsiveness to and recovery from social challenges, a pattern that suggests alternative coping styles ('proactive' vs. 'reactive'). These differences in social coping styles could influence consequences of sexual selection in an urbanised world.

1. Introduction

Most animals show flexibility in their physiological and behavioural responses to changes in their environment. The hypothalamo-pituitary-adrenal (HPA) axis is one of the most robust, generalized, and consistent emergency response pathways in vertebrates, and is known to activate in response to a wide range of environmental and ecological stimuli, from changes in temperature and precipitation levels (e.g. Lobato et al., 2008; Wingfield, 2013), to predation pressure and resource availability (e.g. Bennett et al., 2016; Cockrem and Silverin, 2002; Kitaysky et al., 2001; Thaker et al., 2009). Increased secretion of glucocorticoids and other hormones from the HPA axis (e.g. Oxytocin, ACTH, CRF) directly affect the central nervous system, cardiovascular system, immune system, and reproductive system, thereby stimulating a range of effects, including memory consolidation, cardiovascular tone, immune activation, and reproductive behaviour (reviewed in Sapolsky et al., 2000; Wingfield and Sapolsky, 2003). Thus, activation of the HPA axis in response to stressors directly mediates the behavioural and physiological responses that are needed to maintain homeostasis. All animals, however do not respond to stressors with the

same physiological intensity, and considerable evidence has shown that within species, some individuals can have “proactive coping styles” while others have “reactive coping styles” (reviewed in Koolhaas et al., 1999). A “proactive” coping style is characterised by high aggression and low reactivity and activity of the HPA axis whereas “reactive” coping style is typically expressed as low aggression and high HPA axis reactivity and activity (Koolhaas et al., 1999, see also de Lourdez Ruiz-Gomez et al., 2011; Carere et al., 2010).

For many animals, social interactions can also induce a physiological stress response wherein the type and intensity of the social interaction, as well as the social or dominance status of the interacting individuals, can affect the magnitude of HPA axis activity (Adkins-Regan, 2005; Creel et al., 2013; Dijkstra et al., 2012; Alcazar et al., 2016; Carere et al., 2003). Social interactions also typically involves the activation of the hypothalamo-pituitary-gonadal (HPG) axis (Adkins-Regan, 2005; Creel et al., 2013; Hirschenhauser and Oliveira, 2006; Knapp and Moore, 1997). In vertebrate males, the close functional link between HPA and HPG axes often leads to correlated changes in circulating hormone levels (Lind et al., 2018; Moore et al., 1991; but see Narayan et al., 2013; Thaker et al., 2009, where no correlation was

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Received 18 July 2018; Received in revised form 4 October 2018; Accepted 14 October 2018

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found). The magnitude of change in circulating hormone levels from both these axes and the timing of those changes, however, varies between individuals and across species (Horton et al., 2014; Knapp and Moore, 1996; Yewers et al., 2017). For example, in *Anolis carolinensis*, winners of a fight sustain elevated circulating androgens for at most 1 hr after the male-male interaction, whereas losers experience depressed androgen levels even after 1 week (Greenberg and Crews, 1990). Thus, experiences during a social encounter such as winning or losing competitive interactions not only elicit changes in circulating glucocorticoid and androgenic steroid hormone levels (i.e. ‘winner or loser effects’), these hormones can also mediate behaviours during and after social interactions (Hirschenhauser and Oliveira, 2006; Oliveira et al., 2002; Wingfield et al., 1990).

Population variation in the duration and magnitude of hormonal responses to a stressor are very informative as they reflect differences in the sensitivity of both the HPA and HPG axes to stimuli (*sensu* adrenocortical modulation; Wingfield et al., 2001b). A number of studies have demonstrated that the state of individuals, such as sex, age, body condition, reproductive stage, and social status can influence the adrenocortical response (e.g., Dunlap and Schall, 1995; Grassman and Hess, 1992; Jennings et al., 2000). In addition, differences in the external environment such as rainfall, temperature, food availability, humidity, or habitat alterations can also affect adrenocortical modulation in individuals (e.g., Dunlap and Wingfield, 1995; French et al., 2010; Moore et al., 2000).

One common and dramatic pressure that many animals are currently experiencing is urbanisation, where animals are not only exposed to high human activity, but altered habitats and microclimates, as well as different resources and predator communities (Tuomainen and Candolin, 2011). Therefore, most animals that live in urban areas are forced to cope, which requires behavioural and physiological responses typically mediated by the activation of the HPA axis (Sol et al., 2013; Tuomainen and Candolin, 2011). Not surprisingly, many studies have found differences in circulating glucocorticoid levels and behaviour in animals as a consequence of living in urban environments, but the intensity and direction of responses vary considerably between species (in birds: Abolins-Abols et al., 2016; Angelier et al., 2016; Fokidis et al., 2009; Hayward et al., 2011; in lizards: Romero and Wikelski, 2002; Owen et al., 2014, French et al., 2010, French et al., 2008; in mammals: Scheun et al., 2015). Lack of a consistent directional response (i.e. elevated glucocorticoid levels in urban areas) indicates the importance of understanding the context that results in inter-individual and inter-specific differences.

A growing number of studies in birds and mammals in urban areas have found differences in physiological and behavioural responses during social interactions (Partecke et al., 2005; Hu and Cardoso, 2010; Lowry et al., 2013). The expectation that urbanisation affects social interactions remains untested for reptiles. Using the Indian rock agama *Psammodromus dorsalis* (Gray, 1831, Fig. 1), we examined the effect of urbanisation on social behaviour as well as corticosterone and testosterone levels. We specifically examined responses of males during both inter- and intra-sexual interactions to determine whether courtship and aggressive contexts elicit different responses. We measured behaviours of wild-caught lizards during staged social encounters in the laboratory and quantified the magnitude and time-course of hormone levels after the social interactions. We also examined the potential correlation between the two steroid hormones. In doing so, we provide the first test of whether urban and rural populations of lizards differ in their responsiveness to and recovery from social challenges.

2. Material and methods

The Indian rock agama, *Psammodromus dorsalis*, is a sexually dimorphic species (SVL range: males = 101–140 mm and females = 75–96 mm; Fig. 1) where both males and females are territorial (Deodhar, 2017). Males of this species also develop conspicuous



Fig. 1. Indian rock agamas, *Psammodromus dorsalis* in the suburban habitat. Photo shows the typical close proximity of conspecifics in this habitat with two males (one displaying conspicuous courtship colour on top left and one in neutral dull coloration on bottom left) and one female (top right).

colouration during the breeding season, typically from April to September which become dull at the end of the breeding season (Radder and Saidapur, 2005). Males of *P. dorsalis* also express dynamic physiological colours on their dorsal and lateral body parts that can rapidly change and are specific to the social context. During courtship, the dorsal body region of males shifts to red while the lateral region shifts to black (Batabyal and Thaker, 2017; Fig. 1). During aggressive encounters with other males, these same body regions turn yellow and orange respectively (Batabyal and Thaker, 2017). These different colour patterns are an important component of social interactions as they independently elicit responses from male and female receivers (Batabyal and Thaker, 2018). *Psammodromus dorsalis* occurs in natural rural areas which are predominantly rocky hills and boulders with interspersed scrub vegetation. In addition to these rural areas that lack anthropogenic disturbance, *P. dorsalis* is also found in suburban areas in and around the city of Bangalore, India. Suburban areas, where lizards are found, are mostly empty development plots surrounded by small houses or in and around construction areas with scrub vegetation (majorly invasive *Lantana* sp.) (see Supplementary Fig. S1 for satellite images of rural and suburban areas).

2.1. Experimental design

We performed the following experiments during the breeding season (April–August) over two consecutive years (2013, 2014). Free ranging male lizards from a suburban population ($N = 40$ from 2 sites) and a rural population ($N = 40$ from 2 sites) were captured by noosing and brought into the laboratory. Replicate sites within each habitat were 5–10 km apart, and the suburban and rural habitats were approx. 60 km apart. In captivity, lizards were housed individually in glass

terraria (60 × 30 × 25 cm), that were lined with disposable absorbent paper as the substratum and provided with rocks for refuge. Terraria were covered on all sides to minimize disturbance and were maintained in a room that permitted natural temperature and lighting conditions. Individual 60 W incandescent basking lights were turned on from 0800 to 1200 h and from 1500 to 1600 h, and lizards were provided with live ants, field crickets, and fresh water daily. All lizards were maintained in the laboratory for 7–9 days and were returned to the site of capture after experimental trials were complete.

To quantify the effect of social stimulus on behaviour and hormonal responses, we allowed each focal male ($N = 25$ from suburban and 25 from rural, excluding control animals) to interact with a stimulus male and a sexually mature female separately. Focal males were exposed to stimulus lizards from the same habitat type (suburban, rural), but these individuals were caught from sites that was different from where focal animals were caught, and thus were unfamiliar. Each behavioural trial began with a 30 min acclimation period in a testing terrarium followed by a 30 min interaction period with one of the stimuli (either a male or a female). Social interactions were staged in testing terraria (95 × 45 × 30 cm) that were lined on the bottom with a rubberized sheet marked with 4 × 4 cm grids (Supplementary Fig. S2). A different control set of males ($N = 15$ from suburban and 15 from rural) were also kept in the same testing terrarium for 30 min but were not exposed to any social stimuli. Testing terraria were placed behind a blind to minimize disturbance by observers, and all trials were video recorded with a Canon 550D camera for subsequent quantification of behaviour. After social interactions and blood sampling (see below), lizards were allowed 24 hrs to recover in their home terraria before being exposed to the second social stimulus (see Supplementary Fig. S2 for a schematic of the experiment protocol). Assignment to treatment (social or control groups) was random, and the order of stimulus for the social group (exposure to female or male) was also randomized. All experiments were conducted from 08:00 to 12:00 or from 15:00 to 17:00, which are the peak activity periods for this species. Before the start of the experimental trials, mass (g) and snout-to-vent length (mm) were measured for all individuals using a digital weighing balance and digital callipers respectively.

2.2. Behavioural responses

From the 30-min video recording of social encounters with males and females, we recorded the following behaviours (similar to Deodhar and Isvaran, 2018; Radder et al., 2006).

Simple push-ups and head bobs: Push-up consist of raising and lowering the head and trunk by the straightening of the forelimb. Push-ups are mostly accompanied by head bobs that are either single or double. A single head bob is performed when the animal raises its head ~1 cm from initial position and lowers it. A double head bob or shudder is performed when the animal raises and lowers its head twice in quick succession.

Crouch walk: A male performs a low walk by moving forward slowly with a continuous head shudder. This behaviour is only seen when males interact with females.

Bite: One individual grip any body part of another with its mouth.

Mount: One individual holds down the other, either fully or partially, by climbing on top of it.

2.3. Hormonal responses

To examine the short-term effect of social interaction on hormone levels, we took a single blood sample from each focal male at one of the following time points: 0 min, 10 min, 20 min, 30 min or 120 min after the behavioural trial ($N = 5$ individuals/time point, see Supplementary Fig. S2 for experiment design). A second blood sample was taken at the same time point after the second behavioural trial 24 h later, resulting in two blood samples per individual. As a comparison, one blood

sample was also obtained from the control animals (no social stimulus) at the same time points: 0 min, 10 min, 20 min, 30 min or 120 min post acclimation ($N = 3$ individuals/time point). Blood samples were obtained from the retro-orbital sinus using heparinized microcapillary tubes (following Thaker et al., 2009). Once collected, samples were centrifuged and the plasma was stored at -20°C until analysis. Enzyme-Immuno Assay kits (Arbor Assay DetectX Corticosterone K014-H5; Testosterone K032-H5) were used to measure circulating corticosterone and testosterone levels in the plasma. EIA kits were first optimized as per Wada et al., 2007, and we subsequently analysed the plasma at a dilution ratio of 1:100 for corticosterone and 1:140 for testosterone. For both hormones, samples were analysed in duplicate and a total of 12 assays were run, with a duplicate lab standard in each assay. Percent recovery of corticosterone in the assay was 98.93, with an intra-assay coefficient of variation of 0.12–6.84 and an inter-assay coefficient of variation at 9.51 (Inter-assay CV were calculated from a lab standard of known concentration placed on all plates). For testosterone, percent recovery was 98.54, and the intra-assay coefficient of variation was 0.04–7.62 and inter-assay coefficient of variation was 8.47. Hormone levels were determined in reference to seven-point standard curve with a limit of detection at 0.016 ng/ml for corticosterone and 0.030 ng/ml for testosterone.

2.4. Statistical analyses

We first compared the proportion of individuals that showed at least one overt behavioural response during the social encounters, using a two-sample test for equality of proportion (Chi squared test) with continuity correction across the two habitats. For those individuals that showed some behavioural response (Male-male encounter: $N = 20$; Male-female encounter: $N = 21$), we ran a generalised linear model (negative binomial distribution for count data) with each behavioural display separately as the response variable, using habitat and body condition of the focal male and stimulus (males or females) as fixed factors. Body condition was calculated from mass and snout-vent length as the scaled mass index (as per Peig and Green, 2009).

We first quantified the effect of body condition on circulating hormone levels, using a linear regression for corticosterone and a generalised linear model with a gamma distribution for testosterone, as testosterone had a non-normal distribution (corticosterone: $t = 1.03$, $p = 0.192$; testosterone: $t = -0.83$, $p = 0.406$). No effect of body condition was found on either of the hormone levels, and thus all further analyses were done without body condition as a factor. Using a linear modelling framework, we tested the effect of social context (male-male, male-female, control), time (0, 10, 20, 30, 120 min post-interaction) and habitat (suburban and rural) on circulating corticosterone (lm model) and testosterone (glm model) levels. For each hormone, we first constructed a global model with all three predictor variables [habitat type (suburban, rural), social context (control, male-male, male-female), time of blood sample (0, 10, 20, 30, 120)] and their three-way interaction effect. We then contrasted this global model with subsequent simplified two-way models to determine the most parsimonious model (parsimony was assessed from ANOVA comparison between models). We report the best model fit in the Results section. To determine significance of individual factors, we performed subsequent post-hoc tests using lsmeans function wherever relevant (Lenth, 2016). Outliers of extremely low corticosterone and high testosterone levels (beyond 4 standard deviations from the mean) were excluded before analysis (Corticosterone: Rural: $N = 2$; Testosterone: Rural: $N = 1$, Suburban: $N = 2$). Finally, we performed Spearman's correlation analyses between corticosterone and testosterone values at all time points (0 min, 10 min, 20 min, 30 min and 120 min) and for the two populations (suburban and rural) separately. All statistical analyses were conducted using R Studio (3.0.1) statistical software.

3. Results

3.1. Behavioural responses

In staged encounters with both males and females, a higher proportion of rural males were behaviourally reactive compared to suburban males. During encounters with females, 65% of rural males showed behavioural displays, whereas only 20% of suburban individuals did ($\chi^2 = 6.54$, $P = 0.010$). During encounters with males, 55% of rural males showed some social displays, while only 25% of suburban males did ($\chi^2 = 2.60$, $P = 0.100$). All lizards that showed at least one behavioural display also exhibited some dynamic colour changes that are social context specific (Batabyal and Thaker, 2017). During encounters with other males, the dorsal region of 20 males (out of 50 tested) changed to yellow and the lateral region turned to orange. During encounters with females, 21 males (out of 50 tested) turned red (dorsal region) and black (lateral region). During the control treatment (no social encounter) and before the start of each social trial, all lizards were in their neutral brown colouration (see Fig. 1).

For the individuals that showed at least one behavioural display during the male-male social context, there was no effect of habitat, body condition of focal male, or body condition of stimulus male on the number of head bobs, bites, and mounts shown (see Table 1 for statistical results, see Fig. 2 for head bobs).

During male-female encounters, habitat significantly predicted the number of head bob displays (glm: $z = -3.18$, $P = 0.001$). Rural males performed more head bob displays towards females compared to suburban males (Fig. 2). There was no effect of body condition of the focal male ($z = 1.35$, $P = 0.175$) or the interacting female ($z = 1.01$, $P = 0.311$) on the number of head bobs shown during this social context. There was no significant effect of habitat, body condition of focal male, or body condition of the stimulus female on the crouch walk behavioural display (Table 1).

3.2. Hormonal responses

Corticosterone levels after the social encounters were not significantly affected by the three-way interaction between social context, habitat and time in the global model (Anova model comparison: $F = 0.55$, $P = 0.814$). The best model fit for corticosterone was an additive model of social context, habitat, and time with two additional interaction terms. Therefore, corticosterone was significantly affected by the interaction between habitat and time (Anova model comparison: $F = 4.03$, $P = 0.004$) and by the interaction of habitat and social context (Anova model comparison: $F = 3.46$, $P = 0.035$), wherein suburban and rural males differed in circulating corticosterone levels

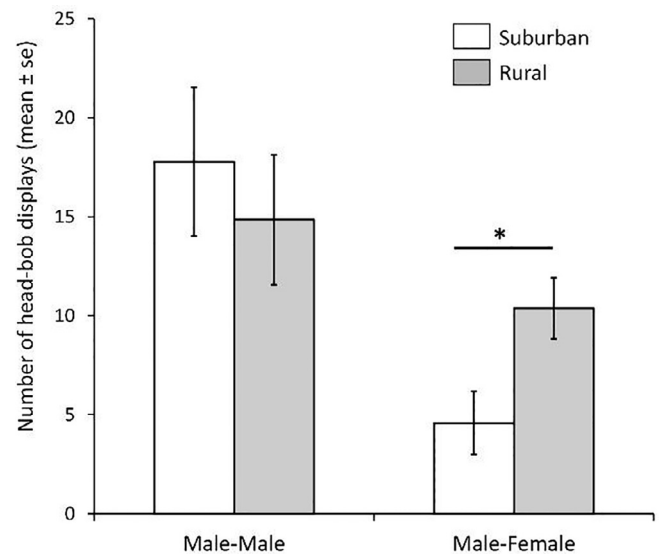


Fig. 2. Number of head bob displays (mean \pm se) shown by suburban and rural males of *Psammodromus dorsalis* during staged encounters with other males (male-male) or females (male-female). Rural males displayed a significantly greater number of head bobs than suburban males during male-female interactions, but not male-male interactions.

across social context and also across time points. We report below the corticosterone response in each social context (Control, Male-male and Male-female) separately from linear models with habitat and time as predictor variables.

Under control conditions (no social encounter), corticosterone was significantly higher in suburban males compared to rural males ($F_{1,20} = 5.77$, $P = 0.026$, open symbols in Fig. 3a, b), with no significant effect of time ($F_{4,20} = 0.52$, $P = 0.715$, Fig. 3a, b) or an interaction between habitat and time ($F_{4,20} = 0.74$, $P = 0.573$). After male-male encounters, we found a significant effect of habitat ($F_{1,35} = 29.29$, $P < 0.001$) wherein suburban males had higher circulating levels of corticosterone compared to rural males (post hoc $p < 0.001$, Fig. 3a). There was no significant effect of time ($F_{4,35} = 1.53$, $P = 0.215$) or an interaction between habitat and time ($F_{4,35} = 2.44$, $P = 0.076$) on corticosterone levels after encounters with other males (Fig. 3a). After male-female encounters, both time ($F_{4,37} = 2.80$, $P = 0.039$) and habitat ($F_{1,37} = 25.55$, $P < 0.001$) significantly influenced circulating corticosterone levels (Fig. 3b). Suburban males had significantly higher circulating levels of corticosterone compared to rural males (post hoc $p < 0.001$, Fig. 3b) and the difference in hormone level was greatest

Table 1

Behaviours shown by males from suburban and rural areas during male-male ($n = 20$) and male-female ($n = 21$) encounters. Reported are the statistical results from a generalized linear model with potential predictors. * denote significant results at $p < 0.05$.

Social encounter	Behaviour shown	Predictor variable	z	P
Male-male	Head bob	Habitat	0.63	0.525
		Body condition of focal male	-0.75	0.447
		Body condition of stimulus male	-0.74	0.458
	Bite	Habitat	1.02	0.307
		Body condition of focal male	-0.29	0.765
		Body condition of stimulus male	-0.50	0.616
	Mount	Habitat	-0.29	0.768
		Body condition of focal male	-0.78	0.435
		Body condition of stimulus male	-0.49	0.619
Male-female	Head bob	Habitat	-2.70	0.006*
		Body condition of focal male	0.80	0.422
		Body condition of stimulus female	0.96	0.334
	Crouch walk	Habitat	0.15	0.880
		Body condition of focal male	0.28	0.774
		Body condition of stimulus female	1.26	0.206

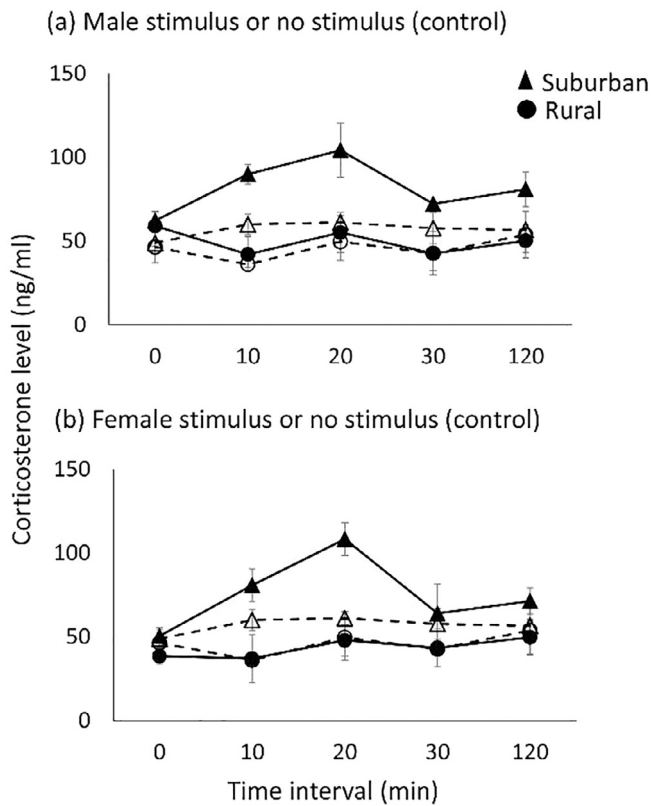


Fig. 3. Corticosterone level (mean \pm 1 se) of males of *Psammophilus dorsalis* across time (0 min, 10 min, 20 min, 30 min and 120 min) after a 30 min interaction period with a (a) male stimulus or a (b) female stimulus. Open symbols in all figures denote the mean hormone levels after no social encounter (control) for both suburban (triangle) and rural (circle) populations across time.

between 0 and 20 mins post interaction (post hoc $p = 0.02$, Fig. 3b).

Testosterone levels were best explained by the global model and the three-way interaction of social context, habitat and time (Anova model comparison: $F = -3.70$, $P = 0.045$). Further subdividing the data according to social context showed that under control conditions (no social encounter) there was no significant effect of habitat ($z = -1.38$, $P = 0.166$) or time ($z < 0.5$, $P > 0.05$ for all time point comparisons) or an interaction between habitat and time ($z = -0.85$, $P = 0.282$) on testosterone levels (open symbols in Fig. 4a, b). Thus, testosterone levels remained low for both suburban and rural males during control conditions when there was no social encounter. After male-male encounters, testosterone levels were affected by time ($z = 2.73$, $P = 0.047$ for 10 min vs 20 min comparison, Fig. 4a), but not by habitat ($z = 0.50$, $P = 0.612$, Fig. 4a) or an interaction of habitat and time ($z = -2.48$, $P = 0.063$, Fig. 4a). Testosterone levels of all males were elevated after encounters with other males and returned to control levels by 20 min post interaction (Fig. 4a). After encounters with females, we found an interaction effect between time and habitat on testosterone levels ($z = -5.36$, $P < 0.001$, Fig. 4b). Social encounters with females resulted in higher testosterone levels for rural males, compared to control levels, which were maintained up to 120 mins post interaction ($p > 0.05$ for all post hoc time comparisons). Suburban males, initially increased testosterone levels above control levels, but those levels declined rapidly within 20 min post interaction (0 min vs 20 min: post hoc $p = 0.042$, Fig. 4b).

Finally, we found negative correlations between circulating levels of corticosterone and testosterone for suburban males at time points 0 min (Spearman's $\rho = -0.8$, $p = 0.33$), 10 min ($\rho = -1$, $p = 0.08$), 20 min ($\rho = -0.8$, $p = 0.33$), 30 min ($\rho = -0.8$, $p = 0.13$) and 120 min ($\rho = -1$, $p = 0.33$) after social encounters with a male

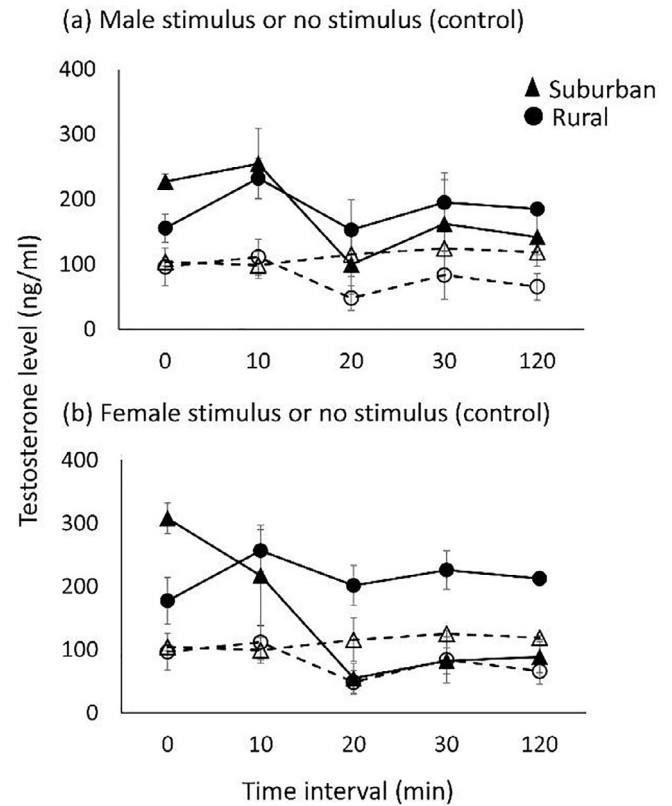


Fig. 4. Testosterone level (mean \pm 1 se) of males of *Psammophilus dorsalis* across time (0 min, 10 min, 20 min, 30 min and 120 min) after a 30 min interaction period with a (a) male stimulus or a (b) female stimulus. Open symbols in all figures denote the mean hormone levels after no social encounter (control) for both suburban (triangle) and rural (circle) populations across time.

(closed symbols in Fig. 5a). Similar negative correlations were also found for suburban males at time points 0 min ($\rho = -0.8$, $p = 0.33$), 10 min ($\rho = -0.6$, $p = 0.41$) and 20 min ($\rho = -0.8$, $p = 0.33$) after interaction with a female (closed symbols in Fig. 5b). For rural males we found no correlations between the two steroid hormones after an encounter with a male or a female at any time point ($\rho < \pm 0.5$, $p > 0.05$ for all time points, open symbols in Fig. 5a, b).

4. Discussion

Social encounters in *P. dorsalis* elicit behavioural responses and induce changes in steroid hormone levels. Differences in behaviours and subsequent corticosterone and testosterone levels, however, were largely driven by population (suburban/rural) rather than the type of social interaction (inter/intra-sexual). In all social contexts, fewer suburban males showed behavioural displays compared to rural males. For those that did display, we found no population differences in the intensity of aggression during male-male encounters. During encounters with females, however, the intensity of courtship behaviour tended to be lower for suburban males compared to rural males. Suburban males had higher levels of corticosterone under both control conditions as well as following intra- and intersexual interactions, while rural males remained at low levels throughout. All social interactions elicited an initial increase in testosterone levels for both suburban and rural males. However, while rural males maintained elevated testosterone levels for at least 30mins after interactions with a female, suburban males showed rapid decline in levels shortly after all social interactions. These results provide the first evidence in reptiles that social behaviour and subsequent hormonal responses are significantly different across a suburban and rural population.

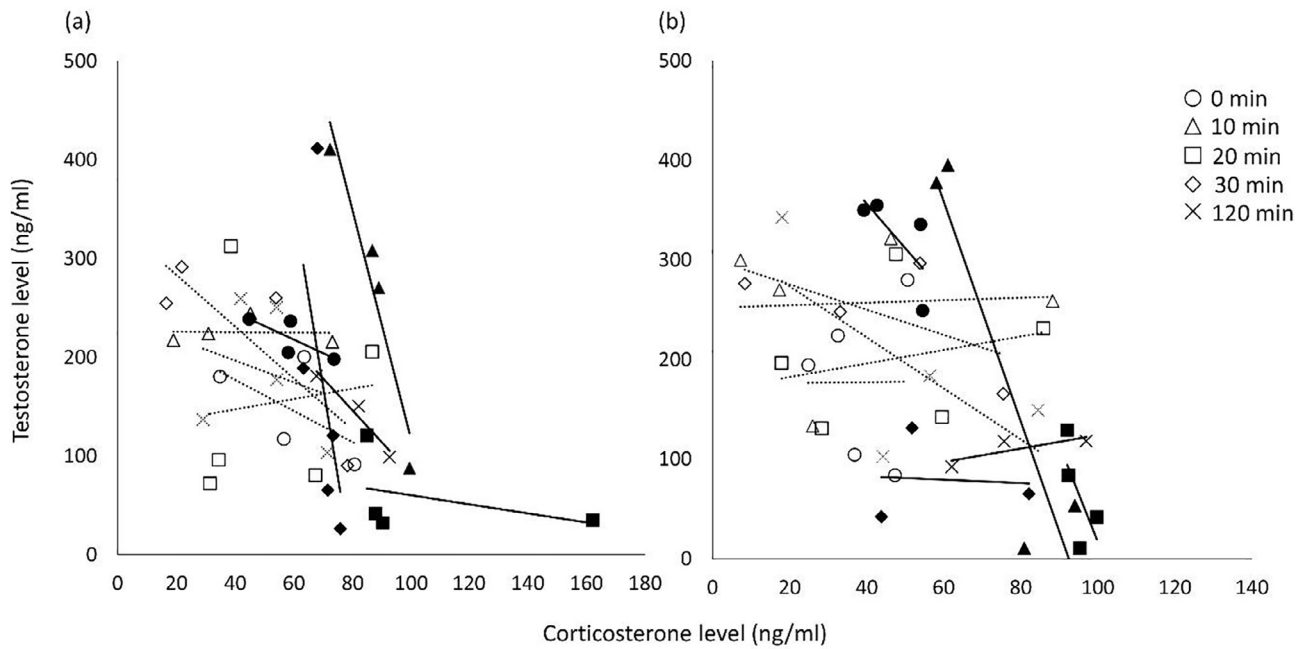


Fig. 5. Correlation between corticosterone and testosterone levels (ng/ml) in males of *Psammophilus dorsalis* from suburban (closed symbol) and rural (open symbol) areas at various time points after social interactions with (a) a male and (b) a female.

Differences in responses to and recovery from social interactions were affected significantly by population of origin of the males rather than the social context. Social behaviour and the subsequent hormonal responses between the suburban and rural populations of lizards were not due to differences in body condition or age or reproductive status. Instead these differences are more likely to be long-term (life-time) physiological and behavioural changes in response to habitat disturbance, such as shifts in predation pressure (Fischer et al., 2012), conspecific density (Kokko and Rankin, 2006), or resources (Balakrishna et al., 2016). By fragmenting natural habitats, urbanisation increases the frequency, distribution, and intensity of multiple perturbation factors that interact to influence social responses of free-living animals. Notably, in our study system, local lizard densities and territory overlap are higher in suburban areas compared to rural areas (Amdekar and Thaker, in prep). These differences in spatial distribution of potential competitors and mates could alter the intensity of social stress. High local density of conspecifics in suburban areas might lead to acclimation to many neighbours and thus lower motivation during staged courtship encounters as availability of females is high (Jirotkul, 1999; Kokko and Rankin, 2006). We have observed that along with low responsiveness during courtship encounters (this study), *P. dorsalis* from suburban habitats also have lower contrast colours during courtship displays (Batabyal and Thaker, 2017). Our finding that suburban males are less likely to engage in aggressive displays toward other males in controlled social settings is also corroborated by our observations under natural conditions, where we often find males perching close together in suburban areas (i.e. greater tolerance or habituation) but not in rural areas (Fig. 1). This less aggressive behavioural strategy, with rapid decline in testosterone levels could be an effective response to modified social stressors in urban environments.

The role of corticosterone and testosterone in responding to the demands of social interactions has been investigated in a variety of reptiles (e.g. Baird et al., 2014; Denardo and Licht, 1993; Gonzalez-Jimena and Fitzte, 2012; Kabelik et al., 2006; Knapp and Moore, 1996). Results from these studies suggest that the behavioural, physiological, and environmental context in which a social encounter occurs is key to understanding the magnitude and duration of the steroid hormones release. For example, in male Eastern fence lizards, *Sceloporus undulatus*, circulating corticosterone levels increase in response to both

male and female encounters during the breeding season but not during the non-breeding season, and only encounters with males result in an increase in plasma testosterone levels (Smith and John-Alder, 1999). In our study, circulating hormonal levels were comparable to that recorded for other lizard species that experience social or environmental challenges (Knapp and Moore, 1997; Graham et al., 2012). Notably, courtship and competitive interactions in *P. dorsalis* elicited a similar pattern of change in corticosterone and testosterone levels within suburban and rural populations (but hormonal responses differed between populations). Similar hormonal responses within populations seems to suggest that the energetic demands during both inter- and intrasexual interactions may be similar. We also find a negative correlation between corticosterone and testosterone levels in some individuals, especially at 0, 10 and 20 min after social interactions with both males and females. This negative pattern in steroid hormone levels was apparent in suburban males, but not rural males. After energetically demanding social encounters, an increase in circulating corticosterone levels in many animals helps mobilise energy and restore homeostasis (Moore and Jessop, 2003; Wingfield et al., 2001a,b). Correspondingly, for males of *P. dorsalis* from the suburban habitat, we find that testosterone levels decline as corticosterone increases, a response which has been hypothesized in other systems to minimize the re-occurrence of immediate and energetically demanding social behaviour (Moore and Jessop, 2003; Wingfield et al., 2001a,b).

Differences in the intensity of behavioural responses and steroid hormone release between suburban and rural males raises an interesting contrast in social strategies, akin to alternative coping styles (sensu Koolhaas et al., 1999). In a study by Knapp and Moore (1996), males of the less aggressive orange morph of the tree lizard, *Urosaurus ornatus*, show elevated plasma corticosterone levels and depressed testosterone levels after winning a staged male-male encounter. In contrast, the more aggressive orange-blue territorial morphs of *U. ornatus* show no elevation in plasma corticosterone and no decline in plasma testosterone levels, similar to males who had not engaged in social interactions (Knapp and Moore, 1996). We find that individuals of *P. dorsalis* from one suburban population seem to have a strategy similar to a “reactive coping style” shown by non-aggressive or non-territorial individuals of other species, typified by low aggression, high corticosterone levels, and weakly sustained testosterone levels

(Denardo and Licht, 1993; Koolhaas et al., 1999). A typical male in the natural habitat would need to respond to competitive encounters with high aggression, generally mediated by an elevation in testosterone. Individuals of *P. dorsalis* from our rural study population show this “proactive coping style”, with high behavioural reactivity, low corticosterone, and sustained levels of testosterone (Koolhaas et al., 1999). Frequent competitive encounters during the breeding season is known to inhibit corticosterone elevation in other lizard species (Knapp and Moore, 1996), which enables testosterone release to be more responsive to immediate social requirements. Thus, when the demand for aggressive encounters is high, it can be energetically efficient and necessary to down-regulate adrenocortical responses (Moore and Jessop, 2003; Wingfield and Sapolsky, 2003). Studies on *Sceloporus undulatus* also find a positive correlation between plasma corticosterone levels and high territory overlap of males and females, similar to the pattern of stress hormone responses that we observe in the males of *P. dorsalis* from suburban areas where multiple males and females are found in close proximity (Haenel et al., 2003; John-Alder et al., 2009). Although our measurements of hormonal and behavioural reactivity were obtained under controlled laboratory conditions and thus may be lower compared to levels exhibited by lizards in the wild, these data reflect interesting relative differences in coping styles between these two populations. Here we suggest that the suite of changes due to urbanisation, which includes a change in the intensity of social stressors, can alter the social coping styles of lizards from the typical “proactive” form to a “reactive” form likely modulated by overall higher corticosterone levels. Differences in social strategies in suburban lizards could result in the reduction of sexual selection opportunities, opening up interesting avenues to test effects of social and environmental stress on mating strategies and fitness in an urbanised world.

Acknowledgements

We would thank Shashank Balakrishna for help in the field.

Funding

This work was supported by DBT-IISc partnership program, DST_FIST, and University Grants Commission (fellowship for AB).

Ethical standards

This species is not covered under the Schedules of the Indian Wildlife (Protection) Act; therefore, collection permits are not required. All capture, handling and experimental protocols were approved by the Institutional Animal Ethics Committee at the Indian Institute of Science (CAF/Ethics/394/2014).

Declaration of interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ygcen.2018.10.007>.

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