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# An Introduced Competitor Elevates Corticosterone Responses of a Native Lizard (*Varanus varius*)

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## ABSTRACT

Glucocorticoid hormone profiles are increasingly used as physiological markers to infer the strength of species interactions that can influence fitness and ensuing population dynamics of animals. Here we investigated two aims. First, we measured the effect of a 90-min capture stress protocol on the plasma corticosterone responses of a large native Australian lizard, the lace monitor (*Varanus varius*). Second, we compared the basal and postcapture stress corticosterone responses of lace monitors in habitats where they were exposed to high or low densities of the European red fox (*Vulpes vulpes*), an introduced competitor. Lace monitors responded to the capture stress protocol by significantly increasing plasma levels of corticosterone above basal at 45- and 90-min-postcapture blood-sampling intervals. In habitats with high fox densities, lace monitors produced a significantly greater basal and capture-stress-induced corticosterone response compared to individuals in low-fox density habitat. A significant interaction among fox density, time postcapture, and body condition was also found to influence plasma corticosterone values. These results suggest competition with red fox, perhaps via nutritional stress and increased hypersensitivity of the adrenocortical axis in lizards. At present, without further research, we do not understand whether such responses mediate lizard fitness or whether they have adaptive or maladaptive consequences for lizard populations in response to red fox competition. Never-

theless, our results help broaden understanding of the physiological implications arising from species interactions and specifically how introduced competitors could mediate diverse impacts on native biodiversity.

## Introduction

Responses in individual- or population-level glucocorticoid (GC) levels are commonly used physiological markers to infer ecological-, evolutionary-, or conservation-related processes of vertebrates (Wingfield et al. 1998; Wikelski and Cooke 2006; Busch and Hayward 2009; Crespi et al. 2013). The rationale underpinning such inference rests on the notion that GC hormones are extremely important in the regulation of complex allostasis (i.e., processes of achieving homeostasis) in vertebrates (McEwen and Wingfield 2003; Romero 2004). Individual variation in GC production to internal or environmental stimuli (e.g., predation pressure) indicates differential investment of resources into an individual's physiology and behavior to maintain allostasis (Ricklefs and Wikelski 2002; Landys et al. 2006; Bonier et al. 2009). Basal or acute stress GC responses to environmental variation can act on behavior or physiology to adjust an individual's phenotype to challenging environmental conditions that can influence its performance or fitness (Ricklefs and Wikelski 2002; Landys et al. 2006). Increasingly, empirical studies report strong causation or correlations among individual- or population-level GC measures and vital rates (e.g., survival; e.g., Romero and Wikelski 2001; Blas et al. 2007). In lieu of more logistically demanding and expensive direct population assessment methods (e.g., mark-recapture studies), the use of GC measurements represents an appealing holistic physiological marker that may correlate with animal fitness or population status (Sheriff et al. 2011).

Elevation of GCs due to stressors can have broadscale phenotypic effects on an individual's performance by the promotion or inhibition of many physiological and behavioral attributes (Sapolsky et al. 2000; McEwen and Wingfield 2003; Romero 2004). Organismal responses from acute elevation of GCs during short-term stressors broadly include increased mobilization and sequestration of energy and activation of diverse behaviors that enable individuals to avoid or mitigate impacts of stressors (Wingfield et al. 1998). Specific responses include elevated glucose production for increased activity and vigilance and inhibition of reproductive and social behaviors (Wingfield et al. 1998; Sapolsky et al. 2000). The acute stress

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response is aptly termed the “emergency life-history stage” to reflect the extent that GC-mediated effects cause holistic reorganization of the phenotype (Wingfield et al. 1998, p. 191). The ultimate consequence of acute elevation in GCs is to potentially influence an individual’s fitness (Love and Williams 2008; Jessop et al. 2013), where fitness, higher or lower, is dictated by the extent that the individual’s GC-mediated phenotype is matched to prevailing environmental conditions (Sheriff and Love 2013; Patterson et al. 2014). Prolonged or chronic stressors caused by long-term uncontrollable and unpredictable factors in the environment can result in sustained elevation of GCs that also trigger adaptive or maladaptive consequences pending context (Romero et al. 2009; Boonstra 2013).

Strong species interactions (e.g., predation, parasitism, and competition) are increasingly viewed as key ecological mechanisms that can elevate physiological stress of animals (Boonstra et al. 1998; Rouf et al. 2006; Creel et al. 2007; Travers et al. 2010; Anson et al. 2013; Clinchy et al. 2013). In particular, predator-prey interactions demonstrate how predators can induce elevated GC levels in prey (Clinchy et al. 2013). This can occur either as a fear response (i.e., predator stress hypothesis) or from predators causing prey to decrease foraging to increase vigilance (i.e., predator-sensitive foraging hypothesis; Boonstra et al. 1998; Creel et al. 2007; Thaker et al. 2010). Decreased foraging time induces nutritional stress through reduced body condition and again elevates GC stress hormone levels (Boonstra et al. 1998; Creel et al. 2007). Elevated GC hormones, reduced nutrition, or lowered body condition can induce physiological dysregulation, enabling predators to decrease prey fitness via reduced reproductive success or lowered survival (e.g., stress-induced immunosuppression; Creel et al. 2007; Sheriff et al. 2009; Travers et al. 2010; Clinchy et al. 2013). Ultimately, these physiological responses constitute sublethal predation costs that add to a predator’s direct kill rate and inflate demographic impacts to prey populations (Creel et al. 2007; Travers et al. 2010; Clinchy et al. 2013).

Introduced species are globally recognized for their capacity to produce strong biotic interactions that could influence physiological responses in native species (Gurevitch and Padilla 2004; Sax and Gaines 2008; Graham et al. 2012). Novel traits of invaders and a commensurate lack of coevolution in native species can result in extremely strong and asymmetrical species interactions (Salo et al. 2007; Sax and Gaines 2008). Altered GC responses could serve as an important indicator of the degree of physiological impact that occurs between introduced species and native species (Berger et al. 2007; Graham et al. 2012). For example, native species exposed to strong asymmetrical resource or interference competition from introduced species could lead to reduced resources or injury that could produce large GC-mediated consequences that further impact phenotypic performance or fitness (Palomares and Caro 1999). To date there have been few studies that have attempted to use GC levels as a marker for inferring competitive dynamics between native species and introduced species (Berger et al. 2007; Graham et al. 2012; Anson et al. 2013; Narayan et al. 2013).

We addressed two aims investigating causes of variation in the corticosterone responses in the lace monitor lizard (*Varanus varius*). This predatory reptile is widely distributed across eastern Australia and because of its large body size functions as a mid- (i.e., mesopredator) to high-order predator in forest ecosystems (Jessop et al. 2012a; Smissen et al. 2013). First, we evaluated whether levels of corticosterone in the lace monitor were responsive to a capture stress protocol. This protocol provides an important validation step necessary to determine whether plasma levels of corticosterone are a responsive physiological marker to external stressors. This is especially important in large reptiles, which can exhibit relatively slow or reduced plasma GC responses (relative to smaller reptiles and other vertebrates) to capture stress protocols, potentially making GCs less useful for gauging the effects of environmental perturbations (Jessop et al. 1998, 2004b, 2013).

Our second aim considered that because the lace monitor’s diet can substantially overlap with other native and introduced predators, it is potentially exposed to resource competition (Triggs et al. 1984; Jessop et al. 2010). In particular, competition with the introduced European red fox (*Vulpes vulpes*) could have multiscale physiological implications for lace monitors (Anson et al. 2013). Our previous research has begun to examine competitive interactions between these two species and indicated that in low-fox density habitats, an advent of conservation management (i.e., lethal poison baiting) caused increased lace monitor densities (Anson et al. 2014). Furthermore, phenotypic differences including significantly reduced body condition also suggested resource competition in habitats where introduced red fox densities are high (Anson et al. 2013). However, it remains unknown whether competition could also directly affect the adrenocortical stress responses of lace monitors or whether competition-induced effects on lizard body condition, a putative mechanism for regulating adrenocortical responsiveness in many vertebrates, also further explains variation in plasma corticosterone responses of lizards (Romero 2004). To investigate these aims, we studied lace monitors across adjacent habitats that possessed high and low red fox densities and associated differences in competitive interactions.

## Material and Methods

### Study Species

The lace monitor is a semiariboreal diurnal reptile that hunts on the ground and in trees. Weighing up to 14 kg, it is the second-largest native predator (after the dingo [*Canis dingo*]) in eastern Australia (Weavers 1988; Guarino 2001). Its activity is seasonal, with home range varying from 185 ha in summer to zero in winter, when animals are inactive (Guarino 2002).

In Australia, a paucity of study means there is little evidence for how large native reptile predators, including varanid lizards, are impacted by introduced carnivores (e.g., red fox, feral cat [*Felus catus*]; Sutherland et al. 2011; Anson et al. 2014).

However, in some habitats there is good evidence for high dietary overlap between native predators and introduced predators (Sutherland et al. 2011). Resource overlap could impose resource competition between varanid lizards and introduced carnivores (Sutherland et al. 2011; Anson et al. 2013). In our study system, adult lace monitors and red fox share extensive dietary overlap in prey, especially for the ringtail possum (*Pseudocheirus peregrinus*; Triggs et al. 1984; Jessop et al. 2010). Moreover, the approximately eightfold-higher field metabolic rate of the red fox indicates their need to consume a much greater mass of food per capita than lace monitors (Nagy et al. 1999; Jessop et al. 2010; Sutherland et al. 2011). This large energetic disparity further suggests that the red fox can exert very strong resource competition on lace monitors (Sutherland et al. 2011).

Intraguild killing consequences of interference competition or direct predation are additional interactions that can occur between sympatric predators (Palomares and Caro 1999). However, killing of lace monitors by red fox is unlikely in our study system. This is because direct interactions between both predators are limited by large temporal and, to some extent, forest strata (i.e., spatial) differences in their daily habitat use. Lace monitors are diurnal and semiarboreal, while the red fox is nocturnal/crepuscular and ground dwelling in habits (Meek and Saunders 2000; Guarino 2002). Furthermore, dietary study suggests that predation by the red fox on lace monitors (or vice versa) is not recorded in our study system (Triggs et al. 1984; Jessop et al. 2010). Thus, resource competition, as opposed to killing/predation, is implicated as the primary interaction between lace monitors and red fox.

#### Field Protocols

During the summer (November–February) of 2008–2009 (aim 1) and 2010–2011 (aim 2), we captured wild lace monitors in coastal forests covering 42,000 ha in the Cape Conran Coastal Park and adjacent Murrungowar State Forest in East Gippsland, Victoria, Australia (37°48/S, 148°52/E). Here, lizards inhabit coastal forests comprising Banksia woodland, heath, and lowland eucalypt forest. All lizards were visually located while moving through habitat on foot or in a vehicle driving along forest management tracks. On sighting, we approached and captured each lizard using a long pole fitted with a noose rope. Once secured, the lizard was then restrained with duct tape around the mouth and limbs and placed into a canvas sack. Three (aim 1) or two (aim 2) consecutive blood samples (1 mL) were then collected from the ventral caudal vein of each lizard using a 21-gauge needle and a 3-mL syringe and placed into a lithium heparin container (BD microtainer tubes, BD Vacutainer Systems, Franklin Lakes, NJ) and stored on ice. Once back at camp (~3 h) samples were centrifuged (5,000 rpm for 5 min) and the plasma was removed and stored at –20°C until corticosterone assay. All animals were individually identified with a passive integrated transponder to prevent repeat sampling of individuals beyond the first capture. On completion of experiments, animals were released at their location of capture.

#### Experimental Protocol for Aim 1

We captured 12 individual adult lizards from forest adjacent to a campground where lace monitors were in high density (Jessop et al. 2012a). A capture stress protocol similar to that utilized in many vertebrate studies was adopted to activate the adrenocortical axis of lace monitors (Wingfield et al. 1983; Elsey et al. 1991; Jessop 2001). Capture stress incorporates the combined disturbances of capture, restraint, and blood sampling until being released. This stress protocol has been effectively used in many reptiles to stimulate their adrenocortical axis (e.g., turtles [Aguirre et al. 1995; Cash et al. 1997], lizards [Dunlap and Wingfield 1995], crocodiles [Jessop 2003]). The response to capture stress was measured by taking three sequential blood samples from individual adult lizards at 0, 45, and 90 min postcapture. Time 0 constituted basal blood samples collected within 2–5 min of locating, noosing, and restraining the lace monitor. After blood sampling, each lizard had its length and body mass recorded, and these were used to calculate individual body condition scores representing the residuals obtained from the regression of both log-transformed metrics.

#### Experimental Protocol for Aim 2

We captured 36 individual adult lizards exposed to either high- ( $N = 18$ ) or low- ( $N = 18$ ) fox density treatments in natural forest. Using methods described above, we collected a basal and 90-min-postcapture blood sample to measure plasma corticosterone responses of lace monitors.

Habitat manipulation of fox densities was achieved by the presence (i.e., low-fox density treatment) or absence (i.e., high-fox density treatment) of lethal fox baiting undertaken by the Department of Sustainability and Environment, Victoria, Australia (Murray et al. 2006; Dexter and Murray 2009). This conservation program (in which our study was conducted) comprised two poison-baited habitat sites and two non-poisoned-baited (i.e., control areas) habitat sites. The area of these four sites ranged from 7,000 to 12,000 ha. Fox suppression was achieved by ongoing deployment of Foxoff Econobaits (Animal Control Technologies, Melbourne), prepoisoned with 3 mg sodium fluoroacetate (“1080” poison). This dose of sodium fluoroacetate is lethal to canids but nontoxic to varanid lizards (McIroy et al. 1985; Twigg and King 1991). Nonlethal baits were also placed within the two control treatment sites to enable comparison of fox bait take between treatments. At the time of study, 10 yr of sustained fox baiting has resulted in a fivefold lower bait take and, by inference, similarly reduced fox density in poison-baited habitats compared to control areas (Murray et al. 2006).

#### Radioimmunoassay

We measured total corticosterone in lace monitor plasma using radioimmunoassay techniques identical to those of Jessop et al. (2012a). Plasma samples (100  $\mu$ L) of lace monitors were

extracted for corticosterone concentrations using a corticosterone 3H kit (MP Biomedicals). Final steroid concentrations were calculated from standard curves and corrected for individual sample recovery, individual plasma volume, and the addition of tritiated steroid. Average ( $\pm$  SE) sample recovery was  $75.7\% \pm 0.028\%$ , with an intra-assay coefficient of variation (CV) of 7.6% and an interassay CV of 13.04%. The antibody had 100% cross reactivity with corticosterone, 11% with 11-Dehydrocorticosterone, 7% with 11-Deoxycorticosterone, and <1% with the following steroids: progesterone, cortisol, aldosterone, testosterone, pregnenolone, and 5 $\alpha$ -DHT.

### Statistical Analysis

For aim 1 we used a full-factorial generalized linear mixed-effect model (GZLMM) to evaluate the effects of time, body condition, and their interaction on plasma corticosterone values. This model was fitted with a Gaussian distribution and an identity canonical link. The structure of the correlation matrix was of an individual function, and individual lizard ID was used as a random effect to account for repeated measures. For aim 2, we again used GZLMM (with the same conditions listed above) and tested for the effects of fox density, time after capture, body condition, and then interactions between fox density and time and fox density, time, and body condition on plasma corticosterone values. Post hoc tests were conducted to determine where statistical significance was obtained within main effects. As both samples (aims 1 and 2) comprised individuals that were strongly biased toward males (a likely advent of sex life-history mortality), we did not consider sex as an additional effect in either model. Statistics were performed using SPSS V.21 (IBM).

## Results

### Aim 1

The capture stress protocol resulted in a linear increase in lizard plasma corticosterone concentrations over the 90-min duration (GZLMM: Wald  $\chi^2 = 25.39$ ,  $P < 0.001$ ; fig. 1). Post hoc tests indicated that among sampling time intervals, basal corticosterone levels differed from the 45-min- ( $P = 0.040$ ) and 90-min- ( $P = 0.001$ ) postcapture values. However, concentrations did not differ significantly between the 45- and 90-min-postcapture intervals ( $P = 0.105$ ). There was no significant effect of an individual's body condition (GLZMM: Wald  $\chi^2 = 1.234$ ,  $P = 0.267$ ) nor was there a time-by-body condition interaction response (GLZMM: Wald  $\chi^2 = 0.17$ ,  $P = 0.917$ ) on lace monitor plasma corticosterone levels.

### Aim 2

Lizards captured in high-fox density habitat had significantly greater corticosterone levels compared to individuals in low-fox density habitats (i.e., due to introduced predator suppression; GZLMM: Wald  $\chi^2 = 6.17$ ,  $P = 0.013$ ; fig. 2*b*). Again, basal and 90-min-postcapture stress corticosterone values were significantly different from one another (GZLMM: Wald

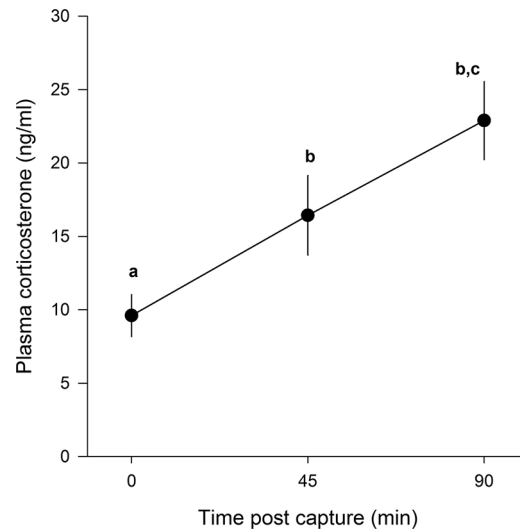


Figure 1. Relationship between plasma corticosterone and time after capture in lace monitors. The results report the mean and standard error of plasma corticosterone levels measured from 12 individuals at three repeated sampling events. The letters denote post hoc differences among corticosterone levels at the three time periods.

$\chi^2 = 18.13$ ,  $P < 0.001$ ; fig. 2*a*). Body condition as a main effect did not cause significant differences among corticosterone values in lizards (GZLMM: Wald  $\chi^2 = 0.82$ ,  $P = 0.775$ ). There was a significant fox density-by-time interaction effect on plasma corticosterone values (GZLMM: Wald  $\chi^2 = 46.85$ ,  $P < 0.001$ ). Here lizards captured in high and low fox density had significant differences in their basal ( $P = 0.04$ ) and 90-min-postcapture ( $P < 0.01$ ) stress corticosterone values (fig. 2*a*). There was also a significant three-way interaction effect among fox density, time postcapture, and body condition in lizards (GZLMM: Wald  $\chi^2 = 8.14$ ,  $P = 0.043$ ). Post hoc testing indicated that significance in this interaction was attained by corticosterone levels in lizards occupying high-fox density habitat sampled at 90 min postcapture that negatively covaried with an individual's body condition (fig. 2*b*).

## Discussion

GC hormones, because of their ability to regulate many traits, have considerable influence on animal performance and fitness (Wingfield et al. 1998; Crespi et al. 2013). Understanding how invasive species physiologically affect native species could provide important insights into their applied ecology or conservation needs (Wikelski and Cooke 2006; Busch and Hayward 2009; Seebacher and Franklin 2012). With respect to competition between native species and introduced species, inference from GC responses could help indicate the degree of coexistence between introduced competitors and native competitors and hence help evaluate short- or long-term impacts of competition dynamics, a major area of conservation management prioritization and investment (Heard and Sax 2013).

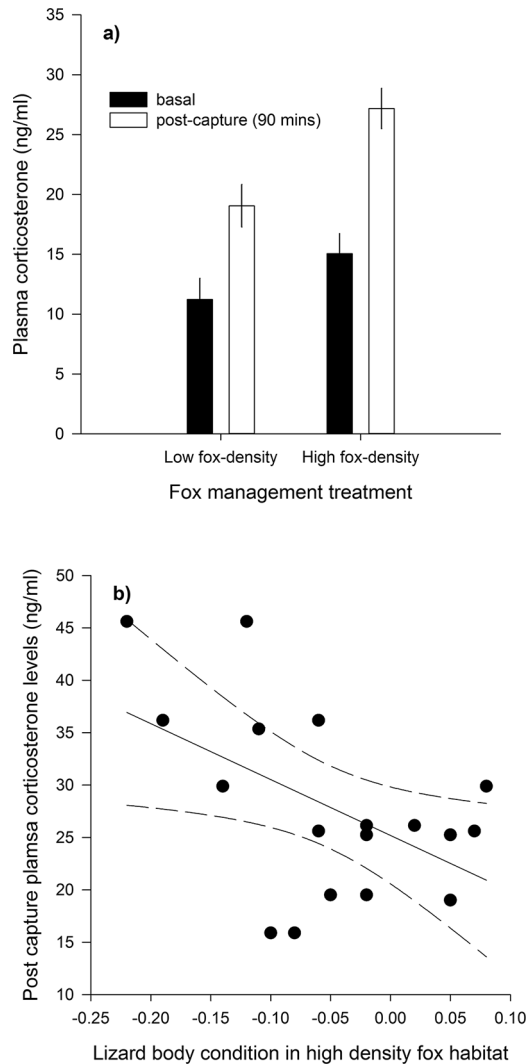


Figure 2. *a*, Comparison of corticosterone levels of lace monitor lizard captured in habitats of high and low fox densities and at basal and 90-min-postcapture time periods. The results report the mean and standard error of plasma corticosterone levels measured from 18 individuals at each fox density treatment. *b*, A scatterplot reporting the significant interaction between capture stress, body condition residual, and high fox density on plasma corticosterone levels of lace monitors. The regression line and associated 95% confidence intervals report the mean predicted response of plasma corticosterone levels as a function of lizard body condition in high-fox density habitat.

We demonstrated that the adrenocortical response of lace monitors was activated by a capture stress protocol as corticosterone synthesis significantly increased with time postcapture. Our capture stress protocol combined the effects of capture, restraint, and serial blood sampling, all components that individually, or cumulatively, can activate the hypothalamopituitary-adrenal (HPA) axis in vertebrates (Wingfield et al. 1997). Increases in plasma corticosterone occurred predominantly over the initial 45-min-postcapture duration. As corticosterone levels had yet to return to basal by 90 min postcapture, it suggests that additional time is needed for negative

feedback to downregulate the HPA axis and decrease plasma corticosterone levels (Romero 2004). Thus, the cadence of the acute stress response could be considered relatively slow in responsiveness and similar to that observed in other large reptiles including seas turtles, crocodiles, snakes, and lizards (Jessop 2001; Jessop et al. 2003, 2004; Romero and Wikelski 2006; Dupoue et al. 2013).

Our results indicated that basal and stressor-induced sensitivity of the adrenocortical axis of lace monitors was influenced by the prevailing habitat density of an introduced competitor, the red fox. Basal corticosterone levels exhibited a significant increase in high-fox density habitats. Such a response could potentially signal reduced food intake or a sustained nutritional or energetic stressor confronting lace monitors in such habitats (Anson et al. 2013). Additionally, increased activity, whereby lace monitors are required to exert higher foraging activity to locate fewer prey in heavily contested high-fox density habitat, could contribute to elevated basal corticosterone levels. Once elevated, basal GC levels promote the energy mobilization needed for heightened metabolic demands during physical activity in vertebrates (Romero 2004; Hamann et al. 2007; Malisch et al. 2007). We think that at their time of capture (between 10 a.m. and 4 p.m.), most lizards were/had been exhibiting some level of activity (i.e., slow walking, with intermittent bouts or resting/basking), suggesting intermittent but low aerobic activity that could influence basal corticosterone levels. Unfortunately, we had little capacity to directly measure levels of individual lizard activity before capture and thus did not incorporate activity as a potential covariate in our analyses. However, for future research that aimed to consider the possible effects of daily activity on lizard basal corticosterone levels, we advocate the use of telemetry to quantify individual movement rates (i.e., an index of activity) before capture and blood sampling (Seebacher and Grigg 2001; Imansyah et al. 2008). These data could then be considered as a covariate in subsequent analyses to directly evaluate the effects of activity on lace monitor corticosterone levels.

Lizards in sites with high fox density also had higher corticosterone responsiveness to the capture stress protocol compared to those from low-fox density sites. Elevated GC responses again suggested that in high-fox density habitats lace monitors are subjected to greater levels of competition (Jessop et al. 2010; Anson et al. 2013). An energetic basis to increased hypersensitivity in acute stress response was also suggested by the significant covariation between lizard plasma corticosterone levels and their body condition. Poor body condition is a commonly ascribed process that can lead to elevation in both basal and stress-induced corticosterone levels in vertebrates (Barton et al. 1987; Kitaysky et al. 1999; Moore et al. 2000; Romero 2004). The rationale for increased adrenocortical hypersensitivity in poor-conditioned animals is to presumably compensate the need for increased energetic demands when animals are under nutritional stress (Jessop et al. 2002, 2004a).

Predators demonstrate how through both nutritional/energetic (i.e., predator-sensitive foraging hypothesis) and fear (i.e., predator stress hypothesis) stressors that they can increase HPA activation in their prey (Boonstra et al. 1998; Boonstra

2013; Clinchy et al. 2013). Nominally, because sympatric predators not only compete but also potentially kill (i.e., predation or interference competition) one another, both nutritional and fear stressors could also explain elevated GC responses in the inferior competitor (Palomares and Caro 1999). Nevertheless, we strongly suspect that hypersensitivity in GC responses of lace monitors in high-fox density habitat is due to nutritional stress and not fear. This reasoning is suggested by a lack of dietary evidence for predation by red fox on lace monitors (Triggs et al. 1984). Further, the large degree of temporal and spatial niche separation between lace monitors and red fox limits their direct contact (Meek and Saunders 2000; Guarino 2002). Thus, if the risk of predation is extremely low, it logically precludes fox from causing fear-induced stress in lace monitors.

Given that variation in adrenocortical responsiveness can be induced by many internal and external stimuli, how certain are we that the observed differences in corticosterone responses of lace monitors are due to resource competition with fox (Dunlap and Wingfield 1995; McEwen and Wingfield 2003; Romero 2004)? The most compelling evidence is that our study is conducted using a landscape-scale manipulation of fox density across replicated sites (Murray et al. 2006). This experimental design controls for the possibility that other spatially variable factors (e.g., prey density, habitat disturbance, anthropogenic stressors) that increase the adrenocortical responses of lizards are minimized (French et al. 2008). Additionally, lizards were sampled across fox density treatments using highly consistent field protocols to ensure that similar experimental conditions (e.g., equal sample effort among treatments and consistent time of blood sample collection) were faced by all individuals. These experimental attributes greatly add to the weight of evidence that fox-induced competition was the most parsimonious explanation for differences in adrenocortical responses of lace monitors.

Is hypersensitivity in the lace monitor HPA axis an adaptive response in high-fox density habitats, especially as resource competition with the red fox nominally represents an ongoing and chronic stressor? In wild animals subjected to anthropogenic or natural chronic stressors, two opposing but adaptive responses in the HPA axis may occur. First, animals exposed to prolonged human-mediated disturbances can mount reduced stress responses in order to minimize the disadvantages thought to be associated with chronically elevated GC levels (Romero and Wikelski 2002; Partecke et al. 2006; Walker et al. 2006; Payne et al. 2012; Owen et al. 2014). Second, Boonstra (2013) argues that in certain contexts chronic elevation and hypersensitivity in basal and acute stress GC levels of prey in coevolved predator-prey systems are adaptive, as elevated GC levels can promote survival and maternal programming of prey to reduce predation risk (Boonstra et al. 1998; Sheriff et al. 2009). In lace monitors, elevated basal and acute corticosterone stress levels in high-fox density habitats suggested that their HPA axis response is also similar to some predator-prey examples. Similarly, as lace monitors have persisted for ~35 generations since introduction of the red fox, it may also suggest that these lizards have evolved adaptive coexistence with this competitor. There are an increasing number of examples of

rapid evolution occurring on ecological timescales that permit species to persist in novel environments (Carroll et al. 2007). Changes in responsiveness of the HPA axis are likely to be a key process that permits broadscale phenotypic adaptation of vertebrates to novel environmental conditions, including persistence with introduced species (Jessop et al. 2012b). Thus, as with Boonstra's (2013) assertion, our interpretation of elevated GC responses in lace monitors is also not aligned with classic biomedical and theoretical expectations of chronic HPA axis activation, which is considered maladaptive (McEwen and Wingfield 2003; Romero et al. 2009).

Clearly, to now understand any long-term fitness and adaptive consequences of hypersensitivity in the HPA axis of lace monitors, we must conduct further research (Malisch et al. 2007). Similar to studies on other large varanid lizards (e.g., Komodo dragons [*Varanus komodoensis*]), we advocate undertaking an extensive mark-recapture study that would permit estimates of recruitment, survival, and population growth (i.e., measures of fitness and population-level adaptation; Jessop et al. 2007; Purwandana et al. 2014). Then, using an information-theoretic approach, we could compare different models that evaluate the effects of habitat-based (e.g., fox management, habitat quality, prey availability) and individual-based (e.g., body condition, basal and acute stress GC levels [total and free measures]) phenotypic parameters on the estimates of lizard immunocompetence, fecundity, recruitment, survival, and population growth (Sinervo and Licht 1991; Berger et al. 2005; Blas et al. 2007; Malisch et al. 2009; Anson et al. 2014; Patterson et al. 2014). If models that considered GC level parameters were ranked highest, it would suggest their importance for affecting lace monitor fitness (e.g., immunocompetence, fecundity, survival, or recruitment) and population growth. Most importantly, if we found that elevated GC levels in lizards occupying high-fox density habitat also maintained stable or positive population growth rates, then we would assume the HPA responses to be adaptive. Conversely, if elevated GC levels were associated with negative population growth, then we would assume the response maladaptive.

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