Glucocorticoids (GCs) are used as biomarkers of physiological stress response in reptiles. Fundamental stress physiology tools including the emergency life history stage (ELHS) and the reactive scope model (RSM) can be useful to determine how individual variation of stress responses shape population ecology. In this perspective, we applied the RSM and ELHS into the context of two urban-dwelling small native Australian reptile species to compare the stress-response patterns in short- and long-breeding lizards. Firstly, by drawing inferences from the ELHS, we presented hypothetical scenarios using sample GC data for a short-breeding species (e.g. common blue-tongue lizard). We showed that activation of the physiological stress response would be non-adaptive due to the consequences of stress on reproduction. Therefore, blue-tongue lizards may become exposed to acute and chronic environmental stressors (e.g. human disturbance and habitat clearance) during the breeding season as they prefer not to activate their hypothalamo-pituitary interrenal (HPI) axis in support of their short-breeding season. On the contrary, long-breeding lizards (e.g. bearded dragons), which have multiple breeding opportunities and are accustomed to living around humans and altered urban environments, tended to operate above the critical adaptive value of the ELHS during their breeding period. This suggests that any future changes to the dynamics of habitat availability and breeding opportunities may favour the dragon differently over the blue-tongue lizard. To further capture the dynamics of stress responses along spatial and temporal scales, we suggested that researchers should collect field data (e.g. blood plasma or faecal GCs) and then use the ELHS and RSM to understand how the environment is shaping the animal’s stress physiology. The application of field stress monitoring and data visualization using the ELHS and RSM could guide environmental monitoring and conservation programs of native wildlife species.

Key words: survival, stress, reproduction, reactive scope model, glucocorticoids, Emergency life history stage

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Introduction

Australia’s ‘megadiverse’ landscape has unique wildlife biodiversity, with 87% of mammal species, 93% of reptiles, 94% of frogs and 45% of bird species only found in Australia (Chapman, 2008). Australia’s unique biodiversity is declining rapidly, with more than 1700 species known to be threatened and at risk of extinction. Human-induced environmental change is one of the biggest environmental threats facing Australian wildlife (Brearley et al., 2009). Further research is needed on causal relationships between environmental factors and host stress physiology (Narayan, 2017).

Recent data from wildlife hospitals and rescue centres in Australia indicate that, over the years, more and more reptiles are being rescued in urban areas due to anthropogenic-induced environmental factors such as habitat disturbance and vehicle collision (Scheelings, 2015; Taylor-Brown et al., 2019). In this perspective article, using hypothetical data, we provide new insights into the potential applications of fundamental stress physiology theory and models in native species conservation and management programs. We will use examples of two local native Australian reptilian species (lizards) to show how stress physiology data when integrated with fundamental concepts, the emergency life history stage (ELHS) and reactive scope model (RSM) could increase our knowledge of species response to extreme environmental change.

Stress, Stressors and Stress Response

Stress is an inevitable part of an animal’s life because of the rapidly changing dynamics of time and space of the environment that it inhabits (Monaghan and Haussmann, 2015). Many of the extrinsic factors that an animal comes across throughout its life history, such as circadian cycles, passing of the seasons, tidal cycles and so forth, are predictable due to intrinsic biological and evolutionary mechanisms such as biological clocks, biological (circadian and seasonal) rhythms, specific movement patterns, activity patterns, etc. These mechanisms allow an animal to cope with predictable changes or, in other words, to survive (Guindre-Parker, 2020; Monaghan and Haussmann, 2015). The physiological stress response is also an important biological mechanism that enables animals to cope with natural and anthropogenic-induced environmental changes (Wingfield, 2013a).

The Concept of Stress and Stressors

A distinct definition of stress cannot be found in the literature and this ambiguity is primarily due to two reasons: firstly, as explained by Berkvens (2012), the concept of stress is complex with synergistic interactions among several intrinsic (animal related) and extrinsic (environmental related) factors that are difficult to ascertain, and hence the definition of stress is vague. Secondly, ‘stress’ is employed to characterize a number of related but distinctly different phenomena (Tokarz and Summers, 2011). This view is supported by Guillette et al. (1995) and Romero (2004), which explains that stress is used to refer to (i) external pernicious stimuli-causing stress, (ii) state of strain produced by the organism due to these stimuli and (iii) overexertion of stress responses causing bodily deteriorations. Although the aforementioned phenomena are closely related to each other, using the same term for defining different phenomena is the reason why ‘stress’ lacks a clear definition (Denardo, 2006).

As described by Selye (1950), this is an individual’s physiological (and behavioural) response to a noxious stimulus, and thus a stimulus that might induce a response from one individual might not induce a response from another individual of the same and/or different species (see Cockrem, 2013 for an extensive review on the importance of accounting for individual variation in stress studies). For example, when a group of eastern fence lizards (Sceloporus undulatus) were exposed to invasive ants, the stress response within experimental population of lizards varied significantly (Graham et al., 2012), highlighting inter-individual differences in stress response. Furthermore, a stressor that induces a stress response at a given point of time might not induce a similar response at a different point in time for the same individual (Romero et al., 2009). For example, as shown by Moore and Mason (2001), red-sided garter snakes (Thamnophis sirtalis) elicited a stress response when manually captured during summer; however, no change in stress response was observed when captured during late spring. This intra-individual variation can thus be regarded as an example of the context-dependent nature of stress responses in animals, which is mostly associated with crucial life history stages such as breeding.

Fundamental stress physiology concepts such as the ELHS and RSM can be customized to suit a specific research program to understand the context-dependent nature of stress responses. They will also allow us to understand and predict normal variation of physiological mediators (such as GCs) over crucial life history stages (Wingfield, 1998, 2013a) and explain the impact of their variation at an inter- and intra-individual level (Romero et al., 2009).

For this review, stress is described as an imbalance in the homeostasis of an individual when it is exposed to any form of stressor (Selye, 1950). Consequently, a stressor is any external stimulus that has the potential to disrupt the homeostatic equilibrium of an individual (Pryce and Fuchs, 2017). When a stressor disturbs the homeostatic equilibrium, the body adopts several physiological (and behavioural) changes to counteract the impact induced by the stressor, and to re-establish homeostasis, and this is termed as a stress response (Denardo, 2006; Tokarz and Summers, 2011). An acute stress response may be necessary to ensure survival and allow adaptation to environmental change; however, chronic stress is a problem as significant modulation of the physiological...
stress response can threaten animal well-being by exerting deleterious effects on the individual’s biological state.

**Mechanism of Stress Response in Reptiles**

When an individual is exposed to a stressor, it makes some basic physiological (and behavioural) alterations that are common regardless of the specifics of the stressor, and these changes allow an individual to maximize its chances of survival (Denardo, 2006). These fundamental alterations involve diverting mobilized energy reserves only to those systems that are vital for survival and inhibiting the energy diversion to non-essential body systems (Denardo, 2006; Norris and Carr, 2020). When an animal is exposed to any physical and/or physiological stressor (e.g. being chased by a predator), it stimulates the paraventricular nucleus of the hypothalamus to secrete a variety of adrenocorticotropic hormone (ACTH)-releasing factors (Aguilera, 1998), of which corticotrophin-releasing hormone (CRH) (Kabelik, 2021; Silvestre, 2014; Sinervo and Miles, 2011; Tokarz and Summers, 2011) and arginine vasotocin (AVT) are of prime importance in reptiles. Predominantly, CRH (and to a lesser extent AVT) is carried to the anterior pituitary via the hypothalamic–pituitary portal system where they stimulate the corticotrophic cells of anterior pituitary to secrete ACTH (Sinervo and Miles, 2011; Tokarz and Summers, 2011). ACTH is then carried via the systemic blood circulation to the interrenal glands where it stimulates the synthesis and secretion of GCs (Carsia and John-Alder, 2003; Sinervo and Miles, 2011).

A characteristic feature in stress response of reptiles (and birds) is the secretion of corticosterone (CORT), instead of cortisol (as is the case in fish and mammals) as the primary stress GC (Berkvens et al., 2013; Scheun et al., 2018). The levels of CORT in the tissues will then rise and assist in sequestering energy to those body systems that will allow the reptile to maximize its chances of survival in that situation, either by fleeing from or fighting off the predator in that situation (Jessop et al., 2015; Neuman-Lee et al., 2020). However, as shown in the recent study by Neuman-Lee et al. (2020) the relationship between CORT and energy mobilization (e.g. glucose availability to tissues) is complex and requires further experimental validation for each species. At a cellular level CORT is thought to stimulate a decrease in cellular metabolism across the body during exposure to acute stressors, therefore transiently increasing the amount of glucose in the blood for the brain’s optimal function (see review by Kuo et al., 2015 for a detailed explanation of how GCs regulate glucose).

On a theoretical perspective, as an example, once the reptile overcomes an acute stressor, the high level of GC is identified by the GC receptors and the GC secretion is inhibited to achieve homeostasis, by inhibiting CRH and AVT secretion at the hypothalamus level and ACTH at the pituitary level via the negative feedback loop (Berkvens, 2012). The aforementioned situation is a classic example of an acute stress response; however, it is important to note that if the reptile is exposed to a stressor for a prolonged period of time (either in terms of duration and/or frequency), it will result in prolonged and/or frequent activation of the HPA axis, which will disrupt the normal functioning of the negative feedback loop mechanism and will eventually have negative impacts on its different body systems (Narayan, 2019). The mechanism of neuroendocrine stress response and its effect on body systems in reptiles is illustrated in Fig. 1. Although not discussed in this paper, it is important to note that the sympatho–adreno–medullary system and neurohormones such as catecholamines are also important aspects of acute stress responses in reptiles (Di Lorenzo et al., 2020).

**GC Plasticity and Role of Stress Physiology Models**

GC plasticity refers to the varying levels of GCs expressed by a single individual across different contexts such as different environmental perturbations (Guindre-Parker, 2020). An extensive review of the literature by Injaian et al. (2020) evaluated baseline and stress-induced CORT levels in reptiles (measured using blood plasma samples), however, could not establish a clear association between CORT and environmental stress. Cockrem (2013) also suggests that there is a significant inter- and intra-individual difference between stress responses evoked by individuals. This variation of individual responses may be influenced by several factors such as sex, pre- and post-natal life experiences, maternal influence, position in the social hierarchy, time of the year and so on (Cockrem, 2013).

Individual variation of stress response is one of the several types of GC plasticity described by Guindre-Parker (2020) and is dictated by baseline and stress-induced GC levels. GC plasticity implies that since individuals not only portray differences in baseline and acute levels of GCs, but also in magnitude of the stress response elicited by them, it is extremely important to account for individual variation when reporting results (Guindre-Parker, 2020). For example, at a population level, urban-wild reptiles might not elicit as strong of a stress response when exposed to humans (as a stressor) as compared to their wild counterparts, since the urban-wild reptiles might be acclimatized to human presence. However, within those populations different individuals might elicit varying degrees of stress response whereas some individuals might not elicit a stress response at all, depending upon aforementioned animal-related factors as well as the context of environmental perturbation (Comendant et al., 2003; Knapp and Moore, 1997; Moore et al., 1991).

Stress physiology models (explained in detail further) tend to categorize individuals based on context-dependent characteristics that can be useful for accounting individual variation.
of stress response. In their original paper, Romero et al. (2009) categorizes organisms based on different characteristics such as social status (dominant versus sub-ordinate), maternal care (handled versus unhandled) and so on. Similarly, several other studies also categorize organisms based on relative extremes (Crespi et al., 2013; Howell and Sanchez, 2011) inferring that although stress levels vary along a continuum, only extreme levels of stress (i.e. either too little or too much) are responsible for deleterious consequences. In our view, the major advantage of complementing stress quantification studies with theoretical models is that it will allow researchers to predict stress responses based on context-dependent categorization and back them up using empirical evidence (e.g. ACTH challenge test). Within a certain population, animal-related categorization—such as male versus female, adult versus juvenile, dominant versus sub-ordinate and so on—may all produce different results and thus categorizing the population based on the context of the study and using stress physiology models to predict and/or justify the results might prove of extreme importance to standardize the methods used to analyse stress and related phenomena.

**Overview of ELHS and RSM**

**Emergency life history stage**

GCs secreted by the activity of the HPA axis play a fundamental role in modulating the transition between life history stages such as hatching, metamorphosis, sexual maturity, reproduction and so on (Crespi et al., 2013). As explained by Wingfield et al. (1998) these 'normal' life history...
transitions are predictable and are thus mediated by intrinsic biological and evolutionary mechanisms such as circadian clock, seasonal cycles, etc. However, when an animal comes across an unpredictable situation (termed as ‘perturbation factors’) (see Wingfield et al., 2011a for direct/indirect labile perturbation factors and permanent perturbation factors), the normal life history stage is disrupted and an ELHS is triggered. The ELHS involves a suite of behavioural and physiological changes that allow the individual to cope with that situation, and once the perturbation has passed, the individual returns to the normal life history stage (Wingfield et al., 1998). The decision of whether or not to activate the ELHS is dependent upon the adaptive value of the ELHS, i.e. organisms are capable of eliciting a stress response or activating the ELHS only during an optimal predictable array of environmental conditions and are incapable of doing so when the environment is extremely unpredictable (highly stable environment) or not predictable at all (highly dynamic environment) (Wingfield et al., 2011b). During these extremes, the adaptive value of eliciting a stress response or entering the ELHS is below the critical adaptive value and is thus insignificant for an animal (see Wingfield et al., 2011b) (Fig. 2). This adaptive value of ELHS varies depending on different life history strategies of individuals/species/populations (Boonstra, 2013; Crespi et al., 2013), and will be discussed in detail further.

Reactive scope model

The RSM proposed by Romero et al. (2009) assists in integrating the activity of physiological mediators with unpredictable environmental changes and different life history traits, to predict the response to and impact of stressors on animals. As per the original model, the concentration of the physiological mediator fluctuates in four general ranges: Predictive Homeostasis, Reactive Homeostasis, Homeostatic Failure and Homeostatic Overload Figure (Fig. 3). The Predictive and Reactive Homeostasis range, together form the Normal Reactive Scope and fluctuation of physiological mediator beyond the Normal Reactive Scope (Romero et al., 2009). The Predictive range constitutes the predictable variation of physiological mediator (i.e. circadian and seasonal rhythms, etc.); however, when an animal comes across any noxious situation (i.e. stressor), the concentration of the physiological mediator (e.g. CORT in context of this review) increases (from predictive range to reactive range, i.e. stress response) to help cope with the stressor (Fig. 3). If the animal comes across a stressor of high magnitude, the concentration of CORT will increase beyond the upper threshold of the reactive range (surpassing the Normal Reactive Scope) (Fig. 3). Long-term exposure to stressors could result in pathology and eventually death if animals are often required to maintain the upper threshold of the reactive range. Similarly, if CORT cannot be maintained above the threshold between Homeostatic Failure and Predictive Homeostasis range, this will result in Homeostatic Failure and rapid death since the physiological mediator can no longer carry out essential physiological processes (Romero et al., 2009). The negative consequences of entering the homeostatic overload and/or homeostatic failure range have been summarized by Romero et al. (2009) in their original paper. An important caveat to note is that two stressors of equal magnitude may or may not cause CORT levels to enter homeostatic overload range depending on various intrinsic and/or extrinsic factors (e.g. life history stage) influencing the ‘normal’ variation of CORT (Romero et al., 2009).
Implication of ELHS and RSM to understand coping mechanisms in reptiles

The ELHS model can be used to predict whether or not a reptile (or any animal) would initiate a stress response (i.e. transition into an ELHS) when exposed to a stressor. This prediction is based on the adaptive value of the ELHS, which is dependent on different life history strategies that have evolved over time (Boonstra, 2013; Crespi et al., 2013). Breeding season is vital to study since it dictates an important life history stage in every animal’s life, i.e. reproduction/mating (Wingfield et al., 1998). Consider, for example, animals with short and long breeding seasons. In case of seasonal animals with a short breeding season, for example, common blue-tongue lizard (Tiliqua scincoides) whose breeding season is only during spring in Australia, there do not exist multiple opportunities to mate and raise the offspring. Since the rewards of raising the offspring prevail the benefits of activating the ELHS, the adaptive value of ELHS plummets during the breeding season to avoid the onset of ELHS. Right-hand panel: Expression of ELHS in P. barbata as an example of an animal with an long-breeding season, illustrating a slight dent in the adaptive value during the breeding season to modulate the expression of ELHS (adapted from Wingfield, 2013a). (Note: Multiple grey tracks are illustrated to indicate repeatability over several seasons/years as indicated by numbers 1–3).

With the availability of the RSM (Romero et al., 2009), researchers then have access to another powerful tool to evaluate the integration of the HPA-axis activity with unpredictable environmental changes and different life history traits, to predict the response to and impact of stressors on animals. By applying the RSM in Galapagos marine iguanas (Amblyrhynchus cristatus), Romero (2012) explains that delayed termination of stress response results in prolonged activation of ELHS and eventually causes mortality in those populations. This delayed termination of the physiological stress response results in progressive reduction of the normal reactive scope (Fig. 3) making these molecules unresponsive to stressors.
populations more vulnerable to any additional stressors. It can be inferred that in order to maximize the chances of their survival, these iguanas should either avoid any further stressors, or avoid eliciting a stress response when exposed to a stressor. The latter would be possible if the adaptive value of the ELHS was below the critical adaptive value, which would allow the animal to inactivate the transition into ELHS (Fig. 2).

Similarly, we apply the RSM to the previous example of short versus long breeding season lizards and predict their response to an acute stressor. Since common blue-tongue lizards have critically low adaptive value of transition into ELHS during the breeding season (Fig. 4), the transition to ELHS is silenced to facilitate the current bout of reproduction (reproduction wins over immediate survival). On the other hand, if the blue-tongue lizard does not silence the ELHS when exposed to an acute stressor during breeding period, this could make it vulnerable to enter into homeostatic overload (referring to the RSM) (Figs 3 and 4). This explanation is in line with the notion that the circulatory levels of physiological mediator (e.g. CORT) might already be within homeostatic range to facilitate the energetic demands of reproduction (Wingfield, 2013a; Wingfield and Sapolksy, 2003).

As explained by Wingfield (2013a), transitioning the HPA-axis response into the ELHS increases the probability of short-term survival of an animal to combat the stressor, through elevation of CORT levels (and other physiological and behavioural mechanisms); however, the probability of reproduction is decreased since majority of energy reserves will be diverted away in overcoming the stressor. Based on this, we predict that the bearded dragon could still afford to eliciting a stress response to overcome the stressor because of two main reasons: (i) it can have several opportunities to mate in the future and (ii) because it is at low risk of entering the homeostatic overload range (Fig. 3). It is, however, important to note that earlier research showed that during breeding season, the bearded dragon also tends to modulate its acute stress responses to physical stressors (e.g. capture). It will be worthwhile to carryout longitudinal monitoring (e.g. within versus outside breeding season) of the stress responses of the bearded dragon to better understand how the species operates under the fundamental theories of the ELHS and RSM.

Conclusions

The ELHS provides a powerful tool for researchers to determine how the study species utilizes its stress endocrine system during exposure to stressors. This can be evaluated by exploring the adaptive value of the ELHS and determining where the stress responses of the study species sits along the predictive range and between the lower and upper levels of the adaptive and critical adaptive values (see Figs 2 and 4). With available field endocrinology data, researchers will also be able to apply the RSM to make long-term assessments of the physiological response and adaptation of their study species across spatial and temporal scales (Fig. 3). We believe that there is a definite value in using these fundamental approaches to study the eco-physiology of native small reptiles in Australia such as the blue-tongue lizard and the bearded dragon and this data could be useful for conservation biologists and urban planners as well. For example, with the identification of the adaptive state of the stress response of the study species using the ELHS and by knowing the pattern of temporal and spatial variation in the stress response (using the RSM), researchers will know exactly whether their species is facing some underlying physiological problems (e.g. lizard species requiring to active the stress response to high levels during the breeding season due to increased severity of environmental stress). We certainly require this type of integrated approach and field endocrinology data to progress our knowledge on the stress physiology of native wildlife and also provide empirical evidence to show how species are responding to and being impacted by extreme environmental change.

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