Stress, reproduction, and adrenocortical modulation in amphibians and reptiles

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Abstract

While the hypothalamo–pituitary–adrenocortical (HPA) response to stress appears to be conserved in vertebrates, the manner in which it is activated and its actions vary. We examine two trends in the stress biology literature that have been addressed in amphibian and reptilian species: (1) variable interactions among stress, corticosterone, and reproduction and (2) adrenocortical modulation. In the first topic we examine context-dependent interactions among stress, corticosterone, and reproduction. An increasing number of studies report positive associations between reproduction and corticosterone that contradict the generalization that stress inhibits reproduction. Moderately elevated levels of stress hormones appear to facilitate reproduction by mobilizing energy stores. In contrast, pronounced activation of the HPA axis and extremely elevated levels of stress hormones appear to inhibit reproduction. Much of these contrasting effects of stress and reproduction can be explained by expanding the Energetics-Hormone Vocalization Model, proposed for anuran calling behavior, to other taxa. In the second topic, a number of amphibians and reptiles modulate their HPA stress response. Adrenocortical modulation can occur at multiple levels and due to a variety of factors. However, we have little information as to the physiological basis for the variability. We suggest that several ecologically based ideas, such as variability in the length of the breeding season and lifetime reproductive opportunities, can be used to explain the utility of adrenocortical modulation in these taxa.

Keywords: Stress; Reproduction; Behavior; Corticosterone; Amphibians; Reptiles

Introduction

In nature animals face environmental, social, and physical perturbations which can jeopardize not only their immediate survival but other key life history factors, such as reproduction. Individuals may need to respond to similar challenges with considerably different strategies depending on the social and environmental context. Increasingly, the hypothalamo–pituitary–adrenocortical (HPA) axis is viewed as a complex physiological system that can mediate large variation in the physiological and behavioral responses of animals to stressors (Sapolsky, 1992). A major function of the HPA axis, and in particular the acute adrenocortical stress response, is to behaviorally or physiologically eliminate or reduce the impact of potential stressors on an animal and thus promote its survival (Balm, 1999). Physiological effects can include mobilizing energy stores, gluconeogenesis, and suppressing growth and reproduction (Greenberg and Wingfield, 1987; Wingfield et al., 1998). Behavioral effects can include suppressing reproductive and territorial behaviors and promoting escape behaviors (Wingfield et al., 1998). In addition to this defensive survival function, the HPA axis may also be modulated or altered to support behavioral and physiological functions necessary to enable animals to undertake specific activities such as reproduction (Wingfield et al., 1998). Thus the HPA axis can function to mediate diverse responses to various stressors that can either increase or reduce the probability of an animal’s survival depending on the individual’s situation.
We attempt to identify recent examples of the complex interplay among stress, corticosterone, and the natural history of amphibians and reptiles. These taxa represent two divergent groups of vertebrates that encompass a wide diversity of reproductive systems and strategies (Crews and Moore, 1986). This diversity is a good basis from which to explore the capacity for complex interactions among stressors, corticosterone, and the subsequent effects on behavior and physiology. We have avoided repeating information covered in several previous and comprehensive reviews of stress studies in amphibians and reptiles (Greenberg and Wingfield, 1987; Guillette et al., 1995; Lance, 1990; Tyrrell and Cree, 1998). Rather, our aim is to provide descriptive accounts of two topics for which amphibians and reptiles are good models: (1) the interplay among stress, corticosterone, and reproduction and (2) adrenocortical modulation of the stress response. Furthermore, we address whether the specific stress literature from amphibians and reptiles support or refute contemporary ecological and evolutionary theories of stress biology. The first topic addresses the capacity for context-dependent variation in interactions among stress, corticosterone, and reproduction. The second topic examines the capacity for adrenocortical modulation in amphibians and reptiles. Adrenocortical modulation is a mechanism by which vertebrates may mediate changes in the rate, duration, and magnitude of glucocorticosteroid synthesis and release in response to stressors (reviewed in Wingfield and Ramenofsky, 1999; Wingfield and Romero, 2001).

Variable interplay among stress, corticosterone, and reproduction

Traditionally, stress is thought to have a negative impact on reproduction at multiple levels (Greenberg and Wingfield, 1987). This is well supported in many amphibian and reptile studies, in which short-term stressors may inhibit physiological aspects of reproduction (Guillette et al., 1995). Yet this inhibitory relationship between stress and reproduction cannot be generalized for at least two reasons. First, it appears that for many animals the relationship between stress and reproduction is highly context-dependent and thus some individuals may exhibit an inhibitory response while others do not. Second, it is evident that during reproduction many amphibians and reptiles display concurrent elevations in plasma levels of corticosterone with no suppression of reproductive behavior or physiology. It is possible that elevated plasma levels of corticosterone may actually facilitate specific behavioral and physiological aspects of reproduction. In this section we examine the capacity for amphibians and reptiles to exhibit context-dependent interactions between stress and reproduction and the capacity of corticosterone to facilitate reproduction.

Context-dependent interactions between stress and corticosterone

The role of corticosterone in mediating and responding to the demands of social interactions, in a reproductive context, has been investigated in a variety of amphibian and reptile systems. Results from these investigations suggest that the behavioral, physiological, and environmental context in which a social encounter occurs can be key to understanding the role of corticosterone in social interactions. For example, male Eastern fence lizards, *Sceloporus undulatus*, display an increase in plasma corticosterone levels in response to male or female encounters during the breeding season but not during the nonbreeding season (Smith and John-Alder, 1999). Interestingly, only the encounters with males resulted in an increase in plasma testosterone levels.

Context dependence in the stress response may arise due to physiological differences that are associated with alternative male reproductive tactics. Two male phenotypes of tree lizards, *Urosaurus ornatus*, are associated with alternative male reproductive tactics, one being territorial and the other being nonterritorial (Moore et al., 1998). Both morphs respond to capture stress with an increase in plasma levels of corticosterone; however, only the nonterritorial males respond with a concomitant decrease in plasma testosterone levels (Knapp and Moore, 1997). In response to winning territorial encounters on the previous day, the nonterritorial males display elevated plasma corticosterone and depressed plasma testosterone levels. In contrast, the territorial males show no change in plasma hormone levels the day after winning an encounter (Knapp and Moore, 1996). It appears that one of the physiological differences between the morphs is the plasma steroid binding globulin capacity. These lizards have a plasma steroid binding globulin that binds both androgens and corticosterone. The binding capacity in territorial males is significantly greater than in nonterritorial males (Jennings et al., 2000). This difference in binding capacity between the morphs likely results in higher plasma levels of unbound corticosterone in the nonterritorial males. This would be especially evident when plasma corticosterone levels are elevated and free corticosterone could then trigger a decrease in plasma testosterone. The difference in free versus bound corticosterone potentially explains the morph difference in testosterone response to similar increases in corticosterone. Such a mechanism could occur in other lizards too, as exogenous corticosterone treatment has been shown to decrease plasma testosterone levels and aggressive behavior in the brown anole lizard, *Anolis sagrei* (Tokarz, 1987).

The social context-dependent nature of increased plasma corticosterone levels on aggressive and territorial behaviors has been investigated in the side-blotched lizard, *Uta stansburiana*. In a laboratory study, corticosterone implants alone or combined with testosterone implants reduced aggressive behavior in males (DeNardo and Licht, 1993). This
study implies that the effects of corticosterone on aggressive behavior are not through the route of decreased plasma testosterone levels, but rather are an effect of corticosterone itself. DeNardo and Sinervo (1994a,b) investigated the interaction between social status and physiological state in a field setting. At three sites, half the males were implanted with either corticosterone or saline, while at a fourth site, all the males were implanted with corticosterone. On the three sites with corticosterone and saline implants, both activity level and home-range size were decreased by corticosterone. However, on the site where all males were implanted with corticosterone, home-range size was not affected. These data demonstrate that increased plasma corticosterone puts males at a competitive disadvantage, but only when neighbor males have low plasma corticosterone levels. These studies demonstrate the importance of considering both physiological and social context when investigating the stress response.

The capacity for elevated corticosterone to facilitate reproduction

There are many recent studies in amphibians and reptiles that report a positive relationship between corticosterone and reproduction. These positive relationships fall into two categories. The first is a seasonal increase in baseline levels of corticosterone associated with the onset of the reproductive season. This elevation appears to be long-lasting (weeks to months). The second is a more pronounced increase in corticosterone which coincides with energetically demanding reproductive behaviors. The increased levels of corticosterone appear to more abbreviated (hours to days).

A number of amphibian and reptile species have higher baseline levels of corticosterone during the breeding season than during the nonbreeding season, including side-blotched lizards (U. stansburiana; Wilson and Wingfield, 1992, 1994), crested newts (Triturus carnifex; Zerani and Gobetti, 1993), Galápagos tortoises (Geochelone nigra; Schramm et al., 1999), and red-sided garter snakes (Thamnophis sirtalis parietalis; Moore et al., 2001). Male and female green turtles (Chelonia mydas) also exhibit an increase in plasma corticosterone with reproduction (Jessop et al., 2002). Gravid tuatara (Sphenodon punctatus) exhibit increased levels of plasma corticosterone compared to nonbreeding females sampled at the same time of year (Tyrrell and Cree, 1998). The red-spotted garter snake (Thamnophis sirtalis concinnus) has a positive relationship between baseline plasma testosterone and corticosterone levels across the year (Moore et al., 2000b). However, there are also species in which plasma corticosterone levels do not appear to be elevated during breeding, such as brown anoles (A. sagrei; Tokarz et al., 1998), gopher tortoises (Gopherus polyphemus; Ott et al., 2000), female alligators (Alligator mississippiensis; Guillette et al., 1997), and bearded dragon lizards (Pagona barbata; Amey and Whittier, 2000).

Many studies in anuran amphibians have demonstrated that plasma corticosterone levels can increase, along with plasma testosterone levels, in response to reproductive behaviors. This is in contrast to more typical suppression of reproduction by stress or corticosterone (eg. Moore and Miller, 1984). Plasma corticosterone and androgen levels both increase in response to amplexus (courtship clasping) in male marine toads, Bufo marinus (Orchick et al., 1988). Male bullfrogs, Rana catesbeiana, display a positive relationship between plasma corticosterone and androgen levels during the breeding period, with a peak in corticosterone at the beginning of the active chorusing period (Licht et al., 1983; Mendonça et al., 1985). Male desert spadefoot toads, Scaphiopus couchi, exhibit elevated plasma androgen and corticosterone levels during the calling and amplexing period of the reproductive cycle (Harvey et al., 1997). Experimental exposure to a male chorus resulted in increased plasma androgen and corticosterone levels in the male treefrog, Hyla cinerea (Burmeister and Wilczynski, 2000).

Free-living male Western chorus frogs, Pseudacris triseriata, displayed a positive relationship between plasma corticosterone and androgen levels within the breeding season (Emerson and Hess, 2001). One correlate of this increased plasma corticosterone during breeding behavior is the energetic costs of the behavior. A study across four neotropical anuran species (Hyla ebraccata, Hyla microcephala, Scinax boulengeri, and Physalaemus pustulosus) demonstrated that interspecific variation in plasma corticosterone levels is positively correlated with calling rate and the rank of relative energy in the call (Emerson and Hess, 2001).

Discussion of the interplay among stress, corticosterone, and reproduction

The role of hormones in advertisement calling in anuran amphibians can provide some insight into the complex relationship between corticosterone and reproduction. Calling is crucial for males of most anuran species, and for many species, the time spent calling is positively associated with male mating success (e.g., Ryan, 1985). In addition, calling behavior is often considered to be one of the most energetically expensive activities for ectothermic vertebrates (Bucher et al., 1982).

Emerson (2001) has proposed an extension of the Challenge Hypothesis (Wingfield et al., 1990), termed the Energetics-Hormone Vocalization (EHV) Model, to explain the reported relationships between calling behavior and testosterone and corticosterone levels in male anuran amphibians. The EHV model proposes that calling behavior drives an increase in plasma testosterone that is accompanied by an increase in plasma corticosterone levels due to the energetic demands of the behavior. Thus, over a period of time, levels of both hormones increase. At some point, plasma corticosterone levels surpass a threshold and trigger a short-term stress response. Plasma testosterone levels then decline, resulting in a negative association between the two hor-
mones (Emerson, 2001). This appears to follow the transition from normal, seasonally variable corticosterone levels (level B) to an emergency life history stage (level C), modeled by Wingfield and Ramenofsky (1999).

There are multiple possible physiological mechanisms that can explain the transition between positive and negative relationships of plasma testosterone and corticosterone. Plasma binding proteins in the bloodstream hold one potential explanation. In birds, corticosterone binding globulin binds testosterone with low affinity and can be displaced by corticosterone in high concentrations, making the testosterone available to be cleared (Deviche et al., 2001). Thus at elevated, but not baseline, levels corticosterone can drive a decrease in plasma testosterone levels. It is possible that a similar situation occurs in reptiles where plasma binding proteins may bind both corticosterone and testosterone (Jennings et al., 2000). A second possible explanation for the interactions between plasma corticosterone and testosterone involves the intracellular mineralocorticoid (MR) and glucocorticoid receptors (GR) (Knapp and Moore, 1997). Due to different binding affinities for corticosterone, at low plasma corticosterone levels the MR is saturated. The GR is only bound when plasma corticosterone levels become elevated, such as during a stress response. It is possible then that the negative effects of corticosterone on plasma testosterone levels occur through activation of the GR when plasma corticosterone levels are high. Plasma steroid binding proteins as well as MRs and GRs need to be described in more amphibian and reptilian species to determine if their binding capacities and specificities can be a mechanism to explain the EHV model.

Expanding the EHV model (Emerson, 2001) to other systems beyond male anuran amphibians holds great promise. Many courtship and aggressive behaviors in amphibians and reptiles are energetically expensive and could display similar hormonal associations to anuran vocalizations [e.g., scramble mating systems such as the green turtle, C. mydas (Jessop et al., 1999) and the red-sided garter snake, T. s. parietalis (Moore and Mason, 2001; Moore et al., 2000a)]. We hypothesize that a positive relationship between plasma corticosterone and reproduction in males occurs when courtship and mating are energetically expensive. This scenario of corticosterone being elevated during reproduction could occur in a variety of mating systems including scramble type (a nonterritorial mate searching mating system), female choice, and male competition. Incorporating the energetic models proposed by Wingfield and Ramenofsky (1999) would be a logical first step toward expanding this hypothesis beyond anurans. Adaptations of the EHV model could explain the relationships between androgens and corticosterone in a variety of systems and could expand our general understanding of hormone–behavior relationships.

In contrast to males, there is less information detailing the effects of stress or corticosterone on reproduction in female amphibians and reptiles. There is anecdotal evidence that some female reptiles are able to maintain reproductive behaviors in the face of extreme stress. For example, many researchers have reported the capacity of female sea turtles to maintain nesting behaviors despite very recent and severe injuries from sharks (Jessop, 2000). Female red-sided garter snakes, T. s. parietalis, mate despite recent injuries from crows or exposure to blizzard or flood conditions (Moore, 1999; Whittier et al., 1987). As females often have the higher energetic investment in reproduction it would not be surprising to see a facilitative role for all but the highest plasma levels of corticosterone in female reproduction.

Maternal stress has been demonstrated to affect offspring behavior in the common lizard, Lacerta vivipara. Experimental treatment of females with corticosterone implants promotes increased offspring philopatry to the natal area (de Fraipont et al., 2000). In the field, gravid lizards in the poorest condition produce offspring that have increased natal philopatry compared to offspring from mothers in good condition. de Fraipont et al. (2000) suggest that poor conditioned females may be chronically stressed and thus elevated levels of corticosterone may represent the proximate mechanism that mediates limited juvenile dispersal in these females. Thus it would benefit offspring of mothers in good condition (i.e., low corticosterone) to disperse farther and minimize the potential for mother–offspring competition.

**Modulation of the stress response**

Most amphibians and reptiles respond to stressors by increasing plasma levels of corticosterone (reviews: Guillette et al., 1995; Lance, 1990; Tyrrell and Cree, 1998). However, it is evident that considerable variation in the rate, duration, and magnitude of the adrenocortical response to the same type of stressor may occur. These differences in adrenocortical responsiveness reflect a change in the sensitivity of the HPA axis to stressors and are often termed adrenocortical modulation (Wingfield and Romero, 2001). A number of studies have demonstrated that differences in physiological state among individuals, such as body condition, reproductive state, disease status, age, sex, genotypic variation, and social status can result in adrenocortical modulation (e.g., Dunlap and Schall, 1995; Grassmen and Hess, 1992; Knapp and Moore, 1996). In addition, differences in external environment such as variation in rainfall, temperature, food availability, and humidity or general habitat quality can result in individual adrenocortical modulation between populations (e.g., Dunlap and Wingfield, 1995; Moore et al., 2001). In this section we detail examples of adrenocortical modulation in amphibians and reptiles at multiple levels and discuss the general ecological and evolutionary implications.
Factors involved in the modulation of the individual adrenocortical response

A number of factors including sex, season, reproductive state, and ontogenetic shifts appear to be associated with individual modulation of the adrenocortical responses between amphibian and reptile populations to stressors. Sexual variation in the adrenocortical responses to capture stress has been noted for breeding marine turtles (*Chelonia mydas*, *Eretmochelys imbricata*, *Lepidochelys olivacea*). In each case, females exhibited reduced stress-induced corticosterone levels compared to males (Jessop, 2001; Valverde et al., 1999a,b; Fig. 1a). Sex-associated differences in adrenocortical response to stress have also been observed during the spring breeding season of red-sided garter snakes (*Thamnophis sirtalis*; Whittier et al., 1987; Moore et al., 2000a). In this instance, plasma corticosterone levels of females decreased but males’ levels remained constant in response to capture stress. There is also evidence for sex based variation in the adrenocortical responses of green frogs (*Rana esculenta*; Zerani et al., 1991). In contrast, there are no sex-associated differences in the adrenocortical response of alligators (*A. mississippiensis*), marine iguanas (*Amblyrhynchus cristatus*), or tuataras (*S. punctatus*) to capture stress (Elsey et al., 1991; Lance and Elsey, 1986; Romero and Wikelski, 2001; Tyrrell and Cree, 1998).

Seasonal variation in the adrenocortical stress response has been recorded in a variety of amphibians and reptiles including male garter snakes (*T. sirtalis*), lizards (*Podarcis sicula sicula*, *Sceloporus occidentalis*) and green frogs (*R. esculenta*) (Manzo et al., 1994; Moore et al., 2001; Paolucci et al., 1990; Zerani et al., 1991). Typically, the adrenocortical response of these animals was lowest during spring, coinciding with breeding activities. It is possible that some seasonal variation observed in the adrenocortical stress response of amphibians and reptiles is associated with changes in reproductive state (i.e., breeding versus non-breeding) as opposed to seasonal changes per se. For example, ovariectomized whiptail lizards (*Chemidophorus uniparentis*) exhibit a greater magnitude of adrenocortical response to capture stress than intact females (Grassmen and Crews, 1990). Green turtles, which breed less than annually, modulate the sensitivity of the adrenocortical response depending on their reproductive state. Breeding turtles exhibited a reduced adrenocortical response to capture stress.
stress when compared to nonbreeding animals at the same time of year (Jessop, 2001, Jessop et al., 2002; Fig. 1b).

Interpopulation differences in the individual’s adrenocortical stress response have been recorded in a variety of reptiles. In fence lizards, S. occidentalis, populations at the periphery of the species range exhibited more pronounced stress responses (Dunlap and Wingfield, 1995). While some of this variation was attributable to the relatively poor body condition of individuals in the peripheral populations, a genotypic component was also suspected, as these population differences persisted under laboratory conditions. A comparison of garter snake subspecies also demonstrated that during the summer, male red-sided garter snakes (T. s. parietalis) exhibited a greater magnitude of adrenocortical response to capture stress than male red-spotted garter snakes (T. s. concinnus; Moore et al., 2001; Fig. 1c).

Facultative modulation of the adrenocortical response between individuals of different populations may also arise due to deterioration in environmental conditions that reduces habitat quality and ultimately alters the physiological state of individuals in the population. Galápagos marine iguanas, in poor physical condition due to a severe El Niño event, increased both basal levels of corticosterone and the magnitude of their adrenocortical response to capture stress (Romero and Wikelski, 2001; Fig. 1d). When sampled under more benign environmental conditions, the adrenocortical responses of marine iguanas were reduced in magnitude. A similar situation occurred in response to oil fouling (Wikelski et al., 2001). Similarly, Southern toads, Bufo terrestris, exposed to coal ash exhibit higher plasma corticosterone and testosterone levels than individuals from uncontaminated sites (Hopkins et al., 1997). In contrast, juvenile alligators (A. mississippiensis) from a population that was exposed to environmental contaminants in ovo exhibited no difference in adrenocortical responsiveness to capture stress compared to alligators from relatively pristine lake systems (Guillette et al., 1997).

Individuals within a population often vary considerably in physical attributes (body condition, health, size, and age). Several studies in amphibians and reptiles have addressed how physical trait differences interact with the sensitivity of an individual’s adrenocortical response to stressors. For example, reptiles may exhibit increased activity of their HPA axis with decreased body condition. Western fence lizards (S. occidentalis) in good body condition (an index based on the residuals of mass over snout-vent length) produced lower levels of corticosterone, in response to capture stress, compared to individuals in poor condition (Dunlap and Wingfield, 1995). Similarly, reciprocal relationships between body condition and the magnitude of the adrenocortical stress response have been described in breeding male green turtles (C. mydas) and freshwater crocodiles (C. johnstoni) (Jessop et al., 2002; Jessop et al., 2003). Basal levels of corticosterone in marine iguanas, garter snakes, and two species of agamid lizard (Amphibolurus nuchalis, Pagona barbatus) are also negatively correlated with body condition (Bradshaw, 1986; Cree et al., 2000; Moore et al., 2000b; 2001; Romero and Wikelski, 2001). It is interesting to note that the dynamics of the association between plasma corticosterone levels and body condition may differ. In fence lizards, plasma corticosterone levels increase linearly with decreasing body condition. In contrast, the relationship in both male green turtles and marine iguanas is nonlinear and thus a threshold of poor body condition is necessary before individuals increase the sensitivity of their HPA axis to stress. While some reptile species exhibit increased sensitivity in the adrenocortical response coinciding with decreased body condition, others do not. The adrenocortical responses of red eared slider turtles (Trachemys scripta) and male red-sided garter snakes (T. s. parietalis) produced in response to capture stress is independent of body condition (Cash et al., 1997; Moore et al., 2000). We do not know why body condition is linked with either basal or stress-induced corticosterone levels in some reptiles but not in others.

Other physical traits also have been associated with differences in the individual adrenocortical stress response. Age is significantly correlated with increased plasma corticosterone levels following exposure to capture stress in male red-sided garter snakes (T. s. parietalis) and freshwater crocodiles (C. johnstoni; Moore et al., 2000; Jessop et al., 2003). Immature sea turtles (Caretta caretta, C. mydas) exhibit greater adrenocortical responses to capture compared to larger animals or adults (Gregory et al., 1996; Jessop, 2000). In addition, the current health or disease status of individuals may also increase or alter the sensitivity of the adrenocortical response to stressors in reptiles. Green turtles (C. mydas) afflicted with severe fibropapillomatosis and fence lizards (S. occidentalis) infected with malaria have increased corticosterone levels following exposure to capture stress compared to healthy individuals (Aguirre et al., 1995; Dunlap and Schall, 1995).

The physiological basis of adrenocortical modulation

Although several examples of adrenocortical modulation exist in reptiles and amphibians, at present there is little understanding of what physiological mechanisms operate within the HPA axis to enable modulation of corticosterone release during stress. Nesting olive ridley sea turtles (L. olivacea) exhibit a very limited adrenocortical stress response to capture stress but dramatically increase plasma corticosterone levels in response to an ACTH challenge (Valverde et al., 1999a,b). This result infers that mechanisms upstream of the anterior pituitary could be responsible for the lack of modulation of stress response in this species. In birds, the ability to modulate the adrenocortical stress response appears to be regulated by mechanisms both upstream and downstream of the anterior pituitary (Wingfield and Romero, 2001).
Discussion on adrenocortical modulation

By utilizing studies from other taxa, it is possible to begin to compare and contrast the ecological basis to adrenocortical modulation and thus consider why amphibians and reptiles may have evolved the capacity to modulate the HPA axis. In arctic and desert breeding birds, a central hypothesis suggests that species reduce their adrenocortical response to stress to offset the relatively short length of the breeding season (Wingfield and Romero, 2001). Consequently, the reduced sensitivity of the HPA system is thought to maximize the birds’ reproductive success by preventing stressors from triggering an adrenocortical stress response. For at least one reptile species this hypothesis could be applicable. Male garter snakes (T. s. parietalis) that breed in high latitude areas exhibit a reduced adrenocortical stress response during the breeding season compared to populations breeding at more southern latitudes with a longer breeding season (Moore et al., 2001).

While the duration of the reproductive season could explain the basis for decreased adrenocortical sensitivity in some reptiles, for others, such as sea turtles, it does not appear applicable. In sea turtles, breeding females of at least three species (half of the family Cheloniidae) exhibit a reduced or slower adrenocortical response to capture stress compared to nonbreeding females (Jessop, 2001; Owens, 1997; Valverde et al., 1999a). The breeding/nesting activities of these reptiles are typically confined to equatorial and warm subtropical habitats where breeding seasons are extended and some populations breed year-round. Similarly, it might be predicted that life history variation in reproductive traits is a basis by which sea turtles exhibit adrenocortical modulation. Sea turtles are generally long-lived with a delayed age to maturity and multiple lifetime breeding events. However, there is still considerable variation in their reproductive life history attributes, such as age to sexual maturity, seasonal nesting episodes, and relative investment in the current reproductive event. Perhaps the explanation for adrenocortical modulation in sea turtles is a phylogenetic constraint.

The capacity to modulate the adrenocortical stress response in vertebrates is being increasingly recognized as a potential mechanism to mediate decisions important to an individual’s fitness (Wingfield et al., 1998). Essentially, as an individual modulates the adrenocortical stress response, it is also modifying its sensitivity to stressors within the environment. In the short term, corticosterone can trigger behavioral and physiological changes that could facilitate the animal’s survival (Wingfield et al., 1998; Wingfield and Ramenofsky, 1999). However, initiating an adrenocortical stress response and thus increasing the odds of immediate survival may be in direct conflict with key life history processes, such as reproduction. Thus during reproduction, it may be necessary for an animal to attempt to endure the stress by downregulating the HPA axis. This may maximize reproductive success although it may also increase mortality (Wingfield et al., 1998).

To our knowledge, there are only correlational studies that suggest that adrenocortical modulation may provide a physiological basis for a trade-off between conflicting life history traits. Marine turtles can maintain both a reduced adrenocortical stress response and reproductive activities in the face of a number of natural stressors, including conspecific competition for nesting habitat and even lethal heat stress (Jessop et al., 1999, 2000; Valverde et al., 1999a). In this latter example, nesting turtles were dying from overheating while maintaining a reduced adrenocortical stress response. It is possible that the lack of adrenocortical responsiveness promoted their death by not triggering a behavioral and physiological response that could have facilitated their immediate survival (Jessop et al., 2000).

There is also correlational evidence from other reptiles that implies increased adrenocortical responsiveness during particular life history phases can promote survival and future reproduction. During pervasive weather events such as storms, floods, and drought, populations of animals may be susceptible to unprecedented levels of mortality. There are relatively few examples in which natural populations of reptiles and amphibians increase the sensitivity of their adrenocortical stress response as a possible mechanism to promote their survival during pervasive and broad-scale stressors. Perhaps the best example is in the Galápagos marine iguanas (A. cristatus). They endure chronic starvation and mass mortality due to El Niño events (Romero and Wikelski, 2001). During a severe El Niño event, several island populations of marine iguanas increased both basal plasma corticosterone levels and their adrenocortical responsiveness to capture stress (Romero and Wikelski, 2001). Romero and Wikelski (2001) hypothesized that for individuals in very poor body condition, the increased capacity to produce corticosterone could be a physiological trait that enhances survival.

Some amphibians and reptiles possess the capacity to modulate their adrenocortical response to stress; however, other species do not. Given both the relatively disparate nature of studies on this subject and the lack of comparative studies between closely related taxa, finding a single unifying hypothesis to explain the ecological basis of adrenocortical modulation is presently difficult. For those amphibian and reptile species that downregulate their adrenocortical response, perhaps the most tentative generalization is that adult females, particularly those in a reproductive state, are more likely to have a suppressed adrenocortical response compared to breeding males or adult nonbreeding females. Finally, integrated studies that combine field endocrinology with a mechanistic approach that assesses factors such as the variation in receptor abundance and type, the role of plasma binding globulins, and the energetic demands of the individual will provide useful future research platforms.
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