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Ethological Aspects of Stress in a Model Lizard, *Anolis carolinensis*¹

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SYNOPSIS. Research on the stress response in reptiles can provide a useful comparative perspective for understanding how the constituent elements of the response can be put into service of diverse behavioral adaptations. A summary of the neural and endocrine causes and consequences of specific behavioral patterns seen in the small diurnal lizard, *Anolis carolinensis*, has provided a model for the exploration of the dynamics of autonomic and neurohormonal contributions to adaptive behavior. In this species, changes in body color provide indices of the flux of circulating stress-relevant hormones, and are seen in situations from spontaneous exploration through agonistic behavior. Furthermore, captive adult males spontaneously and consistently manifest social dominance relationships that provide many of the elements of a stress-mediated adaptive behavioral patterns. These patterns include suppressed reproduction and long-term coping apparently based more on stress-mediated changes in motivation than acquired changes in behavior.

INTRODUCTION

The physiological ethology of stress in reptiles can inform views about the possible evolutionary antecedents of coping responses in other taxa, not least humans. For reptiles, as in other species studied, stressors are real or perceived challenges to an organism's ability to meet its real or perceived needs. Stressors may be internal or external changes and the nature of their challenge can evoke responses from within a nested hierarchy of possible coping responses depending on the severity and duration of their challenge. Several excellent general reviews (Axelrod and Reisine, 1984; Goldstein, 1987; Johnson *et al.*, 1992; Sapolsky *et al.*, 2000) in concert with much work on reptiles (below) provide a useful framework for interpreting the physiological ethology of the reptilian stress response at several levels, from the individual to phylogenetic.

Before 1950, there was little basic knowledge about the adrenal glands in reptiles. This regrettable state began to be corrected with Hebard and Charipper's (1955) comparative study of the morphology and histochemistry of the reptilian adrenal gland and the work of Wright and Chester Jones (1957) on lizards and snakes. Within twenty years, Manfred Gabe (1970) had a significant body of work to summarize, Ian Callard and colleagues (1973) addressed the workings hypothalamic pituitary adrenal axis and Unsicker (1976) described storage of the adrenaline and noradrenaline in chromaffin tissue. In 1978, Lofts summarized the structure (1978) and the Callards discussed the comparative physiology of the reptilian adrenal gland (Callard and Callard, 1978) in a comparative light. The interactions of stress with reproduction, immunology, and intermediary metabolism with an emphasis on reptiles was provided by Guillelte and colleagues (1995).

STRESS-SENSITIVE BEHAVIOR IN REPTILES

Laboratory and field studies of the relationship between the stress response and behavior have proliferated in various reptile taxa to provide a clear sense of the diversity of adaptive functions that stress physiology can serve as well as the utility of reptiles as models. For example, in sea turtles, adrenocortical function is suppressed in the face of highly stressful environmental conditions in an apparent trade-off favoring successful reproduction (Jessop *et al.*, 1999a, b, 2000 in green sea turtles; Valverde *et al.*, 1999 in olive ridley sea turtles). In captive red-eared slider turtles, implants of adrenal steroid resulted in an initial increase in activity (and possible food encounters), but diminished activity (possibly to conserve energy) in subsequent days (Cash and Holberton, 1999). Stress-induced suppression of reproductive behavior is well known in many taxa, including reptiles where diminished androgen is correlated with elevated corticosterone in alligators (Lance and Elsey, 1986) and lizards (*e.g.*, Moore *et al.*, 1991; DeNardo and Licht, 1993; Manzo *et al.*, 1994; Greenberg and Crews, 1990).

Plasma levels of corticosterone is often taken to indicate physiological stress and to suggest how well a population is coping with ecological challenges such altered predator prey relationships, population density, or climatic extremes (Christian, 1980), but as Dunlap and Wingfield (1995) pointed out using free-living lizards, basal adrenal hormone levels must be considered apart from adrenal responsiveness to acute stressors (and see Dunlap, 1995). Such a distinction was useful in a unique test of the utility of the stress response to predict of survival in wild animal populations, Galapagos marine iguanas were studied on six islands in the archipelago, all subject to the stress of local famine attributable to El Nino-related climate change. Baseline corticosterone was not predictive of survival through an El Nino period, but corticosterone response to handling stress was found to be better than body condition at predicting survival (Romero and Wikelski, 2001).

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The behavioral endocrinology of lizards in the laboratory and field has been investigated at length by Michael Moore and his colleagues (*e.g.*, Moore *et al.*, 1991; Knapp and Moore, 1997; Crews and Moore, 1986) who noted in particular the flexibility of responses to sex and stress hormones depending on variables such as ecological context and social status. Moore's approach, by exploring the epigenetics of alternative life history strategies, underscores the adaptive flexibility of hormonally sensitive behavioral mechanisms (Moore *et al.*, 1998).

Anolis lizards

Among lizards, the diverse and wide-spread new world genus *Anolis* is the most studied and has become a useful model for evolutionary ecology (see Losos, 1994). In particular, the green anole, *Anolis carolinensis*, has proved to be a useful model for many phenomena, including some of clear biomedical interest (Greenberg *et al.*, 1989). This small, diurnal, insectivorous lizard of the American southeast is abundant, convenient to observe and easy to maintain in the laboratory (see Greenberg 1992, 1994), qualities which have led to their frequent use in behavioral studies (*e.g.*, Crews, 1979; B. Greenberg and Noble, 1944; Jenssen, 1978; Jenssen *et al.*, 1995). Aspects of *A. carolinensis* relevant to understanding their ethology include behavior inventories that emphasize social dynamics (Greenberg, 1977) and basic ecology (Jenssen *et al.*, 1995) as well as laboratory studies of their behavioral endocrinology (*e.g.*, Crews, 1979). An atlas of the forebrain (Greenberg, 1982) prepared to guide brain lesion experiments (*e.g.*, Greenberg *et al.*, 1984) is useful for analyzing regional histochemical or metabolic changes associated with behavior (*e.g.*, Summers *et al.*, 1998; Baxter *et al.*, 2001).

THE ANOLIS MODEL OF STRESS

Investigations, which began with neural control of aggressive displaying as the key behavioral variable (Greenberg, 1977), broadened into other areas of physiological ethology when it became apparent that body color change is a reliable indicator of the stress response in this species. This fact in concert with the consistent correlation between specific patterns of color change and specific behavioral patterns indicates the participation of stress-sensitive systems at multiple levels of organization.

Stress and body color in A. carolinensis

Body color can be something of a "window" on the internal state of *A. carolinensis*. In this species, dermal chromatophores are known to be free of sympathetic innervation (Kleinholz, 1938b), leaving body color subject only to the influence of circulating chromoactive hormones: epinephrine (EPI), norepinephrine (NE) and melanotropin (MSH). For example, a shift from green to brown, or darkening involving speckling and the appearance of a small "eyespot" just behind the eye, indicate specific patterns of activation of α_2 -

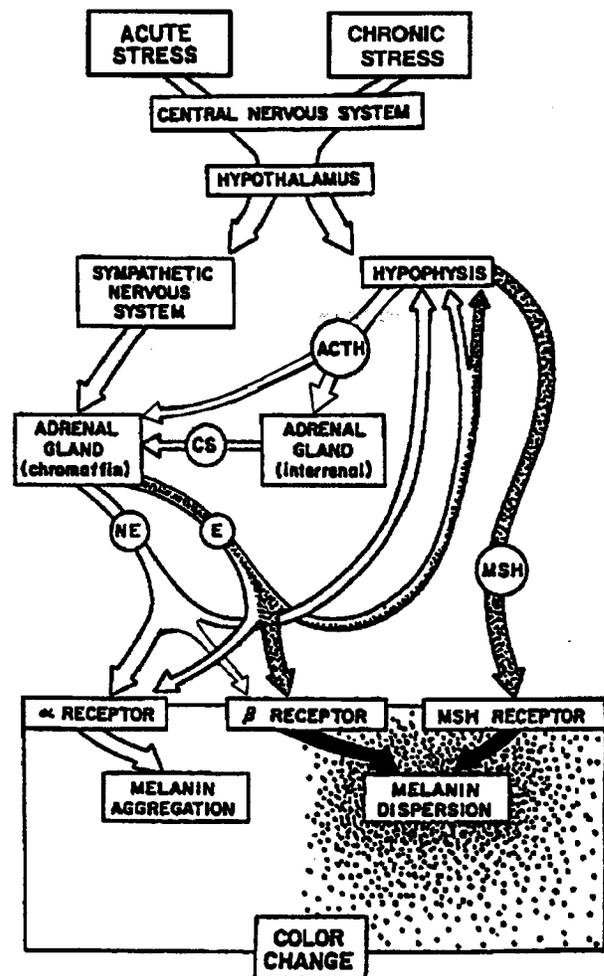


FIG. 1. The effects of stress hormones on a dermal chromatophore of *Anolis carolinensis*. Acute and chronic stressors are integrated to cause the release of hormones that interact with each other and converge in affecting the darkness of a chromatophore. ACTH, adrenocorticotropic hormone; CS, corticosterone; E, epinephrine; MSH, melanocyte stimulating hormone; NE, norepinephrine. CS can elevate the ratio of E to NE by facilitating a key enzyme within the adrenal gland. E stimulates β receptors preferentially and then α receptors resulting in opposing effects. (adapted from Greenberg and Crews, 1983).

and β_2 -adrenoceptors (sympathetic elements of the acute stress response in Fig. 1), and MSH. Despite early beliefs about *A. carolinensis* color matching its background (*e.g.*, Kleinholz, 1938a), more recent studies in the field (Jenssen *et al.*, 1995) indicate that body color is most typically affected by social activities. For example, when male *A. carolinensis* is engaged in behavior such as predator avoidance or the mutual stalking, chases, and retreats of territorial confrontation, color fluctuates in ways strongly suggestive of the hormones associated with the physiological stress response (Table 1).

Although green is the basic color of an unstressed individual's skin, a consistent brown coloration sugges-

TABLE 1. *Body colors of the green anole, Anolis carolinensis, and possible endocrine influences.*

- **Green:** resting state of healthy lizard (normal tonic levels of NE)
- **Green and brown:** transitional color reflecting mild stress (slight EPI and MSH)
- **Brown:** mildly stressed (slight EPI and MSH)
- **Dark brown:** sustained or more intense but not threatening stress (EPI and MSH)
- **Brown with eyespot:** moderate level of stress (high levels of EPI and MSH)
- **Green with eyespot:** high level of stress (EPI sufficient to counter NE effects in skin, but eyespot (with β -adrenoceptors only) not subject to catecholamine reversal of color)
- **Dark green (speckled):** highest level of stress (apparent EPI effect without chronic MSH response; usually includes eyespot)
- **Blotchy green and brown:** morbid stress (competence of catecholaminergic regulation appears compromised)

EPI, epinephrine; NE, norepinephrine; MSH, melanocyte stimulating hormone.

tive of chronic stress is often stable and can be sustained for extended periods without evidence of harmful effects. It is likely that this color change is attributable to MSH, which, like adrenocorticotropin (ACTH), is derived from the precursor molecule, pro-opiomelanocortin (POMC), and can be co-released from the pituitary with ACTH or released by itself (Proulx-Ferland *et al.*, 1982). In the pituitary of *A. carolinensis*, POMC end-products include stress-sensitive opiate-active beta-endorphins (references in Dores *et al.*, 1984). In circulation, MSH promotes melanin dispersion (darkening) by means of stimulation of MSH receptors on chromatophores (Carter and Shuster, 1982), but it also facilitates α -adrenoceptor induction of melanin aggregation (lightening) or β -adrenoceptors promotion of melanin dispersion (darkening) in response to EPI or NE (Goldman and Hadley, 1969). An apparent antagonism exists between MSH receptors and α_2 -adrenoceptors (Carter and Shuster, 1982), while the β_2 -adrenoceptor appears to be linked with the MSH receptor to cause melanin dispersion by stimulating adenylyl cyclase (Vaughan and Greenberg, 1987). While β_1 -adrenoceptors respond to circulating EPI and NE released by sympathetic neurons, the natural agonist for β_2 -adrenoceptors is apparently EPI (Hadley, 1996, p. 325). Hadley and Goldman (1969) observed that dermal chromatophores are similar to many other sympathetic effector cells in which stimulation of α -adrenoceptors tend to override β -adrenoceptor present on the cell, thereby "reversing" the darkening and turning skin color light. Certain patches of skin, however, most notably the post-orbital "eyespot" has β -adrenoceptor only. Thus while skin colors may fluctuate, if EPI is present the eyespot remains dark.

The hormone associated with the chronic stress response, the adrenal glucocorticoid, corticosterone (CS), does not usually affect color directly but can facilitate a key methylating enzyme in the adrenal cortex leading to an increased rate of synthesis of EPI from NE, thereby also contributing to darker color

(hypothalamic-pituitary-adrenal 'cortex' responses in Fig. 1).

Anolis carolinensis, possessed of excellent eyesight and all-cone (color-sensing) retinas, are very sensitive to expressions of arousal in animals around them, most notably the flash of red from a possible adversary's dewlap, usually kept folded beneath the chin. But interestingly, there is little evidence that an acute change in body color—essentially an extended autonomic reflex—has a signal function. There is, however, evidence that the eyespot may function as a social signal to limit aggressive interaction. When Korzan *et al.* (2000) covered a territorial male's stress-evoked eyespot, its aggressive behavior directed toward a mirror were more intense than when the eyespot was not covered or artificially provided. In other words, the perception of an eyespot appeared to suppress aggression. When the brains of such animals were studied, Korzan documented elevations in 5HT and NE in hippocampus as well as several other sites.

The advantage of brown body color on the substrate (to which subordinates in the lab are usually relegated) or with reduced body profile on the trunk of a tree rather than out on a leafy twig (a preferred territorial surveillance site) is obvious, but it is remarkable that there is little evidence that body color has any significance as a social signal with the notable exception of the eyespot.

Many other reptiles are known to change color rapidly in response to environmental stimuli such as light or temperature by means of chromatophore changes mediated by neural or neuroendocrine mechanisms (see Cooper and Greenberg, 1992). The control of long-term color change, however, is in many cases attributable to altered levels of circulating sex steroid hormones as a result of seasonal or developmental changes, or chronic stress affecting steroid hormone secretions. These longer-term changes can then alter the endocrine allostatic "tone" which provides the background for and can affect the expression of more rapid sympathetic neural/adrenomedullary changes that may be expressed in response to potential stressors, the need for crypsis, or the expression of social signals. Externally detectable elements of the stress response have long been believed to be a rich source of potential communicative signals (Morris, 1956).

Stress and behavior in Anolis

The conspicuous color changes during and following competitive interactions between males (Table 1) provide a significant external indication of internal state that enabled us to conduct studies concerned with the neural and endocrine causes and consequences of lizard behavior (Greenberg *et al.*, 1984; Summers and Greenberg, 1994).

Anolis carolinensis in the lab. Like many other lizards (*Amphibolurus*, *Lacerta muralis*, *Uta stansburiana*, and some *Anolis spp.*, see Sugerman, 1990), green anoles in the laboratory provided with basic ethological needs (see Greenberg, 1992) appear to ha-

bituate to discreet human observers, at least in so far as they express a full spectrum of spontaneous activity and maintain a bright green body color. In most research settings, observers sit in the dark watching an illuminated vivarium, peer through gauzy curtains, or observe by means of remote video surveillance. Captive *A. carolinensis* will gradually reduce their defensive immobility responses in response to simulated predation (McNight *et al.*, 1978 and see Hennig, 1979) while other species may manifest a continuing observer effect and will reduce their activity levels (Sugerman and Hacker, 1980 for *Crotaphytus collaris*).

Obvious climatic and physical ecological variables can be easily accommodated in the laboratory but some responses that might constitute a significant dependent experimental variable are quite subtle. It should be a truism by now that the transfer of research into the lab must be highly sensitive to the multiple interacting variables that constrain the behavioral pattern of interest in nature. Accommodation of these needs is what I have characterized elsewhere as "ethologically informed design" (EID) (Greenberg, 1994). For example, slight differences in temperature can evoke alternative defensive behavior (fleeing *versus* freezing) in response to prospective predators (humans) in the lizard *Anolis lineatopus* (Rand, 1964). In the Amazonian *Tropidurus oreadicus*, approach distance is reduced at lower body temperatures (Rociia and Bergallo, 1990), and even in comparable thermal environments approach distance manifest by *Anolis cristatellus* and *A. stratulus* can be significantly affected by the degree of crypsis each enjoys (Heatwole, 1968). In *Anolis carolinensis*, the immobility response to a potential predator's approach is of significantly longer duration when foliage is nearby than when it is absent, but only in the early days of captivity (Hennig, 1979).

Ethological research is deeply informed by a concern for the spontaneity and external validity of observed behavior. A green anole in the lab is not quite the same animal as in the field, but certain benchmark traits such as frequency of spontaneous movements allow us to calibrate the controlled environment in order to evoke a relatively undistorted view of the animal's behavior. For example, use of fluffy sphagnum substrate allows crickets to hide and forces resident anoles to maintain high levels of alertness comparable to those in nature. Simplification of the vivarium by successive reductions in habitat complexity is a key to the confidence one can have in the validity of findings (Greenberg, 1978).

SPECIFIC ASPECTS OF STRESS AND BEHAVIOR IN *ANOLIS CAROLINENSIS*

The *A. carolinensis* model has been employed to explore the effects of stress on several key behavioral or physiological variables. My ambition here is to review the state of research to date on specific behavioral patterns and on hormones associated with stress in the light of adaptive possibilities raised by the more gen-

TABLE 2. *Units of exploratory behavior in Anolis carolinensis.**

- | |
|--|
| <ul style="list-style-type: none"> ● Orientation and locomotor responses <ul style="list-style-type: none"> ○ Posture Change (significantly increased by handling or placement in a new cage) ○ Site Change (significantly increased by handling or placement in a new cage) ● Tongue flick responses <ul style="list-style-type: none"> ○ Tongue-touch (significantly increased by handling but not placement in a new cage) ○ Air-lick (significantly increased by handling but not placement in a new cage) |
|--|

* Adapted from Greenberg, 1985.

eral review above and comparative surveys (such as Greenberg *et al.*, 2002).

Exploratory behavior and stress

"Curiosity" is not a legendary attribute of ectothermic squamates in general, although intensive foraging lizards such the macroteiid, *Ameiva*, may manifest spontaneous rates of exploratory behavior comparable to a gerbil (Regal, 1978). Even in other families generally regarded as "sit-and-wait" predators such as Iguanidae, individual species are remarkable for their exploratory behavior. For example, Rand *et al.* (1975) observed intense curiosity evoked by novel stimuli in *Anolis agassizi*. Seasonal changes are also manifest: in *A. carolinensis*, observed at a field site near Augusta, Georgia, foraging behavior is much greater during the post-breeding season (August to September) than during the breeding season (May to July), presumably in association with relaxed pressure to maintain breeding territories (Jenssen *et al.*, 1995).

Exploratory behavior is observed in several iguanid species when placed in a novel habitat (see Pederson, 1992), presumably to gather ecologically relevant information. In many reptiles, tongue-flicking is a consistent concomitant of novel-habitat behavior but is also seen (at a reduced rate) during movements in a familiar environment. It is readily manifest in the laboratory and field (see Burghardt, 1986 for a coordinated laboratory/field study). While tongue-flicking is likely to gather ecologically relevant chemosensory information, there is also a reasonable possibility that enhanced exploratory behavior is a consequence of non-specific arousal—the "energizing" effect of fear (Halliday, 1966) or relatively mild stress (see Leshner, 1978).

Increased exploratory behavior is associated with mild stress as both a cause and consequence in many taxa. In an experiment in which anoles were mildly stressed by handling before placement in either their home or an unfamiliar habitat, handling was more potent than the unfamiliarity of the habitat in evoking some but not all aspects of exploratory behavior.

Like most reptiles, *A. carolinensis* manifest two forms of tongue flicking, presumably to gather chemosensory information: "tongue-touching" and "air-licking" (Table 2) (Greenberg, 1985). The spontaneous

TABLE 3. *Consequences of a male Anolis carolinensis losing an agonistic encounter in the laboratory.*

PHYSIOLOGICAL

Immediate

- CATECHOLAMINE (EPI and NE) SURGES (body color, nuchal crest erection, Greenberg *et al.*, 1984)
- NE LOWER RELATIVE TO WINNER (Summers and Greenberg, 1994)
- CIRCULATING CORTICOSTERONE INCREASED (Greenberg, Chen, and Crews, 1984)
- MSH INCREASED (relative to winners, Greenberg *et al.*, 1986)
- SEROTONIN ACTIVITY INCREASED IN THE MID-BRAIN, HIND BRAIN (Summers and Greenberg, 1995), HIPPOCAMPUS, AND NUCLEUS ACCUMBENS (Summers *et al.*, 1998)

Long term

- ANDROGEN REDUCED (Greenberg and Crews, 1990)
- CORTICOSTERONE ELEVATED (Greenberg *et al.*, 1984)
- MSH INCREASED (relative to dominants, Greenberg *et al.*, 1986)
- DOPAMINE ACTIVITY DIMINISHED, ADRENERGIC ACTIVITY ENHANCED IN THE MID AND HIND BRAIN (BUT BACK TO CONTROL VALUES BY ONE MONTH) (Summers and Greenberg, 1995)

BEHAVIORAL

Immediate

- BODY COLOR BROWN RELATIVE TO WINNER (indicative of exhaustion of EPI and/or MSH release)

Long term

- BODY USUALLY COLOR BROWN (Greenberg *et al.*, 1984)
- WILL NOT COURT FEMALES (Greenberg and Lumsden, 1990)
- LOWER PERCH-SITE SELECTION (Greenberg *et al.*, 1984) (frequently take cover in leaves or even burrow into loose mossy substrate)

EPI, epinephrine; NE, norepinephrine; MSH, melanocyte stimulating hormone.

rates of posture and site changes (indicative of arousal and attention) and tongue touching and air-licking (to detect gustatory or vomeronasal stimuli, respectively) were observed in both intact and castrated male anoles. When they were in their home cages, spontaneous behavior was comparable, but when they were mildly stressed (by being placed in novel habitat) all indices increased. When, on the other hand, animals were subjected to more intense stress (restraint until an eyespot is elicited) before being placed in a novel habitat, all behavior was significantly depressed with the exception of airlicks, which increased (Greenberg, 1993). Also, as in other studies (*e.g.*, Greenberg *et al.*, 1984), the absence of androgen ameliorated the stress response: castrated males were much less affected by the experience of restraint than were intact animals. Of particular interest was the fact that the familiar energizing effects of mild stress and inhibitory effect of more intense on behavior (Leshner, 1978; Sapolsky *et al.*, 2000) was manifest in most but not all behavioral patterns. Interestingly, it was the least conspicuous of the behavioral patterns (airlick) that was spared, suggesting more adaptive specificity in the inhibitory effect of intense stress than generally appreciated.

Androgen is associated with general arousal in several vertebrates (Archer, 1973; Andrew, 1978). In subjects with reduced androgen levels, stimuli that normally evoke a stress response are significantly less potent. It is also interesting to note that the chemical senses served by tongue-touching and airlicking may be different and involve different neural substrates.

Exploratory behavior was also used to examine the effects of central catecholamines related to the stress response. The catecholamine-specific neurotoxin, N-methyl-4-phenyl-1,2,3,6-tetrahydropyridine (MPTP) was administered to nine adult male lizards to deplete central nervous system catecholamines. Changes in brain content of dopamine (DA), norepinephrine (NE) and serotonin (5HT) were determined in a parallel study (Greenberg, 1993; Greenberg *et al.*, 1990). DA and NE were reduced (to 24% and 7% of control values, respectively) while 5HT increased 200%. In these catecholamine-depleted animals, spontaneous behaviors in the home cage were depressed for all measures, but only orientation and locomotor responses significantly so. In novel habitats, posture changes and tongue-touching were significantly depressed but site-changes and air-licks were unaffected.

Learning and stress

When behavior changes as a result of experience, it qualifies as "learning"—but there are significant differences between circumstances in which (1) behavior changes because the balance between tendencies to approach or avoid a stimulus is altered; or (2) behavior is affected because a specific stimulus is perceived as possessing less adaptive *meaning*; that is, the stimuli no longer have control over behavior because of an altered motivational state. Some optimal level of arousal, anxiety, or stress appears necessary for learning to occur. Mild stress often acts to focus attention on relevant cues while more intense stress impairs learning (see Greenberg *et al.*, 2002, Table 1). This is a clear expression of "optimal arousal," described by the Yerkes-Dodson law (see for example, Mook, 1987); in other words, more or less stimulus intensity than an "optimal" level is less effective in evoking the focal behavioral pattern.

Partly as a result of extraordinary efforts to dispel the view of reptiles as having impoverished learning capacities (Burghardt, 1977), the importance of ecologically relevant stimuli as effective contextual or motivational variables has become progressively more appreciated by ethologists and other scholars and researchers of learning.

Several experimental demonstrations of learning met with a measure of success using ethologically relevant cues (for example, Regal, 1971), but the stress connection has not yet been made clear in reptiles. An implicit role for stress was found in a report from a field study of *Leiocephalus schreibersi* (Marcellini and Jenssen, 1991). Very rapid learning seemed apparent when evoked by a novel predator (human) in 80% of the animals tested.

The hippocampal connection. In mammals and birds, the hippocampus is a target of stress-evoked corticosterone (CS) (McEwen, 1999) as well as a critical mediator of memory and learning (Sapolsky, 1992). It may well be a key structure for establishing connections between phenomena that are discontinuous in time and space (Wallenstein *et al.*, 1998). There is good evidence for homology between reptilian hippocampus and that of mammals and birds. For example, the distributions of GABAergic neurons are similar (Schwerdtfeger and Lopez, 1986); and such neurons, once identified principally as having a damping function on neuron activity are now believed to be actively involved in information processing (Paulsen and Moser, 1998).

Reptiles have a distinct, if modest hippocampus (medial cortex), capable of neurogenesis in response to neurotoxic trauma (Font *et al.*, 1991; Lopez-Garcia, 1992) as well as in the adult brain (Perez-Canellas and Garcia-Verdugo, 1996), in areas implicated in memory and learning (Font and Gomez-Gomez, 1991). There is evidence that the hippocampus of reptiles is both involved in learning and sensitive to stress, however there are as yet only a few studies. Damage to the hippocampus has been known to affect conditioned reflexes since the early 1980s (Ivazov, 1983, in *Ophisaurus apodus*). More recently, the behavioral function of this site, so prominently stress-sensitive in other taxa, was found to be morphometrically correlated with the spatially organized behavioral patterns of a lizard; even though an effective spatial learning test to discriminate specific abilities has eluded invention. The relative volume of hippocampus is larger in the active foraging lizard, *Acanthodactylus boskianus*, than in its sit-and-wait congener, *A. scutellatus* (Day *et al.*, 1999). While the role of hippocampus in learning of *A. carolinensis* is not established, its association with stress is more clear (Summers *et al.*, 1998).

Aggression and stress

The relationships of acute and chronic stress to aggressiveness, and the role of the hypothalamic-pituitary-adrenal axis in particular, has been appreciated since at least the 1960s when a longer latency to manifest aggressiveness was noted in adrenalectomized mice, and mice bred for aggressiveness were found to have heavier adrenal glands (reviewed by Leshner, 1983).

Can we say much as yet about the physiological substrate of this behavior in reptiles? The last two decades have established a site in the basal forebrain apparently responsible for integration of stimuli leading to the expression of aggressive social displays (reviewed in Greenberg, 1983, 1990; Baxter *et al.*, 2001a, b), and brainstem nuclei controlling a key effector of the dewlap displays (Font *et al.*, 1986; Font, 1991). More recently, the darker body color seen in losers of fights provided a key to endocrine variables associated with social subordination and submissiveness. This body color change during aggression, well known in

the laboratory (Greenberg and Noble, 1944) and in the field (Medvin, 1990), presents provocative possibilities because the hormones that affect the chromatophores are also associated with the physiological stress response and, at least in other taxa, have appear to act to suppress aggressiveness and facilitate the expression of social submissiveness (Leshner, 1978).

Body color changes indicative of the involvement of stress physiology in lizard aggression can also provide clues about the temporal dynamic of interactions and the qualities that may allow one combatant or another to prevail. For example, at the conclusions of fights, losers are typically brown (Sigmund, 1979; personal observation) with an eyespot, and winners are green with an eyespot. Further, close observations of agonistic interactions revealed that individuals who were the first to display the eyespot were almost invariably the winners and ultimate social dominants (Summers and Greenberg, 1994). The progress and outcome of fights suggest that losers may lose when they are depleted of reserves of energy or the hormones to mobilize that energy. Such an "exhaustion" hypothesis would suggest a war of attrition in which very slight differences in capacity would make a crucial difference.

Social dominance and stress

The ethological concern with stress and social dominance emerged from the confluence of Hans Selye's clinical concern for "diseases of adaptation" (Selye, 1936, 1976) the ecologist J. J. Christian's (1961) insights about diminished fitness in an ecological stressing context. In particular, observations of reduced fertility at high population densities and the correlation of behavioral dysfunction with adrenal pathology (Christian and Davis, 1964) created an appreciation for the connection between social dominance (see Gauthreaux, 1978) and physiological stress. In little more than a decade, research with reptiles began, reflecting this convergence of physiological ecology and behavior in conjunction with social influences on resource utilization. In the spirit of these early ecologists, Brackin (1978) demonstrated a relationship between social dominance and adrenal volume in the lizard *Cnemidophorus sexlineatus*.

The "dominance threshold." Species possessing the flexibility to shift from strict territoriality to social dominance in response to changing resources exists in many taxa (see Brain, 1981). This phenomenon has also been observed in lizards in the field by Evans (1951) for *Ctenosaura pectinata*; Norris (1953) for *Dipsosaurus dorsalis* as well as in the lab by Hunsaker and Burrage (1969) for various species; Brattstrom (1974); Greenberg (1977) for *Anolis carolinensis*. Indeed, many species may possess an apparent "dominance threshold," unique for each, that reflects a point at which an individual accepts subordination rather than competes for an individual territory. Presumably, after experience in the social environment, such an individual acts to maximize the benefits and minimize

the costs of a particular life history option. Losers could easily escape to neighboring territories, but they may still be at a competitive disadvantage if a more robust male is already resident there or the territory is inferior in other ways. At some point, the interests of a loser of a fight may be better served by remaining in the winner's territory, keeping a low profile, and waiting.

Social dominance in anoles. Social dominance relationships, while rarely seen in the field, are likely a natural feature of at least some anoles, and like exploration (indeed, virtually any behavioral trait) dependant more on habitat and social options available to an evolving species than on taxonomic position. While generally territorial, some anoles are, in the field, seen to manifest hierarchical intermale relations suggestive of social dominance (Trivers [1976] in the giant *A. garmani*, Fleishman [1988] in *A. auratus*, Rand *et al.* [1975] for *A. agassizi*, Jenssen and Feely [1991] for *Chamaelinorops barbouri*). Field data on social dominance in the most fully studied of the anoles, *Anolis carolinensis*, is anecdotal at best, and one extensive field study found no support for the idea (Jenssen *et al.*, 1995). However, in the course of an elaborate field study of the interactions of the sympatric anoles, *A. carolinensis* and *A. sagrei*, on small islands, Campbell (2000) frequently observed that when large territorial males of either species were temporarily removed for marking and measuring, they were replaced by theretofore unseen smaller males within minutes (Campbell, personal communication). The rapidity of replacement by the smaller males suggests they were nearby and alert for an opportunity, much like the situation in a laboratory. In vivaria where dominant and subordinate lizards are living together, if a dominant male falls ill or is removed, it will be replaced on the favored high perch by the subordinate (personal observation). It is likely that males that lose territorial fights in nature will find marginal territories, but on Campbell's islands, as in laboratory habitats, such options are severely limited.

The earliest detailed report on social dominance in *Anolis carolinensis* was that of L. T. Evans (1936) who studied their behavior in large cages. He regarded their formation of social hierarchies as a "modification of the behavior in the field" attributable to the impossibility of retreat to a new territory. He also noted that "the dominant male is commonly green while all the rest are brown."

In the laboratory, *Anolis carolinensis* that fight form social dominance relationships with a rapidity suggestive of a well-established behavioral pattern (Greenberg, 1977; Greenberg *et al.*, 1984). Social dominance, in the conventional sense of one animal manifesting a priority of access to a limited resource over another, is seen in virtually all winners of aggressive interactions between males cohabiting laboratory vivaria. For the first 2–3 days there may be occasional renewals of agonistic interacting, especially in the morning, but these get progressively shorter and less intense. Many

(but not all) animals that establish stable relationships within three days often appear to be able to cohabit indefinitely, suggesting an adaptive resetting of physiological and behavioral tone—"allostasis" in the sense of re-establishing stability through change (Sterling and Eyer, 1988; and see McEwen, 2001).

For green anoles, the physiological and behavioral consequences of losing are extensive relative to those of winning (see Table 1). In one experiment where pairs were tracked for over a month, 25% of subordinate males died or showed signs of morbidity (Summers and Greenberg, 1994), but of these, more than half manifested atypical autonomic reactions early in the relationship.

Winners and losers. In captive green anoles, winners continue to perch at the highest site available and court females, expressing little more than occasional notice of the cohabiting loser. The loser, however, changes markedly: he becomes darker in body color, selects lower perch sites, is less active, and does not court—he has become a social subordinate (Greenberg *et al.*, 1984). Such pairs often share food and water and maintain stable relationships for extended periods, suggesting a pattern well fixed in their behavioral repertoire. But observations from the lab, no matter how consistent, can do no more than suggest ecological hypotheses about the possible advantages accruing from the changes in subordinates: their lower posture, activity levels, darker color, and altered site selection.

Only after stability is attained is a loser of a fight characterized as a social subordinate. During cohabitation in a vivarium, dominants are usually (but not always) green and dominant the highest perch while subordinates are usually (but not always) brown. When at a specific time their relationship is ambiguous, introducing a receptive female decisively confirms status. When the dominant starts courting, the subordinate shows signs of submissiveness. In rare cases where a subordinate also courts, the dominant immediately shifts from courtship displays (with their characteristic rapid head nodding) to aggression (with sagittal expansion of the body profile, eyespot), and subordinates back down. Reversals are very rare, and only seen in our lab when there is an asymmetry in size. In intruder experiments (as opposed to removing a divider between two tanks), residents that are smaller may initially prevail over a slightly larger intruder, but are ultimately unseated as dominants (Alworth, 1986).

Matched antagonists. Are there ever truly matched pairs of antagonists in agonistic encounters? There is a built in asymmetry in the "intruder/resident" paradigm. It is reasonable that, all else equal, an individual in an unfamiliar habitat would be at an initial disadvantage. In nature this might happen when a defeated male escapes and looks further, in the lab this is not usually the case. In one experiment we compared resident and intruder males for whole body lactate concentrations, indicative of glycolysis before and after encounters. All animals engaged in the territorial situation had two to three times the resting levels of lac-

TABLE 4. Putative causes and consequences of MSH release in various taxa.

CAUSES

- CRF increases circulating levels (Proulx-Ferland *et al.*, 1982)
- ACh increases circulating levels (see Hadley and Bagnara, 1975)
- SEROTONIN may be MSH-RF (see Hadley and Bagnara, 1975)
- CATECHOLAMINES (EPI, NE, 5-HT) may inhibit MSH release from pars intermedia (see Hadley and Bagnara, 1975)
- MELATONIN depletes pituitary MSH (after IP injection; see Kastin *et al.*, 1979)
- ENDORPHIN reduces MSH binding
- STRESSORS increase MSH activity: aggression raises pituitary content (Francis and Peaslee, 1974); "non-physical" stress increases release (Sandman *et al.*, 1973); "physical" stress increases release (along with increased ACTH; Sandman *et al.*, 1973); immobilization elevates circulating levels which then modulate prolactin (Khorram *et al.*, 1985).
- BEHAVIOR: acute stress (chase or restraint) reduces MSH, aggression reduces it in winners, increases it in losers; chronic stress (social subordination) increases MSH (Greenberg *et al.*, 1986) (MSH response to aggression in castrates is ameliorated)

CONSEQUENCES

- AGGRESSIVENESS diminished (attributable to MSH suppression of pineal melatonin; Patterson *et al.*, 1980)
- "EMOTIONALITY" is decreased (Golus *et al.*, 1979)
- TONIC IMMOBILITY, the duration of this defensive pattern of behavior, is decreased (Stratton and Kastin, 1976)
- "MOTIVATION" is increased (Stratton and Kastin, 1973)
- ATTENTION is enhanced (Kastin *et al.*, 1979; Sandman *et al.*, 1973)
- LEARNING: delays extinction of passive avoidance response in rats (Datta and King, 1977)
- ANXIETY is reduced (Miller *et al.*, 1974)
- ACTH release is increased (Lis *et al.*, 1982)
- TESTOSTERONE synergizes with MSH to stimulate release of aggression-releasing pheromone (in mice, Nowell *et al.*, 1980)
- TROPHIC PROPERTIES are indicated by stimulation of fetal growth, protein synthesis, wound healing, and liver regeneration (see Swaab and Martin, 1981)

5-HT, 5-hydroxytryptamine, serotonin; ACh, acetylcholine; ACTH, adrenocorticotropic hormone; EPI, epinephrine; NE, norepinephrine; MSH, melanocyte stimulating hormone; MSH-RH, melanocyte stimulating hormone releasing factor.

tate, but a pairwise comparison of animals at the beginning of an encounter showed intruders to be significantly higher than residents, presumably attributable to elevated autonomic arousal (Wilson *et al.*, 1990).

Among the physiological variables that might enable one of a matched pair prevailing in combat and ultimately manifesting dominance is adaptive scope. "Scope" in this sense refers to the tolerance for forced deviations from an optimal physiological state—the capacity to cope—before possibly escalating to or invoking a coping mechanism at another level. "Autonomic tone," that is the resting state of the autonomic nervous system and its reactivity, is also a concern. In our laboratory we generally use the "simultaneous sighting" design to introduce animals to each other. Each individual, in its own compartment of a large vivarium behaves like a dominant, selecting high perches and courting when a female is introduced. They first meet each other when a sliding door between compartments is delicately removed. "Resident advantage" is eliminated and lizards, each on their home ground, apparently perceive each other as intruders. Using this design, evidence (mentioned above) was found that prospective winners are more reactive to the situation and return to a stable state more rapidly than their adversary (Summers and Greenberg, 1994).

But what of losers? Stress is about coping with change, and following fights, winners return much as before. Color changes during fights might be similar, but the immediate consequences are not. The final color of the loser is usually brown with an eyespot while that of the winner is green with an eyespot. The pre-

sent understanding of *Anolis* chromatophore control suggests that losers have either exhausted EPI needed to change the ratio of alpha- and beta-adrenergic receptor stimulation or that MSH may prevail. Darker body color is typically seen in the losers of fights at their conclusion and will also characterize that animal if it remains to cohabit with the winner as a social subordinate. Body color thus suggests that acute responses are reinforced by subsequent allostatic readjustment of tonic hormone levels, particularly that of melanotropin (MSH).

Hormones and behavior

Melanotropin (MSH). It is interesting that in rats, physical stress elevates both plasma MSH and ACTH, while psychological stress evokes only an MSH response (Sandman *et al.*, 1973). If a comparable phenomenon obtains in *Anolis*, we would expect to find both hormones immediately after a rigorous physical encounter, but replaced by MSH with time. The long-term stability often seen in chronically brown lizards, presumed to be chronically stressed, may be in part attributable to some of the unique properties of melanotropin (Table 4). And MSH may in this respect serve a restorative function, helping long-term subordinates cope. In other taxa, melanotropin has found to reduce anxiety. When injected into *A. carolinensis*, it was found to significantly reduce the duration of defensive freezing (tonic immobility) (Stratton and Kastin, 1976). Unlike other stress-related hormones, MSH possesses trophic properties that can stimulate fetal growth, protein synthesis, wound healing, and liver re-

generation (Swaab and Martin, 1981), as well as neural regeneration (Van der Zee *et al.*, 1988).

Corticosterone (CS). In reptiles, much as in other taxa, circulating levels of glucocorticoid is increased by stress (Gist and Kaplan [1976] in *Caiman*; Dauphin-Villemant and Xavier [1987] in *Lacerta*). Corticosterone, the dominant glucocorticoid in reptilia, has apparent reciprocal relations with reproduction (reviewed in Greenberg and Wingfield [1987]; but see Sapolsky *et al.* [2000]). Suppression of reproduction reflects the classic conceptualization of the stress syndrome, as resources are reallocated to cope with needs more urgent than reproduction.

When Richard Tokarz (1987) implanted subcutaneous CS pellets in mature male brown anoles, *Anolis sagrei*. Implanted males manifested significantly fewer approaches and aggressive acts towards stimulus males compared to placebo-implanted individuals. Implanted males also had no detectable circulating testosterone while placebo males were normal. Similarly, side-blotched lizards, *Uta stansburiana*, had significantly depressed testosterone levels after CS pellet implantation (DeNardo and Licht, 1993). The *Uta* experiment, however, went further in utilizing an experimental group in which CS implanted animals also received testosterone. Such animals were also nonaggressive, demonstrating that the suppressive effects of CS was not testosterone-dependent. Further, CS implanted animals did significantly diminish courtship and copulation. The results of the double implants were comparable to those of CS alone, much like the findings in song sparrows (Wingfield and Silverin, 1986).

In a pilot study of the effects of CS implants in *A. carolinensis* in the laboratory, initial aggressive responses to a potential adversary were unimpaired, but even a modest aggressive reply evoked a rapid and complete shut-down of hostilities, subordinate posturing, and skin colors indicative of extreme acute stress (unpublished observation). The impression was one of hyper-responsiveness and underscoring the importance of the research environment.

A field study on *Uta stansburiana* showed significantly reduced activity and home range when some animals were CS-implanted and others saline-implanted, but when all males were CS-implanted there was no change, indicating that the competitive advantage that accrued to unaffected saline animals was nullified (DeNardo and Sinervo, 1994a). In a subsequent study, Testosterone-implanted males manifested a comparable competitive advantage over saline-implanted males; an effect that was nullified by co-implanting testosterone and CS-pellets (DeNardo and Sinervo, 1994b).

This underscores the point that just as CS has a large ensemble of potential effects on stressed organisms, it is likely to affect social relations through multiple routes, some more specific than others. For example, Andrew (*e.g.*, 1972) and Archer (1975) have made convincing cases for the effects of testosterone on attention structure in birds, affecting what stimuli re-

ceive attention as well as how much. In birds and mammals, ACTH, adrenal and gonadal steroids can apparently work through the hippocampus and septum to modulate selective attention (reviewed by Oades, 1979).

Androgen, stress and reproductive behavior

Reproduction is impaired by chronic as well as acute stress responses involving corticotropin releasing hormone (CRH), endogenous opiates, and glucocorticoids (reviewed by Sapolsky *et al.*, 2000). Reproductive suppression is consistent with the general principle of conserving resources when stressed. In dominance relationships, reproductive opportunities are typically the most critical of limited resources which a dominant seeks to monopolize, vividly reflecting at least direct fitness. It is thus reasonable to regard it, as Moberg (1985) puts it, a "barometer of animal well-being"; a sensitive index of the effects of stress. In practical terms such a barometer might be difficult to apply to specific populations. For example, the now familiar phenomenon of stress-sensitivity of offspring as a consequence of severe stress experiences of parents (*e.g.*, Clarke *et al.* [1996] in rhesus macaques; and see Graham *et al.* [1999]), forces us to consider long-term (multi-generational) effects on fitness.

Androgen spike in winners and suppression in losers. While short-term stress might facilitate testosterone secretion and long term stress suppress it (see Moberg, 1985), the experience of winning seems all-important in aggression-induced stress facilitation of androgen. In humans, testosterone elevation after stressful competition is more sustained in winners than in losers (Booth *et al.*, 1989) even *imagining* success in a conflict can elevate testosterone (Schultheiss *et al.*, 1999). Following a territorial dispute between matched adult males, *Anolis carolinensis* winners manifest a dramatic (470%) but transient spike in circulating androgen levels (Greenberg and Crews, 1990). A similar finding in birds led Wingfield *et al.* (1987) to suggest that a supportive or facilitative role for steroid hormones should complement their classic organizing and activating effects on the CNS. Wingfield also cautioned that evolutionary background, experience, social context, and multiple environmental variables are significant constraints on the manner in which testosterone affects social aggression.

In lizards, the hormone profile of subordinates following a fight is different. After combatants occupy the same vivarium for a week, circulating testosterone in lizards that win encounters have returned to control values, while the levels in losers have fallen to about 60% (Greenberg and Crews, 1990). Testicular function in subordinates is not, however, significantly altered. When spermatogenic stage was assessed by the proportion of cell types present in the reproductive tracts of 14 pairs of dominants and subordinates, in only two pairs did dominants manifest significantly more advanced cell types (Greenberg *et al.*, 1984). This indicates that if and when the motivation to court is re-

stored, the animal would rapidly recover sexual competence.

In subordinate lizards, the dynamics of changing stress and sex hormone levels is reflected in the immediate suppression of courtship and also the gradual loss of testosterone. The full suppression of circulating androgen is seen at about the time that dominance relationships are stabilized. It is reasonable that low androgen levels impair reproductive behavior but in the few days preceding this, might the subordinate's behavior in the presence of the dominant be expressing a conditioned avoidance response?

If a subordinate has learned that the presence of the dominant is an indication that courting or seeking an advantageous surveillance post will be punished, we might expect that when the dominant is not present the subordinate will no longer be inhibited. We tested this assumption. If after a week of cohabiting as a stable dominant/subordinate pair, the dominant is removed, effective courtship responses to a receptive female by the subordinate resumes gradually over a period of 18–48 hr (Greenberg and Lumsden, 1990). Interestingly, early responses to females were aberrant, occasionally dysfunctionally violent. It is likely that the recovery of function indicates a resurgence of androgen production after the removal of the presumed tonic suppressive effect of the presence of the dominant.

Is androgen suppression anxiolytic? Androgen reduction apparently ameliorates the effects of at least perceived, behavioral stressors on the system. Body color changes that occur during and after fights indicate that the experience of losing is more stressful than that of winning. The energetic effort of both combatants may appear comparable but there is no testosterone spike that may evoke some transitory metabolic advantage that might compensate for the energy expended. The gradually subsiding testosterone levels of losers may have important effects on motivation. Behavior that may be at first controlled by an avoidance response may, during this time, be gradually become affected by waning motivation such that an ordinarily attractive stimulus such as a high perch or female will no longer evoke an approach response. This would effectively replace a subordinate's stressful approach/avoidance ambivalence about behavior that might result in a punishing conflict with a dominant, with a redirection of attention to other needs. Testosterone is known to enhance motivation, at least for sexual activity (Balthazart *et al.* [1995] in quail; Alexander *et al.* [1994] in rats). In birds and mammals, gonadal steroids can directly affect sensory functions (Gandelman, 1983), selective attention (Oades, 1979), persistence of attention (Andrew, 1978), and have independent rewarding properties in the brain (Packard *et al.*, 1997).

Subordinates in stable relationships, much like castrates, appear to be under less stress. Castration does not eliminate agonistic responding in males, but adrenergic body color responses are retarded, and latency and duration of eyespot expression are both extended

significantly (Summers and Greenberg, 1994). Castrated males will engage in vigorous agonistic interactions in defense of territory but rarely show the enduring darkening effects of losing on body color when they cohabit with the winner. This absence of significant skin darkening in such losers suggested they might not be experiencing chronic stress as intact subordinates clearly are. Indeed, this was the case: corticosterone (CS) levels in castrates that lose was not found to be significantly greater than those of the winners (Greenberg *et al.*, 1984). Castration apparently reduces stress, presumably because the attention to previously provocative stimuli or their motivational significance was ameliorated by reduced androgen. Interestingly, female green anoles will also fight for relative status in which dominance is manifest by expression of the capacity to supplant an adversary. There are no color differences between paired females unless a male is present, in which case the dominant female is darker and would display sexual receptivity more often (Andrews and Summers, 1996). These observations are particularly interesting in light of findings in mammals that intensity and context of stressors (Shors and Servatius, 1997) can evoke different effects in males and females. For example, stress can impair acquisition of a conditioned response in female rats (but not if ovariectomized) while the same stressor facilitates learning in males (Wood and Shors, 1998).

Testosterone implants. The idea of adaptive testosterone reduction was tested in a pilot experiment on green anoles. Reasoning that an inability to reduce testosterone after an agonistic encounter with a superior adversary would lead to a more intense stress response in the defeated animal, *both* animals scheduled for a staged confrontation received testosterone implants. In now familiar fashion, winners occupied higher perches and were brilliant green, losers were brown to dark brown and remained on the substrate. A female was continually present. In these cages there were leaves and twigs to hide under and losers took every advantage of them. In the few tests to date, testosterone-implanted animals created the impression of a "super-subordinate." Such subordinates watch dominants intently and generally lowered their body posture or hid whenever the dominant's gaze went in their direction. Unlike typical subordinates, however (and possibly more like animals in nature), whenever the dominant was removed, the subordinate might immediately begin to court the female (Greenberg *et al.*, 1995). This further reinforces the idea mentioned above that testosterone enhances and may focus attention.

What other behavioral patterns affected by stress may also be modulated by androgen? Melanotropin is depressed by acute stress (Hadley and Bagnara, 1975). In green anoles, chase or restraint or winning an agonistic encounter cause reductions of 34%, 44%, 56% respectively. Losing an encounter, however, evokes a slightly elevated level of MSH. The levels remain elevated relative to the dominant (who returns to slightly more than control levels) during subsequent cohabi-

tation as a social subordinate. The MSH response in subordinates, however is ameliorated in castrates (Greenberg *et al.*, 1986)

Units of behavior documented during exploratory behavior are depressed by stress. but this depression is also ameliorated by castration with the exception of the form of tongue-flick called air-licking, presumed to be related to the vomeronasal chemosensation and mediated through a unique neural pathway (Greenberg, 1985, 1993).

Seasonal influences on the relationship between testosterone and aggressiveness in the field was indicated by artificially increasing testosterone levels in some males lizards, *Sceloporus jarrovi*. Moore and Marler (1987) found that there were significant increases in some, but not all, measures of territorial aggression. Males castrated in the fall when testosterone levels are highest show a dramatic diminution in the intensity of territorial defense, while castration of males during the summer when testosterone levels are only moderately elevated does not affect their capacity to vigorously and successfully defend their territories. Castrated *Anolis carolinensis* also manifest territorial defense when challenged (Greenberg *et al.*, 1984) however indices of stress in both winners and losers are markedly reduced (above). Taken together these findings support the idea that the diversity of endocrine control pathways as well as their multiple targets and diverse effects can provide a rich substrate for evolutionary influences on behavior (see Crews and Moore, 1986; Ketterson and Nolan, 1992).

ENVOI AND DIRECTIONS FOR FUTURE STUDY

One of the most vivid and provocative outcomes of a broad comparative review of stress is the potential of the system to make adaptive contributions in all aspects of life (Greenberg *et al.*, 2002). The multiplicity of hormone functions and the complexity of their participation in behavioral systems creates, as Ketterson and Nolan (1992, p. S33), put it (speaking mainly of testosterone), "ample room for variation on which natural selection can act." Examples of the manner in which control of autonomic reflexes can be brought under the influence of stimuli other than those concerned mainly with physiological homeostasis can be found in all taxa. In reptilia, specific species can provide us with models that can provide insight into this process. Hopefully, continuing work in this area will provide illuminating examples of the manner in which the cascade of effects the stress response represents can integrate all levels of organization into specific evolutionary changes. For example, the biology of stress is likely central to the shift in the control of chromatophores from serving purely homeostatic needs such as thermoregulation, to serving a role in crypsis, and even social communications. The manner in which fragments of motor patterns or autonomic reflexes are transformed into social signals are described in part by the evolutionary process of ritualization (Hinde and Tinbergen, 1958; Morris, 1956).

Sex steroids are the organizing and activating principle of reproductive and social biology and they are also centrally involved in stress biology. The psychoactive effects of two key steroids, corticosterone and testosterone, are becoming better known (see references above and McEwen, 1992), and the dynamic they manifest in reptilian models are consistent with the known effects. It would be interesting to review the interactions of steroids on monoamine expression in brain and chromatophores considering the contrasting effects of glucocorticoids and gonadal steroids (Flugge, 2000).

Stress physiology is likely involved with the life-saving facultative responses to transient, often unpredictable, environmental challenges that constitute an "emergency" stage in their life history (richly illustrated by Wingfield and his colleagues, see Wingfield *et al.*, 1998). These responses can and often are superimposed upon more programmed life history traits in ways that can suggest specific mechanisms by which facultative responses can become obligate.

The richness of steroid hormone genomic and non-genomic influences on electrophysiological responsiveness of neurons and effects on neurotransmitter release (the elegant work of McEwen, Pfaff, deKloet, and others, see Brown, 1994) lays the groundwork for inquiries into specific adaptive phenomena. For example, are the stress-reducing effects of reduced androgen attributable to altered afferent mechanisms, integrative processes, or efferent mechanisms and/or the manner in which these three dimensions of behavior interact? A clarification of information flow through the nervous system must also accommodate complex interactions. For example, gonadal steroids can modulate adrenoceptor responses to catecholamines and even mediate contrary responses depending on their concentration (Hadley, 1996, p. 330). In the orchestration of the stress response there are nested hierarchies that invoke alternative coping strategies, although it is also clear that many apparently specific effects of steroids on behavior are secondary to nonspecific effects in the nervous system.

The dynamics of endocrine responses to sustained stress such as social subordination suggests that there is a release of both MSH as well as ACTH, both derived from the precursor, proopiomelanocortin (POMC). Many subordinates cope well with their status suggesting questions about how these sibling hormones with very different effects are modulated. Is it possible that the processing of POMC is responsive to feedback that affects the varying proportions of its potential products in a manner not unlike the effect of glucocorticoids on the proportions of epinephrine and norepinephrine produced and released from adrenal chromaffin tissue?

The green anole has also been utilized as a model to help understand the role of the basal ganglia of the brain. This site, generally identified as a center of motor coordination, has been revealed in recent decades to be a key element in many cognitive processes in

mammals. Previous work with *Anolis carolinensis* has identified ventral portions of the basal ganglia as essential to the territorial aggression of this species (references in Greenberg *et al.* [1988]; and see Baxter *et al.* [2001a]). In this species, otherwise unimpaired males with lesioned ventral basal ganglia apparently manifest social agnosia and are unstressed and unprovoked by the site of intruding conspecifics. In the light of recent work on the regional localization and activity of stress-related neurotransmitters (Summers and Greenberg, 1995; Summers *et al.*, 1998; Baxter *et al.*, 2001b) this area, which in other taxa is in part responsible for integrating effects of stress as well as affect, motivation, and action, as well as stress (Greenberg, 2002), may be a source of future insight. In summary, we can look forward to deeper understanding of the activation and coordination of the stress response as research into the physiological ethology of this model species progresses.

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