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Corticosterone, locomotor performance, and metabolism in side-blotched lizards (*Uta stansburiana*)

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Abstract

Elevated levels of circulating corticosterone commonly occur in response to stressors in wild vertebrates. A rise in corticosterone, usually in animals of subordinate rank, results in a variety of effects on behavior and physiology. Behavioral and physiological responses to short-term increases in corticosterone are well studied. In contrast, the effects of chronic elevated levels of corticosterone are poorly understood, particularly in lizards. Here, we examined the long-term effects of exogenous corticosterone on locomotor performance, resting and active metabolic rate, and hematocrit in male side-blotched lizards *Uta stansburiana*. Corticosterone implantation resulted in higher levels of stamina relative to sham-surgery controls. In addition, lizards with elevated corticosterone exhibited lower resting metabolic rates relative to controls. Corticosterone had no effect on peak activity metabolism but did result in faster recovery times following exhaustive exercise. We suggest that elevated levels of corticosterone in response to dominance interactions promote enhanced locomotor abilities, perhaps as a flight response to avoid agonistic interactions. Furthermore, stressed lizards are characterized by lower resting metabolic rates, which may serve as strategy to conserve energy stores and enhance survival.

Keywords: Metabolism; Corticosterone; Endurance; Resting metabolic rate; *Uta stansburiana*

Introduction

Stress arising from social interactions can dramatically affect many phenotypic attributes of an organism including physiology, behavior, growth, reproduction, and response to pathogens (Axelrod and Reisine, 1984; Alberts et al., 1992; John-Alder et al., 1996; Fox et al., 1997; Gregory and Wood, 1999; Cote et al., 2006). Accordingly, considerable effort has been expended to understand the mechanisms behind the numerous neural and endocrinological pathways that induce phenotypic changes due to stress (see Johnson et al., 1992; Virgin and Sapolsky, 1997; Orchinik, 1998). Plasma concentrations of corticosterone [B], the primary adrenal glucocorticoid hormone of reptiles (Bentley, 1997; Nelson, 2006), typically rise in response to both a wide array of acute and chronic stressors in multiple contexts, e.g., social, environment, and disease (Orchinik, 1998). In particular, corticosterone concentrations rise in response to both short-term stresses of social and agonistic interactions (Greenberg et al., 1984; Knapp and Moore, 1995; Creel, 2001) as well as the long-term stresses associated with social status, e.g., dominance–subordinate interactions (Fox et al., 1997; Sapolsky, 1988; Creel, 2001).

Recent experiments have documented the behavioral and reproductive consequences of elevated corticosterone in lizards (Moore and Jessop, 2003; Belliure et al., 2004). Chronically increased plasma levels of corticosterone reduce levels of aggressive and reproductive behavior and testis size (Tokarz, 1987; DeNardo and Licht, 1993; De Fraipont et al., 2000). In addition, activity levels and home range size were reduced in response to elevated levels of corticosterone (DeNardo and Sinervo, 1994a). Whereas the behavioral consequences of this suppression are fairly well understood (Tokarz, 1987; DeNardo and Licht, 1993; DeNardo and Sinervo, 1994a,b), the

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physiological effects of elevated levels of corticosterone are largely unknown in lizards. Whether whole-organism traits, such as locomotor performance and energy metabolism, are affected by increased plasma levels of corticosterone arising through social interactions is an underappreciated aspect of the stress response. In a recent paper, Sinervo and Calsbeek (2003) hypothesized that increases in circulating corticosterone would perturb key physiological pathways and ultimately physiological traits such as metabolic rate and endurance. Because traits such as sprint performance or endurance represent the summed effect of many lower level tissue and biochemical characteristics (e.g., muscle fiber composition, enzyme activities; Garland and Losos, 1994), whole organismal traits may give a composite measure regarding the responses of individuals to the effects of stressors. However, it is possible that corticosterone may have contrasting effects on different physiological functions (Wikelski et al., 1999; Meylan and Clobert, 2004).

A link between stress and performance is suggested by several aspects of the action corticosterone. First, glucocorticoids affect intermediary metabolism and are intimately involved in energy balance and homeostasis (Axelrod and Reisine, 1984; Johnson et al., 1992; Bentley, 1998; Nelson, 2005). In particular, corticosterone facilitates transfer of energy from storage to the blood stream by stimulating gluconeogenesis and the generation of glucose substrates from non-carbohydrate sources, e.g., the release of amino acids and mobilization of free fatty acids from muscle, fat tissue, and liver (Johnson et al., 1992). However, prolonged periods of elevated corticosterone also induce the catabolism of muscle tissue (fast twitch muscle fibers), negative nitrogen balance, reproductive suppression, and immunocompetence (Nelson, 2005). Thus, the benefits of elevated corticosterone may entail a cost in terms of diminished reproduction and elevated mortality (but see Cote et al., 2006). Second, corticosterone levels rise after prolonged exercise (Rees et al., 1985; Gleeson et al., 1993; Coleman et al., 1998) or aerobically expensive activities (Emerson and Hess, 2001). Third, implantation of exogenous corticosterone stimulates activity or increases endurance in mammals (Devenport et al., 1993), birds (Breuner et al., 1998), lizards (Belliure et al., 2004; Cote et al., 2006), and turtles (Cash and Holberton, 1999). Furthermore, it has been hypothesized that corticosterone might also facilitate recovery after exercise (Gleeson et al., 1993), perhaps owing to its role in gluconeogenesis (Kraus-Friedmann, 1984).

A first step in understanding the role of corticosterone on whole-organism physiology is to de-couple the social effects from the underlying physiology of the corticosterone response. We use tonic implants to elevate the plasma levels of captive lizards to study the effect of chronically elevated corticosterone on whole-organism physiology. Removing the complexities of the natural environment in the laboratory permits the study of the interactions between stress and physiology while factoring out any potentially confounding social interactions (Dunlap and Wingfield, 1995). We measured one aspect of locomotor performance, endurance, because of its presumed importance in avoidance of predators, prey capture, and dominance displays (Garland and Losos, 1994; Robson and Miles, 2000). In addition, we examined the metabolic responses to elevated levels of corticosterone. We show that lizards implanted with corticosterone have higher stamina relative to control males, and that corticosterone implants have a significant effect on pre- and post-exercise metabolism. We also examined the time course through which the effects of corticosterone on stamina are mediated in the laboratory.

Methods

Species and study site

We obtained lizards from a population of the side-blotched lizard, *Uta stansburiana*, located on the east side of California's coast range during the summer of 1996. The study site, located on Billy Wright Road near Los Banos Grandes, Merced County, California, consists of sandstone rock outcroppings surrounded by grasslands, which are preferentially used by adult lizards. Because each isolated outcrop is separated by fields of grass, dispersal is greatly limited. Therefore, a given neighborhood of adults located on one outcropping is effectively isolated from other neighborhoods.

Males in this study population are characterized by a genetically based throat color polymorphism (orange, blue, or yellow; for a detailed description, see Sinervo and Lively, 1996), which corresponds with their mating behavior and territory status (Calsbeek and Sinervo, 2001; Calsbeek et al., 2001). Blue males defend a single female on a small territory, whereas orange males are ultra-dominant males that defend large territories that have multiple females. Blue males are subordinate to orange males. Yellow males do not defend a territory and instead traverse across a larger home range. In addition, yellow males adopt a female mimicry and sneaker behavior. Blue males actively mate guard to repel yellow females. The frequencies of each morph were blue (50%), yellow (30%), and orange (20%) during the field season. We used only the former throat morph in our experiment since these individuals are most likely to exhibit stress owing to dominance interactions with orange males and intrusions from sneaker males during the breeding season.

Effects of corticosterone on stamina

Lizard husbandry and hormone treatment

Fourteen male lizards were captured from the field site (all blue-throated) in late July toward the end of the breeding season and returned to the laboratory. Each lizard was weighed to the nearest 0.1 g and snout-vent length measured (SVL), to the nearest 1 mm. Males were then implanted intraperitoneally with either corticosterone [B] or a saline sham [S]. Implants were made of silastic brand medical grade tubing (Dow Corning No. 602305), 3 mm in length/0.078 mm i.d. and were sealed with silicone sealant (DeNardo and Sinervo, 1994a,b). The seals were approximately 1 mm long at each end, leaving the central 1 mm of space for corticosterone treatment. Seals on the implants were cured for 24 h and then implants were soaked in sterile saline for 24 h before intercoelomic implantation. These implants are known to keep plasma B levels, in both captive and free-ranging lizards, elevated to 30–50 ng/ml in excess of 3 months (DeNardo and Sinervo, 1994a,b), which is above recorded baseline levels (5–20 ng/ml). Thus, our treatment is likely to have maintained corticosterone levels elevated for the duration of this study (1 month).

We maintained each lizard in separate containers to avoid social interactions and agonistic behaviors. Lizards were fed crickets dusted with a vitamin and calcium supplement during