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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

the experiment. Three to four crickets were provided every other day. We noticed no change in body mass during the course of the experiment. Mean values for mass were not significantly different at the end of the experiment ($t=1.88$, $P<0.2$).

Temporal change in stamina

We estimated the stamina of all lizards prior to conducting the hormone experiment. Because feeding has been shown to reduce stamina in lizards (Martin, 1996), we fasted lizards for 24 h prior to the performance trial. Lizards were warmed to approximately 36 °C for a period of 30 min, which is the field active temperature (Sinervo, unpublished). We measured stamina using a motorized treadmill, which is a standard protocol in studies of physiological performance (e.g., Garland and Losos, 1994; Sinervo et al., 2000). The treadmill was enclosed by two opaque sides and a clear front window. The rear of the track remained open to allow manual motivation during testing. We induced the lizards to run at the pace of the belt (0.5 km/h) by gently tapping on the hind leg. The duration of time lizards maintained their position on the treadmill until fatigued was our estimate of stamina. A lizard was determined to have fatigued if it failed to maintain its position on the belt after three attempts (Robson and Miles, 2000). After determining their stamina, we randomly divided the fourteen lizards into two groups. Seven subjects were implanted with corticosterone, and seven males with saline.

The first post-treatment runs took place 4 days after surgery and continued at a frequency of one test per 2–7 days. Animal mass was recorded after each test. Stamina trials were performed at the same time each day to minimize effects due to diurnal hormonal rhythms. We used repeated measures ANOVA to test for changes in stamina over time in response to treatment. This test is beneficial because of its power, which allowed us to test for treatment effects despite a relatively small sample size during the experiment.

Effects of corticosterone on metabolism

A second sample of 23 male *U. stansburiana* lizards was collected from the field in late August (all blue throated) and randomly divided the individuals into two groups. As in the previous experiment, each lizard was individually maintained in separate terrarium under 40-W incandescent lamps for heat and ultraviolet lighting (11:13 light:dark) simulating the breeding season photoperiod (March–June). Animals were provided crickets and water *ad libitum*. Within 24 h after capture, the lizards were randomly implanted with either corticosterone ($N=12$) or saline ($N=11$) implants.

Measurement of resting metabolic rate and peak oxygen consumption

Lizards were transported to Ohio University (by air) for measuring standard metabolic rate (SMR) and peak oxygen consumption 1 week post-implant. Lizards were allowed to acclimate to laboratory conditions for a minimum of 2 weeks before conducting the respirometry measurements. Therefore, all metabolic tests occurred between 3 and 4 weeks after surgery, which is the approximate time elapsed before a statistical difference in performance was detected.

Standard metabolic rate was determined using an open-flow respirometry system while animals rested in a dark chamber at 36 °C. A dry air stream was passed through the chamber at a flow rate of 100–250 ml/min STPD. Excurrent air was sampled by a Vacumed® O_2 analyzer, with oxygen concentrations recorded every 5 min. Animals were kept in the chamber for 6 h. As an estimate of RMR, we averaged the minimum values for O_2 consumption and CO_2 production over a 15-min interval (Withers, 1977).

Measurement of peak O_2 consumption

Peak rates of O_2 consumption were measured using Vacumed® gas analyzers. Lizards were fitted with a transparent plastic mask through which room air was pulled at flow rates of 250–450 ml/min STPD. We followed previous studies and used masks made from ultracentrifuge tubes (see Garland and Bennett, 1990; John-Alder et al., 1986). The open end of the tube was covered with a latex diaphragm, which firmly held the tube against the neck of the lizard. We placed the lizard on the stationary treadmill belt and measured oxygen consumption for a period of 5 min to establish a baseline value (pre-exercise O_2). This procedure allowed the lizards to become accommodated to the mask, prior to measuring O_2 consumption during running on the treadmill. After 5 min elapsed, we gradually increased the speed of the treadmill to 1.0 km/h and ran the lizards to exhaustion. This was a belt speed that lizards could maintain for 1–3 min and which resulted in peak values for oxygen consumption. Belt speeds faster than 1.0 km/h quickly fatigued the lizards. During the time the lizards were running, we recorded oxygen consumption and carbon dioxide production every 5 s. Overall, most lizards fatigued within 1.5–3 min. The maximum value of O_2 consumption was used as an estimate of peak metabolism (or VO_{2max}). We continued to record O_2 consumption and CO_2 production until both reached their initial resting rate. We also determined the time required to return to resting rates. Males were tested on 2 consecutive days, and the single highest value reached during exercise was used to estimate peak O_2 consumption. From these data, we estimated peak O_2 consumption, mean O_2 consumption, time to reach resting rate (recovery time), and EPOC (Excess Postexercise Oxygen Consumption) and time to EPOC. Furthermore, we obtained respiration rates of the lizards as they recovered from exercise.

Hematocrit

Hematocrit (Hct) was measured on individuals at the end of the experiment. Animals were decapitated and blood samples taken from the neck. Blood was collected in heparinized microhematocrit tubes (75 mm long 1.1–1.2 mm i.d.) and centrifuged for 10 min at maximum speed in a microhematocrit centrifuge.

Statistical analyses

The stamina data were checked to ensure the assumptions of normality and homoscedasticity were met. No transformations were necessary. Pre-treatment values of stamina were compared between treatment groups by a one-way ANOVA. We used a repeated measures ANOVA as implemented using PROC Mixed (SAS v 8.2, SAS Institute, 2000) to ascertain whether corticosterone enhanced or reduced locomotor performance.

Resting metabolic rate as well as the other metabolic variables was non-normally distributed, even after several transformations. Therefore, we compared treatments using a non-parametric one-way ANOVA. In order to assess whether the placement of a mask around the head of a lizard to record oxygen consumption and carbon dioxide production induced additional stress and therefore affected our measurements of activity metabolism, we compared resting metabolic rate to pre-exercise metabolic rate. We used a regression tree analysis to simultaneously investigate which subset of the metabolic variables best explained the variation between treatment groups. Regression tree analysis is a non-parametric procedure that identifies those variables that best explains group membership (Breiman et al., 1984). The goodness-of-fit is ascertained using cross-validation and resampling procedures (De'Ath and Fabricius, 2000).

Results

Change in stamina due to exogenous corticosterone

Pre-treatment values for stamina did not differ between the sham surgery (239 s) and corticosterone (247 s) ($F_{1,7}=0.49$, $P=0.83$). Males with corticosterone implants had significantly higher values for stamina (347.4 s) relative to control males (197.5 s) by the end of the experiment (Fig. 1, $F_{1,5}=12.75$, $P<0.001$). Males implanted with corticosterone showed a significant improvement in running times ($r=0.36$, $P<0.01$). In contrast, we detected no differences in locomotor in the control group (Fig. 1). We found that the stamina of control males remained relatively constant ($r=0.15$, $P=0.30$). A repeated measures analysis of variance revealed a significant time × treatment interaction ($F_{1,70}=5.2$, $P=0.02$), which supports the observation that corticosterone resulted in an increase in performance over time. Also relevant to these results is the time scale in which significant changes in stamina were observed. In an earlier experiment, designed to assess the change in activity and home range behavior in the field, significant effects due to corticosterone arose within 1 month of treatment (DeNardo and Sinervo, 1994a,b). The change in stamina over time as induced by exogenous corticosterone is similar to trend in the field observed by DeNardo and Sinervo (1994a,b).

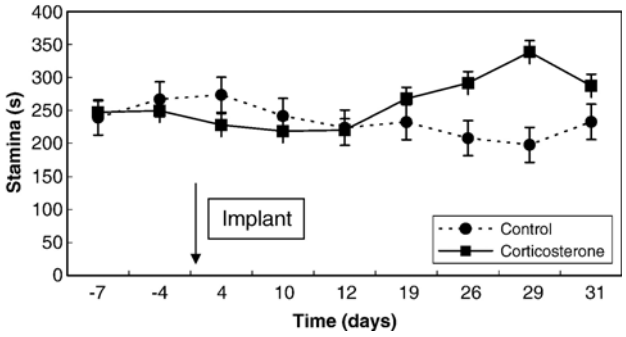

Fig. 1. Temporal variation in stamina as a consequence of exogenous corticosterone. Stamina is the time a lizard maintained its position on a treadmill at a constant speed of 0.5 km/h. Two measurements were made pre-implantation (Days −7 and −4). Surgeries were conducted on day 0. Our first post-implant measurement of stamina began 4 days after surgery and continued for an additional 31 days.

Table 1
Summary statistics from the microrespirometry measurements

Variable	Treatment	
	Control, $N=11$	Corticosterone, $N=12$
Resting O_2 consumption at 36 °C (cc g^{-1} h^{-1})	0.24 (0.031)	0.15 (0.02)
Resting CO_2 production at 36 °C (cc g^{-1} h^{-1})	0.06 (0.004)	0.05 (0.004)
Pre-exercise O_2 consumption (cc·g^{-1} h^{-1})	0.31 (0.051)	0.20 (0.039)
Average O_2 consumption (cc g^{-1} h^{-1})	0.27 (0.052)	0.25 (0034)
Maximum O_2 consumption (cc·g^{-1} h^{-1})	0.62 (0.143)	0.50 (0.089)
Maximum CO_2 production (cc·g^{-1} h^{-1})	0.15 (0.007)	0.13 (0.007)
Time to maximum O_2 consumption (s)	42.0 (5.95)	61.6 (6.06)
Recovery time (s)	77.67 (5.215)	62.30 (5.01)
Recovery O_2 consumption (cc·g^{-1} h^{-1})	0.43 (0.069)	0.40 (0.051)
Excess Post-Exercise Oxygen Consumption (EPOC) (cc g^{-1} h^{-1})	1.79 (0.192)	1.56 (0.28)
Time to EPOC (s)	35.00 (8.62)	20.50 (5.45)
Hematocrit (%)	31.61 (2.27)	35.00 (3.05)
Respiration rate (breathes/min)	35.76 (2.54)	37.7 (2.56)

Values presented are means and standard errors (in parentheses).

Differences in metabolism

Males implanted with corticosterone had significantly lower values for resting O_2 consumption than saline implanted males (ANOVA $F_{1,21}=5.39$, $P<0.02$; Table 1). Treatment males were also characterized by lower values for pre-exercise O_2 consumption (ANOVA $P<0.05$). We detected no statistical difference in pre-exercise metabolic rate relative to resting metabolic rate (paired t-test, $t=1.35$, $P=0.56$). Therefore, we conclude that the performance of lizards while on the treadmill was not affected by the apparatus used in the open-flow microrespirometry. There was no difference in resting CO_2 production between treatment groups (Wilcoxon χ^2 approximation=1.36, $P<0.25$). The time to maximum O_2 consumption was greater in corticosterone males than controls (χ^2 approximation=4.01, $P=0.04$). The remaining variables, maximum O_2 consumption, maximum CO_2 production, average O_2 consumption, recovery O_2 consumption, or Excess Postexercise Oxygen Consumption (EPOC), were not significantly affected by the effects of exogenous corticosterone implants. Note that all estimated values of O_2 consumption were lower in corticosterone males relative to controls. Males with corticosterone exhibited a more rapid recovery time (Table 1; $F_{1,18}=$

4.51, $P<0.05$) than shams. Indeed, corticosterone males returned to baseline values of O_2 consumption 15 s quicker than the shams. Time to reach EPOC also showed the same tendency but was not significant. The remaining variables, hematocrit, respiration rate, and T_b, were not significantly different between the treatments. We used regression tree analysis to determine the parsimonious set of variables that separated treatment groups (De'Ath and Fabricius, 2000). Resting metabolic rate, recovery time, and time to maximum O_2 consumption had the highest explanatory power in separating the treatment groups ($G^2=12.16$, $P<0.001$, $R^2=0.843$).

Discussion

Our study highlights somewhat contradictory effects of corticosterone in response to stress. Circulating levels of corticosterone may rise through social stressors, e.g., dominance interactions, environmental stressors, e.g., reduction in food availability, or disease (Wingfield and Ramenofsky, 1999). Previous experiments have documented a reduction in activity and home range size in *U. stansburiana* after experimentally increasing levels of corticosterone (DeNardo and Licht, 1993; DeNardo and Sinervo, 1994a,b). Field studies of free-ranging side-blotched lizards have shown high plasma levels of corticosterone among individuals that were in poor body condition or inhabiting biophysically stressful environments (Dunlap and Wingfield, 1995). These results show how an increase in corticosterone may play a role in energy conservation by reduction of activity and regulation of metabolic rate. However, elevated levels of circulating corticosterone are also associated with an increase in locomotor performance (Cash and Holberton, 1999).

Chronically elevated levels of corticosterone induced by our experiment resulted in an increase in endurance in male *U. stansburiana*. In addition, experimental males had significantly lower RMR and pre-exercise O_2 consumption, longer times to maximum oxygen consumption, and shorter recovery times. We found no differences between treatment groups in other attributes of metabolic performance or hematocrit.

Endurance, activity, and corticosterone

The effects of decreasing home range size and reducing access to females have led to the preliminary conclusion that corticosterone negatively influences life histories and reproductive success (DeNardo and Sinervo, 1994a,b). Our results in both the field and laboratory suggest that the implications of corticosterone are far more important than simply a means of inhibiting activity. That males implanted with corticosterone experience a significant increase in endurance indicates that corticosterone affects an underlying energetic pathway that plays some as yet to be determined physiological role in improving performance. One potential avenue may involve modification of activity and energy budgets (Cote et al., 2006). Chronic elevation of corticosterone has been shown to alter muscle composition mainly through the loss of glycolytic muscle fibers and the selective retention of oxidative muscle fibers (Fimbel et al., 1993). Although previous studies with corticosterone have addressed issues related to physiological effects of the hormone during and after exposure to a stressor (Coleman et al., 1998), the analysis of corticosterone effects on stamina, or exhaustive exercise, is largely unexplored (but see Gleeson et al., 1993). In an analysis of calling behavior in frogs, Emerson and Hess (2001) noted males with higher concentrations of corticosterone called more frequently than males with lower concentrations. Emerson and Hess (2001) hypothesized that corticosterone influenced the availability of lipids and carbohydrates available to the muscle fibers of the body wall and larynx. Contrary to other studies (e.g., Cash and Holberton, 1999) which show a short-term increase in performance, we found corticosterone to enhance endurance for a long period of time (~2 weeks).

Although the mechanisms by which corticosterone improves stamina are unclear, previous studies with corticosteroids have been shown to have significant effects on endurance-related aspects of physiology. For example, corticosteroids are known to increase protein content in the hearts of rats but have little to no effect on muscle growth (Kelly et al., 1986). Earlier studies showed that corticosterone stimulates hepatic gluconeogenesis in lizards (Gleeson et al., 1993; Nelson, 2005). Additionally, chronic elevation in corticosterone is known to increase lipid metabolism and carbohydrate availability (van der Boon et al., 1991) and endurance in adrenalectomized rats (Devenport et al., 1993). The observed increase in endurance in *U. stansburiana* may result from the action of corticosterone increasing glycogen availability and the resulting hyperglycemia to muscles.

Individuals with higher endurance should have a survival advantage when environmental factors favor dispersal to adjacent habitats (Cote et al., 2006). Moreover, individuals with higher endurance are presumed to have an increased likelihood of repeated escape from predation compared with individuals with inferior stamina. The effective decrease in home range size as a result of increased levels of corticosterone (e.g., DeNardo and Sinervo, 1994a), though previously believed to constrain life histories, may in fact be compensated by a concomitant increase in stamina. Although the complex cascade of events leading to increased stamina can not be reduced to the above examples, corticosterones' effects on endurance clearly deserve additional attention. For example, enhanced corticosterone levels in the lizard *Lacerta vivipara* modified the energy and activity budget as well as resulted in higher survivorship (Cote et al., 2006). Our results demonstrating enhanced stamina may provide a mechanistic explanation for the patterns observed by Cote et al. (2006).

Corticosterone and metabolism

Our estimates of resting metabolic rates for control males were consistent with previously reported values (Roberts, 1968; Andrews and Pough, 1985). A consequence of exogenous corticosterone appears to be a reduction in resting O_2 consumption rates. In addition, the experimental males required less time to recover from fatigue induced by sustained exercise.

The short time for recovery in implanted males may be a consequence of the role of corticosterone in facilitating lactate oxidation (Gleeson, 1996). To our knowledge, this study is the only to examine the metabolic changes induced by elevated levels of corticosterone. Previous work has noted no effect of corticosterone on resting metabolic rate (Wikelski et al., 1999).

The reduction of resting metabolic rates due to corticosterone has several ecological consequences. Principally, lower RMR in males implanted with corticosterone supports the observations described by DeNardo and Sinervo (1994a,b) and DeNardo and Licht (1993). Males with chronically elevated levels of corticosterone showed a significant reduction in home range size and activity relative to pre-implant levels. Blue males in our study population are characterized by smaller territories than the orange males (Sinervo et al., 2000), which may be a consequence of being challenged by territory usurping orange males and sneaker yellow males. DeNardo and Sinervo (1994a, b) suggested that the diminishment in activity and home range size due to corticosterone was a behavioral strategy that favored enhanced survival during stressful episodes by minimizing energetic costs. Our results show that the change in activity and home range size may be accomplished by a reduction in resting oxygen consumption and therefore a reduction in the daily energy requirements during periods of inactivity.

Adaptive basis of the stress response in Uta

Males implanted with corticosterone had both increased stamina and decreased resting metabolic rates. This result is consistent with an adaptive response to social stressors since differences in response to physiological stress should affect male fitness (Wingfield and Ramenofsky, 1999; Meylan and Clobert, 2004; Cote et al., 2006). For example, previous studies have shown that corticosterone levels predict survival in marine iguanas during periods of food stress (Romero and Wikelski, 2001). Blue morphs in *Uta* who are challenged by territorial usurping orange males or yellow sneaker males could benefit from increased plasma levels of corticosterone for enhancing dominance displays. Alternatively, subordinate males would adopt a strategy favoring survival over activity or behavioral aggression. Making a short-term territory sacrifice in favor of survival would allow these males to recoup their former territories or acquire new territories after the disappearance of a dominant male. A reduction in resting oxygen consumption among stressed males would favor survival during episodes of lowered food availability as a result of reduced activity times and smaller territory size. In addition, the increased stamina arising due to chronically elevated corticosterone levels may favor dispersal to a new territory (De Fraipont et al., 2000). Finally, decreased activity levels reflected in the reduction in resting oxygen consumption in stressed males could also enhance the recovery time after extended periods of exertion. We suggest that previous studies of the stress response have underestimated the potential adaptive significance of elevated corticosterone in chronically stressed individuals and overestimated the negative effects that corticosterone may have on the life-history.

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References

Alberts, S.C., Sapolsky, R.M., Altmann, J., 1992. Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. Horm. Behav. 26, 167–178.

Andrews, R.M., Pough, F.H., 1985. Metabolism of squamate reptiles: allometric and ecological relationships. Physiol. Zool. 58, 214–231.

Axelrod, J., Reisine, T., 1984. Stress hormones: their interaction and regulation. Science 224, 452–459.

Belliure, J., Meyland, S., Clobert, J., 2004. Prenatal and postnatal effects of corticosterone on behavior in juveniles of the common lizard, *Lacerta vivipara*. J. Exp. Zool. 301A, 401–410.

Bentley, P.J., 1998. Comparative Vertebrate Endocrinology, 3rd ed. Cambridge Univ. Press.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Wadsworth, Belmont.

Breuner, C.W., Greenberg, A.L., Wingfield, J.C., 1998. Noninvasive corticosterone treatment rapidly increases activity in Gambel's white-crowned sparrow (*Zonotrichia leucophrys gambellii*). Gen. Comp. Endocrinol. 111, 386–394.

Calsbeek, R., Sinervo, B., 2001. Uncoupling direct and indirect components of female choice in the wild. Proc. Natl. Acad. Sci. U. S. A. 99, 14897–14902.

Calsbeek, R., Alonzo, S.H., Zamudio, K., Sinervo, B., 2001. Sexual selection and alternative mating behaviours generate demographic stochasticity in small populations. Proc. R. Soc. Lond., B 269, 157–169.

Cash, W.B., Holberton, R.L., 1999. Effects of exogenous corticosterone on locomotor activity in the red-eared slider turtle, *Trachemys scripta elegans*. J. Exp. Zool. 284, 637–644.

Coleman, M.A., Garland Jr., T., Marler, C.A., Newton, S.S., Swallow, J.G., Carter, P.A., 1998. Glucocorticoid response to forced exercise in laboratory house mice (*Mus domesticus*). Physiol. Behav. 63, 279–285.

Cote, J., Clobert, J., Meylan, S., Fitze, P.S., 2006. Experimental enhancement of corticosterone levels positively affects subsequent male survival. Horm. Behav. 49, 320–327.

Creel, S., 2001. Social dominance and stress hormones. Trends Ecol. Evol. 16, 491–497.

De'Ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192.

De Fraipont, M., Clobert, J., John-Alder, H., Meylan, S., 2000. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. J. Anim. Ecol. 69, 404–413.

DeNardo, D.F., Licht, P., 1993. Effects of corticosterone on social behavior of male lizards. Horm. Behav. 27, 184–189.

DeNardo, D.F., Sinervo, B., 1994a. Effects of corticosterone on activity and home-range size of free-ranging male lizards. Horm. Behav. 28, 53–65.

DeNardo, D.F., Sinervo, B., 1994b. Effects of steroid hormone interaction on activity and home-range size of male lizards. Horm. Behav. 28, 273–287.

Devenport, L., Doughty, D., Heiberger, B., Burton, D., Brown, R., Stith, R., 1993. Exercise endurance in rats: roles of type I and type II corticosteroid receptors. Physiol. Behav. 53, 1171–1175.

Dunlap, K.D., Wingfield, J.C., 1995. External and internal influences on indices

of physiological stress: I. Seasonal and population variation in adrenocortical secretion of free-living lizards. J. Exp. Zool. 271, 36–46.
Emerson, S.B., Hess, D.L., 2001. Glucocorticoids, androgens, testis mass, and the energetics of vocalizations in breeding male frogs. Horm. Behav. 39, 59–69.
Fimbel, S., Abdelmalki, A., Mayet, M.H., Sempore, B., Koubi, H., Pugeat, M., Dechaud, H., Favier, R.J., 1993. Exercise training fails to prevent glucocorticoid induced muscle alterations in young growing rats. Pfluegers Arch. Eur. J. Physiol. 424, 369–376.
Fox, H.E., White, S.A., Kao, M.H.F., Fernald, R.D., 1997. Stress and dominance in a social fish. J. Neurosci. 17, 6463–6469.
Garland Jr., T., Bennett, A.F., 1990. Quantitative genetics of maximal oxygen consumption in a garter snake. Am. J. Physiol. 259, R986–R992.
Garland Jr., T., Losos, J.B., 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright an, P.C., Reilly, S.M. (Eds.), Ecological Morphology: Integrative Organismal Biology. University of Chicago Press, Chicago.
Gleeson, T.T., 1996. Post-exercise lactate metabolism: a comparative review of sites, pathways, and regulation. Annu. Rev. Physiol. 58, 565–581.
Gleeson, T., Dalessio, P., Carr, J., Wickler, S., Mazzeo, R., 1993. Plasma catecholamine and corticosterone and their in vitro effects on lizard skeletal muscle lactate metabolism. Am. J. Physiol. 265, R632–R639.
Greenberg, N.J., Chen, T., Crews, D., 1984. Social status, gonadal state, and the adrenal stress response in the lizard *Anolis carolinensis*. Horm. Behav. 18, 1–11.
Gregory, T.R., Wood, C.M., 1999. The effects of chronic plasma cortisol elevation on the feeding behaviour, growth, competitive ability, and swimming performance of juvenile rainbow trout. Physiol. Biochem. Zool. 72, 286–295.
John-Alder, H.B., Garland Jr., T., Bennett, A.F., 1986. Locomotory capacities, oxygen consumption, and the cost of locomotion of the shingle-back lizard (*Trachydosaurus rugosus*). Physiol. Zool. 59, 523–531.
John-Alder, H.B., McMann, S., Katz, L.S., Gross, A., Green, D.S., 1996. Social modulation of exercise endurance in a lizard (*Sceloporus undulatus*). Physiol. Zool. 69, 547–567.
Johnson, E.O., Kamilaris, T.C., Chrousos, G.P., Gold, P.W., 1992. Mechanisms of stress: a dynamic overview of hormonal and behavioral homeostasis. Neurosci. Biobehav. Rev. 16, 115–130.
Kelly, F., McGrath, J., Goldspink, D., Cullen, M., 1986. A morphological/biochemical study on the actions of corticosteroids on rat skeletal muscle. Muscle Nerve 9, 1–10.
Knapp, R., Moore, M.C., 1995. Male morphs in tree lizards have different testosterone responses to elevated levels of corticosterone. Gen. Comp. Endocrinol. 107, 273–279.
Martin, J., 1996. Effects of recent feeding on locomotor performance of juvenile *Psammodromus algirus* lizards. Funct. Ecol. 10, 390–395.
Meylan, S., Clobert, J., 2004. Is corticosterone-mediated phenotype development adaptive? Maternal corticosterone treatment enhances survival in male lizards. Horm. Behav. 48, 44–52.
Moore, I.T., Jessop, T.S., 2003. Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. Horm. Behav. 43, 39–47.
Nelson, R.J., 2005. An Introduction to Behavioral Endocrinology, 3rd edition. Sinauer Associates, Sunderland, MA.
Orchinik, M., 1998. Glucocorticoids, stress, and behavior: shifting the timeframe. Horm. Behav. 34, 320–327.
Rees, A., Harvey, S., Phillips, J.G., 1985. Transitory corticosterone responses of ducks (*Anas platyrhynchos*) to exercise. Gen. Comp. Endocrinol. 59, 100–104.
Roberts, L.A., 1968. Oxygen consumption in the lizard *Uta stansburiana*. Ecology 49, 809–819.
Robson, M.A., Miles, D.B., 2000. Locomotor performance and dominance in male tree lizards, *Urosaurus ornatus*. Funct. Ecol. 14, 338–344.
Romero, L.M., Wikelski, M., 2001. Corticosterone levels predict survival probabilities of Galápagos marine iguanas during El Niño events. Proc. Natl. Acad. Sci. 98, 7366–7370.
Sapolsky, R.M., 1988. Individual differences and the stress response: studies of a wild primate. Adv. Exp. Med. Biol. 245, 399–411.
SAS Institute, 2000. SAS/STAT Users Guide. SAS Publishing.
Sinervo, B., Calsbeek, R., 2003. Physiological epistasis, ontogenetic conflict and natural selection on physiology and life history. Integr. Comp. Biol. 43, 419–430.
Sinervo, B., Lively, C., 1996. The rock–paper–scissors game and the evolution of alternative male strategies. Nature 380, 240–243.
Sinervo, B., Miles, D.B., Frankino, W.A., DeNardo, D., Klukowski, M., 2000. Testosterone, endurance and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. Horm. Behav. 38, 222–233.
Tokarz, R., 1987. Effects of corticosterone treatment on male aggressive behavior in a lizard. Horm. Behav. 21, 358–370.
van der Boon, J., van den Thillart, G.E.E.J.M.A., Addink, A.D.F., 1991. The effects of cortisol administration on intermediary metabolism in teleost fish. Comp. Biochem. Physiol. A 100, 47–54.
Virgin, C.E., Sapolsky, R.M., 1997. Styles of male social behavior and their endocrine correlates among low-ranking baboons. Am. J. Primatol. 42, 25–39.
Wikelski, M., Lynn, S., Breuner, C., Wingfield, J.C., Kenagy, G.J., 1999. Energy metabolism, testosterone and corticosterone in white-crowned sparrows. J. Comp. Physiol., A 185, 463–470.
Wingfield, J.C., Ramenofsky, M., 1999. Hormones and the behavioral ecology of stress. In: Balm, P.H.M. (Ed.), Stress Physiology in Animals. Academic Press, New York, pp. 1–51.
Withers, P.C., 1977. Measurement of VO_2, VCO_2, and evaporative water loss with a flow-through mask. J. Appl. Physiol. 42, 120–123.