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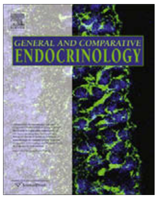

Food deprivation modifies corticosterone-dependent behavioural shifts in the common lizard

J. Cote [a,b,*], J. Clobert [c], L. Montes Poloni [d], C. Haussy [e], S. Meylan [a]

[a] *Laboratoire Fonctionnement et Evolution des Systèmes Ecologiques, UMR 7625, Université Pierre et Marie Curie, 7, quai Saint-Bernard, 75005 Paris, France*
[b] *Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA*
[c] *Station d'Ecologie Expérimentale du CNRS à Moulis, USR 2936, Moulis, 09200 Saint-Girons, France*
[d] *Mécanismes adaptatifs : des organismes aux communautés, UMR 7179 CNRS, MNHN, UPMC, 2, place Jussieu, Case 7077, 75005 Paris, France*
[e] *Laboratoire Parasitologie évolutive, UMR 7103, Université Pierre et Marie Curie, 7, quai Saint-Bernard, 75005 Paris, France*

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ABSTRACT

Stressful events typically induce glucocorticoid production that suppresses unnecessary physiological and behavioural functions. The glucocorticoid production also temporally activates alternative behavioural and physiological pathways. These responses are generally adaptive changes to avoid the negative effects of stressors. However, under low food availability, these behavioural and physiological modifications might lead to energetic costs. We therefore predict that these responses should not be activated when there are energetic constraints (e.g., low food availability). We experimentally tested whether food deprivation modifies corticosterone-induced behavioural and physiological responses in captive male common lizards. We measured corticosterone-induced responses in terms of body mass, metabolic rate, activity level and basking behaviour. We found that corticosterone-induced various behavioural and physiological responses which were dependent on food availability. Well-fed lizards treated with corticosterone were active earlier, and increased their basking behaviour. These behavioural modifications did not occur in food-deprived lizards. This inactivation of stress-related behavioural changes probably allows the lizard to save energy.

1. Introduction

In many species, individuals adjust their phenotype in response to environmental changes (West-Eberhard, 1989). These phenotypic adjustments necessary to face a stressful event often require energetic expenditure that exceeds the energy necessary to maintain all current functions (McEwen and Wingfield, 2003; Romero, 2004; Wingfield, 2003). In many cases, responses to environmental perturbations involve the production of glucocorticoids that often mediate changes in physiological pathways and behavioural expression that minimize energy expenditure (i.e., emergency life history stages; Romero, 2004; Wingfield, 2003). For example, increased glucocorticoid levels can suppress reproductive behaviour (Moore and Jessop, 2003; Silverin, 1998), social activity (DeNardo and Licht, 1993) and partial regulation of the immune system (Berger et al., 2005; Morici et al., 1997), or can increase activity and foraging (Breuner et al., 1998; Cote et al., 2006; Gleeson et al., 1993; Tataranni et al., 1996). These stress responses constitute a set of adaptive changes that should promote survival (Breuner et al., 2008; Cote et al., 2006; Romero, 2004; Wingfield, 2003).

Corticosterone concentrations rise in response to both short-term (e.g., social interactions and food availability; Creel, 2001; Greenberg et al., 1984; Knapp and Moore, 1995; Wingfield and Ramenofsky, 1999) and long-term stressors (e.g., social status; Creel, 2001; Fox et al., 1997; Sapolsky, 1988). While short-term stressors are believed to induce different physiological responses than long-term stressors, the behavioural stress responses are often similar. For example, chronically increased plasma levels of corticosterone also reduce or suppress aggressive and reproductive behaviours (de Fraipont et al., 2000; DeNardo and Licht, 1993; Tokarz, 1987) as well as activity (DeNardo and Sinervo, 1994) in lizards. However, a temporary rise in glucocorticoid level increases energetic expenditure in a lizard species (DuRant et al., 2008). Moreover, a sustained elevation of glucocorticoid production in response to long-lasting stressors requires more energy than a temporary one (Pravosudov et al., 2001; Romero, 2004) and may then have negative consequences, such as catabolization of fast-twitch muscle fibres leading to loss of muscle function, reduced immunocompetence or neural degeneration (Berger et al., 2005; McEwen et al., 1997; Morici et al., 1997; Sapolsky et al., 2000). In many cases, individuals experiencing chronic stress may compensate

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[*] Corresponding author. Address: Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA.
E-mail address: jdcote@ucdavis.edu (J. Cote).

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for the energetic costs by enhancing, for example, food intake (Cote et al., 2006; Kitaysky et al., 2003; Tataranni et al., 1996).

Under some environmental circumstances, however, energetic requirements may exceed available environmental resources. From an evolutionary perspective, stress-induced behavioural and physiological responses should then be modulated according to energetic constraints encountered in the environment or to intrinsic factors such as the ability to mobilize energy from fat reserves. More precisely, in conditions in which resource availability/energetic reserves does not compensate for the energetic requirements of the stress response, the behavioural and physiological modifications may not be activated (Landys et al., 2006). For example, Astheimer et al. (1992) showed that birds modulate their activity and their metabolic rate according to their level of satiety to prevent unnecessary energetic expenditure. Some other studies also showed that corticosterone-induced modifications strongly depend on body condition (Angelier et al., 2007; Loiseau et al., 2008), suggesting the effect of energetic conditions on stress responses. Although previous studies have predicted adaptive responses to long-lasting stress (Cabezas et al., 2007; Cote et al., 2006), the consequences of reduced food availability on the development of behavioural responses to chronic corticosterone elevations still remain unclear. Increasing activity in a food-deprived environment is inefficient and may lead to undesirable increases in energy expenditure; thus, we predict that chronically stressed animals should not exhibit this inefficient stress response in a food-deprived environment.

Here, we experimentally tested whether food deprivation modifies the corticosterone-induced behavioural responses in the common lizard (*Lacerta vivipara*). In this species, a chronic elevation of corticosterone increases energetic expenditure, food consumption, activity and basking behaviour (Cote et al., 2006; de Fraipont et al., 2000). Furthermore, corticosterone has direct and indirect positive effects on male survival via its effects on behaviour and physiology (Cote et al., 2006). Moreover, in this species, food availability is known to affect several important life history traits, for example offspring dispersal (Massot and Clobert, 1995). Thus, we expect that underfed and well-fed lizards will respond to corticosterone treatment in different ways. Based on previous studies we predict that well-fed lizards chronically treated with corticosterone should have greater mass loss and higher metabolic rate, should start their activity earlier and spend a greater proportion of time active compared to control lizards. However, we expect these responses to be reduced or suppressed in food-restricted lizards.

2. Methods

2.1. Species, study-site and housing conditions

The common lizard (*L. vivipara* Jacquin, 1787) is a small lacertid (adult snout–vent length: males 40–60 mm, females 45–75 mm) living in humid habitats in Eurasia. The diet consists of small insects, spiders and earthworms (Avery, 1962).

The experimental design was applied to two separate groups of adult males (>2 years old) in which different variables were measured (because data collection continued on one group for an additional analysis to be reported elsewhere, Fig. 1). These two groups have been collected at the same time (in June 2006) over 4 days from three populations in close proximity (less than 1 km a part) on the Mont Lozère (France, 44°27′N, 3°44′E, average elevation of 1400 m) in Southern France. Group 1 consisted of 36 individuals (9 in each treatment combination) and were used to measure plasma corticosterone levels on day 11. Group 2 consisted of 84 individuals (21 in each treatment combination) and was used to measure body mass on days 1 and 11, standard metabolic rate on day 11 (on a subset of 40 individuals) and behaviour on day 11. Individuals were allocated to hormonal and feeding treatments (described thereafter) in a full crossed design. Half of the males were randomly chosen and treated with corticosterone, while the remaining males were treated with a control treatment. Within each hormonal treatment (corticosterone and control), half of the males were randomly chosen to receive a high feeding treatment, while the remaining males received a low feeding treatment. Treatment groups did not differ in body size (snout–vent length: SVL), body condition or date of capture ($p > 0.20$ for all the simple treatments effects and the interaction) and the same number of lizards from each population were allocated to each of the treatment groups. Prior to the experiment, lizards were individually housed in captivity in plastic terrariums (25 × 15.5 × 15 cm; Le Galliard et al., 2003) containing 3-cm deep litter. In one corner of the terrarium a bulb provided heat for thermoregulation from 09:00 to 12:00 h and from 14:00 to 17:00 h. The bulb created a temperature gradient in the terrarium from room temperature (19–24 °C night–day) to 35–37 °C (below the bulb), encompassing the thermal needs range of this species (Van Damme et al., 1986). An opaque egg carton was added, allowing lizards to hide. Lizards were able to behave normally and behaviour associated with escaping (e.g., scratching on the walls) was rarely observed. Experimental methods adhered to the National Institute of Health Guide for Care and Use of Laboratory Animals. The experiment described below was started 4 days after the capture of the last lizard.

2.2. Experimental treatments

2.2.1. Experimental corticosterone application

The males of each group were allocated to either a corticosterone or a control treatment. The corticosterone treatment consisted of a daily application of 4.5 μl of sesame oil mixed with corticosterone (3 μg of corticosterone/μl oil). Control lizards were treated with 4.5 μl of only sesame oil (for more details, see Cote et al., 2006; Meylan et al., 2003). The treatment was applied on the dorsal surface of the lizard each evening for 10 days (starting on day 1, Fig. 1).

This non-invasive method of corticosterone treatment is similar to that described by Knapp and Moore (1995). It leads to a 5- to 10-fold increase of the basal blood corticosterone levels (equivalent to an absolute increase of about 100 ng/ml) compared to natural populations (Meylan et al., 2003; Cote et al., 2006). Average basal plasma corticosterone levels of individuals that were housed for 1 day in the laboratory day were 21.64 ng/ml for females (max. 101.97 ng/ml, Meylan et al., 2003) and 77.03 ng/ml for males (max. 181 ng/ml, Cote et al., 2006). Our manipulation therefore corresponds to the upper level of corticosterone that naturally occurs in response to acute stress in reptiles (DuRant et al., 2008; Tyrrell and Cree, 1998; see Section 4 for more details).

2.2.2. Feeding treatment

Within each of the hormone treatments (corticosterone and control), half of the individuals were randomly allocated to well-fed and food-restricted treatments. The feeding treatment levels were based on three previous studies of the same species (Cote et al., 2006; Le Galliard et al., 2004; Massot and Clobert, 1995). At the start of the experiment (day 1, Fig. 1), each lizard of the well-fed group was offered one *Pyralis farinalis* larva, whereas lizards of the food-restricted group received no larva to create a diet restriction. Five days later (day 6), all lizards were offered one larva. Only larvae of similar body mass were used to feed the lizards (254 mg ± 12.64 SE). In nature, this species feeds on small insects, spiders and earthworms (Avery, 1962). Our feeding regime is less diverse than in nature, but (1) larvae are part of the feeding regimes of this species and (2) a single specific prey allowed us to precisely control the feeding