General and Comparative Endocrinology 177 (2012) 104–112

Contents lists available at SciVerse ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Ecological correlates of cortisol levels in two bat species with contrasting feeding habits

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ARTICLE INFO

Article history:
Received 19 July 2011
Revised 17 January 2012
Accepted 28 February 2012
Available online 10 March 2012

Keywords:
Glucocorticoid
Cortisol
Seasonality
Food availability
Feeding habit
Phyllostomid bat

ABSTRACT

The immediate release of adrenal glucocorticoids can be crucial for an animal's survival when facing a stressor, but constantly elevated or exceptionally high glucocorticoid levels are usually detrimental for health. Although baseline and maximal secretion of glucocorticoids are regulated within narrow ranges within species, plasma glucocorticoid levels vary largely across vertebrates. We asked what ecological factors affect baseline plasma cortisol levels (CortI) and maximum levels (CortMax) following a physiological challenge through administration of adrenocorticotropic hormone (ACTH). Specifically, we studied whether seasonal fluctuations in food abundance correlate with the capacity of cortisol increases in two phyllostomid bat species with contrasting feeding habits: the sanguinivorous vampire bat (*Desmodus rotundus*) and the frugivorous short-tailed fruit bat (*Carollia perspicillata*). Both species coexist in habitats with various levels of seasonality (dry and rainforest). On a seasonal basis, resource abundance is more stable for vampire than for fruit bats, but previous studies suggested that daily foraging success may vary more for vampire than for fruit bats. CortI and CortMax varied seasonally in *C. perspicillata* from dry and rainforests, with the exception of CortMax in rainforest bats. Although we expected food availability to be stable year-round for vampire bats, we found CortI and CortMax of vampires to be higher during the rainy season than during the dry season. Also, we found CortMax to be higher in vampires from the rainforest than in those from the dry forest. CortMax of vampires were among the highest measured for a free-ranging mammal; a pattern that could be related to the species' vulnerability to starvation. We conclude that food availability modulates cortisol levels in free-ranging species that face seasonally fluctuating resources; in species, however, that benefit from food which is constantly abundant, other factors than food may become more important in modulating cortisol levels.

1. Introduction

The hypothalamus–pituitary–adrenal (HPA) axis is important for all stages of an animal's life history and it becomes particularly relevant when animals experience unpredictable or uncontrollable stimuli that challenge their well-being or survival. If such stimuli bear the potential to disrupt an organism's homeostasis, they are commonly termed 'stressors' [42]. To deal with stressors, such as starvation or social challenges, vertebrates elicit a hormonal stress response via the HPA axis, which culminates in the release of glucocorticoids from the adrenal cortex. These steroid hormones initiate physiological or behavioral modulations in response to the stressor and thus can influence an individual's Darwinian fitness [3,45] or predict survival [47,53]. In birds, stress induced glucocorticoid levels correlate positively with survival rate [29], supporting the role of glucocorticoids in resisting adverse environmental conditions. Generally, the amount of released glucocorticoids correlates with the intensity of a stressor [14]. Whereas temporary elevated glucocorticoid levels might increase an individual's fitness and usually are expected to be adaptive, chronically elevated glucocorticoid levels can be detrimental for the health of an animal [11]. If glucocorticoids persist at high levels, they might even cause damage and pathological changes such as hypertension, immune suppression, energy (fat) depletion and muscle wastage, brain damage and suppression of reproduction (reviewed in [58]) and can even lead to death [56]. Being of pivotal importance for survival and most likely a conserved trait during animal evolution, the hormonal cascade of the HPA axis functions in similar ways in almost all vertebrates [29,58]. However, despite the similarity in the general hormonal pathways along the HPA axis, it is well documented that species show different levels of

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http://dx.doi.org/10.1016/j.ygcen.2012.02.021

glucocorticoids and various thresholds at which a stress response is triggered. This plasticity in the release of glucocorticoids seems to be necessary to allow behavioral and physiological responses to be modulated according to an individual's actual demands [44]. The vulnerability to acute stressors increases when the level of glucocorticoids is at the upper limit of the range determined by normal circadian and seasonal fluctuations ('predictive homeostasis' *sensu* [56]). In this case, glucocorticoid levels are more likely to exceed the reactive homeostasis and reach homeostatic overload, possibly resulting in negative health impacts or even death [56]. Therefore, it is important to understand factors that potentially modulate the predictive and reactive homeostasis range of glucocorticoids.

Besides harsh environmental conditions and risk of predation, chronic malnutrition or acute starvation are the most relevant stressors for free-living vertebrates [56]. The nutritional state and consequently food availability affect glucocorticoid levels, because glucocorticoids are metabolic hormones regulating carbohydrate, protein, and lipid metabolism. Glucocorticoids can increase circulating glucose concentrations for instance by stimulating hepatic gluconeogenesis, by lipolysis in fat cells, and at elevated levels even by proteolysis (reviewed in [58]). Consequently, fasting usually induces an increase in plasma glucocorticoid levels [42]. For example, baseline corticosterone levels of black-legged kittiwakes (*Rissa tridactyla*) are higher when food abundance declines [37], and many free-living birds exhibit low plasma corticosterone levels when receiving additional food [11]. In the common murre (*Uria aalge*), baseline corticosterone levels are inversely related to fluctuations in food abundance [33]. However, acute stress-induced glucocorticoid levels of common murres were best explained by the food availability of the previous month rather than the current situation. This is probably caused by the facilitating effect of repeated glucocorticoid stress responses. This facilitation usually compensates for the negative feedback that elevated glucocorticoid levels exert on subsequent glucocorticoid secretion and thus enables vertebrates to maintain sensitivity to stress. However, this facilitation may become dominant over the negative feedback if an animal is chronically exposed to stress [1], such as under prolonged fasting. Consequently, elevated stress-induced glucocorticoid levels can indicate that an animal has frequently been exposed to a stressor during the past, but not necessarily at the moment. Even though this has been postulated to be generally true across vertebrates [1], only a limited number of species other than birds has been investigated with respect to the modulating capacity of food availability on glucocorticoid levels (e.g. [25,53]).

Species with contrasting feeding habits are probably exposed at varying levels to seasonal fluctuations in food availability. Also, fluctuations in food availability are likely to be related to the seasonality of habitats. Some bat species, such as the short-tailed fruit bat (*Carollia perspicillata*) and the common vampire bat (*Desmodus rotundus*), co-exist in rainforests as well as in tropical dry forests of Central America. Therefore, these bats are good candidates to investigate the relationship between feeding habit, seasonality of food supply, and glucocorticoid secretion. The frugivorous *C. perspicillata* is a specialist consumer of *Piper* fruits (e.g. [32,60]) but feeds occasionally also on other fruits, nectar, pollen, and insects [12,18]. In contrast, the highly specialized sanguinivorous *D. rotundus* feeds exclusively on blood of larger vertebrates, such as peccaries [35]. Close to farmland the major prey of vampires constitutes livestock, such as cattle and horses [38,63,65]. Thus, our study species feed on contrasting diets while being exposed to similar climatic and environmental conditions as they sympatrically occur in dry and rainforests. At our study sites, cattle farming is a major sector of agriculture, resulting in peak densities of livestock populations within Costa Rica [2]. However, cattle and horses move around unpredictably from day to day, therefore constituting a resource that is constantly available throughout the seasons of a year, but not necessarily accessible every night for vampires. *Piper* fruits, which constitute the major diet of *C. perspicillata,* are available almost constantly throughout the year [60]. In general, fruit abundance is high for short-tailed fruit bats in rainforests, even though seasonal fluctuations in fruit availability might occur to a certain extent [20,43]. In contrast, seasonal fluctuation of fruit availability is much stronger in tropical dry forests [19,20,30,43].

In our study, we investigated the relationship between food abundance and glucocorticoid secretion in two tropical bat species with different feeding habits. As a measure of an animal's responsiveness to stress, we quantified the adrenal response to injections of exogenous adrenocorticotropic hormone (ACTH) that stimulates adrenal glucocorticoid secretion. Elevated stress- or ACTH-induced glucocorticoid levels are probably not biased by stressful events which might have happened shortly before sampling, since facilitation compensates for the fast negative feedback glucocorticoids exert on the HPA axis, thereby enabling proper subsequent stress responses [1]. Stress- or ACTH-induced glucocorticoid levels integrate over a longer period of time and reflect the physiological challenges or, more general, the cumulative stress of several days [33]. Therefore, maximum glucocorticoid levels are better suited than baseline levels to draw conclusions about an individual's general ability to respond to stress. In contrast, baseline levels are more related to an animal's actual physiological state and could be elevated due to preceding stressors without being noticed. In particular, we asked whether the degree of seasonal fluctuations in food availability influences blood plasma cortisol levels in frugivorous mammals under natural conditions. Furthermore, we asked whether cortisol secretion in a syntopic species exhibiting stable, non-fluctuating food availability would be equally constant over seasons and habitats.

Due to the metabolic role of glucocorticoids for body homeostasis and their actions in energy allocation and appetite promotion, we expected cortisol levels of *C. perspicillata* to be inversely related to seasonal fluctuations in food availability in the dry forest, i.e. to reach higher levels when ripe fruits are scarce and lower levels when food availability is high. We did not expect such seasonal differences in the rainforest population because of assumed constant food availability. We expected *D. rotundus* to reach similar CortMax levels in both habitats and seasons, since livestock was available in proximity to both study sites year-round.

2. Material and methods

2.1. Study sites

We conducted our study at La Selva Biological Station (LSBS; Heredia Province, Costa Rica, 10°26′N, 83°59′W) and at Sector Santa Rosa (SSR; Guanacaste Province, Costa Rica, 10°50′N; 85°37′O), both of which adjoin pastures. LSBS is covered mainly by primary and old secondary tropical wet forest [40]. Depending on the site of bat capture, distance to the closest pasture ranged from 150 to 1400 m. The relative proportion of area covered by pasture amounts to 23% for the Sarapiquí region, i.e. the canton surrounding LSBS, with a cattle density of 1.2 individuals/ha of pasture [16]. Rainfall in LSBS amounts 4000 mm/m^2 per year with a minor dry season in January through April but exceeds 150 mm/m^2 in all months [57]. In contrast, SSR exhibits a distinct six month dry season with hardly any precipitation from mid-November to mid-May; total annual rainfall varies around 1500 mm/m^2 (data from Santa Rosa weather station, http://investigadores-sacg.org/blog/?page_id=117&lang=es, accessed 31.07.2010). The vegetation at SSR is classified as predominantly deciduous tropical dry forest [4,26]. We estimated the distance to the closest pasture