Behav Ecol Sociobiol
DOI 10.1007/s00265-013-1591-9

ORIGINAL PAPER

Carotenoid-based plumage coloration reflects feather corticosterone levels in male house finches (*Haemorhous mexicanus*)

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Received: 10 January 2013 / Revised: 28 June 2013 / Accepted: 1 July 2013

Abstract Indicator models of sexual selection predict that exaggerated traits communicate information about sender condition or quality to conspecific receivers. Environmental challenges have often been considered as one such condition that could be encoded in an ornamental trait, and there is now extensive evidence showing how different stressors (e.g., nutritional, parasitological, and environmental) impact sexual signal elaboration. One of the primary means of assessing stress is by quantifying glucocorticoid (corticosterone or cortisol (CORT)) levels. For many ornaments, CORT impairs trait expression; however, the evidence is limited and mixed for one of the classic honest signals in animals, ornamental carotenoid coloration. In a model species for studies of carotenoid ornamentation (the house finch, *Haemorhous mexicanus*), we examined the relationship between male plumage redness and feather CORT levels, which serve as an integrated measure of hormone concentration during feather growth. We measured CORT in both tail (melanin-containing) and breast (carotenoid-containing) feathers and found that CORT levels were not different between body regions, but they were negatively correlated with plumage hue, with redder birds having more CORT in feathers. Despite opposing traditional views on stress and ornamentation, our results actually corroborate three other studies showing positive relationships between carotenoid coloration and CORT levels. Though the molecular mechanisms underlying such a relationship are still unclear, our results suggest that CORT should not be considered as a simple indicator of individual quality but rather as a mediator of complex allocation decisions or signals of metabolic activity that could link up with more elaborate expression of ornamental traits.

Keywords Honest signaling · Plumage ornamentation · Sexual selection · Stress hormones · Stress response

Communicated by E. Fernandez-Juricic

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Electronic supplementary material The online version of this article (doi:10.1007/s00265-013-1591-9) contains supplementary material, which is available to authorized users.

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Introduction

Condition-dependent traits can reflect various aspects of phenotypic quality, such as foraging efficiency, resistance to oxidative damage, or parasite susceptibility (Kodric-Brown and Brown 1984; Folstad and Karter 1992; von Schantz et al. 1999; Maynard-Smith and Harper 2003). Many of the environmental and physiological challenges associated with trait production may act as stressors, defined as an adverse and unpredictable change in environmental conditions (Buchanan 2000). Stressors may come in many forms—including nutritional, parasitological, oxidative, and behavioral—virtually all of which have been identified as modulators of sexual signal expression in animals (e.g., Nowicki et al. 2002; Korzan and Summers 2007; Bortolotti et al. 2009a; Mougeot et al. 2010; Roulin et al. 2011).

Published online: 11 August 2013

Among the many ways to physiologically assess the presence or degree of stress in animals is via levels of circulating glucocorticoid hormones (i.e., corticosterone or cortisol; CORT) (Sapolsky et al. 2000). CORT is part of the hypothalamic–pituitary–adrenal (HPA) axis of the endocrine system, whose adrenal secretion relates to the body's response to a stressful event by activating energy mobilization and many other vital cellular and metabolic processes. Chronically elevated CORT plays a central role in the development and maintenance of several condition-dependent signals, largely by inhibiting the expression of traits such as vocalizations (Spencer et al. 2005; MacDougall-Shackleton et al. 2009), courtship behavior (Moore and Miller 1984), and coloration (Roulin et al. 2008).

Carotenoid-based coloration is a classic example of a condition-dependent signal of sexual attractiveness and competitive ability (McGraw 2006; Hill 2006) because animals must acquire carotenoid pigments from food (i.e., a limiting resource) and because these pigments are also used to boost health, as antioxidants and immunomodulators (Blount et al. 2003; McGraw and Ardia 2003). Thus, animals displaying the most intense coloration are those in the best nutritional and health condition or oxidative status and hence can devote substantial amounts of pigment to coloration (Faivre et al. 2003; McGraw 2006). In this sense, carotenoid color signals can encode information about many types of stressors including parasites (McGraw and Hill 2000c), calorie restriction (Hill 2000), and oxidative challenges (Mougeot et al. 2010).

However, for carotenoid coloration, the role of the HPA axis has been understudied (Fitze et al. 2009; McGraw et al. 2011). While some studies have found the predicted negative association between color signal expression (e.g., melanin-based coloration, ornament size) and CORT (Saino et al. 2002; Roulin et al. 2008; Douglas et al. 2009; Lobato et al. 2010), to our knowledge only two studies have found similar results for carotenoid coloration. Experimental CORT elevations decreased pigmentation in the mouth flanges of house sparrow (*Passer domesticus*) nestlings, which is a signal to parents but not an adult sexual signal (Loiseau et al. 2008). In the red grouse *Lagopus lagopus scoticus*, a species possessing carotenoid-based supra-orbital red combs, individual variations in CORT levels were negatively associated with the increase in comb area (Bortolotti et al. 2009a). By contrast, three recent studies in different taxa have found a positive effect of high CORT exposure on adult carotenoid-based signals (Fitze et al. 2009; Cote et al. 2010; McGraw et al. 2011). At present, the mechanism(s) by which CORT positively affect(s) carotenoid-based coloration is unknown. It may either be direct (e.g., CORT may make carotenoids more available) or indirect, by inducing a higher metabolic rate that may be required for redder plumage (Hill and Montgomerie 1994; Hill 2000).

Expanding beyond traditional shorter-term analyses of CORT in animals (i.e., baseline and stress-elevated levels in blood or feces), analyses of CORT in bird feathers have emerged relatively recently (Bortolotti et al. 2008; Bortolotti et al. 2009b) as a technique that permits measurement of long-term baseline and elevated CORT levels during the full process of feather growth (see also Sheriff et al. 2011; Lattin et al. 2011). Although corticosteroids may also be externally deposited on the feathers (e.g. from the preen oil) or may be produced locally (in the feather follicle) it is unlikely to significantly bias the hormone concentrations that originate from the bloodstream (Bortolotti et al. 2008; Stalder and Kirschbaum 2012; Lattin et al. 2011). Therefore, measuring CORT in the feathers may give us valuable information about how animals endure the stressful molt period to become colorful (Hill and Montgomerie 1994). In this study, we studied the relationship between carotenoid-based plumage coloration and feather CORT levels in the house finch, *Haemorhous mexicanus*, a songbird that has served as a model for studies of sexual selection (Hill 2002). Males show large variation in ornamental plumage coloration, ranging from yellow to orange to red, with females preferring redder males as mates (Hill 2002). Near the end of the molt period, we plucked freshly grown feathers from two body regions—tail and breast—and tested the hypothesis that the expression of plumage coloration depends on the CORT levels deposited in the feathers during molt. If plumage coloration reflects exposure to stressors during molt, then we predict that plumage hue in recently developed colorful feathers is negatively correlated with feather CORT levels. On the other hand, if plumage coloration reflects the elevated physiological costs of ornament production, then we predict a positive correlation between plumage hue and feather CORT levels.

Methods

Study animals

On 20 and 24 October 2011, we captured 31 hatch-year male house finches using baited basket traps (McGraw 2006) on the campus of Arizona State University, Tempe, AZ, USA. At capture, we weighed birds to the nearest 0.01 g with an electronic balance and measured tarsus length to the nearest 0.01 mm with digital calipers. Then, we collected 15 fully grown colorful feathers from a standardized part of the breast and the two outermost tail feathers for later measurement of CORT levels (see methods below).

Plumage coloration

Plumage coloration was quantified using digital photography of colorful breast feathers, following standard published

methods for this species (Oh and Badyaev 2006; Giraudeau et al. 2012) and others (e.g., McGraw et al. 2002). Because house finch plumage does not reflect significantly in the UV (Keyser and Hill 1999; McGraw and Hill 2000a), techniques that rely on visible light are sufficient to capture variation in bird-visible and carotenoid-relevant coloration (Butler et al. 2011). Using a Canon PowerShot SD1200S camera (Lake Success, NY, USA), we took two separate photographs of the breast of each bird against a neutral gray-board, using identical distance from camera to object, shutter, exposure, and flash settings for each photograph and including a color/size standard in each photo to control for any slight variations in object illumination. We chose to analyze coloration of the breast because birds were molting into new plumage at this time, and this was the body region where birds most consistently had already grown in new ornamental feathers. Digital images (JPEG, 3648×2736 pixels) were imported into Adobe Photoshop (San Jose, CA, USA) to determine plumage hue, brightness, and saturation of the breast; we used the lasso marquee to select the carotenoid-pigmented plumage regions. This is a semi-automated procedure, where one has to locate a specific area of picture, and the software extends the selection automatically to similarly colored areas. Further extension of the selected area is possible by the user if needed; therefore, the method involves some subjectivity. To account for this, coloration values for the two pictures of each bird were analyzed independently by two people and averaged for statistical analyses. The color measurements were highly repeatable (R=0.983, $F_{30,93}$=238.447, p<0.001, brightness: R=0.945, $F_{30,93}$=70.337, p<0.001, saturation: R=0.792, $F_{30,93}$=16.228, p<0.001).

CORT measurements

We measured CORT in both tail feathers separately and in all breast feathers. The reason for using different feathers from the same individual was to account for CORT differences between individual feathers. The two tail feathers collected were in the same position, so assuming symmetrical molt; it is likely that these feathers were grown at the same time. However, breast feathers may be grown at a different time period than tail feathers, so by measuring CORT in breast feathers we could measure CORT deposited during the growth of colorful feathers.

Feather CORT concentrations were measured by radioimmunoassay (RIA) following a methanol-based extraction using the method of Bortolotti et al. (2008). Briefly, the calamus of the feathers was cut and the remaining part of the feather was minced into pieces less than 2 mm^2 into a test tube. The total mass of the cut feather fragments was weighed to the nearest 0.1 mg. We then added 5 mL methanol to the feather fragments, and the solution was placed in a sonicating water bath for 30 min then incubated for at least 20 h in a heated shaker (at 50 °C). The methanol was removed from the feather particles by filtration through a syringe filter (PTFE filter with 0.45 μm pore size, VWR). The tube with the remaining feather particles was washed and filtered twice again with additional 2×2.5 mL volumes of methanol. The methanol was then evaporated under a fume hood at room temperature under a current of air. The extraction was reconstituted with PBS buffer used in the RIA. To determine the efficiency of the extraction, we included samples spiked with a low amount (4,000 dpm) of radioactive CORT. Mean recovery was 81 %, and final concentrations were corrected by the recovery percentage. We used a commercial antiserum, raised in rabbits against CORT-3-(O-carboxymethyl) oxime bovine serum albumin conjugate (Sigma-Aldrich, St. Louis, MO; product number C8784). According to the manufacturer, the antiserum showed 4.5 % cross-reactivity with cortisol and 3.2 % with cortisone (for a full list see Lattin et al. 2011). The reconstituted extracts were incubated for 48 h at 4 °C with 100 μL of [3H]CORT (Perkin Elmer; product number, NET399250UC) and antiserum. The total volume of the assay was 1 mL. The radioactively labeled CORT had an activity of cca. 10,000 dpm. Bound and free CORT were separated by adding 100 μL dextran-coated charcoal. After centrifugation, the 800 μL of the bound fraction was added to 6 mL of scintillation cocktail (Optima Gold, Perkin Elmer) and counted in a liquid scintillation counter (Tri-carb 2800TR, Perkin Elmer). The minimum detectable level of CORT was 3.90-pg/tube (lowest measurement, 13 pg/tube). Intra-assay coefficient of variation was 5.06 %.

Statistical analyses

All data processing and statistical analyses were performed in the R computing environment (version 2.12.1, R Development Core Team 2011). We analyzed our data by linear models using hue, brightness and saturation as a dependent variable. Initial models contained tarsus length (as a measure of body size), scaled body mass index (as a measure of body condition; see more below), feather CORT concentration, and an interaction between feather CORT and scaled mass index because body condition may affect the relationship between CORT and coloration. Model selection was based on the second order Akaike Information Criterion for small sample sizes (AICc). We report parameter estimates for the final top-ranked model.

Total CORT found in feathers was divided by the mass of the feathers. Although Bortolotti et al. (2008) suggested that CORT values should be corrected for the length of the feathers rather than mass, the length of breast feathers could not be measured as reliably as their mass; therefore, we corrected all these samples by mass as in Koren et al. (2012). To facilitate comparisons between tail and breast feathers, tail feathers were also corrected for their mass. However, we also measured length of tail feathers to the

nearest 0.1 mm from digital photographs using a millimeter paper as the background. Since feather mass and feather length were highly correlated, the CORT levels corrected for mass and length were also highly correlated (R=0.99, p<0.0001). Also, Lattin et al. (2011) found that, when the feather sample is small (less than 25 mg), the mass of the sample may have an effect on the mass-corrected CORT values. Our results did not show any pattern with the mass of the original feather (Supplementary Fig. 1, p=0.959).

To estimate body condition of the birds, we calculated scaled body mass index, which is the predicted body mass of an individual when the structural body measure (here tarsus length) is standardized to the mean value for the study population (Peig and Green 2009). This measure of body condition has been shown to be more reliable than OLS residuals from a mass-structural size regression (Peig and Green 2009). All data conformed to assumptions of parametric tests and linear models. Assumptions and model fit were verified using graphical diagnostic tools (Faraway 2006; Zuur et al. 2009). Influence of individual data points in the model fit was estimated by Cook's distance (the effect of deleting a given observation; Zuur et al. 2009).

Results

CORT concentration did not differ between tail and breast feathers ($F_{2,50}$=0.816, p=0.447; Fig. 1). CORT levels were significantly repeatable between individual feather samples (R=0.43, $F_{30,52}$=3.015, p<0.001). Therefore, in further analyses, we use the mean CORT level of tail and breast feathers.

According to the best supported model, plumage hue was negatively related to feather CORT and body size, with redder males having higher feather CORT (t=−2.225, p=0.034; Table 1; Fig. 2) and larger body size (t=−2.326, p=0.027). Model validation showed that residuals were homogenous and showed no pattern; however, there were two data points with disproportionate influence in the model (Fig. 2; Cook's distances were 0.49 and 0.44); therefore, we refitted this model without these data points. Removing these data points improved the model fit (adjusted R^2 increased from 0.23 to 0.32), and the relationship between CORT and plumage hue became even stronger (p=0.001). However, in the refitted model, the effect of body size did not remain significant (p=0.202). Repeating the model selection without the influential data points did not alter our conclusions (see Supplementary Table 1). Models including body condition or its interaction with CORT levels were less supported, indicating that body condition was not related to plumage hue (note that Table 1 reports model results on the full dataset).

Plumage brightness and saturation were not explained by any of the predictors (last model that still included feather CORT for brightness; tarsus: t=−0.869, p=0.392, feather CORT: t=−1.506, p=0.143; for saturation, tarsus: t=−0.892, p=0.380, feather CORT: t=0.280, p=0.781; see Supplementary Tables 2 and 3 for results of model selection).

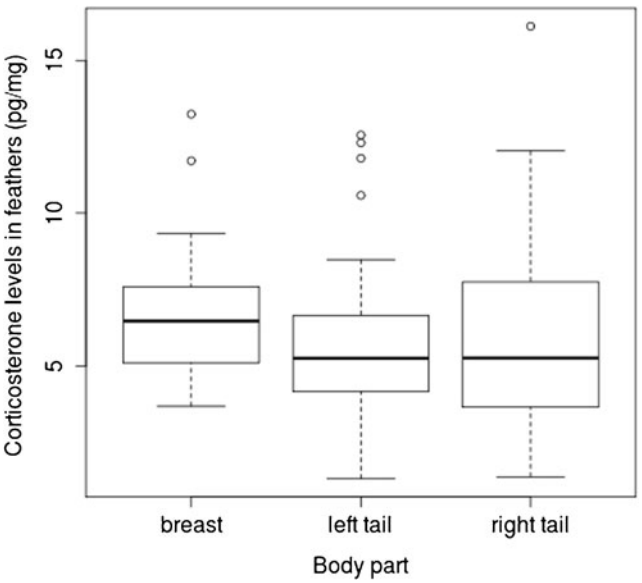

Fig. 1 Corticosterone (CORT) levels in freshly molted, carotenoid-containing breast and two outermost tail feathers of free-living male house finches do not differ significantly but show individual consistency. For each box, the *central line* represents the median and the bottom and the top of the box are the lower and upper quartiles, respectively. The whiskers extend to the lowest and highest observations, respectively, which are no more than 1.5 times the interquartile range from the box. The *dots* indicate data points beyond this range

Discussion

We investigated the relationship between carotenoid-based plumage coloration and an integrated measure of CORT

Table 1 Comparison of linear models for plumage hue levels in male house finches (N=31 individuals)

Predictors in the model[a]	k	AICc	Δ_i	ω_i
Tarsus + CORT	4	189.45	0.00	0.57
Tarsus + SMI + CORT	5	191.59	2.14	0.20
Tarsus	3	191.82	2.37	0.17
Tarsus + SMI + CORT + SMI × CORT	6	194.24	4.79	0.05
CORT	3	198.02	8.57	0.01
(Intercept only)	2	199.86	10.41	0.00

Akaike's Information Criterion corrected for small sample size (AICc), number of estimated parameters (k), AICc difference between the best model and each candidate model (Δ_i), and Akaike weight (a relative estimate of the probability that a given model is actually the best model in the model set; ω_i) are given for each candidate model

CORT feather corticosterone level, *SMI* scaled body mass index, a measure of body condition

[a] Dependent variable: plumage hue

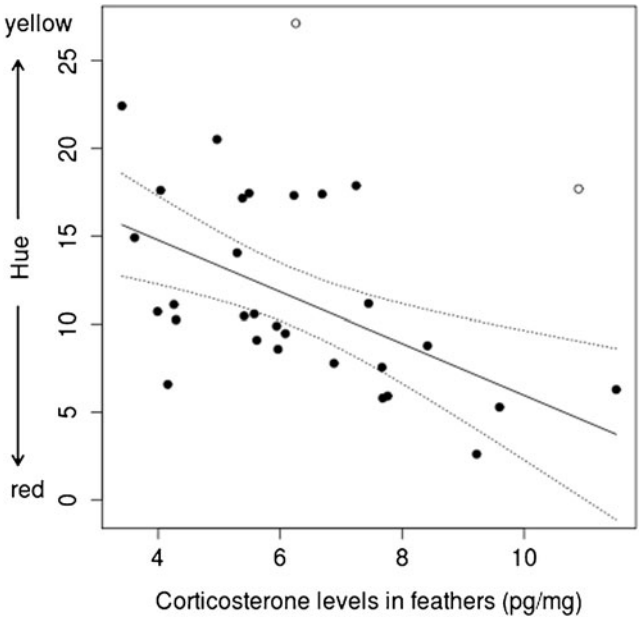

Fig. 2 Mean individual corticosterone (CORT) levels of free-living male house finches are negatively related to the hue of the breast feathers. In other words, feathers from redder males contain more CORT. Two *open circles* show influential data points. The model was refitted without these points, and the *solid line* shows the new model fit; the *dashed lines* show 95 % confidence interval of the fit. See further details in the text

(from feathers) and found that redder male house finches had higher feather CORT concentrations than less red males. As our study is correlative, we cannot ascertain causal relationships between these variables. We discuss three alternative explanations below: (1) CORT directly influenced coloration, (2) CORT levels match the metabolic requirements of different degrees of coloration, and (3) CORT and coloration are related through a third, unmeasured variable.

Our findings are consistent with three recent experiments suggesting a direct positive link between CORT and carotenoid coloration (Fitze et al. 2009; Cote et al. 2010; McGraw et al. 2011). When viewed in light of the traditional assumption that high CORT levels reflect a low-quality stressed individual (i.e., in worse condition, with impaired fitness prospects), these results appear surprising. However, this postulation is no longer considered to be universally valid (Sapolsky et al. 2000; Bonier et al. 2009). In fact, when viewed as an agent affecting energy-allocation processes, we may expect to uncover complex relationships between CORT, coloration, and fitness in house finches. House finches from the western US vary in reproductive strategy as a function of plumage color, with redder males pairing earlier in the season but investing very little energy in provisioning incubating females and nestlings, while yellow/drab males pair late in the season and invest heavily in provisioning (Badyaev and Hill 2002). These reproductive tactics are flexible, and the pituitary hormone prolactin has an important role both in their regulation (Badyaev and Duckworth 2005) and that of molt (Badyaev and Vleck 2007). Elevated CORT levels can have a negative effect on prolactin and are also known to affect reproductive decisions (e.g., Angelier et al. 2009; Lendvai and Chastel 2010; but see Crossin et al. 2012). If inter-individual variation in hormone levels is consistent over time in house finches, it may lead to a phenotype in which elevated CORT levels during molt (either directly or through the effect of prolactin) favor resource allocation toward redder plumage and away from parental investment later, during reproduction.

CORT (and its cascade of effects) may also modulate carotenoid pigments per se. First, CORT may facilitate the release of carotenoids from internal tissue reserves (e.g., body fat, which is rich in carotenoids) and may therefore make carotenoid pigments more available for coloration. In agreement with this idea, Costantini et al. (2008) found that dietary administration of CORT increased circulating carotenoid levels (but also increased reactive oxygen metabolites) in kestrels (*Falco tinnunculus*). Second, an increase of CORT levels may have an indirect effect by stimulating carotenoid-transporting proteins and/or on carotenoid-metabolizing enzymes. Finally, in contrast with chronic stress, which is known to be immunosuppressive, moderately elevated CORT levels have stimulatory effects on both the cell-mediated and the humoral aspects of the immune response (Buchanan 2000). In this case, if CORT levels found in our study reflect the latter, CORT may free up extra carotenoids and a part of this may be allocated to the plumage.

We must also consider the prospects that development of red coloration triggered high CORT levels in males. Given that red coloration is energetically costly to produce (Hill and Montgomerie 1994; Hill 2000), the finches may adjust their metabolism to meet such caloric requirements and an elevated CORT level may be a signal of this adjustment. Finally, there is also the possibility that CORT and carotenoid coloration are not mechanistically linked per se, but connect to a third variable, such as behavior. Redder males may have higher feather CORT levels, for example, because they are dominated by drab males in agonistic interactions (Brown and Brown 1988; Belthoff and Gauthreaux 1991; McGraw and Hill 2000b), including during the molt period in our study population (McGraw et al. 2007). Social subordination in fact can elevate CORT levels in house finches (Belthoff et al. 1994), though a link was not made to plumage coloration in the latter study, nor was it conducted during the molt period. Manipulative experiments are now needed in house finches to disentangle possible mechanisms that link CORT, behavior, and coloration.

To interpret our study, it is important to understand how CORT is deposited in the feathers. Feather is only vascularized during growth; therefore, CORT is thought to be deposited from the bloodstream during molt, although the relationship between circulating and feather levels are not

always tight (Bortolotti et al. 2008; Bortolotti et al. 2009b; Lattin et al. 2011). Molt pattern is highly variable in house finches (Badyaev et al. 2012), but most individuals molt again after fledging (Michener and Michener 1940) including birds in southwestern AZ, where our study was conducted (Badyaev and Vleck 2007). Depending on the hatching date of the individuals, molt can be initiated simultaneously or sequentially in different body parts (Michener and Michener 1940). In the latter case, body parts may reflect different time periods when the growing feathers were exposed to circulating hormones. Although in our study, CORT levels in breast feathers seemed to be slightly higher than in tail feathers (Fig. 1); this difference was not significant, and more importantly, the within-individual variation in CORT levels were smaller than the between-individual differences. Another interesting possibility is that differently colored feathers may take up CORT with different affinity. For instance, it has been shown that more melanized hairs take up more stanozolol (an anabolic steroid) than less pigmented hair in rats (Höld et al. 1996). A recent study in red-winged blackbirds (*Agelaius phoeniceus*) did not find difference in feather CORT between black (melanin-containing) and red (carotenoid-containing) feathers and found that difference in color accounted for 0 % of the variance in feather hormone levels (Kennedy et al. 2013). The latter study also found that CORT concentrations correlated with mean brightness and red brightness of epaulet feathers but not with red chroma or hue. It is noteworthy though that four outliers in that study with the highest CORT values were also the ones among the reddest feathers (Kennedy et al. 2013). Further studies in more species are needed to establish how general the relationship is between CORT and plumage coloration.

In summary, we reveal a positive relationship between levels of feather CORT and exaggeration of a sexually selected plumage trait. This result is not consistent with the hypothesis that plumage redness reflects the exposure to stressors during the molt but rather suggests that this plumage trait may incorporate the physiological and metabolic costs associated with ornament production. As indicator traits are now argued to capture the degree to which animals buffer themselves from allostatic load (McEwen and Wingfield 2003; Hill 2011), we must now comprehensively track the range of costs and benefits associated with CORT elevation to understand how and when we expect CORT to impair or enhance trait expression for different individuals (e.g., at different life stages, with different fitness tactics) and species.

Acknowledgments ÁZL and JN were supported by the Hungarian Research Fund grants (OTKA PD76862 and K75965) and ÁZL by the Bolyai fellowship of the Hungarian Academy of Sciences and by the Eötvös State Grant by the Hungarian Scholarship Board. During the preparation of the manuscript, ÁZL was supported by an NSF grant (1145625) to Frances Bonier and Ignacio T Moore. KJM was supported by a National Science Foundation grant (IOS-0923694). We thank anonymous reviewers and the associate editor who provided helpful and constructive comments on the manuscript.

Ethical standards The study was approved by the Arizona State University Institutional Animal Care and Use Committee, and it complies with the current laws of the USA and Hungary.

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