Effects of Captivity and Body Condition on Plasma Corticosterone, Locomotor Behavior, and Plasma Metabolites in Curve-Billed Thrashers

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ABSTRACT

The acute stress response involves the secretion of catabolic glucocorticoids, such as corticosterone (CORT) in birds, that mobilize intrinsic energy stores primarily through a gluconeogenic pathway involving fat breakdown, thus linking body condition and stress. We measured changes in CORT and gluconeogenic metabolites (triglycerides, free glycerols, glucose) during handling stress in curve-billed thrashers *Toxostoma curvirostre* from two habitats (urban vs. desert) that may differ in food abundance in the wild, in captivity, and in response to both food restriction and subsequent recovery. Urban thrashers were heavier and secreted more CORT than desert birds in the field, but differences did not persist in captivity. Decreased access to food resulted in decreased body mass and a diminished ability to elevate plasma CORT in response to handling stress. However, the opposite effect was observed as these birds recovered from food restriction. Plasma levels of glucose and triglycerides did not change with stress. Food restriction also increased locomotor activity, which likely further exacerbated energy loss. These observations suggest that body condition and stress differences between urban and desert birds may be related to differences in their relative energetic states, possibly due to food availability. Body condition may affect the extent to which an individual can elevate CORT and use free glycerol as energy during acute stress.

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Introduction

Body condition is widely used in studies that investigate the energy reserves, performance, and fitness of organisms. In free-living animals, body condition (often assessed as a body mass to size relationship) has been linked to differences in food availability across habitats (Cypher and Frost 1999; Owen et al. 2005; Brown and Sherry 2006; Auman et al. 2008), reproductive effort (Korpimaki et al. 2000), immunocompetence (Acquarone et al. 2001; Ewenson et al. 2001; Møller and Erritzoe 2003), and survival (Morrison et al. 2007; Bender et al. 2008). Body condition has also been related to circulating glucocorticoid (GC) levels. Here there is a tendency for a negative association between either the baseline ("nonstressed") or stress-induced GC levels and body condition (e.g., Smith et al. 1994; Romero and Wikelski 2001; Cabezas et al. 2007; Schoech et al. 2007). Secreted by the adrenal (interenal) glands, GCs increase in circulation in response to stress, where they are involved in glucose production and can induce hyperglycemia in fasted laboratory mammals (Bizzi et al. 1972; Clore and Thurby-Hay 2009; Beddow and Samuel 2010).

During a stress response (i.e., within minutes), GCs—such as corticosterone (CORT) in birds—induce the mobilization of free glycerol derived from the catabolism of triglycerides in fat reserves (Warne et al. 2009). Free glycerol can then be converted to glucose by gluconeogenesis (Warne et al. 2009). This metabolic pathway thus links GC secretion during stress to the current availability of energy reserves (i.e., body condition) in an effort to increase glucose availability. We have previously modeled how plasma metabolites vary relative to plasma CORT in response to acute stress in several bird species (H. B. Fokidis, unpublished data). This data suggested an association between body condition and CORT secretion, with CORT primarily acting to release glycerol. Along with metabolic effects, CORT also influences foraging behavior (Kitaysky et al. 2001*b*; Pravosudov 2003; Bates et al. 2007; Foster et al. 2009; Warne et al. 2009) and locomotor activity (Lynn et al. 2001, 2003), which can further alter energy balance.

Birds are attractive models to study relationships between body condition and stress for several reasons. First, free-living birds have been extensively used to explore the life-history consequences of elevated CORT levels, demonstrating close links between CORT and fitness (e.g., Bonier et al. 2007; Schoech et al. 2009). Second, the high mass-specific metabolic

rates and elevated glucose turnover in birds compared with mammals (Braun and Sweazea 2008) result in avian body masses being highly susceptible to short-term food restriction (Williams et al. 1999; Kitaysky et al. 2001*a*; Guglielmo et al. 2002*b*; Walker et al. 2005). Third, plasma metabolites, and particularly lipids, are catabolized to provide energy during migratory flight and have been directly linked to changes in body mass (Williams et al. 1999; Guglielmo et al. 2002*b*). Finally, birds inhabit many environments, including human-modified ones, that can differ in their food availability. Several studies have demonstrated variation in body condition between habitats (Owen et al. 2005; Fokidis et al. 2008; Geens et al. 2009).

Curve-billed thrashers *Toxostoma curvirostre* are in better body condition (i.e., higher body mass to size ratio) in the city of Phoenix, Arizona, than in surrounding Sonoran Desert habitats (Fokidis et al. 2008). This may stem from higher plant productivity in Phoenix compared with the desert because of the presence of exotic mesic vegetation and persistent artificial water sources (Martin and Stabler 2002; Stabler and Martin 2004). These human-based changes may have altered the seasonal patterns of CORT secretion in urban thrashers (Fokidis et al. 2009). Experimental studies indicate that urban compared with desert birds (including thrashers) alter their foraging behavior in response to reduced predation risk (Shochat et al. 2004). Although cities can have feral or introduced predators (e.g., cats), the effect of these predators on adult birds is debated (Sims et al. 2008; Van Heezik 2010).

We used adult male thrashers caught from urban and desert sites to test whether experimentally altering body condition (via food availability) affects CORT secretion and the mobilization of metabolites during a stress response. We also investigated how identical captive conditions can equalize differences in stress physiology between urban and desert birds that vary considerably in the field. First, we predicted that if body condition was made equal between urban and desert birds in captivity, the CORT levels between these two populations would be similar. Second, we predicted that increased body condition results in a more robust CORT response to acute stress and an increased mobilization of lipids. Third, we predicted that increased CORT levels would result in an increase in locomotor activity (i.e., more energy expenditure).

Material and Methods

Procedures were approved by the Arizona State University Institutional Animal Care and Use Committee and were done under scientific collecting permits from the U.S. Fish and Wildlife Service, the U.S. Forest Service, and the Arizona Game and Fish Department and by permission from local landowners.

Study Populations

Desert thrashers were captured from the unpopulated Four Peaks Mountains Wilderness Area (Tonto National Forest), located 10 km northeast of the suburban fringe development of Fountain Hills, with vegetation typical of the upland Sonoran Desert (Fokidis et al. 2009). Urban thrashers were caught in east-central Phoenix and Tempe, Arizona, primarily in small city park edges adjacent to middle-income residential areas and commercial areas with mesic-style landscaping, including deciduous trees and palm trees.

Field Sampling and Captivity Study

Twenty-seven adult male thrashers (13 urban, 14 desert) were captured between March 29 and June 23, 2009 (mean capture date: urban, June 5; desert, June 11). This period coincides with the incubation and nestling stages of the reproductive cycle of the species (Tweit 1996). Birds were captured between 0530 and 0957 hours (mean capture time: urban, 0736 hours; desert, 0708 hours). Birds were lured to mist nets using conspecific song playback. Within 3 min of capture, a blood sample (200 μL) was collected from the right jugular vein into a 0.30-mL heparinized syringe with a 29.5-gauge needle for measuring plasma baseline levels of CORT and metabolites (glucose, free glycerol, and triglycerides). Birds were then kept in cloth bags for 30 min, and a second blood sample was collected as above to measure stress-induced CORT and metabolite levels. This technique is widely used in birds to induce an acute stress response (Wingfield et al. 1992; O'Reilly and Wingfield 2001; Arnold et al. 2008). All birds were captured in the field in the early morning, and previous research demonstrates little circadian variation in plasma CORT levels except for a decline in the early afternoon (around 1400 hours) in this species (H. B. Fokidis, unpublished data). This procedure was repeated after birds had been held captive for 45 and 80 d. Time of blood sampling in captivity occurred within the same range (0700–0900 hours) as with field sampling. Blood was stored on ice until plasma was separated by centrifugation and then stored at -80°C until assays were run.

Birds were identified as breeding adult males by the presence of a developed cloacal protuberance (CP), indicating reproductive condition (Pyle 1997). Body mass (± 0.1 g), CP width (± 1 mm), and tarsus length (± 1 mm) were also measured.

Birds were transported to Arizona State University and individually housed in 76 × 46 × 46-cm cages in a single room with cardboard between neighboring birds. The room was maintained at 22°C, with lights on at 0700 hours and off at 2100 hours. The day each bird was caught was defined as day 0, with day 1 being the first day of captivity. Birds were fed an insectivore diet (5MM3; PMI Nutrition, St. Louis) ad lib. for 80 d. This diet consists of 28% protein, 11% fat, 13% fiber, and 8% ash. The daily food intake (DFI) of each bird was monitored (± 0.01 g) for 45 consecutive days, beginning on day 20. To minimize spillage (about 0.05 g/d), food dishes were partially covered with cardboard, allowing only a small opening to access food. Birds were weighed weekly, shortly after lights on and before they started feeding that day. On days 45 and 80, baseline (<3 min of entering the room) and stress-induced (30 min) blood samples were collected.

Body Condition Experiment

The goal in this experiment is to assess how metabolic, hormonal, and behavioral variables vary with changes in body condition using body mass as a proxy. To manipulate body condition, birds were food restricted (to lose body mass) and later allowed to recover (to regain body mass) by being given access to food ad lib. Starting on day 81, birds received an amount of food equivalent to 80% of their individual DFI for 10 d and were then randomly assigned to either a loss-gain (LG) or a gain-loss (GL) group. This 80% DFI food restriction served two purposes: (1) to ensure a similar physiological starting point between birds in the two treatments and (2) to provide incentive for birds in the GL group to feed more and hence gain mass. Birds (half from each habitat) in the LG group were then food restricted (60% of DFI) for 5 d. After this period of food restriction, birds then received food ad lib. for 5 d, which is consistent with preliminary research that showed it took from 3 to 5 d (with food ad lib.) for birds to return to their average body mass (H. B. Fokidis, unpublished data). After 10 d at 80% DFI, birds in the GL group (also half from each habitat) then received food ad lib. for 5 d, and after this period they were food restricted (60% of DFI) for 5 d. Thus, birds received an equivalent duration of 80% DFI (10 d), 60% DFI (5 d), and access to food ad lib. (5 d).

During the treatment period, blood samples (<3 and 30 mins) were collected, and body mass data were recorded on days 5, 12, 15, and 18 from the start of the body condition experiment. Individual food consumption was also monitored daily. The days for blood sampling were used to provide measurements during baseline (day 5), at the midpoints of either food restriction (LG: day 12; GL: day 18) or access to food ad lib. (LG: day 18; GL: day 12), and the shift from one treatment to the next (day 15).

To determine locomotor activity, birds were video recorded ($n = 4$ birds/d, one from each site and treatment) for 2 h daily (1100–1300 hours) throughout the duration of the experimental treatments. This sampling time was well after the initial feeding for the day and thus ensured that birds were not primarily engaged in feeding. Video recordings were analyzed with no knowledge of treatment to determine (1) the number of hops (i.e., movement from perch to perch or to the cage floor) and (2) the time spent perching (i.e., bird inactive on perch and not preening). At the conclusion of the study, birds received food ad lib. for 15 d, and the study was repeated but with individuals now assigned to the alternate treatment group. The order of treatments to which each thrasher was assigned was included in the statistical analyses.

CORT Assays

Total plasma CORT was measured using validated commercial competitive enzyme-linked immunoassays (Assay Designs, Ann Arbor, MI; Fokidis et al. 2009, 2011). The sensitivity of the assay ranged from 11.3 to 19.3 pg/mL, depending on the assay plate. The mean intra- and interassay coefficients of variation were 14.1% and 18.3%, respectively ($n = 4$ plates; 156 samples assayed in duplicate).

Plasma Metabolite Assays

Plasma free glycerol and total triglycerides were measured using a sequential color endpoint assay (reagents F6428 and T2449, Sigma-Aldrich; described in Guglielmo et al. 2002*a*, 2002*b*). Plasma glucose was measured using a colorimetric enzyme endpoint assay (10009582; Cayman Chemical, Ann Arbor, MI). Mean intra- and interassay coefficients of variation for all assays ranged from 9.8% to 14.6% and 11.7% to 23.1%, respectively, with samples assayed in duplicate.

Statistical Analyses

Body condition was calculated from standardized residuals of a linear regression between body mass and tarsus length (Fokidis et al. 2009). The validity of such associations being used as indexes of energy reserves is debated in part because they do not account for growth and how use of reserves may change with body size (Peig and Green 2009, 2010). Although this is a valid concern, in this species the relationship between body mass and tarsus length is linear for the range of values in this study based on comparisons with a larger data set (H. B. Fokidis, unpublished data). In addition, our experimental design focused on changes in condition that occurred within a short time frame. We used Student's *t*-tests to compare body mass, CP width, tarsus length, and body condition between bird populations (urban and desert) in the field. To compare body condition, CORT, and metabolite levels (dependent variables) at the time of capture and during captivity, we used repeated-measures ANOVA (rmANOVA) with individual as the identifying variable and treatment time (baseline or stress induced), origin (urban or desert), and day of sampling (day 0, 45, or 80) as the independent variables. If individual differences in traits observed in free-ranging birds reflect environmental influence, we predicted that this variation would be reduced with captivity. This prediction was tested by comparing the percentages coefficients of variation in the above dependent variables between birds sampled at the time of capture and during captivity using Levene's test of homogeneity of variances.

We also used rmANOVA to examine changes in CORT and metabolites, body masses, and time spent perching in response to experimental treatment. Origin (urban, desert) and treatment (GL, LG) were independent variables, and order of treatment was included as a cofactor. Before analysis, data were tested for the sphericity assumption using Mauchly's test, and data not meeting this assumption were further tested using χ^2 analysis, and the degrees of freedom were deflated using ε-derived Greenhouse-Geiser or Huynh-Feldt corrections (Sokal and Rohlf 1995). We compared sampling time points using least significant difference post hoc tests. The number of hops was analyzed using the nonparametric Friedman's test (Sokal and Rohlf 1995).

To explore further how metabolites and CORT changed with

body condition, we calculated the daily change in body mass (g/d), glucose, triglycerides, free glycerol (nM/d), and CORT (ng/mL/d) during food restriction and recovery from food restriction. These data were assessed using linear regression analysis. All data were normally distributed except for glucose, which was log transformed before analysis.

Statistical analyses were performed using SPSS (ver. 13.0; SPSS, Chicago) with α levels set at 0.05. All data in the text are presented as mean ± SE, and all graphs depict untransformed data.

Results

Differences between Urban and Desert Thrashers in the Field

Body mass was linearly related to tarsus length ($r^2 = 0.80$, $P = 0.029$), and urban thrashers were heavier (urban: 86.3 ± 3.7 g; desert: 81.9 ± 4.8 g; $t_{26} = 2.11$, $P = 0.041$) but did not have longer tarsi (urban: 30.9 ± 1.1 mm; desert: 31.6 ± 2.7 mm; $t_{26} = -0.62$, $P = 0.512$) or a wider CP (urban: 8.3 ± 0.6 mm; desert: 8.3 ± 0.4 mm; $t_{26} = 0.48$, $P = 0.520$) than desert birds. Thus, at capture (day 0), urban thrashers were in better body condition than desert birds ($t_{26} = 2.64$, $P = 0.010$; Fig. 1).

In the field (day 0), baseline CORT ($F_{2,26} = 0.96$, $P = 0.306$; Fig. 2*A*), glucose ($F_{2,26} = 1.03$, $P = 0.317$; Fig. 2*B*), free glycerol ($F_{2,26} = 1.00$, $P = 0.349$; Fig. 2*C*), or triglycerides ($F_{2,26} = 0.18$, $P = 0.857$; Fig. 2*D*) did not differ between urban and desert birds. After 30 min of stress, urban birds had higher levels of CORT ($F_{2,26} = 20.88$, $P \leq 0.001$; Fig. 2*A*), free glycerol ($F_{2,26} = 14.38$, $P \leq 0.001$; Fig. 2*C*), and triglycerides ($F_{2,26} = 7.04$, $P = 0.007$; Fig. 2*D*), but not glucose ($F_{2,26} = 0.75$, $P = 0.205$; Fig. 2*B*), than desert birds. Both free glycerol (origin × treatment time: $F_{2,26} = 3.91$, $P = 0.042$; Fig. 2*C*) and triglycerides (origin × treatment time: $F_{2,26} = 4.16$, $P = 0.035$; Fig. 2*D*) decreased in desert but not urban birds.

Effects of Captivity

Urban and desert thrashers were in similar body condition on days 45 and 80 ($F_{2,25} = 1.22$, $P = 0.384$; Fig. 1). Day of sampling (day 0, 45, or 80) significantly influenced baseline but not stress-induced CORT levels (baseline: $F_{2,25} = 24.76$, $P \leq 0.001$; stress induced: $F_{2,25} = 3.13$, $P = 0.080$; Fig. 2*A*). Urban thrashers had higher baseline CORT than desert birds on day 45 ($P = 0.022$) but lower amounts on day 80 ($P = 0.041$; Fig. 2*A*). Day of sampling did not affect glucose levels (baseline: $F_{2,25} = 0.22$, $P = 0.739$; stress induced: $F_{2,25} = 1.02$, $P = 0.306$; Fig. 2*B*) but affected both stress-induced free glycerol ($F_{2,25} = 4.78$, $P = 0.036$; Fig. 2*C*) and triglycerides ($F_{2,25} = 3.35$, $P = 0.048$; Fig. 2*D*), but the latter was population specific (day 45: $P = 0.019$; day 80: $P = 0.037$). Urban and desert birds had a similar DFI during the 80 d of captivity (urban: 11.39 + 1.27 g; desert: 11.84 + 1.35 g; $F_{2,25} = 0.27$, $P = 0.741$). Body mass, stress-induced levels of CORT, triglycerides, and free glycerol were individually more variable at capture than during captivity (Table 1).

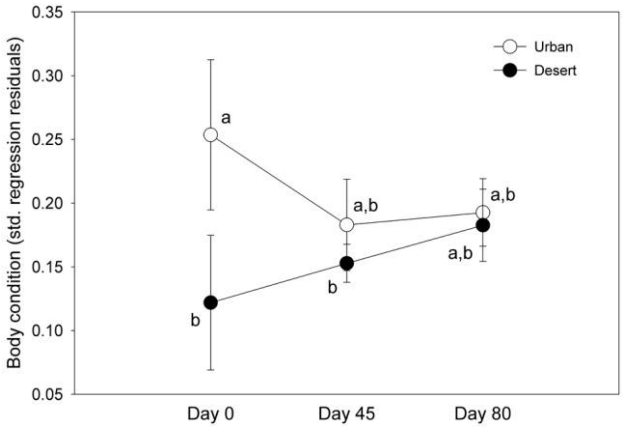

Figure 1. Changes in body condition (i.e., residuals of a body mass-size regression) in curve-billed thrashers *Toxostoma curvirostre* sampled from urban ($n = 13$) and desert ($n = 14$) habitats from capture in the field (day 0) and after 45 and 80 d in captivity with access to food ad lib. Data points are means ± SE, and points with identical letters do not differ at $P \leq 0.05$.

Body Mass Varies with Food Treatment

Order of treatment did not influence any results (all $P \geq 0.259$; η^2 range, 0.063–0.12), and thus data for the two treatments were pooled for further analyses. Likewise, the origin of the bird did not influence any variables (all $P \geq 0.163$; η^2 range, 0.058–0.103). Body mass decreased by 16%–25% of the initial mass during the transition from 80% to 60% DFI in the LG group ($P = 0.007$; Fig. 3), but this was reversed with food ad lib. ($P = 0.253$; Fig. 3). In contrast, the transition from 80% DFI to food ad lib. increased the body mass of only 23 birds (10 urban, 13 desert); thus, the increase in body mass was not statistically significant ($P = 0.189$; Fig. 3). However, food restriction after this period decreased the body mass of all birds ($P = 0.015$; Fig. 3).

Changes in Body Mass Influence Plasma CORT during Acute Stress

Changes in body mass with food restriction and during recovery were inversely related to baseline CORT levels (Fig. 4*A*) but were positively correlated to stress-induced CORT levels (Fig. 4*B*). The magnitude of the stress response (stress-induced CORT/baseline CORT levels) was enhanced by increasing body mass with the GL treatment ($F_{2,25} = 4.37$, $P = 0.042$; Fig. 5*A*), and this effect was eliminated by food restriction ($P = 0.329$; Fig. 5*A*). No obvious change in the CORT response to stress was observed in birds that did not increase body mass, but a very low sample size did not allow for statistical testing. Food restriction in the LG treatment decreased the magnitude of the CORT response to stress ($F_{2,25} = 4.77$, $P = 0.030$; Fig. 5*A*), and this pattern was reversed with access to food ad lib. ($P = 0.033$).

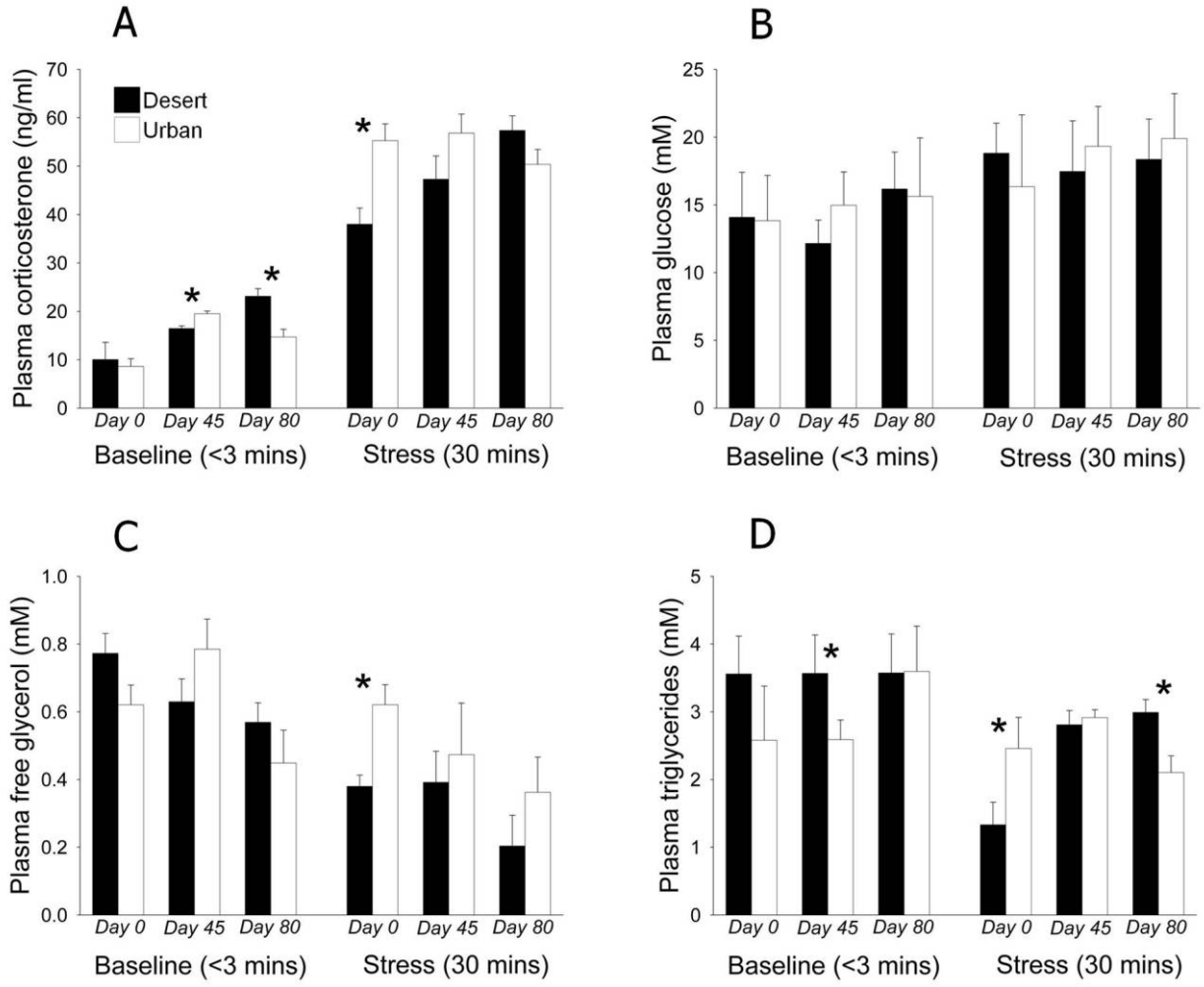

Figure 2. Plasma baseline (within 3 min of capture) and stress-induced (30 min postcapture) corticosterone (*A*), glucose (*B*), free glycerol (*C*), and triglycerides (*D*) in urban (open bars; $n = 13$) and desert-caught (solid bars; $n = 14$) curve-billed thrashers *Toxostoma curvirostre* sampled in the field (day 0) and after 45 and 80 d in captivity. Data points are means ± SE, and asterisks indicate significant site differences ($P \leq 0.05$).

Body Mass Affects Metabolic Changes during Acute Stress

Plasma glucose did not change in response to changes in body mass (Fig. 4*C*). In contrast, as thrashers gained body mass, baseline levels of free glycerol decreased (Fig. 4*D*), whereas triglycerides increased (Fig. 4*E*). Food treatment also did not influence how glucose changed with acute stress (GL: $F_{2,25} = 0.65$, $P = 0.504$; LG: $F_{2,25} = 0.92$, $P = 0.581$; Fig. 5*B*). Food restriction (LG) caused a smaller decrease in free glycerol with acute stress ($F_{2,25} = 3.16$, $P = 0.021$; Fig. 5*C*), but food availability ad lib. (GL treatment) did not affect this free glycerol decline during stress ($F_{2,25} = 0.96$, $P = 0.368$; Fig. 5*C*). Plasma triglycerides were not affected either by the GL or by the LG treatment (GL: $F_{2,25} = 0.27$, $P = 0.730$; LG: $F_{2,25} = 1.02$, $P = 0.285$; Fig. 5*D*).

Behavioral Responses to Changing Body Mass

The GL and LG treatments influenced the time spent perching (GL: $F_{2,25} = 10.66$, $P = 0.005$; LG: $F_{2,25} = 3.92$, $P = 0.033$; Fig. 5*E*) and the number of hops (GL: Friedman's test: $\chi^2 = 16.37$, df = 3, $P = 0.003$; LG: $\chi^2 = 17.09$, df = 3, $P = 0.008$; Fig. 5*F*). Thrashers were more active during food restriction than when they had access to food ad lib., as shown by an increased number of hops ($P \leq 0.028$) and less time spent perched ($P \leq 0.017$).

Discussion

Previous research documented differences in body condition and CORT secretion between free-living urban and desert-dwelling curve-billed thrashers (Fokidis et al. 2008, 2009). This

Table 1: Coefficients of variation (%) for corticosterone (CORT) and plasma metabolites in curve-billed thrashers *Toxostoma curvirostre* sampled in the field (day 0) and after 45 and 80 d of captivity

	Field	Captivity	
	Day 0	Day 45	Day 80
Body mass	14.4[A]	9.9[B]	10.3[B]
Baseline CORT	9.2[A]	4.2[A]	3.3[A]
Stress-induced CORT	36.8[A]	12.2[B]	14.8[B]
Heterophil to lymphocyte ratio	17.2[A]	29.2[A]	20.3[A]
Baseline glucose	13.5[A]	13.4[A]	15.3[A]
Stress-induced glucose	15.2[A]	13.6[A]	16.4[A]
Baseline free glycerol	2.0[A]	2.9[A]	2.3[A]
Stress-induced free glycerol	19.5[A]	9.9[B]	9.3[B]
Baseline triglycerides	6.6[A]	11.2[A]	7.8[A]
Stress-induced triglycerides	14.6[A]	5.2[B]	6.8[B]

Note. Identical letters for a given parameter indicate no significant difference ($P > 0.05$, Levene's test of homogeneity of variances).

study explored links between body condition and CORT secretion by manipulating body mass through changes in food access. Plasma CORT secretion in response to capture stress and body condition differed between urban and desert birds in the field, but these differences disappeared when birds were held captive. Experimental manipulations of food availability revealed associations between changes in body mass and in CORT levels at both baseline and stress-induced levels. Increases in body mass resulted in declines of baseline free glycerol levels and locomotor activity and increases in triglycerides, whereas glucose levels were unaffected by mass changes.

During capture stress, birds had elevated and lowered plasma levels of CORT and free glycerol, respectively, and these effects occurred to a greater degree as body mass increased than when mass decreased during food restriction. These findings suggest that population differences in body condition are a contributing factor to the observed differences in stress physiology.

Local Environment Accounts for Differences between Urban and Desert Thrashers

Captivity is clearly a stressor to wild animals and can alter CORT secretion (Marra et al. 1995; Dickens et al. 2009; Dickens and Romero 2009). We compared thrashers before and during captivity to assess whether differences in stress responses between bird populations can be equalized under identical conditions. At capture, urban thrashers were in better condition than desert birds, but during captivity, urban but not desert birds lost body mass, resulting in no between-population differences in body condition. This mass decrease may have resulted from the catabolic effects of CORT, because food intake was similar between populations. However, the CORT results in this study are inconclusive, because on day 45, stress-induced CORT levels did not differ with habitat, but urban thrashers had higher baseline CORT than desert birds, whereas the opposite pattern was observed on day 80. Regardless, birds from both habitats tended to increase CORT levels with time spent in captivity, suggesting that these birds did not "habituate" (defined here as decreased adrenocortical activity) to captive conditions. Previous studies have reported decreases in circulating GC levels with transition from the wild to captivity (Dickens et al. 2009), although other studies report increases (Marra et al. 1995; Dufty and Belthoff 1997) or no net change in baseline levels (Vera et al. 2011). How captivity alters the stress physiology of a chosen free-living animal model can have important consequences for the outcome of an experiment and may be worth investigating before initiating study (Calisi and Bentley 2009).

Variation in traits that are directly influenced by environmental factors often decrease with captivity (Calisi and Bentley 2009). Supporting this proposition, variation in body mass and plasma CORT of thrashers was greater at capture than during captivity. Thus, captivity negated field-observed differences in body condition and stress physiology. This suggests a primary role for environmental factors influencing variation in these measures as compared with genetic or developmental differences between bird populations. However, an alternative explanation for the lack of differences with captivity may be differences in life-history stages. Male urban thrashers may be capable of breeding earlier (~2 wk) than desert conspecifics on the basis of testes size data (Deviche et al. 2010). Although CP width did not differ between birds for the two populations and all birds were physiologically capable of breeding, we did not know the current breeding status of individual birds (i.e., incubating vs. raising nestlings). Many aspects of stress physiology and body condition vary throughout the reproductive period,

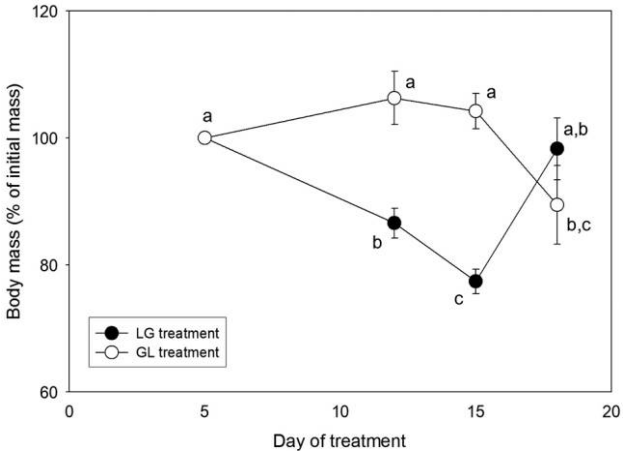

Figure 3. Percentage changes in body mass in 27 curve-billed thrashers *Toxostoma curvirostre* during the course of two feeding treatments: (1) loss-gain (LG), where mass is lost and then regained, and (2) gain-loss (GL), where mass is gained and then lost. Data point at day 5 represents the initial body mass (100%) for all birds. For details on study design, see "Material and Methods." Data points are means ± SE, and points with identical letters do not differ at $P \leq 0.05$.

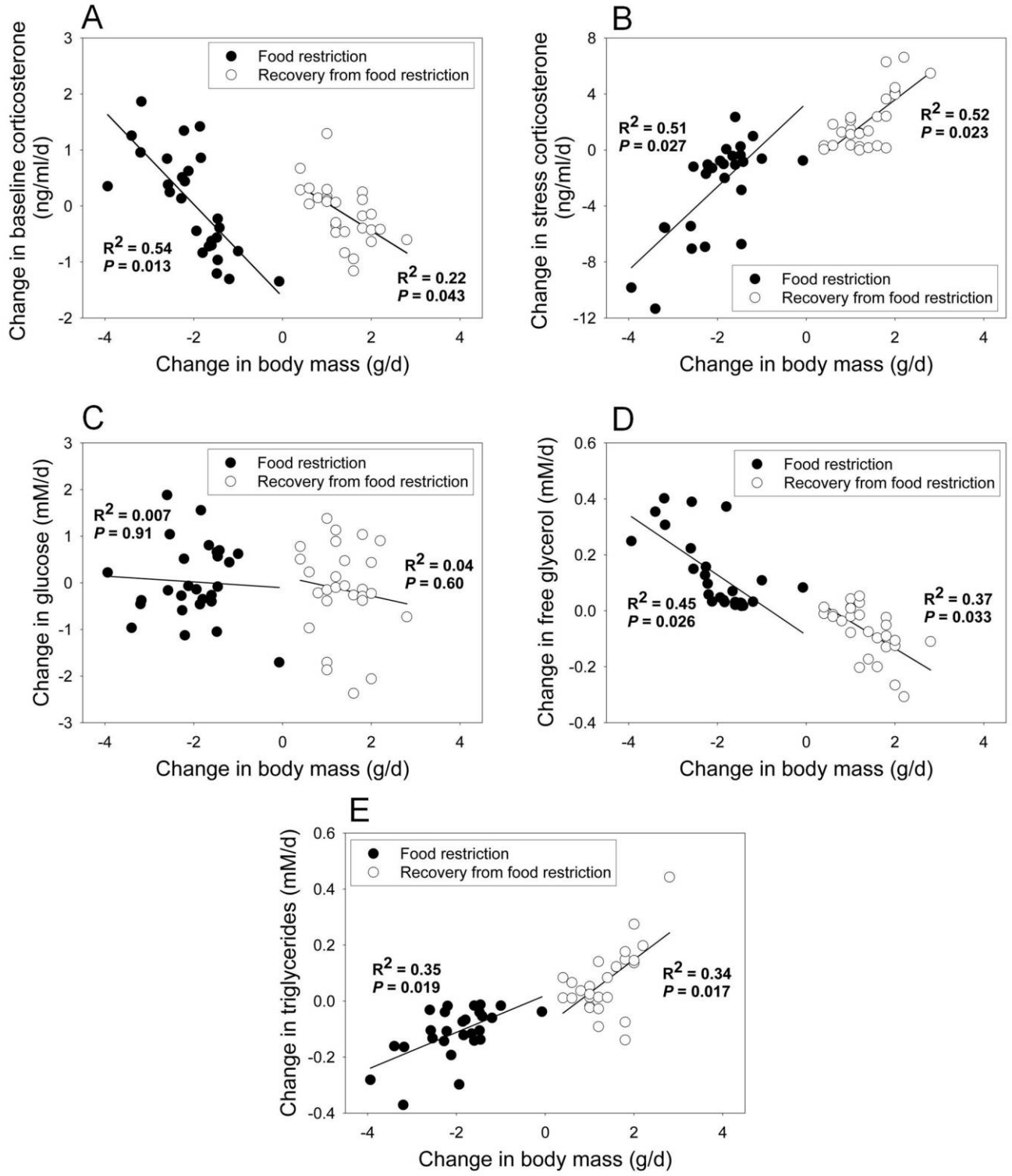

Figure 4. Daily changes in plasma baseline (≤3 min postcapture; *A*) and stress-induced (30 min postcapture; *B*) corticosterone, glucose (*C*), free glycerol (*D*), and triglycerides (*E*) associated with daily changes in body mass in 27 curve-billed thrashers *Toxostoma curvirostre* induced with food restriction and recovery. Each circle represents one individual bird sampled between days 12 and 15 (gain-loss) or days 15 and 20 (loss-gain). Coefficient of determination (r^2) is statistically significant if $P \leq 0.05$.

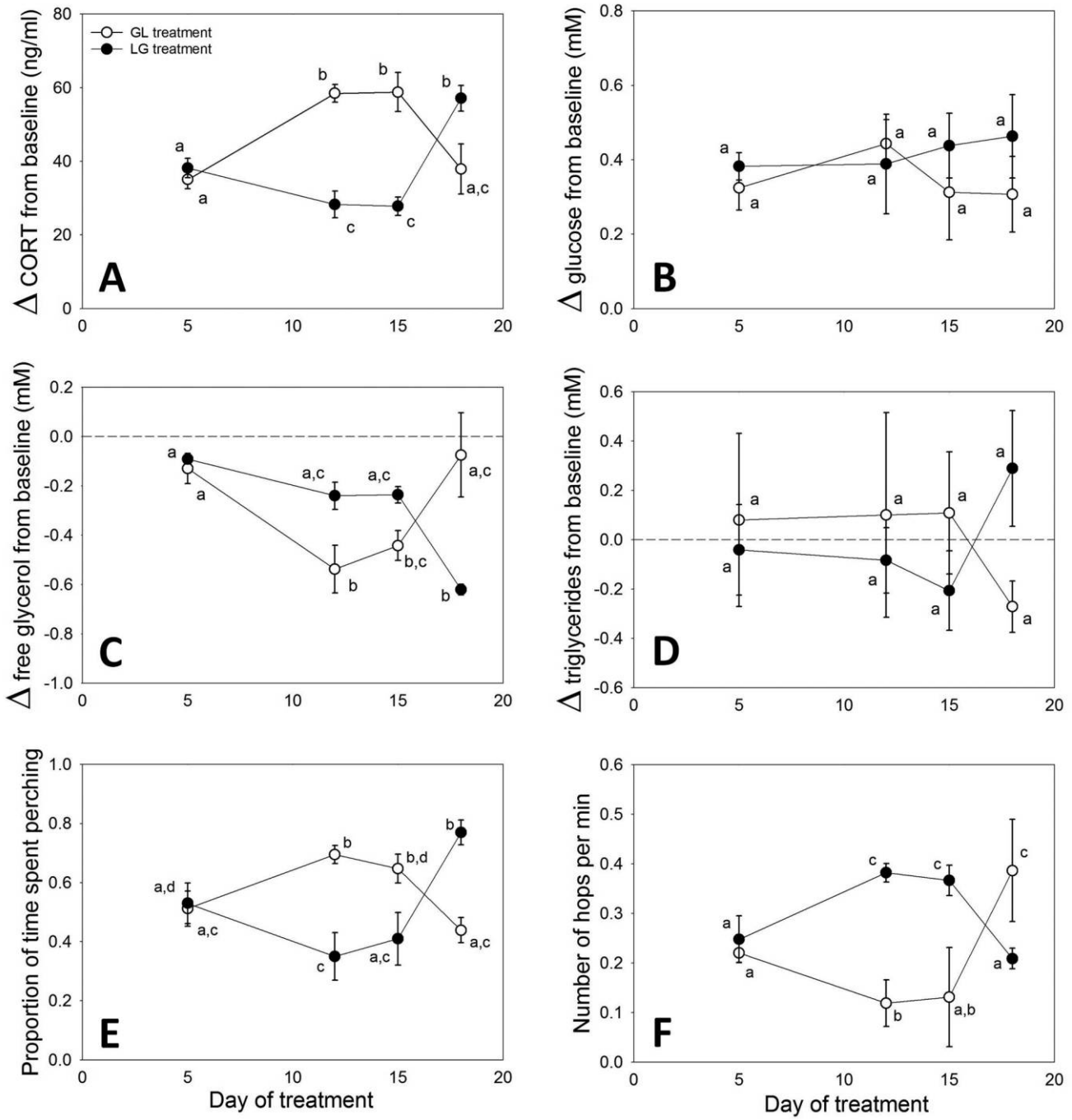

Figure 5. Changes (Δ) in plasma corticosterone (*A*), glucose (*B*), free glycerol (*C*), and triglycerides (*D*) from baseline levels to after 30 min of capture stress and locomotor activity; proportion of time spent perched (*E*) and number of hops from perch to perch per minute (*F*) in 27 curve-billed thrashers *Toxostoma curvirostre* during the course of two feeding treatments (gain-loss [GL] and loss-gain [LG]). For details on study design, see "Material and Methods." Data points are means ± SE, and points with identical letters do not differ at $P \leq 0.05$.

and bringing birds into captivity may have resulted in all reaching an equivalent "nonbreeding" reproductive state.

Changes in plasma metabolites associated with fat deposition and recent foraging activity (triglycerides) or fat mobilization (free glycerol) were also monitored (Williams et al. 1999; Guglielmo et al. 2002*b*, 2005) during the transition from field to captivity. Plasma free glycerol decreased with acute stress in desert and not urban birds, but levels differed between populations only in the field. In contrast, thrashers decreased triglyceride levels with stress during captivity, but only when data from both populations were pooled. Desert thrashers increased triglyceride levels with stress in captivity. The higher triglyceride

concentrations in desert thrashers may indicate that fat deposition is not inhibited during stress or that triglycerides may represent fat mobilization before the cleaving of the free glycerol component. In a study of three migratory songbirds during nighttime flights, plasma triglycerides were elevated compared with periods of inactivity (Jenni-Eiermann and Jenni 1992), suggesting that triglycerides could also increase during catabolic events.

Body Mass: Relationships to Metabolic and Hormonal Status

In thrashers, body mass is negatively related to baseline CORT and free glycerol levels and positively related to stress-induced CORT and triglyceride levels. However, plasma glucose levels were always maintained at a consistent homeostatic concentration regardless of these factors. Under fasted conditions, CORT can induce hyperglycemia in mammals during acute stress, typically acting in a permissive role alongside other glucoregulatory hormones (Armario et al. 1990; Yamada et al. 1993; reviewed in Sapolsky et al. 2000). In this study, plasma glucose did not change with capture stress. One explanation is that glucose mobilization was matched by tissue glucose uptake, resulting in no net change in circulating levels. In most vertebrates, gluconeogenesis is the predominant mechanism by which GCs increase plasma glucose. This mechanism is associated with fat and protein catabolism to provide substrates and increases in gluconeogenic enzyme activity (Schmoll et al. 1999; Altuna et al. 2006; reviewed in Sapolsky et al. 2000). Birds have higher mean glucose levels and metabolic rates than mammals (Braun and Sweazea 2008) and therefore may need to maintain constant glycemia via a rapid uptake of energy substrates (e.g., glycerol) by the liver and kidneys, the major gluconeogenic sites in birds (Scanes 2009). This rapid uptake may explain why many migratory bird species rely primarily on glycerol and fatty acids as fuel for flight muscles (Gannes 2001; Maillet and Weber 2006; Lyons et al. 2008), which may further assist in glucose sparing. Similarly, in some nonmigratory species, glucose does not increase with acute stress (H. B. Fokidis, unpublished data). Some studies report decreases in free glycerol with capture stress (Guglielmo et al. 2002*b*), whereas others report increases (Kern et al. 2007) or no change (Seaman et al. 2005). The linking of CORT and glycerol in birds requires further research, especially in reference to the stress response and glucose production.

Individuals with persistently high CORT levels may catabolize lipids, resulting in a lowered body condition. Inversely, individuals with low circulating CORT levels can accumulate lipid reserves, thus increasing body condition. However, the interplay between GCs and body condition is complicated by the fact that hypercortisolism (usually in response to pathological conditions) can induce fat accumulation in humans (reviewed in Macfarlane et al. 2008) and laboratory rat models (Michel et al. 2003; Campbell et al. 2011; Solomon et al. 2011). However, such an effect of chronically elevated CORT levels on adiposity in birds has not been demonstrated and remains unlikely. Glucocorticoids can also act centrally to stimulate appetite for high-fat, high-sugar (i.e., calorie rich) foods in mammals (Dallman et al. 2004, 2007). Thus, increased CORT secretion during stress may occur in response to greater body condition (i.e., more energy reserves being available).

Some evidence in the literature supports the hypothesis that the current state of energy reserves (i.e., body condition) influences the ability to elevate CORT levels during acute stress. A comparative study of migratory songbirds found that increased handling time is associated with increased CORT levels only in birds with large fat stores (Jenni et al. 2000). This observation is consistent with the hypothesis that the amount of stored energy influences the capacity to mount a stress response. Another study that compared CORT responses of marine iguanas (*Amblyrhynchus cristatus*) across the Galapagos Islands found a consistent "threshold value" for body condition. Below this threshold, body condition and baseline CORT secretion were negatively correlated (Romero and Wikelski 2001). Thus, the effects of elevated CORT secretion may be mitigated by having a certain threshold level of energetic reserves.

In addition to direct metabolic effects, CORT also induces behaviors that can influence energy balance. Food restriction increases perch-hopping activity in white-crowned sparrows *Zonotrichia leucophrys*, and this increase is mirrored by an increase in baseline CORT levels (Lynn et al. 2003). Similarly, CORT administered to white-crowned sparrows through their diet also increased perch-hopping activity (Breuner et al. 1998), suggesting these changes in activity are CORT mediated. In this study, thrashers also increased activity during periods of food restriction, which would promote a negative energy balance. However, this appears disadvantageous, but in both birds and mammals, CORT stimulates foraging (Landys et al. 2004; Pecoraro et al. 2004), which increases body condition, and in captivity this may correspond to increased activity.

Linking Energy Balance and the Acute Stress Response

This study contributes to our understanding of how energy reserves and the stress response interact. Supplementation studies in the field have shown that food availability can alter CORT secretion (Clinchy et al. 2004; Schoech et al. 2007), and this interaction is likely an important ecological mechanism dictating the habitats that animals occupy. However, to properly link food availability and the stress response will require knowledge of how current energetic status is intrinsically monitored. Recent research focusing on how neural mediators (e.g., neuropeptide Y, orexin, agouti-related protein) and peripherally secreted metabolic hormones that can act on the brain (e.g., leptin, ghrelin, insulin) interact with CORT (Heiman et al. 1997; Chang et al. 2005; Schmidt et al. 2008; Warne et al. 2009) provides a myriad of potential mechanisms that can link current energy reserves with the ability to cope with stress.

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