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Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbehSteroid hormone levels in calling males and males practicing alternative non-calling mating tactics in the green treefrog, *Hyla cinerea*

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ARTICLE INFO

Article history:

Received 12 July 2012

Revised 7 November 2012

Accepted 8 November 2012

Available online 15 November 2012

Keywords:

Alternative mating tactics

Androgens

Anuran

Corticosterone

Satellite behavior

Vocalization

ABSTRACT

Circulating glucocorticoids and androgens often figure prominently in mating tactic expression in vertebrates. In anuran amphibians (frogs and toads), for example, recent models predict that the depletion of energy reserves during vocalization will result in increased glucocorticoid levels; high glucocorticoids are expected to negatively affect androgen level to mediate transitions from calling to non-calling behavior. Consistent with these predictions, we show that male green treefrogs (*Hyla cinerea*) adopting an alternative non-calling “satellite” mating tactic were in poorer condition and had higher circulating corticosterone levels and lower androgen levels than calling males. Body condition was inversely related to corticosterone level and positively related to testosterone, but not dihydrotestosterone, level. Corticosterone level was inversely related to testosterone level but not dihydrotestosterone level. Lastly, we show that calling males that were involved in aggressive bouts had higher corticosterone levels than calling males that were not involved in aggressive bouts. Our results are thus consistent with the prediction that aggressive interactions with conspecific males contribute to high corticosterone levels in satellite males that were observed to lose aggressive contests with larger calling males.

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Introduction

Variation in male mating behavior frequently takes the form of alternative mating tactics where individuals conditionally alternate between an energetically demanding dominant tactic and a less energetically demanding alternative (reviewed by [Taborsky et al., 2008](#)). Males exhibiting different mating tactics thus often differ in circulating levels of glucocorticoids ([Oliveira et al., 2008](#)) that play a primary role in mobilizing energy reserves ([McEwen and Wingfield, 2010](#); [Sapolsky, 1992](#)). Circulating glucocorticoid levels and interactions between circulating glucocorticoids and sex steroid hormones, in particular, often figure prominently in mating tactic expression across vertebrates ([Oliveira et al., 2008](#)). In anuran amphibians (frogs and toads), for example, the depletion of energy reserves during vocal production is thought to drive elevations in circulating glucocorticoid levels ([Emerson, 2001](#)). High glucocorticoid levels are expected to eventually suppress the production of androgens and, thus, the production of androgen-dependent vocalizations (as described in the “Energetics-Hormone Vocalization” model, [Emerson, 2001](#)). We examined predictions of the Energetics-Hormone Vocalization model ([Emerson, 2001](#)) in the context of mating tactic expression in green treefrogs, *Hyla cinerea*. Male *H. cinerea* conditionally alternate between a dominant calling mating tactic and a non-calling “satellite” tactic within and between nights of chorus activity ([Perrill et al., 1978, 1982](#)); satellite males characteristically reside in close

proximity to calling conspecific males and attempt to intercept females approaching calling “host” males (reviewed by [Gerhardt and Huber, 2002](#); [Halliday and Tejedo, 1995](#); [Zamudio and Chan, 2008](#)). We examined body condition measures (a proxy for energy reserves), glucocorticoid levels, and androgen levels of calling males and males adopting non-calling satellite mating tactics to determine whether these measures differed between callers and satellites in a fashion that is consistent with predictions of the Energetics-Hormone Vocalization model ([Emerson, 2001](#)).

We also examined steroid hormone levels in male *H. cinerea* in the context of aggressive interactions. Male *H. cinerea* defend calling sites against intruders and often engage in aggressive interactions with other males using aggressive acoustic signals, grappling, or both ([Wells, 2007](#)). Such interactions could modulate circulating hormone levels and contribute to variation in calling behavior. In the highly territorial bullfrog (*Lithobates catesbeianus*), for example, calling males have higher levels of glucocorticoids and lower levels of androgens than non-calling satellite males ([Mendonça et al., 1985](#)). Lower androgen levels in calling males could result from stress responses (i.e., interactions between glucocorticoids and androgens) associated with territorial defense (male bullfrogs aggressively defend territories and frequently engage in combat; [Howard, 1978, 1984](#)) or from the energetic stress related to calling ([Emerson, 2001](#)). Comparing the hormone levels of calling males with varying levels of aggression, which has not been done in anurans, would help to resolve this issue. Nonetheless, smaller satellite male bullfrogs, which are typically the losers in aggressive territorial bouts ([Howard, 1978, 1984](#)),

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appear to maintain relatively high levels of circulating androgens. This is surprising because the losers of aggressive interactions often experience elevations in glucocorticoids that negatively affect circulating androgen levels in many vertebrate species (reviewed in Adkins-Regan, 2005; DeVries et al., 2003). One possibility is that calling male bullfrogs holding territories are subject to unstable social circumstances wherein a relatively high frequency or duration of challenges by a surplus of smaller subordinate males drives elevations in corticosterone levels that negatively affect circulating androgens (see Knapp and Moore, 1995, 1996; Sapolsky and Ray, 1989). We thus measured circulating glucocorticoid levels and androgen levels in calling male *H. cinerea* that were recently involved in aggressive interactions and males that were not recently involved in aggressive interactions to determine if the two groups differed with respect to circulating hormone levels.

Lastly, chorus activity for *H. cinerea* is prolonged (often spanning the spring and summer months) and may be important in the context of steroid hormone profiles and hormone interactions in callers and satellites. Current evidence, for example, suggests that a reciprocal interaction between corticosterone level and androgen level occurs in prolonged breeding anuran species but not explosive breeding species (reviewed by Leary, 2009). These findings are consistent with predictions of the Emergency Life History Stage theory (Wingfield et al., 1995, 1998). Selective pressures imposed on explosive breeding bird species (e.g., time constraints), for example, appear to favor individuals that are capable of buffering against the negative effects of high glucocorticoid level on the reproductive axis (i.e., by altering plasma binding proteins and or receptor levels) (Wingfield et al., 1995, 1998). Such selective pressures, however, may be relaxed in more prolonged breeding species because individuals are provided with the opportunity to return to the pool of conspecifics engaged in breeding activity in the event that a reciprocal interaction between the two steroids occurs (Wingfield et al., 1995, 1998). Hence, based on predictions of Energetics-Hormone Vocalization model (Emerson, 2001) and concepts of the Emergency Life History Stage theory (Wingfield et al., 1995, 1998), we predicted that non-calling satellite male *H. cinerea* would be in poorer condition and have higher corticosterone levels and lower androgen levels than calling males; an inverse relationship between glucocorticoid level and androgen level was expected to be evident in this prolonged breeding species.

Material and methods

Behavioral observations

Choruses of green treefrogs (*H. cinerea*) were studied throughout much of the breeding season (~April–August) over two consecutive years (2010–11) at the University of Mississippi Field Station located in Lafayette County, MS. This facility consists of approximately 740 acres of lowland forest with over 200 ponds; *H. cinerea* are abundant at many of these ponds. All data described in the present study came from 3 widely separated ponds located on this property.

Focal observations were made for a minimum of 20 min (range = 15–80 min, mean = 40 min) on calling males and caller-satellite associations using low powered LED headlamps. Males were classified as satellite males if they did not call during the period of observation and adopted a crouched position in close proximity (~1 m) to calling conspecific males. Satellite males were often observed approaching nearby incoming individuals (males and females) and, in some cases, were observed to successfully amplex (mount) females presumably attracted to the vocalizations of host males. Our observations thus indicated that these males were not merely non-calling males awaiting the vacancy of calling sites nor was there evidence that available calling sites were limited at these ponds (i.e., there was abundant emergent vegetation from which males typically call).

During periods of observation, aggressive interactions between males were logged and a series of approximately 20 consecutive vocalizations were recorded using a Marantz PMD 222 cassette recorder equipped with a Sennheiser directional condenser microphone (Model ME-66). Individuals were subsequently captured by hand and blood samples (~100 µl) were obtained in less than 1 min via cardiac puncture using a sterile 27 gauge heparinized hypodermic needle and syringe. Individuals were then measured from the tip of the snout to the end of the ischium (snout-ischial length, SIL), weighed, marked on the venter with a portable tattoo device (Tattoo-A-Pet, Fort Lauderdale, FL) for future identification (unique tattoo numbers were clearly visible throughout the duration of a single breeding period but not across years), and released. Acquisition of blood and body weight/size measures and application of tattoos was typically completed in 3 min or less and did not appear to have any immediate or long term effects on reproductive behavior; calling individuals typically resumed calling behavior within minutes of release and were often found calling on subsequent nights of chorus activity. Blood samples were stored on ice and subsequently centrifuged at 2200 rpm upon return to the lab (<6 h). Plasma was stored at –20 °C until dihydrotestosterone (DHT), testosterone (T), and corticosterone (CORT) levels were quantified using radioimmunoassay (described below).

Column chromatography and radioimmunoassay procedures

Hormone separation and quantification of hormone concentrations followed the protocol described by Knapp and Moore (1995), Knapp et al. (1999), and Leary et al. (2004). Briefly, plasma samples were incubated overnight with radiolabeled hormone (PerkinElmer, Inc. Hebron, Kentucky) for determination of recoveries for each sample. Steroids were then extracted from plasma using diethyl ether, dried under nitrogen gas at 40 °C, and resuspended in 10% ethyl acetate in iso-octane. Samples were then loaded onto diatomaceous earth columns containing a 3:1 diatomaceous earth:distilled water “glycol trap” and a 1:1 propanediol:ethylene glycol mixture. Mixtures of 10%, 20%, and 52% ethyl acetate in iso-octane were then used to collect DHT, T and CORT, respectively. Fractions were dried under nitrogen and resuspended in phosphate buffered saline containing 0.3% gelatin for use in radioimmunoassay. Testosterone antibody was obtained from Fitzgerald Industries International, Inc (Acton, Massachusetts) and used for both T and DHT assays. Corticosterone antibody was purchased from MP Biomedicals, LLC (Solon, Ohio). All samples were assayed in duplicate.

Plasma samples were analyzed for DHT, T and CORT levels in 4 assays. Assay sensitivities were approximately 0.13 ng/ml for DHT, 0.12 ng/ml for T, and 0.45 ng/ml for CORT. Mean intra-assay coefficients of variation for DHT, T, and CORT were 14%, 9%, and 10%, respectively, based on 3–4 standards run with each assay (standards were known amounts of unlabeled hormones in distilled water that were ether extracted and separated via column chromatography just like plasma samples). Interassay coefficients of variation for DHT, T, and CORT were 19%, 18%, and 19%, respectively. Steroid hormone levels for callers and satellites were analyzed using ANOVA.

For CORT, a total of 19 samples were considered non-detectable because they fell outside the steep portion of the sigmoid standard curve. In these cases, the standard curve equation still allowed estimation of low CORT levels. All 19 non-detectable samples were from calling males and, hence, to be conservative in our approach to examining potential differences in CORT levels for calling males and satellite males, separate analyses were done with and without non-detectable CORT levels.

Body condition estimates

Body condition estimates were used as a proxy for energy reserves. Body condition was calculated by obtaining the residual

values from a linear regression of the cubed root body mass on SIL and dividing those values by the SIL, following the approach described by Baker (1992), Howard et al. (1997), and Howard and Young (1998). This was done for all individuals collectively across years and ANOVA was used to examine body condition estimates for callers and satellites.

Vocal analysis

For the purposes of the present study, recorded vocalizations were used to assess whether males produced pulsed aggressive calls (containing $\geq 50\%$ depth of the amplitude modulation) or unpulsed advertisement calls (with $< 50\%$ depth of the amplitude modulation) during the sampling period (see Oldham and Gerhardt, 1975; Gerhardt, 1978 for description of these two call types). Calls were categorized by examining waveforms using Raven software (Cornell Bioacoustics Laboratory).

Scientific collecting permits were provided by the Mississippi Department of Wildlife, Fisheries and Parks. All procedures were approved by the University of Mississippi Animal Care and Use Committee.

Results

Satellite males and calling males differed with respect to circulating levels of DHT, T and CORT; satellite males had significantly lower levels of DHT ($F_{1,142} = 3.65$, $p = 0.05$) and T ($F_{1,142} = 4.78$, $p = 0.03$) and significantly higher levels of CORT ($F_{1,142} = 16.86$, $p < 0.0001$) than calling males (Fig. 1). CORT levels were still significantly different for the two behavioral phenotypes when the 19 calling males with non-detectable levels of CORT were removed from the analysis ($F_{1,123} = 14.43$, $p = 0.0002$). Simple regression indicated that there was no significant relationship between CORT level and DHT level ($r^2_{1,142} = 0.008$, $p = 0.28$) but there was a significant inverse relationship between circulating CORT level and T level ($r^2_{1,142} = 0.03$, $p = 0.04$, Fig. 2). Overall, there was not a significant relationship between CORT level and total androgen level (DHT + T) ($r^2_{1,142} = 0.02$, $p = 0.10$, data not shown).

We then examined body condition estimates and body size measures for the two behavioral phenotypes. Satellite males were in poorer condition than calling males ($F_{1,140} = 7.24$, $p = 0.008$, Fig. 3A) and were smaller than calling males ($F_{1,140} = 33.92$, $p = 0.0001$, Fig. 3B); reported degrees of freedom differ from those reported for hormone analyses because body weight measures were not available for two calling males for which hormone data was obtained. Simple regression analysis indicated that body condition was negatively related to CORT level ($r^2_{1,140} = 0.07$, $p = 0.001$, Fig. 4A) and positively related to total androgen (DHT + T) level ($r^2_{1,140} = 0.04$, $p = 0.01$, Fig. 4B); these results were

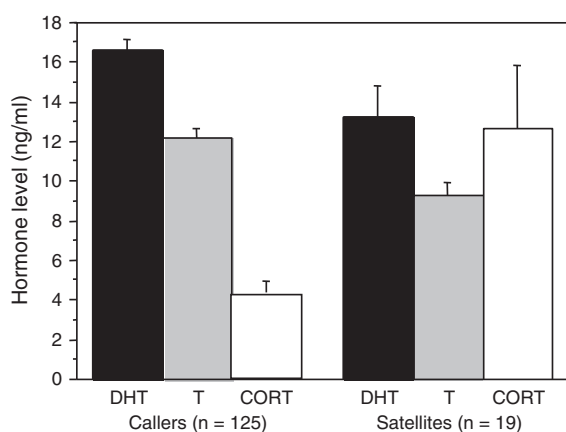


Fig. 1. Mean (\pm SE) dihydrotestosterone (DHT), testosterone (T), and corticosterone (CORT) levels for calling and satellite male *Hyla cinerea*.

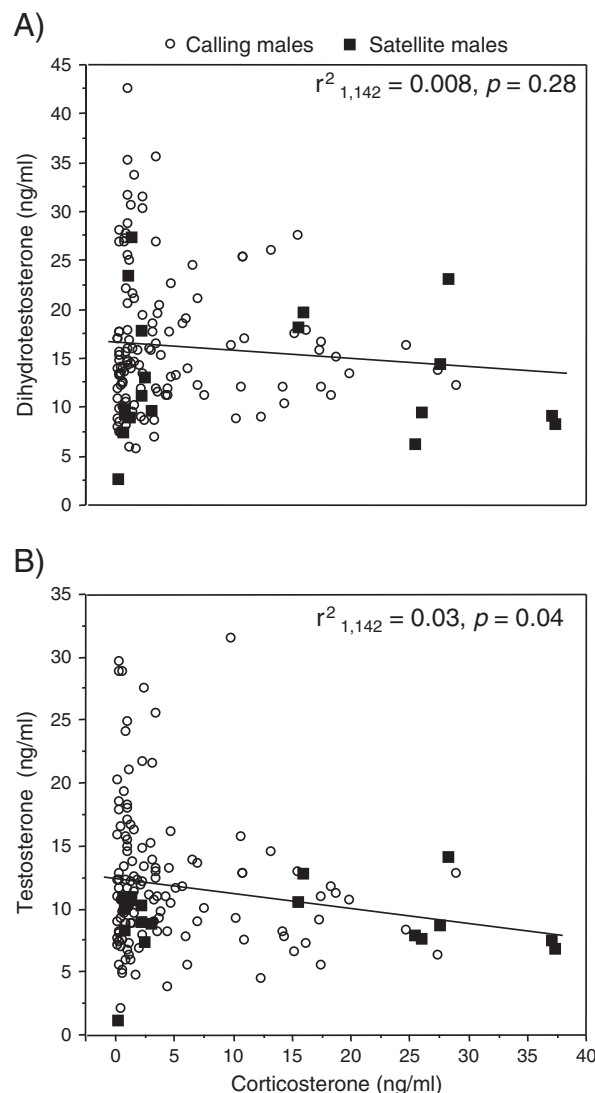


Fig. 2. Relationship between corticosterone level and A) dihydrotestosterone level and B) testosterone level for all males in *Hyla cinerea*. Behavioral phenotypes are designated with different symbols (callers = open circles, satellites = filled squares).

largely attributable to a positive relationship between body condition and T level ($r^2_{1,140} = 0.08$, $p = 0.0005$) but not DHT level ($r^2_{1,140} = 0.01$, $p = 0.2$).

Males for which we had continuous and prolonged focal observations (≥ 30 min), were then partitioned into callers that were not involved in aggressive interactions during the focal observational period ("non-aggressive" males) and callers that were involved in aggressive interactions during the focal observational period ("aggressive" males). There was a significant difference in circulating CORT level between the two groups: non-aggressive males had significantly lower levels of CORT than aggressive males ($F_{1,102} = 9.43$, $p = 0.003$, Fig. 5). Non-aggressive and aggressive males did not, however, differ with respect to circulating DHT ($F_{1,102} = 0.32$, $p = 0.57$) or T levels ($F_{1,102} = 2.56$, $p = 0.11$, Fig. 5). Differences in circulating CORT levels for non-aggressive and aggressive males were not attributable to differences in body condition for these two groups ($F_{1,102} = 0.065$, $p = 0.79$).

Discussion

Male green treefrogs adopting an alternative non-calling satellite mating tactic had, on average, lower circulating androgen levels and higher circulating CORT levels than calling males. CORT level was

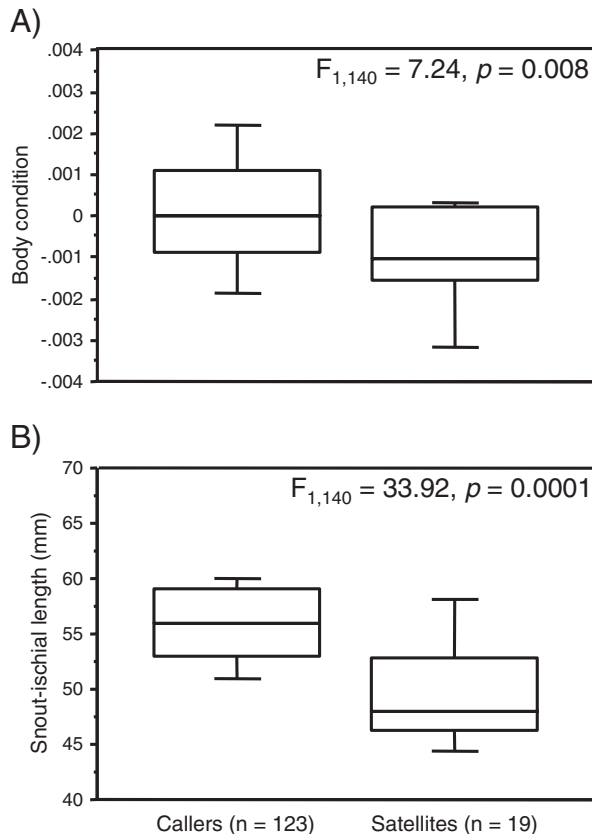


Fig. 3. Box plots depicting A) relative body condition and B) snout-ischial length for calling and satellite *Hyla cinerea*. Height of boxes reflects 75th to 25th percentiles with median horizontal line. Whiskers depict 90th and 10th percentiles.

inversely related to circulating T level but not DHT level across males. These results are largely consistent with predictions of the Energetics-Hormone Vocalization model (Emerson, 2001) that proposes a negative effect of elevated CORT level on circulating androgen level to explain transitions from calling to non-calling behavior in anuran amphibians. Although a causal relationship between CORT level and satellite tactic expression was not established in the current study, CORT administration has previously been shown to decrease the probability of vocalization in *H. cinerea* (Burmeister et al., 2001) and other anuran species as well e.g., túngara frogs, *Physalaemus pustulosus* (Marler and Ryan, 1996), Great plains toads, *Anaxyrus cognatus*, and Woodhouse's toads, *Anaxyrus woodhousii* (Leary et al., 2006a,b). In *A. cognatus* and *A. woodhousii*, CORT administration also results in an increased probability of satellite tactic expression (Leary et al., 2006a,b). The available information thus adds to a growing data set suggesting that elevated CORT, whether by acting directly on central and/or peripheral structures or by negatively affecting circulating androgens, mediates transitions between calling and non-calling behavior in anurans (reviewed by Leary, 2009).

Steroid hormone profiles for caller and satellite green treefrogs (present study) contrast with those reported for other anuran species. In the three other species in which androgens and CORT have been measured, calling males have higher levels of CORT than satellite males (*A. cognatus* and *A. woodhousii*, Leary et al., 2004; *L. catesbeianus* Mendonça et al., 1985). Male *A. cognatus* and *A. woodhousii* appear to experience high levels of CORT while calling and subsequently clear circulating CORT as satellites (Leary et al., 2004, 2006b). Longitudinal data are undoubtedly important in understanding the hormonal mechanisms regulating tactic expression (see Schradin and Yuen, 2011; Oliveira et al., 2008) and we are currently examining how hormone levels change during transitions from calling to satellite behavior (and

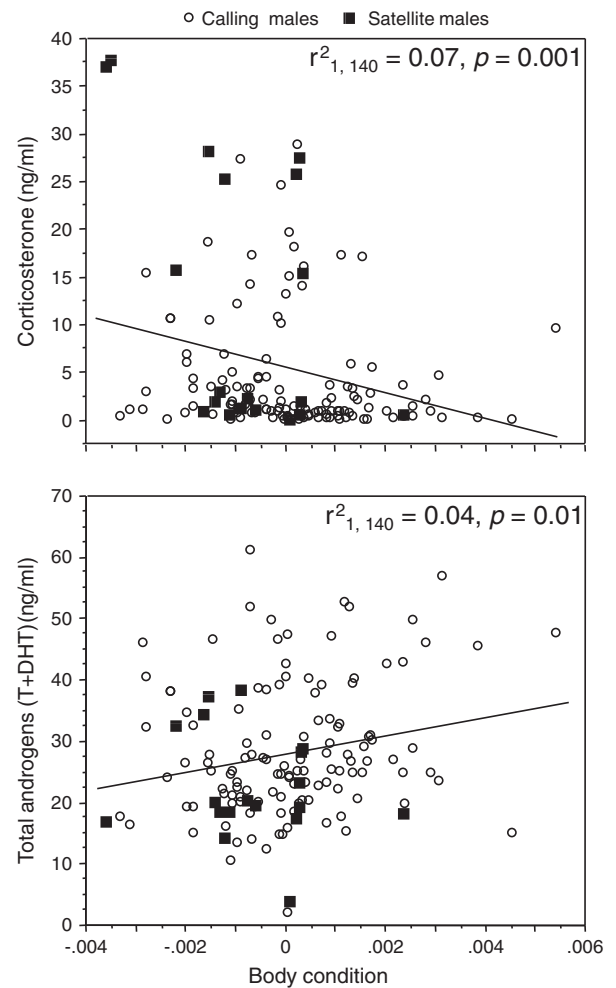


Fig. 4. Relation between relative body condition and A) corticosterone level and B) total androgen level (dihydrotestosterone and DHT + testosterone, T) for all males in *Hyla cinerea*. Behavioral phenotypes are designated with different symbols (callers = open circles, satellites = filled squares).

vice versa) within individual *H. cinerea*. It is not currently clear, for example, whether transitions between calling and satellite behavior in small males are associated with changes in circulating hormone levels (representative of the hormone profiles for callers and satellites

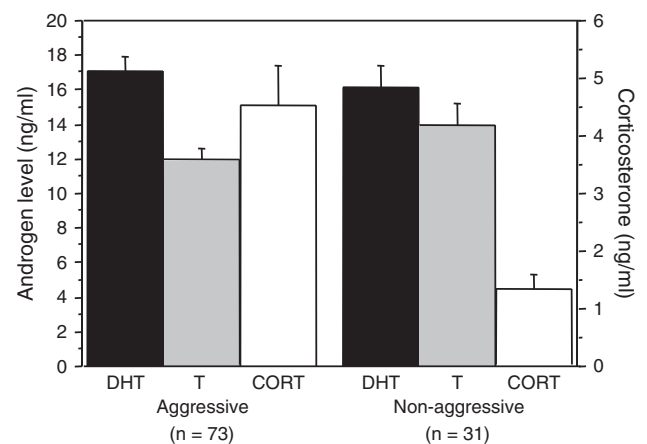


Fig. 5. Mean (\pm SE), dihydrotestosterone (DHT), testosterone (T), and corticosterone (CORT) levels for calling males that were involved in aggressive interactions ("aggressive males") versus calling males that were not involved in aggressive interactions ("non-aggressive males") during the focal observational period.

described in the present paper) or whether small males represent a class of males with chronically elevated CORT levels and low androgens that decrease the propensity to vocalize.

The Energetics-Hormone Vocalization model (Emerson, 2001) predicts that males will experience elevations in CORT levels as a result of the depletion of energy reserves during vocalization. Our results are consistent with this prediction; satellite males had higher CORT levels and were in poorer condition than calling males, and body condition was inversely related to circulating CORT level across males. Our results also suggest, however, that aggressive interactions among males could contribute to variation in CORT level as well. Calling males that were observed to interact aggressively with conspecific males, for example, had significantly higher CORT levels than other calling males that were not observed to interact aggressively during focal observations; circulating androgen levels did not differ for the two groups. Importantly, differences in CORT level for aggressive and non-aggressive males were not related to differences in body condition suggesting that CORT level may be modulated independently of body condition during aggressive encounters. Males involved in aggressive interactions in our study always produced amplitude-modulated aggressive calls (see Gerhardt, 1978; Oldham and Gerhardt, 1975 for description of calls) but only a small proportion of them (20%) engaged in physical combat. We are currently pursuing whether exposure to aggressive calls increases CORT levels in smaller males that typically lose aggressive encounters and that adopt the non-calling mating tactic. Such information may help to explain differences in body size for the two behavioral phenotypes.

The picture that is beginning to emerge from the available hormone data for calling and satellite anurans suggests broad applicability of the Energetics-Hormone Vocalization model (Emerson, 2001) but modifications may be required that incorporate concepts of the Emergency Life History Stage theory (Wingfield et al., 1995) to reflect hormone patterns for explosive breeding versus prolonged breeding anurans. Specifically, current data for two prolonged breeding species (*L. catesbeianus*, Mendonça et al., 1985 and *H. cinerea*, the present study) suggest that reciprocal interactions between corticosterone and androgens potentially mediate behavioral transitions from calling to non-calling behavior and are consistent with predictions of the Energetics-Hormone Vocalization model (Emerson, 2001). In explosive breeding anuran species, however, an inverse relationship between CORT level and androgen level does not appear to occur; in *A. cognatus* and *A. woodhousii*, for example, CORT level is positively correlated with androgen level (Leary et al., 2004). Regardless of these potential differences in steroid hormone interactions among species, it appears that elevated CORT may be the proximate signal that decreases the probability of calling behavior in anurans (Leary, 2009). Given the scarcity of hormone data for calling and satellite anurans, further comparative studies will be required to determine whether the current hormone patterns for explosive versus prolonged breeders hold across a broader range of species.

Acknowledgments

We thank Rosemary Knapp for assistance and guidance with radioimmunoassay procedures. Funding for this research was provided through the University of Mississippi College of Liberal Arts Summer Research Awards to CJL.

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