



Within seasons and among years: When are corticosterone levels repeatable?

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ABSTRACT

Hormones play a central role in integrating internal and external cues to help mediate life-history decisions as well as changes in behavior and physiology of individuals. Describing the consistency of endocrine traits within and among individuals is an important step for understanding whether hormonal traits are dependable predictors of phenotypes that selection could act upon. However, few long-term field studies have investigated the individual consistency of hormonal traits. Glucocorticoid hormones mediate homeostatic responses to environmental variation as well as stress responses to acute, unpredictable disturbances. We characterized the repeatability of plasma corticosterone concentrations in two species of free-living passerines across multiple years. We found repeatability in baseline corticosterone concentrations in both sexes of great tits (*Parus major*) and in female tree swallows (*Tachycineta bicolor*) within the breeding season but no repeatability of this trait among seasons or across years. Stress-induced levels of corticosterone were only assessed in great tits and were not repeatable in either sex. Our data suggest that in line with their function in mediating responses of individuals to longer-term and acute demands, both baseline and stress-induced plasma corticosterone concentrations are rather plastic traits. However, individuals may differ in their degree of trait plasticity and hence in behavioral and physiological responses to a variety of organismal challenges.

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Introduction

Recent studies have characterized the functional significance of individual variation in physiological traits within single populations (Angelier et al., 2010; Bonier et al., 2009a; John-Alder et al., 2009; McGlothlin et al., 2010; Ouyang et al., 2011; Pride, 2005; Romero and Wikelski, 2010; Sinervo et al., 2000; Storey et al., 2006). However, because several studies assessed the hormonal state of an individual only at one point in time and correlated this value with behavior or fitness measures obtained at later stages, the relationship between endocrine traits and behavior or fitness measures is not always present or consistent between studies (Bonier et al., 2009b). One important reason for a failure to find such relationships may be the existence of high intra-individual variation in hormone concentrations, advising caution in assuming that one sample is representative of an individual's endocrine phenotype (Romero and Reed, 2008; Vitousek et al., 2008). Therefore, in order to better understand an individual's physiological phenotype we need to determine the individual consistency of hormonal traits, especially in wild populations (Angelier et al., 2010; Rensel and Schoech, 2011) and across different life-history stages.

Furthermore, knowing the degree of individual consistency in hormonal traits, and their relationship to behavior or fitness can increase our understanding of evolutionary dynamics, such as whether selection is acting on absolute or plastic hormone concentrations (Dohm, 2002; Williams, 2008; Zera et al., 2007). Williams (2008) has proposed that individual variation in endocrine traits might actually be larger than variation in many other physiological traits because hormones integrate external cues and internal condition to regulate optimal life-history, as well as behavioral and physiological strategies. Determining the degree of plasticity in endocrine traits will also contribute to the current knowledge about why certain behaviors are repeatable whereas others are not (Bell et al., 2009). For example, risk-taking is a repeatable and heritable trait (van Oers et al., 2004), and a comprehensive understanding of behaviors under selection can only be achieved with a comparable investigation of the mechanisms that regulate such behaviors (King et al., 2004; Koolhaas et al., 1999; Øverli et al., 2004).

Glucocorticoid hormones (in most rodents and all birds: corticosterone) are ideal for the study of how individuals respond to environmental variation because they are the main mediators of allostasis under changing conditions (McEwen and Wingfield, 2003; Sapolsky et al., 2000). Glucocorticoids rise in response to environmental challenges, such as inclement weather (Gesquiere et al., 2008; Wingfield et al., 1983), or to challenges associated with life-history stages, such as increased energy demands (Romero, 2002). When the individual experiences an acute and unpredictable noxious stimulus, baseline

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corticosterone levels rise within the first 3 min, reaching high stress-induced concentrations, that among many other effects have been linked to decreases in reproductive investment (Angelier et al., 2007; Silverin, 1986). Recent studies have begun to examine the degree of consistency in baseline and stress-induced corticosterone concentrations within individuals, but more commonly in lab settings and over short time spans and only rarely across years in wild populations in a natural setting (Bonier et al., 2009b; but see Rensel and Schoech, 2011). Furthermore, in studies investigating individual consistency in hormonal traits within years, repeatability estimates appear to depend on the study setting (field or captive), time of year, and number of individuals sampled (see Table 1; Angelier et al., 2009, 2010; Ouyang et al., 2011; Rensel and Schoech, 2011; Romero and Reed, 2008; Wada et al., 2008).

Repeatability (*R*) is an index for quantifying the consistency of individual phenotypes and is measured as the fraction of phenotypic variation that is due to differences among individuals relative to differences within an individual (Lessells and Boag, 1987). We tested for repeatability in individual corticosterone levels in two cavity-nesting passerine species with high breeding site fidelity, using data collected during long-term studies of known free-living individuals. We obtained measures of baseline and stress-induced corticosterone concentrations in male and female great tits (*Parus major*) and baseline corticosterone concentrations in female tree swallows (*Tachycineta bicolor*) across multiple years. This approach allowed us to evaluate for each species the repeatability of these endocrine traits within and across years and to compare between-species differences in individual consistency.

Materials and methods

Great tits

Adult great tits were captured in mist nets at feeding stations in MÖggingen, Germany (47°N, 8°E) for two weeks each in March 2009, January 2010, and March 2010. They were also captured at the nest box using an automatic metal trap that closed the entrance hole when they were feeding their 8- or 9-day old young during the breeding seasons of 2009 and 2010 (May–June). All blood sampling took place between the hours of 08:00 and 12:00. We collected blood from the brachial vein (80–120 µl) within 3 min of entrapment in the nest box

or entanglement in the mist net (mean: 1.9 min ± 0.9 standard deviation; *n* = 238) to measure baseline corticosterone levels. We then placed the bird in a cloth bag and collected another blood sample (50 µl) 30 min later to measure stress-induced corticosterone concentrations. The blood samples were kept on ice and centrifuged (822 × *g*, 10 min) within 3 h, and the plasma was separated and stored at –80 °C until analysis for hormone concentration. The work for the great tits was approved by the state of Baden-Württemberg under permit number G-09/102.

Corticosterone concentrations were determined using enzyme immunoassay (EIA) kits (Cat. No. 901-097, Assay Designs) following a diethyl-ether extraction of 5 µl sample volume. After drying the extract under N₂ stream, 400 µl of Assay Buffer 15 (Tris-buffered saline) was added (1:80 dilution), and the samples were allowed to reconstitute overnight. Two separate, stripped-chicken plasma standards with a known amount of added corticosterone (20 ng/ml) as well as two blank samples containing only assay buffer were taken through the entire assay procedure. The next day, 100 µl of each sample (in duplicate) was added to individual wells on the assay plate alongside a standard curve with 5 standards ranging from 32 to 20,000 pg/ml. The samples were added randomly within and across plates but an individual's 0 minute and 30 minute samples were always included on the same plate. The plate was shaken for 2 h to bind the conjugate corticosterone and the antibody. The wells were then washed 4 times with 200 µl of wash solution. After adding 200 µl of p-nitrophenyl phosphate to each well, the plate was incubated in darkness for another hour. Stop solution was then added and the plate was read on VERSA_{max} microplate reader at 405 nm. The lower sensitivity of the assay was at 18.8 pg/ml and the corresponding lower detection limit was at 0.033 ng/ml (determined by the lowest standard). The blank wells were always below the detection limit. Double diethyl ether extractions of samples spiked with a small amount of radioactive corticosterone in our laboratory yield an average recovery of around 90% (extraction efficiency for stripped plasma (*n* = 3 samples): 89.7%, CV 6.1%; extraction efficiency for European blackbird, *Turdus merula*, plasma (*n* = 6 samples): 91.4%, CV 2.2%). Given the high recoveries and low variation in extraction efficiency between samples, we added 10% to all our values to account for extraction efficiency. The mean intra-plate (16 plates) coefficient of variation of two replicate standards per plate was 11.8% and the inter-plate coefficient of variation was 4.9%.

Table 1
Summary of the currently available studies in repeatability of baseline and stress-induced corticosterone concentrations. Studies are sorted by whether baseline corticosterone concentrations were repeatable.

Species	Sex	Average body mass (g)	<i>N</i>	Baseline corticosterone repeatable?	Stress-induced corticosterone repeatable?	Time measured	Time line	Citation
American red starts ^a	Both	7	24	No	Yes	Autumn–spring	1 year	Angelier et al. (2009)
Domestic jungle fowl	Females	2700	10	No	Yes	NA	21 days	Littin and Cockrem (2001)
Adelie penguins ^a	Both	4050	18	No	Yes	Breeding	12 days	Cockrem et al. (2009)
Zebra finches	Females	12	19	No	Yes	Feb–Aug	3 months	Wada et al. (2008)
	Males	12	19	No	No	Feb–Aug	3 months (1 × juvenile)	Wada et al. (2008)
House sparrows ^a	Both	27	40	No	No	Pre-breeding to breeding	3–4 months	Ouyang et al. (2011)
Florida scrub jay ^a	Both	80	37	Yes/no ^b	NA	June	3 years (1 × juvenile)	Rensel and Schoech (2011)
House sparrows	Both	27	19	Yes/no ^c	NA	October	2 months	Romero and Reed (2008)
Greylag geese	Males	3300	10	Yes ^d	Yes ^d	Aug–Jan	6 months (3 ×)	Krajc-Fiser et al. (2007)
Great tit	Both	17	13	Yes	Yes	October	15 days	Cockrem and Silverin (2002b)
Black-browed albatross ^a	Both	3500	8	Yes	NA	Breeding	1 year	Angelier et al. (2010)

NA represents data not available in the study.

^a Indicates if study was performed in the wild.

^b Calculated relative baseline corticosterone by subtracting raw value from cohort mean; baseline corticosterone was only repeatable from the nestling to yearling stage.

^c Ranked individuals at each stage and then calculated repeatability estimates; relative ranks were only consistent during the night and on short days.

^d Fecal metabolites.

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