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Baseline and stress-induced glucocorticoid concentrations are not repeatable but covary within individual great tits (*Parus major*)

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ABSTRACT

In evolutionary endocrinology, there is a growing interest in the extent and basis of individual variation in endocrine traits, especially circulating concentrations of hormones. This is important because if targeted by selection, such individual differences present the opportunity for an evolutionary response to selection. It is therefore necessary to examine whether hormone traits are repeatable in natural populations. However, research in this area is complicated by the fact that different hormone traits can be correlated. The nature of these trait correlations (i.e., phenotypic, within-, or among-individual) is critically relevant in terms of the evolutionary implications, and these in turn, depend on the repeatability of each hormone trait. By decomposing phenotypic correlations between hormone traits into their within- and among-individual components it is possible to describe the multivariate nature of endocrine traits and generate inferences about their evolution. In the present study, we repeatedly captured individual great tits (*Parus major*) from a wild population and measured plasma concentrations of corticosterone. Using a mixed-modeling approach, we estimated repeatabilities in both initial (cf. baseline; CORT0) and stress-induced concentrations (CORT30) and the correlations between those traits among- and within-individuals. We found a lack of repeatability in both CORT0 and CORT30. Moreover, we found a strong phenotypic correlation between CORT0 and CORT30, and due to the lack of repeatability for both traits, there was no among-individual correlation between these two traits—i.e., an individual's average concentration of CORT0 was not correlated with its average concentration of CORT30. Instead, the phenotypic correlation was the result of a strong within-individual correlation, which implies that an underlying environmental factor co-modulates changes in initial and stress-induced concentrations within the same individual over time. These results demonstrate that (i) a phenotypic correlation between two hormone traits does not imply that the traits are correlated among individuals; (ii) the importance of repeated sampling to partition within- and among-individual variances and correlations among labile physiological traits; and (iii) that environmental factors explain a considerable fraction of the variation and co-variation in hormone concentrations.

1. Introduction

1.1. Theoretical background: levels of phenotypic variation

Evolution requires heritable variation, but estimating the heritability of traits in free-living animals is often impractical due to the absence of pedigree information. Under these conditions it is often useful to estimate the repeatability of traits, which sets an upper limit to heritability (Lessells and Boag, 1987; but see Dohm, 2002). Evidence for repeatable variation therefore provides clues as to whether the observed trait can in principle evolve in response to selection (e.g., Dingemanse and Dochtermann, 2014).

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Morphological measures such as wing length or body size are examples of traits that typically have high repeatability. Repeatability is the proportion of phenotypic variance explained by among-individual variance—thus, traits with low within- and high among-individual variance have high repeatability. Within-individual variance describes the amount of phenotypic variation among observations of the same individual over time (Fig. 1) and therefore represents the plasticity (as well as stochasticity and measurement error) of an individual's phenotype in response to external (e.g., ambient temperature) and internal variables (e.g., nutritional status, age). Within-individual variation is therefore not synonymous with plasticity, which instead represents only the portion of this within-individual variation that is due to the individual's response to environmental change.

Among-individual variances describe how much individuals differ from each other in their average phenotype (Fig. 1). Among-individual variation, therefore, represents the more static aspects of the phenotype, which can arise due to 'permanent' external factors (e.g., maternal effects or environmental influences that are stable over the course of the measurements) or heritable genetic differences—fulfilling, in the case of the latter, a prerequisite for evolutionary responses to selection. Within- and among-individual variances thus represent two hierarchical levels of variation and jointly contribute to the phenotypic (i.e., total) variance (Westneat et al., 2014; Fig. 1).

Using heritability estimates (h^2), it is then possible to calculate the evolutionary response (R) to selection (S) using the classic breeder's equation ($R = h^2 * S$). Evolution, however, will proceed very differently if the focal trait is genetically correlated with other traits under selection (Lande and Arnold, 1983). It is therefore imperative that we quantify correlations between traits in order to be able to properly predict how they might evolve. The most pressing consequence of genetic correlations is that they can impose constraints on evolution; the constraining effects of these correlations can be substantial for behavioral (Dingemanse and Dochtermann, 2013) and endocrine traits (Ketterson et al., 2009).

Phenotypic correlations between two traits are sometimes used to infer their genetic correlation, which might be a suitable assumption for certain classes of traits, particularly non-labile (i.e., fixed) traits such as morphological dimensions (cf. Cheverud's conjecture; Dochtermann, 2011). This inference, however, is more complicated for labile (i.e., plastically varying) traits. Raw phenotypic correlations for labile traits are the weighted outcome of two processes: (i) 'within-individual correlations' which are the integration of plasticity between two focal traits (cf. both traits change in concert within the same individual due to one or more environmental variables); and (ii) 'among-individual correlations' which are proximately underpinned by the effects of maternal, 'permanent' environmental and genetic correlations between the traits, with genetic correlations occurring either because of

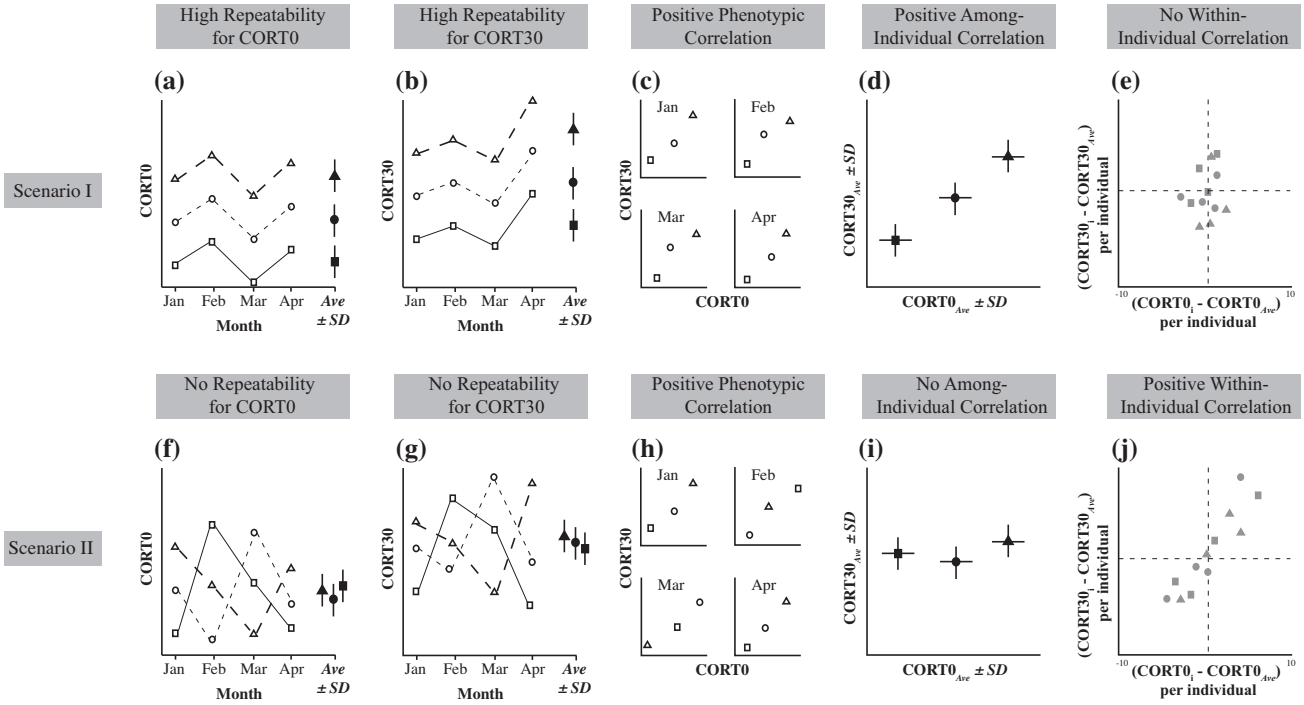

Fig. 1. Illustrations of two hypothetical scenarios in which concentrations of CORT0 and CORT30 are measured at four time points in each of three individuals (square, circle, triangle). Scenario I depicts a situation in which the three individuals differ consistently from each other in both CORT0 and CORT30, as indicated by the consistent rank order of each subject (e.g., triangles are always above circles at any given month) in (a) and (b). Therefore, averages for both CORT0 and CORT30 in these three individuals are distinct (solid symbols in (a) and (b)) and correspondingly, repeatability (i.e., among individual variance) is high. In any given month, the rank order of individuals for CORT0 is the same as that for CORT30, leading to a positive phenotypic correlation between these two hormone concentrations (c). This positive phenotypic correlation is driven by a positive among-individual correlation, and can be illustrated by showing the individual averages for CORT0 versus CORT30 (d), which is due to the fact that the rank order of individuals is stable across months (e.g., triangles are always highest for both CORT0 and CORT30). Note that error bars in (d) illustrate that there is also some within-individual variance in both CORT0 and CORT30. Within-individual correlations can be depicted by plotting the deviation from the average per individual for each measure (i) of CORT0 (x-axis) versus the deviation from the average per individual for each measure (i) of CORT30 (y-axis). The lack of a within-individual correlation is depicted in (e), indicating that the phenotypic correlations in (c) are driven principally by the among-individual correlation (d). Scenario II depicts an alternative situation in which each individual varies considerably from one month to the next leading to a lack of repeatability (i.e., no among-individual variance) for both CORT0 (f) and CORT30 (g). Nevertheless, in any given month, the ranking of individuals for CORT0 is the same as that for CORT30, leading to a phenotypic correlation (h) similar to Scenario I. Because of the lack of repeatability, this phenotypic correlation cannot be driven by an among-individual correlation, which is depicted by the lack of relationship in the average CORT0 and CORT30 phenotypes (i). Instead, it must be driven by a within-individual correlation (j), indicating the role of environmental factors in co-modulating CORT0 and CORT30 concentrations simultaneously within the individual. Scenario II better illustrates the results from the present study.