

Baseline hormone levels are linked to reproductive success but not parental care behaviors



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ABSTRACT

Consistent behavioral differences among individuals, or personalities, have been hypothesized to arise as a result of consistent individual differences in hormone levels. Individual variation in baseline hormone levels or hormonal similarity within a breeding pair may be related to reproductive success, as suggested by the corticosterone-fitness hypothesis and the hormonal similarity hypothesis, respectively. In a population of Eastern bluebirds (*Sialia sialis*) with repeatable behavioral expression and coordination of behavior within pairs, we tested if baseline androgen and corticosterone levels are related to behavioral expression, if coordination in behavior within pairs is facilitated by hormonal coordination, and if baseline hormone levels are related to fledging success at the individual or pair level. We found no significant relationship between hormone levels and nest visit rate or nest defense for either sex. Androgen and corticosterone levels were not correlated within pairs, but pairs in which males exhibited more aggressive nest defense behavior than females were also more different in androgen levels. Females with higher baseline corticosterone levels fledged more young, but hormonal similarity within pairs was not related to fledging success. Our results provide support for the corticosterone-adaptation hypothesis, which suggests that elevation of baseline corticosterone levels may occur during breeding to meet increased energetic demands.

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1. Introduction

The ability to modify behavioral expression in response to changes in the physical and social environments may enhance an animal's ability to behave adaptively in a particular circumstance (Sih et al., 2004a,b; Schuett et al., 2010). However, a number of studies have now documented that individuals do not exercise the full range of behavioral traits demonstrated in the population, but are instead constrained by consistent individual differences in behavior when confronted with environmental and social challenges (reviewed in Wilson, 1998; Dall et al., 2004; Sih et al., 2004a; Réale et al., 2007; Stamps and Groothuis, 2010). Consistent differences in the behavior of animals across time and in different contexts are also called animal personalities (Réale et al., 2007). Despite substantial evidence supporting the existence of animal personalities and behavioral syndromes across many taxa (e.g., invertebrates: Johnson and Sih, 2005; fish: Wilson and Godin, 2009; mammals: Réale et al., 2000; birds: Dingemanse et al., 2003), relatively little is known about the proximate mechanisms that may contribute to variation in personalities within a

population. Differences in circulating hormone levels, particularly corticosterone (CORT) and androgens such as testosterone, have been suggested to contribute to consistent behavioral differences observed within populations (reviewed in Koolhaas et al., 1999; Sih et al., 2004b; Cockrem, 2007) as hormones may influence multiple correlated traits (Ketterson and Nolan, 1999). These proximate mechanisms are important to understand as they may enable an organism to better adapt to a fluctuating environment but may also constrain independent trait evolution by selecting linked behavioral traits (McGlothlin and Ketterson, 2008).

In socially monogamous species with biparental care, similarity in behavioral expression may increase reproductive success (Dingemanse et al., 2004; Spoon et al., 2006; Burtka and Grindstaff, 2015) by facilitating coordination of parental care. Hormones may facilitate this coordination of behavior within pairs by mediating reproductive and social behaviors (Adkins-Regan, 2005; Ouyang et al., 2014). Pair members sharing a territory are likely to be exposed to similar physical and social environments that may cause hormone levels of individuals to resemble one another over time. In great tits (*Parus major*), pairs with increased similarity in baseline CORT levels across the breeding season fledged more young and were more likely to remain paired across years than pairs that did not increase in hormonal similarity (Ouyang et al.,

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2014). In a population of eastern bluebirds (*Sialia sialis*), male feeding rate was positively correlated with female CORT levels within pairs (Davis and Guinan, 2014).

Thus, in socially monogamous species there are at least three potential ways baseline hormone levels may relate to reproductive success (Fig. 1). The first is outlined in the CORT-fitness hypothesis: individuals with higher CORT levels are expected to be in lower condition and fledge fewer young (Bonier et al., 2009b). Second, the hormonal similarity hypothesis predicts that pair members with more similar baseline hormone levels will fledge the most young, regardless of the absolute level of individual hormone levels (Ouyang et al., 2014). Finally, both absolute hormone levels and similarity within the pair may be important such that pairs in which both individuals have lower baseline hormone levels fledge the most young (Fig. 1).

To investigate the complex interaction between animal personality and circulating hormone levels, we tested a wild population of Eastern bluebirds for nest defense behavior against an invasive nest-site competitor, the house sparrow (*Passer domesticus*) and quantified parental feeding rates. In the study population, nest defense behavior is an established component of personality with females demonstrating strong repeatability and males having moderately repeatable behavior (Burtka and Grindstaff, 2013). Nest visit rates are also significantly repeatable in both males and females (Burtka and Grindstaff, 2015). Furthermore, similar expression of aggressive nest defense behavior between pair members is associated with increased nesting success in this population (Burtka and Grindstaff, 2015). Thus, in this study, we asked: (1) if baseline levels of CORT and androgens are related to the expression of nest defense behavior or parental visit rates, (2) if hormone levels of one pair member are related to the behavior of the mate (Davis and Guinan, 2014), (3) if coordination in nest defense behavior and parental visit rates are facilitated by coordination of hormone levels between pair members (Fig. 2), and (4) if baseline hormone levels are related to nesting success at either the individual (e.g., CORT-fitness hypothesis) or pair (e.g., hormonal similarity hypothesis) level (Fig. 1). We predicted that Eastern bluebirds engaging in a more aggressive nest defense strategy would have higher levels of baseline androgens because androgen levels are often positively associated with territory defense behavior (Wingfield et al., 1990) and we predicted that individuals with higher nest visit rates would have reduced baseline CORT levels because baseline CORT has been shown to influence parental investment in some species (e.g., Horton and Holberton, 2009,

Female corticosterone concentration	CORT-fitness hypothesis: Female: low RS Male: high RS Hormone similarity hypothesis: Pair: low RS	CORT-fitness hypothesis: Female: low RS Male: low RS Hormone similarity hypothesis: Pair: high RS Hormone similarity + CORT levels: Pair: low RS
	CORT-fitness hypothesis: Female: high RS Male: high RS Hormone similarity hypothesis: Pair: high RS Hormone similarity + CORT levels: Pair: high RS	CORT-fitness hypothesis: Female: high RS Male: low RS Hormone similarity hypothesis: Pair: low RS
Male corticosterone concentration		

Fig. 1. Potential relationships between baseline corticosterone levels in male and female bluebirds and reproductive success as predicted by the CORT-fitness hypothesis, hormonal similarity hypothesis, and a combination of the CORT-fitness and hormonal similarity hypotheses. RS: reproductive success, CORT: corticosterone.

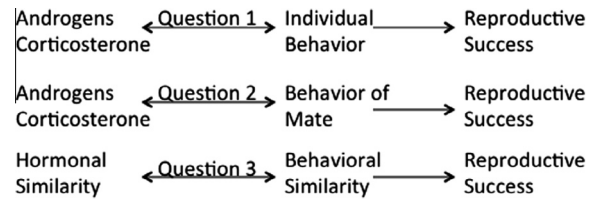


Fig. 2. Schematic to illustrate how baseline hormone levels of individuals and differences in hormone levels within pairs may be related to behavior and reproductive success in relation to the research questions posed in the current study.

2010). We anticipated that pair members would have similar CORT levels (Ouyang et al., 2014). We also predicted that elevated circulating androgens and CORT would negatively influence nesting success at the pair level. Pairs with elevated androgen levels were expected to have reduced nesting success because of a reduction in visit rates (Ketterson et al., 1992). In this population, we have not detected a relationship between nest defense intensity and nest success at the individual level (Burtka and Grindstaff, 2015).

2. Methods

2.1. Model organism and interspecific competitor

Eastern bluebirds are socially monogamous passerines that readily nest in constructed nest boxes and typically maintain the same mate throughout the breeding season (Gowaty and Plissner, 2015). Females lay one egg per day and may have up to six eggs in a clutch (Gowaty and Plissner, 2015). Both parents participate in rearing nestlings and in nest defense behavior (Gowaty and Plissner, 2015). Eastern bluebirds in the study population have two to four broods per season and overwinter in the area or arrive at the study site in late February. Breeding begins as early as late March.

House sparrows represent a threat to Eastern bluebird adult and nestling survival. House sparrows typically colonize near or within human-made structures (Lowther and Cink, 1992) and Eastern bluebirds prefer open habitats (Gowaty and Plissner, 2015). However, both species readily nest in and compete for access to constructed nest boxes (Pogue and Schnell, 1994). House sparrows can displace bluebirds from an established nesting site (Estabrook, 1907; Zeleny, 1976; Burtka, pers. obs.) and will destroy eggs and kill both adults and nestlings for access to nest-box space (Gowaty, 1984; Burtka, pers. obs.).

2.2. Study site and nest monitoring

This study was conducted on seven Eastern bluebird nest box trails located in and around Stillwater, Oklahoma (36° 06' 56.57" N 97° 03' 35.15" W) between March and September in 2009 and 2010. Nest boxes ($N = 144$) were mounted on metal t-posts or wooden fence posts bordering private or public land. Boxes were monitored twice weekly for the appearance of a first egg. Boxes were then checked daily 10 days after the ultimate egg was laid in order to determine hatch day (day 0). Finally, nests were monitored daily after nestling day 14 to quantify the number of young surviving to fledging.

2.3. Nest defense behavior

Nest defense behavior for both parents was quantified using simulated territorial intrusions conducted between nestling days 7–9 ($N = 164$ total trials). A male house sparrow was captured from

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