



## Phenotypic plasticity in hormonal and behavioural responses to changes in resource conditions in a migratory songbird



Sara A. Kaiser <sup>a, b, \*</sup>, T. Scott Sillett <sup>c</sup>, Michael S. Webster <sup>a, b</sup>

<sup>a</sup> Department of Neurobiology & Behavior, Cornell University, Ithaca, NY, U.S.A.

<sup>b</sup> Macaulay Library, Cornell Lab of Ornithology, Ithaca, NY, U.S.A.

<sup>c</sup> Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, D.C., U.S.A.

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An emerging question in animal behaviour is whether and how behavioural plasticity will enable organisms to adjust to human-induced, rapid environmental changes that affect breeding conditions. Adaptive behavioural plasticity in response to changing resource conditions will depend on the sensitivity of the neuroendocrine system to food stimuli and on constraints in the mechanisms mediating the expression of reproductive behaviours. We tested the hypotheses that food availability mediates plasticity in androgen and corticosterone (CORT) responses, and that circulating concentrations of these hormones in turn mediate investment into competing mating and parental behaviours in a migratory songbird. We provided supplemental food to black-throated blue warblers, *Setophaga caerulescens*, breeding in habitats with natural low and high food abundance. The effects of supplemental feeding were most pronounced in food-poor habitat. During their social mates' fertile stage, fed males sang less near their nest sites, had lower plasma androgen and CORT levels, and had higher residual mass than control males. Fed males benefited indirectly from their mates' access to supplemental food because fed females provided more parental effort than control females. Fed males did not increase their own parental effort. Our results suggest that fed males increased mate-guarding effort over extrapair mate attraction while their social mates were fertile and invested additional resources into territorial defence or self-maintenance during the parental stage. These findings reveal plastic patterns of covariation among endocrine parameters and mating behaviours, but not parental behaviours, in response to food supplementation. These responses enabled individuals to adjust their reproductive effort rapidly to changes in resource conditions. Our findings suggest that adaptive reproductive investment in response to environmental change is unlikely to be constrained by the hormonal mechanisms underlying the mediation of competing mating and parental behaviours.

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A major question in animal behaviour is whether and how organisms will respond to human-induced, rapid environmental change (Sih, Ferrari, & Harris, 2011; Tuomainen & Candolin, 2011; Wingfield, 2003). Behavioural plasticity is one potential mechanism that can buffer individuals within a population against environmental change and facilitate adaptive evolution (Duckworth, 2009; Ghalambor, McKay, Carroll, & Reznick, 2007; Snell-Rood, 2013). Such plasticity depends on both the sensitivity to environmental stimuli and the physiological mechanisms that animals use to regulate seasonal reproduction (Dawson, 2008; Lessells, 2008). A strong candidate proximate mechanism underlying adaptive behavioural plasticity is the neuroendocrine system, and its

downstream mechanisms (i.e. hypothalamic–pituitary–gonadal and hypothalamic–pituitary–adrenal axes) (Wingfield, 2008). Steroid hormone levels and the responsiveness of target tissues are seasonally dynamic and mediate suites of reproductive behaviours that can enhance fitness (Ketterson, Nolan, Wolf, & Ziegenfus, 1992; McGlothlin, Jawor, & Ketterson, 2007; Ricklefs & Wikelski, 2002; Sinervo & Svensson, 1998). A critical gap in our knowledge, however, is how environmental stimuli are perceived and then translated by the neuroendocrine system to mediate phenotypically plastic expression of reproductive behaviours (Wingfield et al., 2011; Wingfield, Visser, & Williams, 2008). Understanding these links is especially timely given that rapid environmental change has exposed animals to modifications in habitat quality and environmental stimuli such as food availability (Both et al., 2010; Visser, Holleman, & Gienapp, 2006). These changes in breeding condition can influence reproductive decisions and reproductive success

\* Correspondence: S. A. Kaiser, Cornell Lab of Ornithology, 159 Sapsucker Woods Rd, Ithaca, NY 14850, U.S.A.

E-mail address: [sak275@cornell.edu](mailto:sak275@cornell.edu) (S. A. Kaiser).

(Both, Bouwhuis, Lessells, & Visser, 2006; Visser, van Noordwijk, Tinbergen, & Lessells, 1998). Sensitivity of the neuroendocrine system to environmental stimuli, as well as plasticity and constraints in the signalling mechanism, will determine the extent to which animals will be able to respond and the rate at which they will do so (Hau, 2007; Ketterson, Atwell, & McGlothlin, 2009; Lessells, 2008). A mechanistic understanding of behavioural responses to changing environmental stimuli is therefore necessary to determine the potential evolutionary constraints on these responses and whether adaptive plasticity in behaviour is sufficient to compensate for rapid environmental change (Adkins-Regan, 2008; Wingfield, 2008, 2013; Wingfield et al., 2011).

The multiple effects of steroid hormones on behavioural traits has led to the question of whether this signalling mechanism constrains or permits adaptive physiological and behavioural plasticity (Adkins-Regan, 2008; Hau, 2007; Ketterson et al., 2009; Lessells, 2008; McGlothlin & Ketterson, 2008; Sinervo & Svensson, 1998). When suites of traits depend on a shared mechanism, adaptive responses may be constrained because each trait is not controlled independently and their expression may show limited plasticity (Hau, 2007; Ketterson et al., 2009). When suites of traits are independently regulated, these traits may have a greater potential to adapt rapidly to changing environmental conditions and exhibit greater plasticity (Adkins-Regan, 2008; Ketterson et al., 2009).

Studies of birds have been especially valuable in advancing our understanding of complex relationships among hormones, reproductive behaviours and changing environmental stimuli (Adkins-Regan, 2005; Ball & Ketterson, 2008; Hau, 2007; Wingfield et al., 2011). Research focused on the effects of social stimuli on short-term hormonal responses has revealed that individuals can respond rapidly and flexibly to environmental challenges (Kempnaers, Peters, & Foerster, 2008). Less empirical work has investigated neuroendocrine responses to nonsocial environmental stimuli, such as food availability (Goymann, Landys, & Wingfield, 2007). Yet, one of the major impacts of climate change on breeding birds has been the reduced availability of food (e.g. insect prey) with shifting spring phenology (Visser et al., 2006). Although food availability is known to influence the hormones regulating the onset of reproduction in birds (reviewed in: Ball & Ketterson, 2008; Schoech, Rensel, Bridge, Boughton, & Wilcoxon, 2009), we know less about the interaction between food availability and the steroid hormones that may mediate plasticity of mating and parental behaviours (Schultner, Kitaysky, Gabrielsen, Hatch, & Bech, 2013).

Steroid hormones appear to be important mediators of reproductive trade-offs between mating effort (e.g. pursuit of extrapair mating), parental effort and self-maintenance behaviours in birds (Hau, 2007; Ketterson & Nolan, 1999; Ketterson, Nolan, Cawthorn, Parker, & Ziegenfus, 1996; Magrath & Komdeur, 2003; Wingfield, Hegner, Dufty, & Ball, 1990). Testosterone (T) and corticosterone (CORT) regulate key behavioural and physiological processes and can have interactive effects on reproductive performance (Hau, 2007; Hau, Ricklefs, Wikelski, Lee, & Brawn, 2010). Androgens, such as T, generally support behaviours that increase male fecundity and, when elevated for long durations, can reduce survival (Reed et al., 2006). Hormone manipulations have demonstrated causal links between T and both sexual and aggressive behaviours (reviewed in Fusani, 2008). The suppression of male parental behaviours by T, however, has received mixed support (e.g. DeVries & Jawor, 2013; Lynn, 2008). Correlative evidence also suggests a potential role for glucocorticoids, such as CORT, in regulating parental effort in response to resource conditions (Jenni-Eiermann, Glaus, Gruebler, Schwabl, & Jenni, 2008). Baseline CORT concentrations, which regulate metabolic functions, can be indicative of energetic reserves, and thus may balance reproductive effort with self-

maintenance (i.e. the likelihood of survival) given local resource conditions (Schoech, Bowman, Bridge, & Boughton, 2007). Elevated CORT affects self-maintenance behaviours that promote adult survival (reviewed in Wingfield & Ramenofsky, 1999), at a cost to parental care of nestlings (Almasi, Roulin, Jenni-Eiermann, & Jenni, 2008; Silverin, 1998). Evidence is also accumulating that higher baseline CORT levels during the nestling stage are adaptive when positive feedback results in increased parental provisioning effort (reviewed in Bonier, Martin, Moore, & Wingfield, 2009). Alternatively, elevated baseline CORT levels may prepare individuals for investment in energetically expensive parental activities (Love, Madliger, Bourgeon, Semeniuk, & Williams, 2014). Selection on hormone-mediated trade-offs between mating and parental effort in response to food availability should occur at the level of the individual (Eikenaar, Whitham, Komdeur, van der Velde, & Moore, 2011). Therefore, it is also important to examine individual variation in plasma hormone concentrations and their relationships to mating and parental effort.

Here, we experimentally tested the hypotheses that food availability mediates plasticity in androgen and corticosterone responses, and that circulating concentrations of these hormones in turn mediate investment into competing mating and parental behaviours. To do so, we provided supplemental food to a free-living, Nearctic-Neotropical migratory songbird, the black-throated blue warbler, *Setophaga caerulescens*, breeding in habitats with low and high food abundance at the Hubbard Brook Experimental Forest (HBEF), New Hampshire, U.S.A. We predicted that (1) relative to controls, fed males would invest additional resources into mating effort and reduce parental effort and (2) increased mating effort would be associated with higher plasma androgen and lower baseline CORT levels. We also expected that male reproductive effort and hormone levels would be positively associated with energetic reserves during their social mate's fertile stage (i.e. egg laying) and during periods of biparental care (i.e. provisioning nestlings). In the context of habitat quality, we predicted that supplemental feeding would significantly mediate hormonal and concomitant behavioural responses in low-quality habitat, but have a reduced or negligible effect in high-quality habitat. Finally, our hypothesis predicts that hormonal responses should covary with an individual's behavioural responses and energetic reserves. Accordingly, we examined whether circulating steroid hormones mediate male reproductive trade-offs between mating and parental effort for all sampled males (fed and control combined). We predicted that androgen concentrations would be (1) higher in males during their social mate's fertile stage than during the parental stage, (2) positively correlated with mating effort and (3) negatively correlated with parental effort. We predicted that elevated baseline CORT concentrations in males would be associated with lower energetic reserves, but higher parental effort.

## METHODS

### Study Population

We studied a marked population of black-throated blue warblers breeding in mature northern hardwood forest in the 3160 ha HBEF, Woodstock, New Hampshire, U.S.A. (43°56'N, 71°45'W). We collected data over a 4-year period (May–August, 2009–2012) on three, gridded study plots established at low (250–350 m; 85 ha), mid (450–600 m; 65 ha) and high (750–850 m; 35 ha) elevations (Rodenhouse, Sillett, Doran, & Holmes, 2003). The abundance of Lepidoptera larvae, the primary food source and important predictor of territory quality for black-throated blue warblers (Holmes, Rodenhouse, & Sillett, 2005), is positively correlated with elevation at the HBEF (Cline, Strong, Sillett, Rodenhouse, & Holmes, 2013;

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