



Novelty induces behavioural and glucocorticoid responses in a songbird artificially selected for divergent personalities



Alexander T. Baugh^{a,*}, Kailyn R. Witonsky^a, Sarah C. Davidson^{b,c}, Laura Hyder^a, Michaela Hau^{d,e}, Kees van Oers^f

^a Department of Biology, Swarthmore College, Swarthmore, PA, USA

^b Department of Migration and Immuno-ecology, Max Planck Institute for Ornithology, Radolfzell, Germany

^c Department of Civil, Environmental and Geodetic Engineering, The Ohio State University, Columbus, OH, USA

^d Evolutionary Physiology Group, Max Planck Institute for Ornithology, Seewiesen, Germany

^e Department of Biology, University of Konstanz, Konstanz, Germany

^f Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

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Stress physiology is thought to contribute to individual differences in behaviour. In part this reflects the fact that canonical personality measures consist of responses to challenges, including novel objects and environments. Exposure to novelty is typically assumed to induce a moderate increase in glucocorticoids (CORT), although this has rarely been tested. We tested this assumption using great tits, *Parus major*, selected for divergent personalities (bold-fast and shy-slow explorers), predicting that the shy birds would exhibit higher CORT following exposure to a novel object. We also scored behavioural responses to the novel object, predicting that bold birds would more frequently approach the novel object and exhibit more abnormal repetitive behaviours. We found that the presence of a novel object did induce a moderate CORT response, but selection lines did not differ in the magnitude of this response. Furthermore, although both selection lines showed a robust CORT elevation to a subsequent restraint stressor, the CORT response was stronger in bold birds and this effect was specific to novel object exposure. Shy birds showed a strong positive phenotypic correlation between CORT concentrations following the novel object exposure and the subsequent restraint stress. Behaviourally, the selection lines differed in their response during novel object exposure: as predicted, bold birds more frequently approached the novel object and shy birds more strongly decreased overall locomotion during the novel object trial, but birds from both selection lines showed significant and similar frequencies of abnormal repetitive behaviours during novel object exposure. Our findings support the hypothesis that personality emerges as a result of correlated selection on behaviour and underlying endocrine mechanisms and suggest that the relationship between endocrine stress physiology and personality is context dependent.

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Wild animals regularly cope with challenges in their natural environments and benefit from behavioural flexibility. Individuals are not infinitely flexible, however, and constraints on plasticity can generate consistent behavioural differences (i.e. personality), which have been described in a variety of taxa (Gosling, 2001). Personality is often measured using assays of exploratory behaviour (e.g. spatial and object neophobia) with responses that can be described along a shy–bold continuum (Carere, Drent, Privitera,

Koolhaas, & Groothuis, 2005). These personality traits show an established set of correlated physiological and behavioural characteristics that are stable across time and contexts in both free-living (reviewed in Carere, Caramaschi, & Fawcett, 2010) and captive populations (Groothuis & Carere, 2005). Past studies have shown that more shy personalities ('slow explorers') are more sensitive to environmental changes and often perform better in dynamic environments, whereas bolder personalities ('fast explorers') may be better adapted to stable environments (Dingemans, Both, Drent, & Tinbergen, 2004; Drent & Marchetti, 1999; Korte, Koolhaas, Wingfield, & McEwen, 2005; Marchetti & Drent, 2000; Verbeek, Drent, & Wiepkema, 1994). These findings suggest that personalities might also differ in the frequency of

* Correspondence: Alexander T. Baugh, Swarthmore College, 500 College Avenue, Martin Biological Laboratory, Swarthmore, PA, 19081, USA.

E-mail address: abaugh1@swarthmore.edu (A. T. Baugh).

routine-forming behaviours (i.e. stereotypies; abnormal repetitive behaviours), which are often observed in stable captive populations (Garner, Mason, & Smith, 2003; Keiper, 1969; Mason, 1991), with bolder individuals predicted to exhibit a higher frequency of abnormal repetitive behaviour.

A variety of neural and hormonal adaptations underlie behavioural responses to environmental challenges. A growing body of research on the proximate correlates of animal personality has demonstrated that endocrine phenotypes can be individually consistent and associated with personality (reviewed in Hau, Casagrande, Ouyang, & Baugh, 2016; Koolhaas, de Boer, Buwalda, & van Reenen, 2007; but see Bell, Hankison, & Laskowski, 2009; Pavitt, Walling, Möstl, Pemberton, & Kruuk, 2015). Because of their systemic nature and pleiotropic effects, steroid hormones have been proposed as key mechanisms that organize behavioural traits into correlated suites (Carere et al., 2010; Ketterson, Atwell, & McGlothlin, 2009; Koolhaas et al., 1999). However, the extent to which hormonal mechanisms evolve alongside behavioural mechanisms and are responsible for individual variation in behaviour remains under debate (Carere et al., 2010; Mutzel, Kempenaers, Laucht, Dingemans, & Dale, 2011).

Several of the behaviours that typify personality variation (e.g. shyness in nonhuman animals, neuroticism in humans; Gosling, 2001) are thought to be related, either directly or indirectly, to differences in how animals cope hormonally with stress (Koolhaas et al., 1999). Indeed, the proactive–reactive coping model described in Koolhaas et al. (1999) suggests individual covariation in boldness, environmental sensitivity and endocrine stress responsiveness. Therefore, the hypothalamic–pituitary–adrenal (HPA) axis, which produces glucocorticoids as its main end product, is often studied in this context (Hau et al., 2016). The principal glucocorticoid in birds is corticosterone (CORT), which serves primarily metabolic functions at baseline levels but becomes elevated shortly after the perception of a stressor, and continues to increase until a process of negative feedback permits baseline levels to be re-achieved (i.e. the glucocorticoid stress response; Romero, 2004). This endocrine stress response is conserved across vertebrates (Ellis, Jackson, & Boyce, 2006; Wingfield, 2003) and functions as a critical adaptation that enables organisms to regain homeostasis following acute challenges. Given the speed with which the stress response can be initiated (<3 min; Baugh, van Oers, Naguib, & Hau, 2013; Baugh, Davidson, Hau, & van Oers, 2017; Heading, Nisbet, & Ketterson, 2006; Romero & Reed, 2005; Small et al., 2017), it is also conceivable that the CORT response plays a direct role (through activational effects) in modulating behavioural responses to stressors in addition to the more rapid response mediated by the sympathetic nervous system (reviewed in Axelrod & Reisine, 1984).

Indeed, several lines of evidence suggest that shyer individuals have, on average, a more potentiated HPA axis, typically including one or more of the following characteristics: a faster onset of the glucocorticoid response, higher peak levels and weaker negative feedback (Baugh et al., 2012, 2013, 2017; Baugh, Davidson et al., 2017; Carere & van Oers, 2004; Koolhaas et al., 1999; Korte, Beuving, Ruesink, & Blokhuis, 1997; Martins, Roberts, Giblin, Huxham, & Evans, 2007; Satterlee & Johnson, 1988; van Oers, Buchanan, Thomas, & Drent, 2011), including in humans (reviewed in Ellis et al., 2006). Such studies have also been carried out using individuals derived from artificial selection experiments in both mammals (Harri, Mononen, Ahola, Plyusnina, & Rekilä, 2003) and birds (Cockrem, Candy, Castille, & Satterlee, 2010; Jones, Satterlee, & Ryder, 1992), thus providing an opportunity to identify genetically correlated traits.

Most of our understanding of interindividual variation in stress physiology and its relationship to personality stems from studies

applying a standardized handling-restraint stressor (reviewed in Cockrem, 2007). This method is easy to apply uniformly across studies and species, universally induces a strong and rapid CORT response, and likely reflects the HPA response to one type of potent stressor: interaction with predators (Canoine, Hayden, Rowe, & Goymann, 2002; Cockrem & Silverin, 2002a; Jones, Smith, Bebus, & Schoech, 2016; Wingfield & Ramenofsky, 1999). However, restraint methods are probably not representative of other less potent real-world stressors that often provide opportunities for behavioural coping, thus potentially revealing ethologically relevant individual differences. Interestingly, conventional exploratory assays, which often involve exposure to novel environments or novel objects, are typically assumed to induce a mild stress response, but this is rarely tested in a rigorous manner (but see Cavigelli & McClintock, 2003). These assays more closely resemble natural scenarios in which individuals experience novel physical or social environments, and therefore provide an opportunity to test this broader hypothesis about the link between personality and glucocorticoid phenotypes.

Here we evaluate the assumption that behavioural responses to novelty are directly related to stress physiology in a species that has served as a model for personality studies, the great tit, *Parus major*. In great tits, novel environment exploration and boldness towards novel objects are phenotypically correlated and individually consistent over time, and artificial selection experiments have demonstrated a heritable component (Drent, van Oers, & van Noordwijk, 2003). Furthermore, this heritable combination of behaviours ('fast-bold'/'slow-shy') correlates phenotypically and genetically with other behavioural tendencies, such as risk taking (van Oers, Drent, de Goede, & van Noordwijk, 2004), aggression and dominance (Verbeek, Boon, & Drent, 1996). Earlier work has also demonstrated that great tits selected for a combination of slow exploration and shyness ('slow explorers') show elevated CORT concentrations compared to 'fast explorers' in response to social challenges (faecal CORT: Carere, Groothuis, Möstl, Daan, & Koolhaas, 2003) and handling-restraint stress (plasma CORT: Baugh et al., 2012). These results imply a genetic correlation between behavioural and hormonal traits.

We tested four specific predictions: (1) exposure to a novel object should induce a mild CORT increase; (2) this novelty-induced CORT response should be higher in slow explorers; (3) the elevation in CORT should be further amplified following a subsequent restraint stressor, again with slow explorers experiencing a higher secondary stress response due to a predicted positive correlation between initial and subsequent stress responses; and (4) slow explorers should less frequently approach a novel object and show a lower frequency of routine-forming (route-tracing) behaviour.

METHODS

Subjects, Novel Object Exposure and Hormone Sampling

At the Netherlands Institute of Ecology (NIOO-KNAW, Wageningen, NL), we tested birds from the fourth generation of lines bidirectionally selected for fast exploration and boldness (fast explorers) and slow exploration and shyness (slow explorers). For details on the parental population and the artificial selection process, including the behavioural screening, see Drent et al. (2003), van Oers, Drent et al. (2004), van Oers, de Jong, Drent, and van Noordwijk (2004) and Verbeek et al. (1994).

Three weeks prior to the start of our experiments, adult birds were transferred from a group-housed aviary to singly housed cages in three rooms of an indoor–outdoor aviary facility, where

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