ARTICLE IN PRESS

General and Comparative Endocrinology xxx (2015) xxx-xxx

Contents lists available at ScienceDirect



General and Comparative Endocrinology



journal homepage: www.elsevier.com/locate/ygcen

An experimental examination of interindividual variation in feather corticosterone content in the house sparrow, *Passer domesticus* in southeast Australia

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ARTICLE INFO

Article history: Received 20 April 2015 Revised 8 December 2015 Accepted 13 December 2015 Available online xxxx

Keywords: Avian Endocrine Stress response Behaviour

ABSTRACT

Non-invasive techniques for measuring glucocorticoids (GCs) have become more prevalent, due to the advantage of eliminating the effects of animal disturbance on GC levels and their potential to provide an integrated, historic estimate of circulating GC levels. In the case of birds, corticosterone (CORT) is deposited in feathers, and may reflect a bird's GC status over the period of feather synthesis. This technique thus permits a retrospective view of the average circulating GC levels during the moult period. While it is generally assumed that differences in feather CORT content (CORT_f) between individuals reflects their different stress histories during either natural or induced moult, it is not clear how much of this variation is due to extrinsic versus intrinsic factors. We examined this question by determining CORT_f in free-living house sparrows (Passer domesticus) from two populations, one urban and the other rural, that were plucked before and after exposure to different plasma CORT levels while held captive. We experimentally manipulated plasma CORT by implanting birds with either a corticosterone-filled, metyrapone-filled, or empty ('sham') silastic capsule as replacement feathers first emerged. The pattern of post-treatment CORT_f was consistent with our expectations, based on plasma CORT levels of an experimentally implanted reference group. However, there was no statistically significant difference in CORT_f between these treatment groups unless sex, population origin, and CORT_f of original feathers for each individual were included in a model. Thus, birds with higher CORT_f in feathers removed for this experiment tended to have higher CORT_f in post-treatment replacement feathers, irrespective of treatment. In addition, we found that feather fault bar scores were significantly higher in CORT-treated birds than in the other two treatment groups, but did not vary directly with CORT_f level. Our study therefore broadly confirms the use of feathers as a non-invasive tool to estimate plasma CORT during moult in birds, but importantly demonstrates the potential for intrinsic differences in stress characteristics between populations and individuals to obscure the effects extrinsic stressors might have on CORT_f.

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1. Introduction

In dealing with a changing environment, an animal's stress response is a critical element for maximising its survival. A stress response consists of a suite of physiological and behavioural coping mechanisms to maintain homeostasis (Selye, 1973) and may include prioritising allocation of resources towards selfmaintenance functions (Jenni et al., 2000). When a vertebrate responds to a stressor, its hypothalamic–pituitary–adrenal (HPA) axis is activated and releases glucocorticoids (GC) from the adrenal

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http://dx.doi.org/10.1016/j.ygcen.2015.12.010 0016-6480/© 2015 Elsevier Inc. All rights reserved. cortical tissues for minutes up to hours (Sapolsky et al., 2000). This response redirects an animal from its normal activities to a 'lifesaving' or 'emergency' state (Wingfield et al., 1998), which facilitates their ability to overcome stress and restore homeostasis (Bortolotti et al., 2008; Charmandari et al., 2005; Wingfield and Romero, 2001).

Chronically elevated levels of glucocorticoid hormones (GC), e.g., cortisol and corticosterone may have detrimental health consequences. These include declines in immune function, body condition, growth, reproduction and survival (Blas et al., 2007; Boonstra et al., 1998; Charmandari et al., 2005; Sapolsky et al., 2000). Increased glucocorticoid levels are also associated with greater susceptibility to parasites, and may activate latent infections due to their suppressing effects on the immune system (Gylfe et al., 2000; Mougeot et al., 2010).

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The process of capturing and handling an animal when obtaining blood samples to evaluate GCs levels provokes a stress response, which starts within minutes of an animal first being disturbed. Consequently, obtaining baseline plasma GC requires blood to be collected within 2-5 min of initial disturbance (Romero and Reed, 2005). An animal's GC levels continues to rise following capture, and the extent of this rise over a known period after capture gives insight into an individual's stress sensitivity. These two measures provide valuable insight into processes underlying seasonal and life-stage related changes in vertebrate stress physiology (Romero, 2002). More recently, researchers seeking insight into an individual's integrated GC levels over longer periods have explored the use of non-invasive methods to examine the relationship between variation in individual GC levels and particular ecological conditions (Fairhurst et al., 2012; Harms et al., 2010; Koren et al., 2012; Legagneux et al., 2013; Will et al., 2014). These methods assess the content of GC and their metabolites in an individual's hair, feathers, or the GC metabolite content of their excreta (Goymann, 2005; Sheriff et al., 2011). Feathers, hair and excreta are thought to accumulate GC (and/or their metabolites) in accordance with the circulating CORT levels during their production. Because of this, examining GC content noninvasively has the potential to provide a retrospective view of an individual's integrated GC levels during the period of feather or fur replacement. Although there is great potential for using these non-invasive techniques to assess stress levels, validation in relation to plasma GC levels is essential (Buchanan and Goldsmith, 2004).

During avian moult, corticosterone (CORT) and its metabolites are incorporated into developing feathers via diffusion from the blood quill (Jenni-Eiermann et al., 2015) and are believed to reflect plasma levels during the period of feather synthesis (Bortolotti et al., 2008, 2009; Jenni-Eiermann et al., 2015). If this assumption is valid, CORT levels in feathers will represent an integrated average of plasma CORT levels over the period of that feather's maturation. Despite good evidence that CORT can be measured in feathers, the reliability of this method to reflect stress status during moult and, further, the ability to discern the chronology of plasma CORT levels during moult have seldom been validated. Following the first study examining CORT_f in relation to plasma CORT (Bortolotti et al., 2008), validation studies confirmed that experimentally increased plasma CORT does result in increased CORT_f in the European starling Sturnus vulgaris (Lattin et al., 2011), tree swallows Tachycineta bicolor (Fairhurst et al., 2013), as well as in feral pigeons Columba livia domestica (Jenni-Eiermann et al., 2015). In validating this method several notes of caution have been raised. Firstly, it has been found that antibodies with high specificity to CORT failed to detect CORT in feathers from starlings (Lattin et al., 2011), but were successful in detecting CORT_f in pigeons (Jenni-Eiermann et al., 2015). Determinations of CORT_f have also been found to vary according to the mass of sample being analysed. Using pooled samples of starling feathers (Lattin et al., 2011) and ruddy turnstones (Aharon-Rotman et al., 2015), these studies independently demonstrated that decreasing feather sample mass below a critical amount leads to overestimation of CORT levels, as well as decreased repeatability. Considering the low correlation repeatedly found between plasma CORT and CORT_f (Fairhurst et al., 2013; Jenni-Eiermann et al., 2015; Lattin et al., 2011), the potential limitations of inferring plasma CORT levels and, in turn, stress status, during moult from CORT_f are important to recognise.

Feather quality is known to reflect the health status of moulting birds and, consequently, feather quality has the potential to serve as a biomarker for stress while moulting. CORT stimulates protein breakdown and, as feathers are mainly keratin proteins, high plasma CORT can have negative effects on feather growth and structure (DesRochers et al., 2009; Jenni-Eiermann et al., 2015; Strochlic and Romero, 2008). Fault bars, which are structural

defects caused by protein reduction during feather growth (Riddle, 1908), appear at higher frequency when birds are malnourished (Murphy and King, 1982) or under greater predation risk (Witter and Lee, 1995). Thus, fault bars should provide an indication of a bird's stress status during moult. There is evidence that feather quality correlates directly with fitness, with birds having a greater number of fault bars suffering lower reproductive success and reduced longevity (Bortolotti et al., 2002). When fault bars do occur, there is suggestion that they are distributed non-randomly among flight feathers, with occurrence least likely in feathers with highest importance for flight performance (Jovani and Blas, 2004). Thus, we expected that the occurrence of fault bars would be higher in tail than in wing feathers because the wing primary and secondary feathers we sampled are more important for generating force during flight than the tail feathers, which are mainly used for stability, balance and turning (Sarasola and Jovani, 2006).

Our objective in this study is to examine for the first time whether individual-level differences in $CORT_f$ persist in the following round of feather replacement in a wild-caught bird and, further, to see if this relation is affected by imposition of different circulating CORT levels. Using experimental manipulations of plasma CORT, we determined $CORT_f$ in both pre- and posttreatment feather samples and the extent of fault bars on feathers synthesized during these treatments.

2. Methods

House sparrows Passer domesticus were first introduced in Melbourne in 1863 and are now well established throughout urban areas of eastern Australia. For our study, we captured sparrows at Torquay (Victoria, Australia 38.3°S, 144.3°E) in summer 2012 and at Werribee, (Victoria, Australia 37.9°S, 144.65°E) in autumn 2013. After capture, sparrows were placed 2 per cage (ca. $40 \times 60 \times 60$ cm) and held in a room with temperature maintained at 25 °C and photoperiod set to 14L:10D. Commercial finch seed mix, grit and water were provided *ad libitum*. After at least 1 week of adjustment to captivity, we removed birds from their cages. anaesthetized them with methoxyflurane before plucking 12 feathers from their wings and tail (five primaries, five secondaries and two rectrices), to be used as a reference for individual CORT_f values. After recovery from anaesthetic, birds remained in their holding cages until feather regrowth was noted (14 and 12 days after plucking in the Torquay and Werribee population, respectively). We then manipulated corticosterone levels by implanting each bird with either a single corticosterone-filled (Sigma-Aldrich, Sydney, New South Wales, Australia; catalogue number 27840), metyrapone-filled (Sigma-Aldrich; catalogue number M2696), or empty silastic capsule (referred to as "sham" in this paper). Because we wanted to examine whether individual differences in stress characteristics persisted under different extents of plasma CORT and to see if differences in CORT_f between treatment groups were similar in magnitude to those of implanted reference birds, we chose to maximise plasma CORT differences between treatment groups by giving one group CORT implants known to be superphysiological (Buttemer et al., 1991) and the other groups treatments intended to result in far lower plasma CORT levels. Thus, the other two groups received either an empty implant (sham treatment) or an implant filled with metvrapone, known to reduce glucocorticoid synthesis by its inhibition of steroid 11βhydroxylase (Drouet et al., 2010). The capsules were prepared from 10 mm lengths of medical-grade silastic tubing (1.47 mm inner diameter; 1.96 mm outer diameter; Dow Corning, Sydney, New South Wales, Australia), which were sealed at each end with silastic glue in metyrapone and control capsules and at one end for those filled with corticosterone. A single capsule per bird was

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