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The effects of chronic psychological and physical stress on feather replacement in European starlings (*Sturnus vulgaris*)

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Abstract

Corticosterone (CORT) is seasonally modulated in many passerines, with plasma CORT concentrations lowest during the prebasic molt, when all feathers are replaced. Recent evidence indicating that CORT implants slow the rate of feather regrowth in molting birds suggests that plasma CORT concentrations are downregulated during molt in order to avoid the inhibition of feather growth caused by the protein catabolic activity of CORT. To further test this hypothesis, we examined whether endogenous CORT release, stimulated by exposure to either psychological stress or physical stress (food restriction), could inhibit feather regrowth rates or decrease feather quality in birds undergoing an induced molt (feather replacement after plucking). European starlings (*Sturnus vulgaris*) were exposed to chronic psychological stress or food restriction for three weeks of the feather regrowth period. Throughout this time, the length of growing primary, secondary, and tail feathers was measured and blood samples were collected to measure baseline and stress-induced CORT concentrations. Upon completion of growth, feather quality was analyzed via measurements of mass, rachis length, feather area, and presence of fault bars. Both psychological and physical stress protocols elevated circulating plasma CORT but significantly less than implants from an earlier study did. Psychological stress had no effect on feather regrowth rates or feather quality. Food restriction had no effect on feather growth rate but caused asynchronous feather replacement. When combined with psychological stress, physical stress also resulted in smaller feather area. Results indicate that CORT implants may not accurately represent chronic stress physiology. Additionally, the purpose for downregulating CORT concentrations during molt appears to be more complicated than simply protecting feather production from CORT's catabolic effects.

Keywords: Birds; Molt; Corticosterone; Stress; Chronic stress; Food restriction; Implant

1. Introduction

The annual replacement of flight and body feathers by passerines in the late summer and early fall, the prebasic molt, is a tightly regulated process that requires significant metabolic investment (Murphy and King, 1992). Though the end result of a successful molt is a complete set of structurally sound feathers, the costs associated with this period of feather loss and subsequent regrowth are impressive. Two important challenges faced by molting birds are (1) obtaining the necessary protein to support such body rebuilding and (2) coping with decreases in flight performance and thermoregulation resulting from a reduced number of feathers while new pins are emerging (Swaddle et al., 1999). In order to both successfully prepare for the approaching migration and winter by replacing worn feathers and to survive the immediate feather replacement period, a delicate metabolic balance must exist. It is likely that unforeseen metabolic demands during the molt, such as those created by physical and psychological stressors, could disrupt this balance and negatively impact both immediate and future survival.

Recent work has begun to examine the effects of such additional demands on molting birds. Romero et al. (2005) demonstrated that high circulating levels of corticosterone (CORT), the principal glucocorticoid released by avian adrenal tissue in response to the activation of the hypothalamic–pituitary–adrenal (HPA) axis by a stressor, can slow the rate of

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feather growth in both naturally molting birds and birds undergoing an induced molt (plucked). CORT was originally implicated in disrupting feather growth due to the observation that the majority of passerines sampled in the field show a distinct downregulation of CORT release, both baseline and stress induced, during the prebasic molt (reviewed by Romero, 2002). This nadir follows the annual peak in CORT release, which occurs during the breeding months. Based on the metabolic actions of CORT, Romero et al. (2005) hypothesized that the low circulating levels seen during molt were directly related to the costs associated with feather growth.

CORT is thought to be a major regulator of the metabolic pathways involved in the cascade of physiological events that comprise the stress response (Sapolsky et al., 2000). In contrast to the nearly instantaneous initiation of the short-lived "fight or flight" response by catecholamines, CORT acts on a longer time scale by slowly increasing and maintaining elevated energy levels for many hours. Inhibition of protein synthesis and stimulation of gluconeogenesis via protein catabolism are two of the mechanisms through which CORT acts to increase energy levels. It is believed the CORT-induced increase in energy levels sustains the period of heightened alertness following a stressor, allowing an animal to recover from a stimulus and better respond to a subsequent stressor (Sapolsky et al., 2000). Additionally, high CORT concentrations can trigger increased activity associated with irruptive migration, are permissive for foraging behavior, suppress reproductive behaviors and reduce metabolism at night (Wingfield and Romero, 2001). Through its permissive, suppressive, and stimulatory actions, CORT serves to maintain or restore homeostasis in wild animals, thereby improving the likelihood of surviving a stressful episode (Sapolsky et al., 2000).

The hypothesis proposed by Romero et al. (2005) suggested that passerines downregulate CORT release during molt in order to avoid the protein catabolic activity of CORT from directly inhibiting the protein deposition necessary to produce feathers. Feathers are composed of 95% protein, particularly the amino acids cysteine and methionine (Murphy and King, 1992), and account for as much as 40% of the dry weight of an individual (Ginn and Mellville, 1983). If CORT interfered with this protein deposition, it could slow the overall pace of molt. Since molting birds experience an increased risk of predation (Swaddle et al., 1999), a slower rate of feather replacement could potentially negatively impact survival. Additionally, because molt duration is extremely time-sensitive, so as to temporally separate this energetically costly life-history stage from breeding and migration, most species complete molt in a narrow time window (Hemborg and Lundberg, 1998; Rubolini et al., 2002). Changes to the species-specific optimal molt duration have been shown to have consequences on feather quality, over-winter survival, and future reproductive success (Dawson et al., 2000; Nilsson and Svensson, 1996).

The finding that implantation of CORT capsules in both naturally molting European starlings (*Sturnus vulgaris)* and starlings undergoing an induced molt resulted in slower rates of feather regrowth compared to birds given sham implants supports the hypothesis that passerines downregulate plasma CORT concentrations during molt in order to minimize any curtailment of feather growth induced by the metabolic actions of CORT (Romero et al., 2005). To further test this hypothesis and to examine the potential effects of unforeseen perturbations on molt, in this study we examined whether endogenous CORT release, stimulated by exposure to chronic psychological stress or physical food-deprivation stress, could also inhibit feather regrowth in European starlings.

2. Methods

2.1. Birds

Thirty-nine wild European starlings (*Sturnus vulgaris*) were captured on February 9, 2005 in Eastern Massachusetts and housed in an indoor flight aviary at Tufts University. The European starling, like other passerines, initiates a prebasic molt in the late summer following breeding and the entire molt takes approximately 100 days to complete (Ginn and Mellville, 1983; Rothery et al., 2001). To prevent the start of a natural molt, subjects were maintained on a short day light cycle (10L:14D) for 7 months, mimicking the winter months. Three weeks prior to the start of experimentation, birds were transferred to individual laboratory cages under the same photoperiod conditions. Birds were maintained at room temperature and were provided Purina Mills® Start and Grow® chick feed and water *ad libitum*. All experiments were performed according to AALAC guidelines and approved by the Tufts University Institutional Animal Care and Use Committee.

2.2. Induced molt

On day 0, all birds were subjected to an induced molt. Starlings were briefly anesthetized with halothane, an inhalable anesthetic, administered in a nose cone and feathers were plucked by hand. Plucking a feather results in the tearing away of the distal portion of the papilla, thereby stimulating the growth of a new feather (Watson, 1963). Primary flight feathers 4, 5, 6, and 7 and secondary flight feathers 1, 2, and 3 were removed (representing approximately 40% of flight feathers),

Fig. 1. Induced molt wing, demonstrating removal of primaries 4–7 and secondaries 1–3. Left and right wings were plucked. Additionally, all 12 retrices were plucked.