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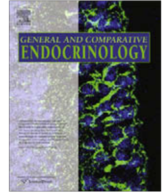

Seasonal changes in concentrations of plasma LH and prolactin associated with the advance in the development of photorefractoriness and molt by high temperature in the starling

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ABSTRACT

In a study on starlings (*Sturnus vulgaris*) kept on a simulated annual cycle in photoperiod, temperature had no effect on the timing or rate of testicular maturation but high temperature resulted in an advance in the timing of testicular regression and molt (Dawson, 2005). This study asks whether the earlier gonadal regression in response to higher temperature represents a central neuroendocrine response to temperature, and secondly, whether prolactin plays a role in the earlier regression. Castrated starlings were kept on a simulated annual cycle of photoperiod at either 8 or 18 °C. Circulating LH and prolactin concentrations were measured and the progress of the post-nuptial molt was recorded as an external indicator of the development of photorefractoriness. Additionally plasma prolactin was measured in samples taken from intact male and female starlings in the 2005 study. In castrated birds, LH concentrations decreased three weeks earlier at 18 °C. These birds also showed the same three week advance in molt as males and females in the earlier study. This demonstrates that the advance in regression caused by higher temperatures probably results from a central neuroendocrine mechanism, i.e., an advance in photorefractoriness, rather than an effect at the level of the gonads. Temperature had a highly significant effect on the changes in prolactin – peak prolactin occurred three weeks earlier at 18 °C. However, there was no clear consistent significant difference in prolactin between the two temperatures in advance of the onset of photorefractoriness, so the advance in photorefractoriness may not be mediated by prolactin. The higher temperature resulted in a significantly earlier decrease in prolactin and this may be causally related to the advance in molt.

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1. Introduction

Birds use the annual cycle in photoperiod to time their breeding attempts so that maximal nestling growth rate coincides with peak food availability (Dawson et al., 2001; Sharp, 2005). Consequently, both gonadal maturation and regression need to be timed appropriately. Although increasing photoperiods during spring lead to gonadal maturation, they also initiate the development of long day photorefractoriness, resulting in gonadal regression, and this essentially dictates the latest date that eggs can be laid. The time of gonadal regression is closely related to the beginning of the post-nuptial molt (Dawson, 2005, 2006).

Climate change may lead to increased spring temperatures and advance the time of the peak abundance of invertebrates on which many birds rely to feed their young. If a bird relies entirely on changes in photoperiod to time breeding, it may be unable to compensate by adjusting the time of breeding and a mismatch will develop between the time of invertebrate abundance and peak nestling growth. This has already been observed in some song birds (Coppack and Pulido, 2004; Visser et al., 2004; Gienapp et al., 2006; Both et al., 2009). In a study on starlings (*Sturnus vulgaris*) kept on a simulated annual cycle in photoperiod at low (5 or 8 °C) or high (20 or 18 °C) temperatures, temperature had no effect on the timing or rate of testicular maturation but high temperature resulted in an advance in the timing of testicular regression and molt (Dawson, 2005). Similar studies on great tits (*Parus major*) (Silverin et al., 2008) and mountain white crowned sparrows (*Zonotrichia leucophrys oriantha*) (Wingfield et al., 2003) have also shown an accelerating effect of high environmental temperature on the development of long day photorefractoriness. If climate warming induces such a response, it could lead to shorter breeding seasons, i.e., fewer breeding attempts in multi-brooded species. In great tits there is evidence that this may be happening (Husby et al., 2009).

The aim of this study is to investigate the endocrinology underlying the accelerating effect of high environmental temperature on the development of photorefractoriness in the starling. Two specific questions are addressed: does the earlier gonadal regres-

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sion in response to higher temperature represent a central neuroendocrine response to temperature, and secondly, does prolactin play a role in the earlier regression?

The annual cycle of gonadal development in the starling appears to involve two distinct neuroendocrine responses to photoperiod (Dawson and Goldsmith, 1997; Dawson et al., 2001, 2002; Watanabe et al., 2007; Stevenson et al., 2009a,b). Gonadal development during early spring is the consequence of an increase in the rate of secretion of GnRH, driven by increasing photoperiod. However, gonadal regression is not the reverse of this process. Regression results from the onset of photorefractoriness. This occurs during longer photoperiods than initially induced maturation and appears to result from a decrease in GnRH synthesis rather than secretion. Recovery of photosensitivity (resumption of GnRH synthesis) occurs during short photoperiods (Dawson and Goldsmith, 1997) in the autumn. In castrated starlings, circulating LH concentrations reflect GnRH synthesis; they are high in photosensitive birds irrespective of photoperiod, decrease dramatically at the onset of photorefractoriness and increase as photosensitivity is regained (Dawson and Goldsmith, 1984). If the earlier gonadal regression seen in birds at higher temperatures reflects a central neuroendocrine response to temperature, then this should be apparent as an earlier decrease in plasma LH in castrated birds at the higher temperature.

Seasonal changes in prolactin secretion are also controlled by photoperiod with the peak values lagging those of plasma LH and coinciding with the development of photorefractoriness (Sharp and Sreekumar, 2001). Prolactin may therefore have a role in gonadal regression in birds (Dawson and Sharp, 1998, 2007; Sharp et al., 1998; Reddy et al., 2007; Small et al., 2008a). This has been demonstrated in the starling in which removal of the suppressive effect of prolactin by active immunization against the avian prolactin releasing hormone, vasoactive active intestinal polypeptide, delays, but does not prevent the development of photorefractoriness (Dawson and Sharp, 1998) Prolactin may exert anti-gonadal effects centrally through an effect on GnRH dynamics (Buntin et al., 1999) and/or directly at the gonads via gonadal prolactin receptors (Leclerc et al., 2007). If higher temperatures cause the vernal photoinduced secretion of prolactin to increase sooner or at a greater rate, then a potential threshold concentration of prolactin could be attained sooner leading to an acceleration in the development of photorefractoriness. There is evidence that high temperatures may enhance photoinduced prolactin secretion in female turkeys (Gahali et al., 2001), and similar observations have been reported in male, but not in female *Z. l. oriantha* (Maney et al., 1999). However, high temperature has no effect on photoinduced prolactin secretion in either sex of *Zonotrichia leucophrys gambelli* or *Zonotrichia leucophrys pugetensis* (Maney et al., 1999), nor in male song sparrows (*Melospiza melodia morphna*) (Perfito et al., 2005).

To investigate whether accelerated gonadal regression in response to higher temperature represents a central neuroendocrine response to temperature, and whether prolactin plays a role in this, castrated starlings were kept on a simulated annual cycle of photoperiod at two different temperatures. Circulating LH and prolactin concentrations were measured and the progress of the post-nuptial molt was recorded as an external indicator of the development of photorefractoriness. Additionally plasma prolactin was measured in samples taken from intact male and female starlings in the 2005 study in which it was first observed that high temperature advances the onset of photorefractoriness (Dawson, 2005).

2. Materials and methods

2.1. Animal husbandry and experimental procedures

Juvenile starlings were trapped from the wild during the autumn and kept in outdoor aviaries (latitude 52°N). During May of the following year, 20 males were anesthetised with isoflurane, an incision was made between the caudal pair of ribs on the left side and the left testis was removed with fine curved forceps. The birds were returned to the outdoor aviary. Three weeks later, the operation was repeated on the right side and the right testis was removed (Home Office Licence PPL 80/1521). In early December the birds were divided into two groups of 10 and moved into two indoor rooms ($3.1 \times 3.1 \times 2.6$ m) in which they were allowed to fly freely. One room was kept at 8 °C and the other at 18 °C with 15 changes of air per hour. These temperatures were chosen to represent, but be well within, the range experienced at 52°N during the annual cycle. Lighting was provided by three cool white fluorescent tubes and one grolux tube (to provide UV) per room resulting in about 1500 lux at perch height. Photoperiod was changed each day to simulate changes at 52°N as calculated from the Astronomical Applications Department of the U.S. Naval Observatory (http://aa.usno.navy.mil/).

In late December a blood sample was collected from each bird. About 300 μl of blood was collected into capillary tubes after pricking the brachial vein and stored in a centrifuge tube for a few hours to allow clotting. Samples were centrifuged and serum aspirated and stored at −20 °C until assayed for LH and prolactin. Further samples were collected at intervals over the next 12 months. Birds began to moult in May and the progress of moult was recorded thereafter at weekly intervals and scored as a proportion of final primary feather mass (Dawson and Newton, 2004).

Serum samples that had been collected from intact male and female starlings held under identical conditions during a previous year (Dawson, 2005) were also assayed for prolactin. Molt in these birds was used as a surrogate for the time of photorefractoriness onset to compare with equivalent data from the castrates.

2.2. Radioimmunoassays

LH was assayed in duplicate 20 μl aliquots of plasma, in a micro-modification (Deviche et al., 2008) of a homologous chicken LH radioimmunoassay (Sharp et al., 1987). The antiserum was IRC2 202 at a 1:5000 dilution. The sensitivity of the assay was 0.05 $\mu g\,l^{-1}$, and 50% displacement was obtained with 2.4 $\mu g\,l^{-1}$. All samples were assayed in one assay with 6.4% and 8.1% variation for a high- and a low-value pool, respectively.

Prolactin was assayed in duplicate 20 μl plasma samples in a recombinant-derived starling prolactin assay (Bentley et al., 1997). The sensitivity of the assay was 4.5 $\mu g\,l^{-1}$, and 50% displacement was obtained with 150 $\mu g\,l^{-1}$. Intra-assay variance was 6.8%.

2.3. Statistical analyses

Two birds in each group died during the year and were removed from analyses. Data were log transformed to normalise data before analysis. Statistical differences in LH and prolactin between the warm and cold groups were assessed with two-way analysis of variance with repeated measure (RM ANOVA) with temperature and date as factors. Bonferroni post-tests were used to determine differences between the treatments at specific dates. Statistical differences within each group with date were assessed using one-way RM ANOVA and differences between specific dates were assessed with Tukey's Multiple Comparison tests. For prolactin data, the dates of peak prolactin values for individual birds were compared between warm and cold groups using two-tailed *t*-tests. Moult start dates were calculated by regressing individual moult scores for the first 4 weeks after the start of moult back to zero, and two-tailed *t*-tests used to assess differences in start dates and molt duration between the groups.

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