

# Circulating prolactin and corticosterone concentrations during the development of migratory condition in the Dark-eyed Junco, *Junco hyemalis*

Rebecca L. Holberton <sup>a,\*</sup>, Timothy Boswell <sup>b,1</sup>, Meredith J. Hunter <sup>a,2</sup>

<sup>a</sup> Department of Biology, P.O. Box 1848, University of Mississippi, University, MS 38677, USA

<sup>b</sup> Division of Genetics and Genomics, Roslin Institute (Edinburgh), Roslin, Midlothian EH25 9PS, UK

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## Abstract

Endogenous plasma prolactin and baseline corticosterone concentrations were measured in Dark-eyed Juncos (*Junco hyemalis*,  $n = 27$ ) photostimulated into migratory condition to look at how these hormones may be linked to the development of migratory condition. In addition to the commonly used assay for corticosterone, a recombinant-derived European starling prolactin assay validated for Dark-eyed juncos was used to measure endogenous prolactin in order to detect small but significant changes in plasma prolactin levels. In response to transfer from short (10.5L:13.5D) to long (18L:6D) days, the birds increased in body mass, fat score, daily food intake, and nocturnal migratory locomotor activity (*Zugunruhe*). On short-days, both hormones were low (corticosterone mean = 2.89 ng/mL  $\pm$  0.48 SE; prolactin mean = 6.43 ng/mL  $\pm$  1.31 SE). But, within 14 days of photostimulation both hormones increased significantly (Day 14: corticosterone mean = 5.71 ng/mL  $\pm$  0.77 SE; prolactin mean = 19.67 ng/mL  $\pm$  2.81 SE), rising further by Day 48 (corticosterone mean = 8.41 ng/mL  $\pm$  0.72; prolactin mean = 112.67 ng/mL  $\pm$  9.18 SE). On Day 48, birds with the most fat (fat score = 3) had significantly higher corticosterone levels than those with less fat (fat score = 2). This pattern, albeit not statistically significant, was similar for prolactin. These results illustrate that, independent of the seasonal peak in prolactin associated with the onset of photorefractoriness, plasma prolactin levels can rise, in concert with corticosterone, as birds come into spring migratory condition, providing some support for earlier hypotheses that these two hormones play an integral role in the development of migratory condition. Whether similar changes in plasma prolactin occur with respect to autumn migration, as does baseline corticosterone, has yet to be determined.

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## 1. Introduction

Migratory birds undergo significant changes in a suite of behavioral and physiological activities as they prepare for migration. For most birds, the development of migratory

disposition entails adjustments in food intake and diet preference. These are coupled with changes in digestive processes that lead to transitions in body composition, such as muscle hypertrophy and fat deposition, as well as shifts in daily activity patterns (Bairlein, 2002; Berthold, 1996; Gaunt et al., 1990; Gwinner, 1996a,b; Long and Stouffer, 2003; Marsh, 1984; McWilliams and Karasov, 2001; for review see Holberton and Dufty, 2005; Ramenofsky and Wingfield, 2007). While these adjustments in migratory behavior and physiology have been recognized for decades, the underlying mechanisms organizing them are still not well understood. Meier and colleagues proposed that seasonal changes in diel secretion patterns of corticosterone and prolactin act as pri-

\* Corresponding author. Present address: Laboratory of Avian Biology, 221 Murray Hall, School of Biology and Ecology, University of Maine, Orono, ME 04469, USA. Fax: +1 207 581 2537.

E-mail address: [rebecca.holberton@maine.edu](mailto:rebecca.holberton@maine.edu) (R.L. Holberton).

<sup>1</sup> Present address: School of Biology, Ridley Building, Newcastle University, Newcastle upon Tyne, NE1 7RU, UK.

<sup>2</sup> Present address: 73067 Meadowlark Dr., Abita Springs, LA 70420-2531, USA.

mary cues regulating changes in food intake, fat deposition, and preferred orientation direction (e.g. Meier and Farner, 1964; Meier et al., 1965). Unfortunately, the model has not been rigorously tested and recent studies have shown that a suite of endocrine signaling pathways are involved with regulating the complex adjustments in migratory behavior and physiology (Ramenofsky et al., 1999; Richardson et al., 1995; Totzke et al., 1998; for review, see Holberton and Dufy, 2005; Ramenofsky and Wingfield, 2007).

Corticosterone's well-established relationship with behavior and physiology associated with energy regulation in birds has caused it to remain a focus of migration research. Laboratory and field studies on a variety of bird species have shown that patterns of corticosterone secretion (baseline corticosterone and the sensitivity of the hypothalamic-hypophyseal-adrenal response to an acute stressor) can change significantly between the non-migratory and migratory period (Holberton, 1999; Holberton et al., 1996, 1999; Long and Holberton, 2004; Piersma et al., 2000; Romero et al., 1997, 1998). During migration, baseline corticosterone levels can become moderately elevated above non-migratory levels when migrants are putting on fat (Holberton, 1999; Holberton et al., 1996, 1999; Landys et al., 2004a,b; Long and Holberton, 2004; Piersma et al., 2000). Laboratory studies have demonstrated that this range of moderately elevated corticosterone supports increased migratory food intake (Landys et al., 2004a,c, 2006) and, if an increase in endogenous baseline corticosterone is prevented, migrants are unable to fatten (Holberton et al., 2007; Holberton, unpubl. data). However, although an elevation in baseline corticosterone may be needed to regulate these activities, the hormone's actions are likely integrated with those of other feeding-related hormones and neuropeptides from the brain, gut, and other organs (Boswell, 2005; Koch et al., 2002; Kuenzel, 1994). In addition to its role in promoting migratory feeding and fattening, corticosterone, directly or indirectly through its influence on energy stores, may serve as a "readiness" or departure cue (Landys-Ciannelli et al., 2002; Lohmus et al., 2003). Corticosterone has even been proposed as a hormone that interacts with spatial orientation mechanisms enabling birds to select the appropriate direction for a bout of migratory flight (Piersma et al., 2000).

In comparison to corticosterone, prolactin's relationship to the development of migratory condition and behavior is much less understood. It has been well-established that, in birds, an annual peak in circulating prolactin plays an integral role in the development of photorefractoriness and the onset of post-nuptial molt (Sharp et al., 1998), but little is known about the role that prolactin plays in regulating migratory feeding and fattening. Several decades of research have shown that central or peripheral administration of mammalian prolactin can increase food intake and/or fat stores in both non-migratory and migratory avian species (Boswell et al., 1995; Buntin and Tesch, 1985; Meier and Farner, 1964). However, a number of studies involving the use of both heterologous (e.g. using antibodies raised

against mammalian prolactin, Campbell et al., 1981; Hall et al., 1987; Schwabl et al., 1988) and homologous (e.g. using antibodies raised against recombinant avian prolactin, Boswell et al., 1995) prolactin radioimmunoassays have failed to demonstrate a close temporal association between circulating prolactin levels and the development of migratory condition. This may have been overlooked in migratory songbirds, owing to the fact that a passerine-specific prolactin assay sensitive enough to detect subtle but biologically significant changes in plasma prolactin had yet to be used to examine how circulating prolactin levels may change during the development of migratory condition.

The availability of a sensitive homologous assay for passerines (Bentley et al., 1997) enabled us to begin investigating the possibility that changes in plasma prolactin levels may promote development of migratory condition, and to begin to examine how circulating prolactin levels may be associated with simultaneous changes in circulating corticosterone levels. In the present study, we measured endogenous plasma corticosterone and prolactin concentrations in a group of Dark-eyed Juncos, *Junco hyemalis*, as the birds were brought into migratory condition. This species is an annual obligate middle-distance migrant in North America and has been used extensively in a wide variety of laboratory and field studies on migration. In the present study, we looked at how these hormones may be linked with changes in food intake, fat deposition, and migratory restlessness, employing the standard corticosterone radioimmunoassay that entails the use of an antibody raised against a ligand well-conserved across most vertebrate species, and the relatively new homologous passerine prolactin radioimmunoassay previously validated for Dark-eyed juncos.

## 2. Methods

Dark-eyed Juncos ( $n = 27$ : 11 males, 13 females, 3 unknown) were captured on their wintering grounds in Yalobusha County, MS in November–December, 1998, and early January, 1999, using mist nets and potter traps. At the University of Mississippi's avian facilities, the birds were initially housed as flocks in large free-flight aviaries and then transferred in January, 1999, to individual commercial birdcages (40 cm × 40 cm × 40 cm). The birds were maintained on a 60:40 mix of white millet and turkey starter, with water also provided *ad libitum* throughout the study. Minerals and vitamins were provided regularly. Each bird was given a unique combination of color bands for individual identification. Initial photoperiod was set to reflect that of local winter conditions (10.5L:13.5D).

The birds were sampled for endogenous corticosterone and prolactin before and after the transition from short- to long-days on 24 March (referred to as Day 0, the first long-day). The increase in daylength was made at the end of the light period so that the timing of the lights on for the birds remained the same with respect to our time of day. Throughout the entire study, blood collection, body measurements and food intake determinations were always made at the same time with respect to lights on regardless of photoperiod schedule, with measurements beginning at least 1 h after lights came on (to allow the birds to break their nocturnal fast) and completed within 2 h. The birds were never disturbed during the nighttime period and all maintenance and data collection were done while the birds were being handled in order to minimize disturbance time.

Blood collection for all of the birds at each sampling period was spread over 3 days so that each bird could be effectively captured and sampled for baseline corticosterone and prolactin well within 5 min of the initial distur-

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