Differential migration and an endocrine response to stress in wintering dark-eyed juncos (*Junco hyemalis*)

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The dark-eyed junco (*Junco hyemalis*) exhibits differential migration in autumn that, in general, results in females overwintering south of males, and young within each sex overwintering north of older birds. Individuals overwintering at higher latitudes face less predictable and more challenging environmental conditions. Rapid increases in circulating levels of the energy-regulating glucocorticosteroid, corticosterone, occur in response to environmental stressors. To establish whether the strength of acute corticosterone secretion was correlated with the probability of encountering poor environmental conditions, we compared the corticosterone stress response (e.g. initial plasma concentrations at the time of capture and 30 min later) in dark-eyed juncos overwintering in Mississippi (MS), USA, near the southern limit of their wintering range, with juncos overwintering in New York (NY), USA, near the northern limit of their wintering range. During two winters, 22 males and one female were sampled in NY; 13 males, 12 females and one bird of undetermined sex were sampled in MS. Not unexpectedly, NY birds carried greater fat reserves that resulted in a significantly higher value of energetic condition (mass corrected for wing cord cubed). There was no difference between the two winters sampled at either site, nor was there an effect of sex on patterns of corticosterone secretion in MS birds. With sexes pooled, MS and NY birds had similar baseline corticosterone levels. However, as predicted, NY birds exhibited significantly higher corticosterone concentrations 30 min after capture. These results support the hypothesis that birds wintering in less predictable, more extreme environments show a higher amplitude corticosterone response, which may enable them to adjust their behaviour and physiology more rapidly in response to environmental stressors such as storms. Adrenocortical sensitivity may be a part of the physiological milieu associated with differential migration in juncos; whether it results from endogenous differences in the migratory programmes of individuals or from acclimatization to local environmental conditions remains to be determined.

Keywords: corticosterone; hypothalamic–pituitary–adrenal (HPA) axis; dark-eyed junco; *Junco hyemalis*; winter stress; differential migration

1. INTRODUCTION

In many species of birds, age and/or sex classes often demonstrate non-random, differential use of habitats in winter. In particular, the dark-eyed junco, *Junco hyemalis*, exhibits a distinct pattern of differential migration in autumn that results in the age and sex classes being distributed non-randomly along a latitudinal gradient in winter (Ketterson & Nolan 1976, 1979; Chandler & Mulvihill 1990). In general, females, which are usually smaller than males, winter farther south than males, and, within the sexes, first-winter birds remain farther north than adults (Ketterson & Nolan 1976, 1983). Several hypotheses have been proposed to explain the ultimate factors influencing differential migration. These include differential advantages between the classes in the time of arrival on the breeding grounds (Ketterson & Nolan 1976; Myers 1981), the effects of social dominance on an individual's ability to gain access to resources in winter (Lack 1944; Kalela 1954; Balph 1975; Gauthreaux 1978, 1982; Ketterson & Nolan 1979) and physiological constraints on the ability of smaller individuals to meet

their energetic demands in winter (Ketterson & Nolan 1976, 1979; Ketterson & King 1977; Stuebe & Ketterson 1982). None of these hypotheses are mutually exclusive and various studies on the proximate mechanisms influencing differential-migration patterns have provided support for each in turn.

In general, the body-size hypothesis focuses on differences in the onset of hypothermia as an expression of cold tolerance (Swanson 1990) and fasting endurance (Stuebe & Ketterson 1982) associated with latitudinal differences in weather and food availability. However, the endocrine basis of behavioural and physiological mechanisms needed to respond to challenges in energy demand by animals expressing differential migration is less well understood. The regulation of energy reserves is an important component of homeostasis and may become more challenging to individuals living in relatively less predictable environments.

One of the most commonly studied endocrine responses to homeostatic challenges in birds is the ability to respond to stressors with an increase in the energy-regulating glucocorticosteroid, corticosterone. In birds, plasma concentrations of corticosterone can rise rapidly above normally low maintenance levels in response to a variety

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of perturbations such as storms or predation risk (Harvey *et al.* 1984; Wingfield 1994; Smith *et al.* 1994; Wingfield *et al.* 1983, 1992). Increases in corticosterone are believed to redirect ongoing behavioural and physiological activities towards immediate life-saving activities such as an increase in food searching or food intake, and to promote gluconeogenesis, using protein reserves as an energy source, if needed (Wingfield & Silverin 1986; Cherel *et al.* 1988; Gray *et al.* 1990; Wingfield 1994; Bruener *et al.* 1998). Chronic high levels of corticosterone are believed to be immunosuppressive and incompatible with reproduction, growth and development in a variety of vertebrate taxa (Sapolsky 1987; Greenberg & Wingfield 1987; Elsey *et al.* 1990; Paolucci *et al.* 1990; Wingfield *et al.* 1992, 1995a; Wingfield 1994). For many species of songbirds, maximal levels of corticosterone in the plasma are usually reached in about 30–60 min after the initial disturbance, with corticosterone concentrations returning to pre-disturbance levels if an individual is able to meet an energetic challenge successfully or if the perturbation passes (Dawson & Howe 1983; Holberton *et al.* 1996; Holberton 1999; Astheimer *et al.* 1992, 1995; Romero *et al.* 1997; Schwabl *et al.* 1991).

Acute corticosterone secretion from adrenocortical tissue in birds is primarily under the control of chemical signals (adrenocorticotrophic hormone, ACTH) from the pituitary, which are, in turn, under the control of several releasing hormones, primarily corticotropin-releasing factor (CRF) from the hypothalamus (Holmes & Phillips 1976; Harvey *et al.* 1984). The rapidity of this cascade and the resulting rate of change in corticosterone concentration in plasma, can be assessed by taking an initial blood sample immediately at the time of capture (the best estimate of the pre-disturbance value and referred to as 'baseline' throughout this study), followed by subsequent samples taken at specific intervals after capture. The resulting profile of acute corticosterone secretion illustrates an individual's adrenocortical response to the stress of capture and handling and is the accepted paradigm for measuring the sensitivity of the hypothalamic–pituitary–adrenal (HPA) axis.

Recent studies have shown that the sensitivity of the HPA axis can vary between and within individuals. In birds, reduced responses often occur when reproductive success may be most compromised by the deleterious effects of high levels of corticosterone (Astheimer *et al.* 1994, 1995; O'Reilly & Wingfield 1995; Wingfield *et al.* 1992; R. L. Holberton and J. C. Wingfield, unpublished data) or when a delay in muscle protein catabolism may be most beneficial for an individual (Cherel *et al.* 1988; Holberton *et al.* 1996, 1999; Holberton 1999; Marra & Holberton 1998). Several studies have also found that the strength of the corticosterone response may be correlated with energy reserves, with greater increases in corticosterone often occurring in birds exhibiting greater fat stores (Wingfield *et al.* 1994, 1995a). Conversely, reduced adrenocortical responses have been observed in birds in poorer energetic condition who, as a consequence of occupying sub-optimal winter habitats, may be trying to conserve energy reserves by delaying the onset of protein catabolism (Marra & Holberton 1998).

Presumably, an individual with a greater ability to increase plasma corticosterone concentration quickly

would be able to readjust its behaviour and physiology more rapidly in order to meet efficiently the energetic challenges encountered in unpredictable environments. In this study, we investigated the possibility that adrenocortical sensitivity may be part of the physiological milieu associated with differential migration patterns in juncos. Specifically, we predicted that birds wintering farther north, where environmental conditions may be less predictable and more challenging, would show a faster rate of acute corticosterone secretion in response to capture and handling stress than those birds wintering at the southern end of their winter range where temperature and food availability are more predictable.

2. STUDY AREAS AND METHODS

All juncos were captured with mist-nets or potter traps at baited sites in Water Valley, Yalobusha County, Mississippi, USA (MS, 34°09'N, 89°37'W) and in Berne, Albany County, New York, USA (NY, 42°37'N, 74°08'W) well after the period of autumn migratory activity for this species (see Terrill 1987; Holberton 1993). Sampling occurred during daylight hours from 1 January to 21 February 1998, and 19 December 1998 to 3 January 1999 in MS, and from 28 December 1997 to 18 January 1998, and 26 December 1998 to 1 January 1999 in NY (table 1). Local temperatures (to nearest °C) at the time of sampling were either determined by outdoor yard thermometers or obtained from the nearest (within 32 km) National Weather Service database.

The time that each bird was captured in the trap or net was recorded as the initial time of disturbance. A baseline blood sample (referred to as time 0 in all figures and analyses) was taken within 5 min of capture for all birds. A second sample taken 30 min after capture (referred to as time 30 in all figures and analyses) was used to assess the rate of change in plasma corticosterone concentration over the period of time in which most passerine corticosterone profiles begin to become asymptotic. Between samplings, birds were held individually in dark, cloth bags or small boxes. The degree of fat deposition in the furcular fossa on a scale closely based on that described by Helms & Drury (1960) was recorded for each bird. Briefly, this scale is as follows: 0, no visible fat in the fossa; 0.5, trace of fat at the base of the fossa; 1, fat lining the furculum but not filling the fossa; 2, fat completely filling the fossa; 3, fat beginning to bulge beyond the fossa; and 4, fat beginning to spread across the abdomen. For each bird, body mass was recorded (to the nearest 0.5 g) and sex was determined by wing cord (to nearest 0.5 mm) and plumage characteristics (Wood 1951; Grant & Quay 1970). While the degree of skull ossification can be used to distinguish those birds hatched in the current year from those hatched in any previous year, the dates of our sampling made this criterion unreliable for assigning age (Pyle *et al.* 1987). Therefore, we did not distinguish first-winter birds from older ones at either site.

At each time of capture and again 30 min later, *ca.* 80 µl of whole blood was collected in heparinized microcapillary tubes following venipuncture with either a lancet or a 27 G needle. The blood was kept refrigerated for 2–3 h until centrifuged. The plasma was then collected and kept frozen until assayed by radioimmunoassay in Oxford, MS, as described in Cash & Holberton (1999). The samples from both sites for each year were analysed within a single assay to eliminate inter-assay variation for within-year comparisons. Intra-assay coefficient of

Table 1. Ambient air temperature during the sampling periods and the number of juncos (by sex, if known) captured and sampled for the corticosterone stress response (initial and 30 min after capture) for each sampling period in MS and NY during the winters of 1997–1998 and 1998–1999

site, year	males	females	unknown	total birds	days	ambient temperature range (°C)
MS, 1997–1998	4	9	0	13	3	+ 2 to + 9
MS, 1998–1999	9	3	1	13	4	+ 3 to + 11
NY, 1997–1998	11	0	0	11	4	– 1 to + 1
NY, 1998–1999	11	1	0	12	5	– 1 to + 3

variation (c.v.) for the 1997–1998 samples was based on a plasma pool (c.v. = 3.7%) and a corticosterone standard (c.v. = 4.0%). The measures of intra-assay c.v. for the 1998–1999 samples were 3.7% and 5.5%, respectively.

3. RESULTS

The period of sampling, the number of days on which sampling occurred and the number of birds captured each year at each site are presented in table 1. Trapping effort was spread equally across years and sites. Not unexpectedly for this species, only one female was captured in NY while both sexes were equally represented in MS. In general, temperatures during the sampling periods in NY were lower than those in MS, with several sampling days in NY occurring during periods of frost (table 1).

(a) Site-based differences in energetic condition and fat score

An index of energetic condition (body mass per wing cord cubed) was used to correct for possible differences in body size within and between groups (Cash *et al.* 1997; Marra & Holberton 1998). NY birds had a significantly higher index of energetic condition than MS birds (Student's *t*-test, two-tailed: $p < 0.01$; figure 1). Birds sampled in NY were more likely to have greater fat reserves, with the majority of NY birds (21 out of 23) exhibiting a fat score of 3 as compared to the majority of MS birds (19 out of 26) with fat scores of 0.5 or 1 (figure 2).

(b) Site-based differences in corticosterone secretion

There was no difference in baseline corticosterone concentrations between years at either site (MS 1997–1998, mean $\pm$ s.e.m. = 4.06 ± 0.8 ng ml⁻¹, $n = 13$ versus MS 1998–1999, mean = 3.61 ± 1.0 ng ml⁻¹, $n = 13$; NY 1997–1998, mean = 4.72 ± 0.7 ng ml⁻¹, $n = 11$ versus NY 1998–1999, mean = 4.98 ± 1.4 ng ml⁻¹, $n = 12$); time 30 corticosterone levels also did not differ across years at either site (MS 1997–1998, mean = 13.41 ± 1.4 ng ml⁻¹, $n = 13$ versus MS 1998–1999, mean = 14.08 ± 1.6 ng ml⁻¹, $n = 13$; NY 1997–1998, mean = 16.21 ± 1.3 ng ml⁻¹, $n = 11$ versus NY 1998–1999, mean = 17.93 ± 2.4 ng ml⁻¹, $n = 12$; Student's *t*-test, $p > 0.05$). Therefore, we pooled samples from the two years for further analyses. The single female from the NY samples precluded analyses for an effect of sex at that site. However, there was no difference in baseline (males, mean = 3.12 ± 1.0 ng ml⁻¹, $n = 13$ versus females, mean = 4.52 ± 0.8 ng ml⁻¹, $n = 12$; Student's *t*-test, $p > 0.05$) or time 30 (males, mean = 12.66 ± 1.3 ng ml⁻¹,

Figure 1. Mean ($\pm$ s.e.m.) indices of energetic condition (body mass corrected for wing cord cubed (g mm^{-3})) for dark-eyed juncos wintering in NY ($n = 23$) and MS ($n = 26$) during the 1997–1998 and 1998–1999 winters (years pooled).

Figure 2. The frequency distributions of fat scores for dark-eyed juncos captured at wintering sites in NY (open bars) and MS (solid bars) during the 1997–1998 and 1998–1999 winters (years pooled).

$n = 13$ versus females, mean = 15.44 ± 1.6 ng ml⁻¹, $n = 12$; Student's *t*-test, $p > 0.05$) corticosterone concentrations between males and females sampled in MS, allowing these samples to be pooled for further analyses. When only males from each site were considered, baseline corticosterone values did not differ between MS and NY birds (MS, mean = 3.24 ± 1.0 ng ml⁻¹, $n = 13$ versus NY, mean = 4.95 ± 0.8 ng ml⁻¹, $n = 22$; Student's *t*-test, $p > 0.05$; figure 3a), but NY males showed significantly higher concentrations of corticosterone at time 30 than males sampled in MS (MS, mean = 12.3 ± 1.3 ng ml⁻¹, $n = 13$ versus NY, mean = 16.99 ± 1.5 ng ml⁻¹, $n = 22$; Student's *t*-test, $p < 0.05$; figure 3a). When data from MS males and females were pooled and compared to those from NY birds, there was no difference in baseline corticosterone concentration (MS, mean = 3.83 ± 0.6 ng ml⁻¹, $n = 26$ versus NY, mean = 4.86 ± 0.8 ng ml⁻¹, $n = 23$; Student's *t*-test, $p > 0.05$; figure 3b) but NY birds had a significantly higher concentration of corticosterone 30 min after capture than those birds sampled in MS (MS, mean = 13.75 ± 1.0 ng ml⁻¹, $n = 26$ versus NY, mean = 17.11 ± 1.4 ng ml⁻¹, $n = 23$; Student's *t*-test, $p < 0.05$; figure 3b).

At the NY sampling site, about 30 cm of snow fell overnight on 29–30 December 1997. On 30 December, two juncos were captured. Both were assigned fat class 3 and both had unusually high time 30 corticosterone levels (30.99 ng ml⁻¹ and 26.11 ng ml⁻¹ above baseline levels of 8.24 ng ml⁻¹ and 3.66 ng ml⁻¹, respectively). These 30 min sample values are well above the average time 30 values for birds sampled at the same site under more moderate conditions. This is, of course, an anecdote, but it suggests that adrenocortical responsiveness may be facultatively modulated in response to short-term changes in local conditions.

(c) Energy reserves and corticosterone secretion

There was no correlation between corticosterone concentration at time 30 and the residuals of a linear regression model of body mass versus wing cord cubed (mass corrected for body size; Cash *et al.* 1997; Marra & Holberton 1998) for birds sampled in NY ($r = 0.09$, $r_{\text{crit}} = 0.41$, $p > 0.05$, $n = 23$; figure 4) or MS ($r = 0.03$, $r_{\text{crit}} = 0.39$, $p > 0.05$, $n = 26$; figure 4). While there was a significant correlation between fat score and temperature when the data were pooled across both sites ($r = -0.57$, $r_{\text{crit}} = 0.29$, $p < 0.05$, $n = 47$; not shown; weather data for two samples were not available), variation in corticosterone levels at time 30 was not associated with fat score ($r = 0.14$, $r_{\text{crit}} = 0.27$, $p > 0.05$, $n = 49$; not shown). There was no correlation between baseline corticosterone and either the residuals of mass corrected for body size, or fat score at either site (residuals of mass corrected for body size versus baseline corticosterone: MS, $r = 0.18$, $r_{\text{crit}} = 0.39$, $p > 0.05$, $n = 26$; NY, $r = 0.003$, $r_{\text{crit}} = 0.41$, $p > 0.05$, $n = 23$, not shown; fat score versus baseline corticosterone: MS, $r = 0.14$, $r_{\text{crit}} = 0.39$, $p > 0.05$, $n = 26$; NY, $r = 0.29$, $r_{\text{crit}} = 0.41$, $p > 0.05$, $n = 23$, not shown) or when the sites were pooled (residuals of mass corrected for body size versus baseline corticosterone: $r = 0.10$, $r_{\text{crit}} = 0.27$, $p > 0.05$, $n = 49$; fat score versus baseline corticosterone: $r = 0.09$, $r_{\text{crit}} = 0.27$, $p > 0.05$, $n = 49$, not shown).

Figure 3. The corticosterone stress profiles (mean $\pm$ s.e.m. (ng ml⁻¹)) of (a) male juncos and (b) dark-eyed juncos (sexes pooled) captured in NY (open circles) and MS (solid circles) during the winters of 1997–1998 and 1998–1999 (years pooled). Note that in both cases there was no difference in the initial sample taken immediately after capture (time 0) but NY juncos showed a significantly higher corticosterone concentration 30 min after capture (time 30).

4. DISCUSSION

Ketterson & Nolan (1983) determined that, while annual survivorship was equal for northern and southern winter populations of dark-eyed juncos, overwinter survivorship differed significantly along a latitudinal gradient. Their study showed that, although northern-wintering juncos did not incur the higher mortality associated with the longer migrations experienced by more southerly wintering juncos, northern-wintering birds had a lower probability of surviving until spring and this was most probably due to the higher risk of starvation. Our results show that the ability to respond more quickly to rapidly

Figure 4. Plasma corticosterone concentrations 30 min after capture (time 30) as a function of energetic condition (i.e. the residuals of a linear regression of body mass on wing cord cubed, see text for details) for dark-eyed juncos wintering in NY (open circles, $n = 23$) and MS (solid circles, $n = 26$). There was no correlation between energy reserves and time 30 corticosterone concentration at either site.

changing conditions is correlated with the degree of environmental predictability: juncos wintering at higher latitudes exhibited faster adrenocortical responses to stress than those individuals wintering in the south, a pattern that was consistent over the two years in which data were collected. Specifically, juncos sampled in NY exhibited significantly higher plasma corticosterone concentrations 30 min after capture than did juncos sampled in MS. Such differences in the sensitivity of the HPA axis should be indicative of an individual's ability to adjust its behaviour and physiology to cope with changing environmental conditions in a timely manner. By this criterion, juncos overwintering in NY that have a higher probability of encountering severe winter weather may be better prepared to deal with these exigencies.

This pattern is supported by earlier work on wintering dark-eyed juncos. Based on single blood samples taken *ca.* 20–40 min after capture, Rogers *et al.* (1993) found that juncos overwintering in Michigan were likely to have higher plasma corticosterone concentrations than those overwintering in Tennessee. There was no apparent difference between birds in Michigan and Indiana, separated by a smaller latitudinal distance. While the study of Rogers *et al.* (1993) did not examine the corticosterone stress response directly, their corticosterone values are comparable to ours at time 30, with the same magnitude of difference in corticosterone levels found at different latitudes. Wingfield *et al.* (1995b) found that Japanese bush warblers (*Cettia diphone*) breeding at higher latitudes exhibited a steeper adrenocortical stress response than those breeding in a more southerly location. That study may not be strictly comparable to ours because the pattern of corticosterone secretion in breeding birds is often influenced by time and energy constraints associated with the degree of parental care (Wingfield 1994; O'Reilly & Wingfield 1995; Wingfield *et al.* 1995b; Silverin

& Wingfield 1998). However, the authors found that male parental care is absent in the bush warbler, thereby making the similarity in the patterns observed in wintering juncos and breeding bush warblers more likely to be the result of analogous factors modulating the corticosterone stress response with respect to environmental predictability (Wingfield 1994).

In our study, juncos wintering in NY exhibited higher indices of energetic condition, a result of greater fat reserves, than those exhibited by juncos in MS. Although MS may experience 2–7 cm of snow every other year or so, extended periods of frost and ice storms, which may make foraging difficult for ground-feeding birds such as the junco, are infrequent and rarely persist for more than a day or two (R. L. Holberton, personal observation). This is in clear contrast to NY where several centimetres of snow may fall frequently throughout the winter period and snow cover may persist for weeks or even months. Many studies have shown that, in wintering birds, lipid deposition responds to short- and long-term environmental conditions (e.g. temperature and snowfall; Helms & Drury 1960; Evans 1969; Rogers 1995; and unpublished data referred to in Rogers *et al.* (1993)). Corticosterone is intimately involved in the regulation of energy reserves and is believed to be a major facilitator of lipogenesis (Wingfield & Silverin 1986; Gray *et al.* 1990; Astheimer *et al.* 1992). The amount of fat reserves that birds deposit can play a role in the milieu of metabolic processes associated with seasonal acclimatization in populations at higher latitudes or altitudes (O'Connor 1996). However, unlike many non-passerines living at higher latitudes, passerines do not rely on fat reserves for insulation, nor can they modulate feather density to meet higher energetic costs in winter (Marsh & Dawson 1989; Swanson 1991). Several studies have found that small birds, including juncos, increase basal metabolic rate and/or use muscle shivering as a way to meet their thermal energy demand (Dawson & Carey 1976; Swanson 1991; Liknes & Swanson 1996). Both responses require increasing energy intake, which can be difficult at higher latitudes in winter. Under these conditions, the enhanced responsiveness of the HPA axis, which quickly redirects ongoing activities towards those facilitating greater food encounter and intake rates, can lead to greater fat deposition and increased overwinter survival. It is possible that differences in HPA-axis sensitivity may be an intrinsic component of the acclimatization process, but we know of no studies that have linked seasonal acclimatization abilities with glucocorticosteroid activity in birds.

Despite the fact that juncos sampled in NY had both higher fat scores and higher time 30 corticosterone levels than MS birds, there was no correlation between these two variables at either site. Several studies have also failed to find a consistent relationship between variation in fat reserves and patterns of corticosterone secretion at a particular time of year. In Alaskan common redpolls (*Acanthis flammea*) there was a non-significant trend for leaner birds to have higher maximal corticosterone levels in January, but that pattern was even less apparent in February (Wingfield *et al.* 1994). On the other hand, American redstarts (*Setophaga ruticilla*), which overwinter in Jamaica, rarely carry detectable fat reserves. However, thinner birds occupying poorer-quality habitats had

reduced adrenocortical responses, a mechanism by which birds faced with chronic food deprivation may be able to protect skeletal muscle from corticosterone's catabolic effects for as long as possible (Holberton *et al.* 1996; Marra & Holberton 1998). The lack of a strong relationship between the strength of the adrenocortical response and energy reserves in wintering juncos and other birds suggests that the hormonal responsiveness is only weakly tuned to the immediate state of fat reserves but often serves as a stress-avoidance mechanism enabling an individual to respond to environmental exigencies before becoming compromised (Sapolsky 1987).

Several important questions remain regarding the nature of latitudinal differences in adrenocortical sensitivity and its relationship to differential migration in dark-eyed juncos. The pattern of latitudinal segregation in the wintering grounds is strongest between males and females (Ketterson & Nolan 1985) and this difference has an endogenous basis (Holberton 1993). It seems possible that adrenocortical responsiveness could be a component of an endogenous migratory programme (Berthold 1996) but our data suggest that any endogenous difference is not a simple, gender-based one. This is in light of the fact that, at one site (MS), there was no difference between the sexes in adrenocortical secretion, precluding a strong, sex-linked expression of the trait, regardless of latitude. Others have also failed to find differences in corticosterone concentration between the sexes when sampled at the same sites during the non-breeding season (Rogers *et al.* 1993; Wingfield *et al.* 1994; Holberton *et al.* 1996; Holberton 1999; R. L. Holberton, unpublished data; Marra & Holberton 1998). However, Ketterson & Nolan (1979, 1983, 1985) report that, within each sex, first-winter birds remain further north of adults as a way in which first-year breeders can maximize their probability of acquiring a territory by arriving as soon as possible on the breeding grounds in spring. If adrenocortical responsiveness is an intrinsic constraint on how far north a given individual can overwinter, it may be part of an ontogenic process; young birds within each sex that are attempting to remain as close to the breeding grounds as possible in winter may be able to do so through the advantage of a faster adrenocortical response. While intrinsic age-related differences in the ability to respond to stress pose potentially interesting areas of research, our data could not address the effects of age at either site. However, Rogers *et al.* (1993) failed to find age-related differences in corticosterone secretion at any latitude in their study, making a weak argument for an age-related constraint in HPA-axis activity. If the degree to which an individual can modulate the corticosterone stress response has a genetic predisposition, experience, as always, may play an important role in its expression. Controlled laboratory experiments would be needed to determine whether variation in the strength of the corticosterone stress response has an endogenous basis, with either sex or age, and how environmental factors such as weather and social conditions could affect its expression.

To date, however, the evidence is more consistent with acclimatization to local conditions (within and across latitudes) than it is with an age- or sex-related endogenous constraint. Rogers *et al.* (1993) found that, regardless of age or sex, juncos responded with higher plasma cortico-

sterone levels and an increase in adrenal mass during the same day that a snowfall and sharp drop in temperature occurred, even at the most southerly site sampled (Tennessee). Our two birds sampled in NY following a large snowfall behaved similarly. Collectively, these data from field studies suggest that juncos wintering at a given latitude are able to respond to local conditions and short-term changes in energy demand (Rogers *et al.* 1993) and that temperature may act as a proximate cue influencing rapid fat deposition (Rogers 1995).

In summary, the latitudinal differences in the corticosterone response in our juncos may have been the result of responses to proximate differences in temperature and snow cover, with or without a genetically based difference in their capability to do so. Whether modulation of the corticosterone stress response is an intrinsic component of the seasonal acclimatization milieu associated with increased basal metabolic rate and shivering capability is unknown. The biological basis of the expression of this characteristic, comprising both a behavioural and physiological component, is most probably a complex interaction of environmental factors and genetic constraints. Clearly, further work is needed to elucidate the relative roles of endogenous and exogenous factors influencing winter-distribution patterns of a differential migrant like the dark-eyed junco.

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