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PLASMA CORTICOSTERONE, ADRENAL MASS, WINTER WEATHER, AND SEASON IN NONBREEDING POPULATIONS OF DARK-EYED JUNCOS (*JUNCO HYEMALIS HYEMALIS*)

CHRISTOPHER M. ROGERS[1,4], MARILYN RAMENOFSKY[2,3], ELLEN D. KETTERSON[1], VAL NOLAN, JR.[1], AND JOHN C. WINGFIELD[2,3]

[1]*Department of Biology, Indiana University, Bloomington, Indiana 47405, USA; and*
[2]*Rockefeller University Field Research Center, Tyrrel Road, Millbrook, New York 12545, USA*

ABSTRACT.—Plasma levels of corticosterone (B) have been measured in free-living Dark-eyed Juncos (*Junco hyemalis hyemalis*) wintering in Michigan, Indiana, and Tennessee. Total adrenal dry mass also was determined for a large number of wintering juncos collected at these three locations. All populations had access to supplemental food. When Michigan, Indiana, and Tennessee winter populations were compared, plasma B was significantly greater when new snow had fallen on trap days (midwinter) than when it had not (early winter). However, the relative importance of a direct response to proximate snowfall and a seasonal change as independent causes of this pattern could not be determined. In the Tennessee population in early January, plasma B was greater on two days with new snowfall than on two days without new snowfall. Total adrenal dry mass was significantly and positively correlated with recent snowfall, possibly in support of elevated plasma B on snowy days. Together with studies showing increased fat reserves shortly after new snowfall in the Dark-eyed Junco, these results suggest that corticosterone might be involved in directing increased feeding and associated lipogenesis as inclement weather sets in. Although a direct response to snowfall is suggested, factors correlated with snowfall (e.g. barometric pressure) also may cause elevated titers of B during inclement weather. *Received 14 October 1991, accepted 4 March 1992.*

DURING WINTER, many species of birds at temperate latitudes increase their stored lipid reserves (recently reviewed by Blem 1990). Winter fat serves to supply metabolic fuel for nocturnal thermoregulation (Lehikoinen 1987) and as an emergency energy supply during periods of resource shortage (e.g. snowstorms and windstorms; Rogers 1987, Rogers et al. 1991). In temperate North America, fat reserves are generally greater in populations residing in more northern latitudes (Nolan and Ketterson 1983, Rogers et al. 1993). In some species, the fat reserve also increases toward midwinter at single locations (e.g. Rogers and Rogers 1990).

Despite extensive knowledge concerning spatial and temporal variation in the winter fat reserve of small birds, the mechanisms regulating the fat reserve in response to winter conditions are largely unknown. However, birds are known to respond to a wide variety of proximate environmental factors by increasing plasma levels of corticosterone (B), an adrenal glucocorticosteroid possibly involved with fat metabolism in small birds in winter (Schwabl et al. 1985, Gray et al. 1990). Such factors include temperature extremes in addition to capture and collection of a blood sample (Harvey et al. 1984). The role of weather as an environmental stressor is not well understood, although in a wintering population of Harris' Sparrows (*Zonotrichia querula*) a sudden drop in temperature accompanied by a new snowfall caused a rise in plasma B (Rohwer and Wingfield 1981). Schwabl et al. (1985) suggested that increased plasma B stimulates foraging behavior and fat deposition as inclement weather sets in; such extra energy reserves could enhance survival during harsh environmental conditions.

If inclement weather causes an elevation of plasma B, this steroid should increase when winter weather changes from relatively mild to

[3] Present address: Department of Zoology, University of Washington, Seattle, Washington 98195, USA.
[4] Present address: Department of Biological Sciences, University of Iowa, Iowa City, Iowa 52242, USA.

TABLE 1. Temperature, new snowfall, and snow cover for each of four trap efforts. Temperature and total snowfall data also shown for five days preceding each effort. Traces are amounts of new snowfall less than 0.25 cm deep.

Trap day				Five days prior to trap day		
Temperature (°C)		New snowfall (cm)	Snow cover	Temperature (°C)		New snowfall (cm)
Minimum	Maximum			Minimum	Maximum	
			Indiana (December 1984)			
7.2	15.6	0.0	None	4.1	15.2	0.0
			Michigan (December 1984)			
−4.6	2.6	0.0	Patchy	0.6	9.9	5.1
			Tennessee (January 1984)			
−2.5	2.4	1.3	None to complete	11.2	20.6	0.0
			Michigan (January 1985)			
−8.6	−3.6	Two traces	Complete	−11.9	−3.7	23.4

relatively harsh conditions. To test this prediction, we sampled plasma B in three populations of the Dark-eyed Junco (*Junco hyemalis hyemalis*) wintering at different latitudes in eastern North America. Although winter weather changed little while populations were being sampled, a sudden winter snowstorm at one latitude allowed comparison of plasma B between mild and harsh winter conditions in the same population. Finally, latitudinal and seasonal variation in adrenal mass of juncos was analyzed in relation to environmental factors in order to elucidate the role of this endocrine gland in responses to weather. Our results support the hypothesis that sudden snowfall causes a rise in plasma B and adrenal hypertrophy, which in turn are associated with increased fat reserves.

METHODS

Sample collection.—The Dark-eyed Junco is an abundant passerine breeding in the boreal forest that covers much of Alaska, Canada, and the extreme northern United States (Bent 1968). The winter populations, established in eastern North America between 50°N and 28°N by early December, begin to migrate back to breeding habitat in early March (Ketterson and Nolan 1976).

Blood samples were obtained from juncos for determination of plasma B by specific radioimmunoassay. Three junco populations were sampled during four trap efforts: in Bloomington, Indiana (39°10'N, 86°31'W, elevation 250 m) on 15-19 December 1984; near Kalamazoo, Michigan (42°17'N, 85°36'W, elevation 288 m) on 20-22 December 1985 and again on 26-27 January 1985; and near Nashville, Tennessee (36°07'N, 86°41'W, elevation 180 m) on 2-5 January 1985. All study sites were provided with supplemental food (white millet, mixed wild bird seed, cracked corn) at least one week before sampling. Juncos were trapped in four-cell Potter ground traps and mist nets set at these feeding sites. The time that birds spent in traps was minimized to avoid possible increases in plasma B caused by struggling. After capture, birds were held individually in darkened bags until blood samples were taken. Blood samples were collected from the alar vein into heparinized capillary tubes. Time in minutes elapsing between capture and the completion of blood sampling (hereafter, bleeding time) was recorded. Next, blood samples were separated by centrifugation and plasma was aspirated and stored on dry ice in the field pending storage in the laboratory at −20°C. Samples were collected at the same time of day to avoid diel variation in plasma corticosterone (Dusseau and Meier 1971, Joseph and Meier 1973). Visible fat class (Rogers 1991), age and sex (Ketterson and Nolan 1976, 1982), total body mass (Pesola spring scale), and length of the flattened wing chord (mm) were determined. Individual birds retrapped within trap efforts were not resampled.

Weather conditions before and during sampling.—Table 1 summarizes weather data for each trapping period and also for the five days preceding each effort (weather data obtained from Climatological Data, U.S. Weather Service, 1984-1985 and supplemented with on-site observations). Temperature, new snowfall, and snow cover varied among the three sites in Indiana and Michigan, but no severe weather changes occurred during the sampling at these three sites (Table 1). In contrast, a snowstorm occurred in Tennessee during the 2-5 January 1985 trapping period. This weather change allowed evaluation of the effect of sudden inclement weather on plasma corticosterone within the same population. No snow had fallen at the Tennessee site during the previous month, and these conditions persisted through 2 January; on this day minimum and average daily temperatures were 0.6 and 1.4°C. Between nightfall on the 2nd and dawn of the 3rd, 0.25 cm of new snow fell, covering the ground with a thin layer of snow; minimum and average temperatures were 0.0 and 1.4°C on the 3rd. Between nightfall of the 3rd and dawn of the 4th, 1.0 cm of new snow fell, again covering the ground completely; minimum and average daily temperatures were −5.0 and −1.7°C on the 4th. By dawn on the 5th, most of the snow cover had melted; minimum and average temperatures were −5.6 and 1.4°C on this day.

Determination of plasma corticosterone.—Circulating levels of plasma B were determined by specific radioimmunoassay following the chromatographic procedures described by Wingfield and Farner (1975) and Ball and Wingfield (1987). Initially, 2,000 CPM of ^{3}H-corticosterone (New England Nuclear) was added to each plasma sample that served as an internal standard and was used to measure the percentage of recovery following the extraction and chromatographic steps. Next, 4 ml of redistilled dichloromethane were added to each sample for extraction of the endogenous and ^{3}H-steroid. Extracts were evaporated and redissolved in 10% ethyl acetate in isooctane and placed on Celite : propylene glycol : ethylene glycol (W:V:V;6:1:1) microcolumns for chromatographic separation. The B fraction was collected in 50% ethyl acetate in isooctane, evaporated, and redissolved in phosphate buffer with 0.1% gelatin. Concentration of B in the purified eluate was measured by specific radioimmunoassay with ^{3}H-corticosterone standard and specific antibody (Endocrine Sciences). Duplicate values of each sample were read off a standard curve that ranged in concentration from 7.8 to 1,000 pg. All samples were adjusted for percentage of recovery of the internal standard. The range of recovery values for all samples was from 65 to 85%. Concentrations are given in nanograms per milliliter (ng/ml).

Determination and statistical analysis of adrenal dry mass.—Total dry mass of the paired adrenal glands was used as a general indicator of secretory activity. Adrenals were removed from wintering juncos collected (in connection with a separate study of the regulation of winter lipid storage) at the above Michigan, Indiana, and Tennessee locations during the 1982–1983 and 1983–1984 winters (Rogers et al. 1993). Adrenals were weighed together (nearest 0.01 mg) on a Mettler analytical balance after oven-drying (48 h at 90°C) in an aluminum-foil envelope.

Stepwise multiple-linear regression (Nie et al. 1975) was used to separate possible independent influences of environmental, temporal, morphological, and population factors on adrenal mass. Environmental data were obtained from Climatological Data, U.S. Weather Service (1982–1984). Minimum daily temperature is the minimum temperature that occurred on the night immediately preceding trapping. Change in minimum daily temperature is the difference between minimum daily temperature on trap day and minimum daily temperature on the previous day. Snowfall was represented by snow0–5, the total snowfall (cm) occurring during the six-day period including trap day and the five days immediately preceding trap day. Season is the number of days after 1 December (fall migration in this species typically ends in late November) that blood samples were taken. Wing length was used as a general measure of overall body size. Population of winter origin was represented by two dummy variables, Michigan-Tennessee and Indiana-Tennessee; Tennessee was the reference population (Nie et al. 1975). Age (birds hatched during the preceding breeding season designated as young; those hatched earlier designated as old), sex, and year (1983 or 1984) also were represented by dummy variables.

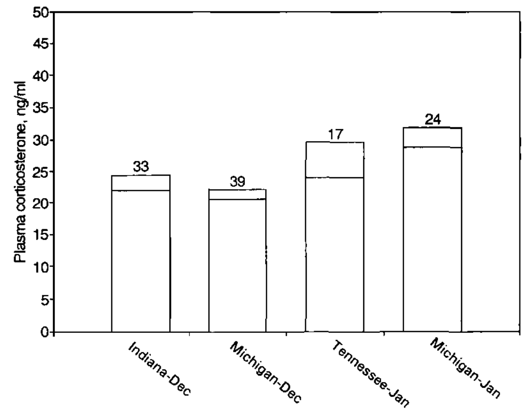

Fig. 1. Plasma B ($\bar{x}$ + 1 SE) for the four winter sampling periods (trap efforts). Sample sizes shown above bars. Horizontal lines within bars indicate 1 SE.

Results

Initial analyses indicated the four age-sex classes to be similar in plasma B; in addition, all four age-sex classes showed similar increases in plasma B in response to bleeding time (capture stress). When data from the age-sex classes were pooled, plasma B was lower during the December samplings in Indiana and Michigan than during the Tennessee and Michigan-January efforts (Fig. 1; Kruskal-Wallis H_c = 16.31, two-tailed $P < 0.001$, $n = 113$). The time of day that samples were obtained was similar for all sampling efforts, averaging 3.5, 4.2, 4.9, and 4.9 h after dawn for Indiana, Michigan-December, Tennessee, and Michigan-January efforts, respectively. Bleeding time averaged 32.8, 27.9, 29.7, and 21.0 min.

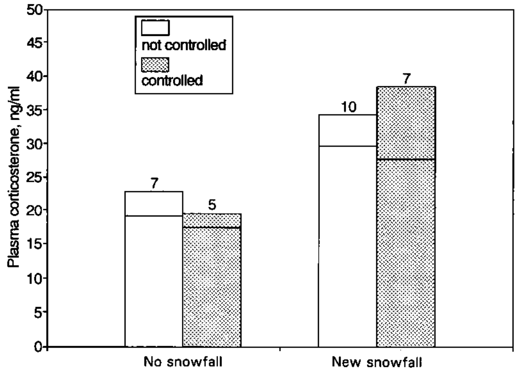

Fig. 2. Plasma B ($\bar{x}$ + 1 SE) for birds trapped in Tennessee, January 1985 on two days without new snowfall (2 and 5 January) and on two days with new snowfall (3 and 4 January). Sample sizes shown above bars. Plasma B indicated when controlled and not controlled for bleeding time. Horizontal lines within bars indicate 1 SE.

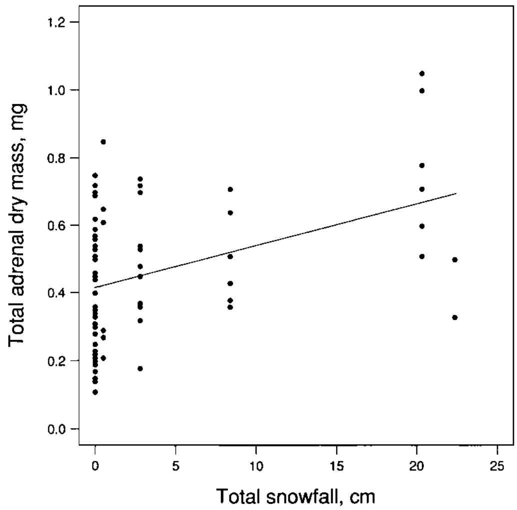

Fig. 3. Relationship between total adrenal dry mass and snowfall (n = 79 individual juncos). Snowfall represented by total amount of snow falling on the trap day and the five days preceding it.

An analysis of plasma B statistically corrected for bleeding time yielded the same pattern of statistically significant variation among sampling efforts. In a multiple-regression analysis, trap effort (P = 0.0003) and bleeding time (P = 0.022) were statistically significant; age (P = 0.206), sex (0.570), the age-bleeding time interaction (P = 0.454), the sex-bleeding time interaction (0.266) were not. Thus, statistical control of bleeding time increased the significance of variation among trap efforts. In addition, the response to bleeding time apparently did not differ between age classes or between the sexes.

Snowfall that occurred during the Tennessee sampling effort was accompanied by changes in plasma B. This variable was significantly higher (Mann-Whitney U = 13.0, two-tailed P = 0.032; Fig. 2) on 3 and 4 January, when new snow had fallen by dawn, than on 2 and 5 January, days on which no new snow had fallen by dawn (2nd) or no new snow had fallen by dawn and recent snowfall had almost melted completely (5th). Samples were obtained, on average, 2.7 h after dawn (civil twilight) on 2 and 5 January, and 1.2 h after dawn on 3 and 4 January. Bleeding time averaged 38.9 and 23.3 min for nonsnowy and snowy periods, respectively. When bleeding times were nearly equalized (30.4 min nonsnowy, 27.9 min snowy), the result was an even greater difference (Fig. 2; two-tailed P = 0.012). Small sample sizes precluded meaningful analysis of day-to-day variation in plasma B. The age-sex classes were distributed nearly equally between nonsnowy and snowy conditions (numbers of young males, young females, and old males for nonsnowy and snowy periods were 2, 3, 2 and 5, 4, 1, respectively; no old females were trapped).

Multiple-linear regression of total dry mass of both adrenals indicated the strongest correlate of adrenal dry mass was snow0–5 (Fig. 3). With snow0–5 held constant statistically, no other factors independently explained variation in adrenal dry mass, including population, season, age, sex, wing length, and the two temperature factors.

DISCUSSION

Weather, season, and plasma corticosterone.—Our original goal was to evaluate the relationship between plasma B and winter weather as weather changed during the period in which a population was sampled (trap effort). Unlike the Indiana and Michigan findings, the Tennessee data are unique because they allow an evaluation of snowstorm effects on plasma B; blood samples were collected immediately before, during, and immediately after new snowfall. For these reasons, the Tennessee data are discussed first, followed by their significance for understanding the seasonal variation in plasma B observed among the four trap efforts.

What factors might be responsible for the significant variation in plasma B observed in Tennessee? Time of day, bleeding time, age, and sex were similar between samples from snowless and snowy days; hence, they cannot explain the variation. Temperature varied little among the four sampling days. However, higher plasma B on days with new snowfall by dawn than on snowless days (Fig. 2) suggests a role for this short-term factor, or a correlate thereof, in elevating plasma B.

Data from Michigan and Indiana support this suggestion. Plasma B was high in Michigan in January 1985 when new snow fell on trap days, and temperature was much lower during this Michigan effort than in Tennessee, but B was similar during these two efforts. In early winter, the Michigan-December and Indiana trap efforts lacked snowfall, and daily temperatures differed between these efforts (Table 1), but plasma B did not (Fig. 1). Although only snowfall is implicated as causing elevated B, the snow response might be dependent on low temperature (Rohwer and Wingfield 1981).

These data also suggest a complex aspect of the possible snow response. Plasma B was high in Tennessee in apparent response to snowfall, but was high in Michigan in January when only traces of new snow fell on trap days (Table 1, Fig. 1). However, the five days immediately preceding the Michigan-January effort had heavy snowfall and very cold temperatures; heavy snow cover persisted throughout the trap effort (Table 1). Snow also fell immediately before the Michigan-December effort, but B was relatively low; however, by dawn of the first trap day this snowfall had largely melted and snow cover was patchy. Together these results support the interpretation that: (1) plasma B rises in response to new snowfall, but drops quickly if conditions ameliorate; and (2) heavy snow cover and cold conditions maintain high levels of plasma B.

Although a response to snowfall can explain the significant variation in plasma B among trap efforts, these results do not necessarily rule out additional factors. For example, the variation among trap efforts possibly represents a response to local conditions superimposed on a seasonal fluctuation in plasma B that is independent of proximate weather conditions. Seasonal changes in plasma (Macchi et al. 1967) and adrenal (Peczely 1976) corticosterone levels have been demonstrated for other species of birds (Harvey et al. 1984). The significance of seasonal rises in B independent of the proximate environment deserves further attention.

Factors influencing adrenal mass.—Snowfall on trap day and the five days preceding it was the strongest correlate of temporal and spatial variation in adrenal mass of juncos (Fig. 3). Of a large set of independent variables, many of which are known to influence adrenal size or activity, no variable was a significant explanator of variation in adrenal dry mass after the effect of snow0–5 was removed statistically. Seasonal changes in size/activity of the avian adrenal are documented (Lorenzen and Farner 1964, Hohn et al. 1965, Moens and Coessens 1970, Silverin 1978, Chaturvedi and Thapliyla 1979). The significance of snow0–5 implicates a proximate factor in causing the observed seasonal variation in adrenal size. This result suggests that upon snowfall, the adrenal glands of juncos increase in size (and possibly secretory activity) in support of elevated plasma corticosterone. Changes in total adrenal dry mass are assumed to reflect changes in that portion of the interrenal tissue responsible for corticosterone synthesis and release. However, it is possible that changes in adrenal mass reflect changes in chromaffin tissue; unfortunately, at present there are no data with which to address this possibility in the study species.

Role of hypothalamic-pituitary-adrenal axis in winter physiology.—Corticosterone has diverse effects in birds (reviewed by Holmes and Phillips 1976, Harvey et al. 1984). Many of these studies have focused on domestic species; as a result, little is known about the role of this steroid in natural populations. In our study, the Dark-eyed Junco apparently responded to the onset of snowstorms with a rapid increase in plasma B. The elevation of B as environmental conditions degrade might direct an increase in foraging rate (Nagra 1965, Wingfield 1984, Wingfield and Silverin 1986); if sufficient food is available, storage of lipids may be possible (see Dulin 1956, Baum and Meyer 1960). Such "extra" reserves could enhance fasting capacity during prolonged food shortages should severe conditions persist. This hypothesis is consistent with the observations that: (1) in the Tennessee population in January, visible fat class was significantly greater after the snowstorm than before (Rogers in prep.); (2) Michigan, Indiana, and Tennessee winter populations of the Dark-eyed Junco have greater fat stores shortly after new snowfall than before (Nolan and Ketterson

1983, Rogers et al. 1993); (3) plasma B administered in silastic capsules increased fat stores in wintering juncos (Gray et al. 1990) and breeding Song Sparrows (*Melospiza melodia*; Wingfield and Silverin 1986), and increased feeding rates in breeding Pied Flycatchers (*Ficedula hypoleuca*; Silverin 1985).

Our results compared with those of similar studies of wintering birds suggest that plasma B has different physiological roles in different species exposed to inclement weather. To illustrate, this steroid might be involved in utilization of stored fat reserves in breeding passerines experiencing food shortage caused by heavy rains (Wingfield et al. 1983), and might stimulate feeding (and associated lipogenesis) in wintering juncos at the onset of snowstorms. A final point is that, although these results are framed in terms of a direct endocrine response to snowfall, alternative proximate factors (e.g. barometric pressure; Kreithen and Keeton 1974) may instead be responsible for the observed patterns in plasma B. Further work is needed that addresses different hypotheses concerning the role of plasma B in winter physiology of small birds, possible seasonal changes in plasma corticosterone that are independent of the proximate environment, and causal factors underlying "emergency" responses to inclement weather.

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