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AN ANALYSIS OF BODY MASS, WING LENGTH, AND VISIBLE FAT DEPOSITS OF DARK-EYED JUNCOS WINTERING AT DIFFERENT LATITUDES

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During winter, many bird species at temperate latitudes increase their stored fat (see King and Farner 1966, King 1972 for review of older literature; O'Connor 1973, Evans and Smith 1975, Biebach 1977, Vincent and Bédard 1976, Carey et al. 1978, Blem 1978 for more recent findings). Winter fattening is considered an adaptive response to the increases in thermoregulatory costs, duration of nocturnal fasting, and risk that in severe climates snow or ice storms will curtail or prevent daylight feeding.

If climate (including day length) is the ultimate cause of winter fattening, then in much of the world populations of the same species wintering at different latitudes should differ in amount of fat stored (King and Mewaldt 1981). In certain sedentary species, higher body mass (wet weight) and thus perhaps greater fat stores have been found to be characteristic of more northern populations (e.g., the Great Tit [*Parus major*], compare van Balen 1967 and Haftorn 1976; and the House Sparrow [*Passer domesticus*] Blem 1973); but studies of migratory birds have produced conflicting results. Several species of shorebirds exhibit the expected trend (Pienkowski et al. 1975, Dick and Pienkowski 1979), but neither White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) (King and Mewaldt 1981) nor American Goldfinches (*Carduelis tristis*) (Wiseman 1975, Carey et al. 1978) are heavier farther north. The European Starling (*Sturnus vulgaris*), a partial migrant, exhibits still a different pattern, carrying more fat at mid-latitudes than it does to the north or south (Blem 1981).

In this paper we analyze, according to sex and age, variation in body mass of 1835 migratory Dark-eyed Juncos (*Junco hyemalis*) from six wintering locations in the eastern United States. Juncos have been the subject of numerous studies of body mass in the laboratory and field (Helms and Drury 1960, Johnston 1962, Weise 1963, Farrar 1966, Helms et al. 1967, Knowles 1972, Swanson 1975, Holmes 1976, Prescott 1978), but sex and/or age was not determined in most of these. Juncos are known to fatten in winter (Helms et al. 1967, Bower and Helms 1967, Holmes 1976); and in one geographic comparison, mass was greater at a higher latitude (Massachusetts) than at a lower (Delaware), even when temperatures were warmer at the more northerly location (Helms and Drury 1960, Knowles 1972). Here we ask whether body mass varies with latitude and whether any variation that is found can be attributed to differences in fat storage.

We also consider possible advantages of fatness and leanness to wintering juncos, as well as what environmental cues might elicit (or suppress) fattening and thus account for any geographic patterns that exist.

METHODS

Sampling.—Locations and dates of sampling appear in Table 1 (for further details, see Ketterson and Nolan 1982). Early-winter sampling (on or before 9 January) was carried out during 2–5 winters in Michigan (N = 5), Indiana (N = 2), Tennessee (N = 3), South Carolina (N = 4), and Alabama (N = 2). Late-winter sampling (2 February–15 March) took place during one to two winters in Indiana (N = 2), Tennessee (N = 1), South Carolina (N = 2), and Mississippi (N = 1). Michigan and Indiana we refer to as northern, and other locations we regard as southern.

Subjects were captured, usually by netting, at sites baited with millet and cracked corn. They were banded, weighed to the nearest 0.1 g (50 g Pesola spring balance), measured (flattened wing), and sexed by methods previously described (Ketterson and Nolan 1976, 1982). Age was determined by examining skull pneumatization and/or a combination of eye color and plumage traits in early winter, by eye color, plumage, and wing length in late winter. Birds were categorized either as having hatched during the preceding breeding season (hereafter, young) or in an earlier season (adult). Reliability of aging approached 100% in early winter; it was slightly greater than 90% in late winter, as we determined by re-aging at that time juncos whose skulls had been examined in November and December (Ketterson and Nolan 1982). Most weights were taken within 1 h of capture, none more than 2 h after capture. Visible fat was classified using a modified version of the scale of Helms and Drury (1960): 0 = no fat on abdomen (A) or in furcula (F); 1 = F < 33% full, A < 50% covered; 2 = F 33–66% full, A 50–100% covered but surface not even with pectoral region; 3 = F filled, A covered and flush with pectoral region, neither A nor F bulging; 4 = either F or A bulging; 5 = both F and A bulging. Scoring was done before weighing and therefore was not influenced by results of weighing. Because we did not begin to score fat until midway in the study, this data set is smaller than that for body mass. Sampling efforts lasted several days each time we visited a particular location; when juncos were caught more than once during an effort, only the mass at first capture was included in the analysis.

Environmental data.—Air temperatures before and during sampling were determined from Climatological Data (1976–1980, U.S. Weather Bureau). Reporting stations were within 16 km of their respective sampling locations. "Prior temperature" is the mean of daily mean ([maximum + minimum]/2) temperatures during the 3 days immediately preceding the first day of sampling. "Immediate temperature" is the mean of daily means on the days on which we sampled. "Day length" is the period between morning and evening civil twilight (Nautical Almanac, 1981). From our field observations we characterized snow as falling, on the ground but not falling, or absent. These environmental data appear in Table 1.

Data analysis.—Statistical analyses were done using the Statistical Package for Social Sciences (SPSS, Nie et al. 1975). A three-way analysis of variance was employed to analyze the effect in early winter of sex, age, and location on body mass and wing length. First we tested both dependent variables for heterogeneity across years; using one-way ANOVAs of mass and wing length by year, each sex-age class was treated separately at each location (Table 1 shows data in summary form). Wing lengths were homogeneous except that adult males in Michigan were smaller in the first year of the study than thereafter. Body weight exhibited heterogeneity in the following instances: in Michigan and Indiana (adult and young males, young females), Tennessee (adult females), and South Carolina (young males, adult females). Despite heterogeneity, we combined data across years because a four-way analysis of variance (one that partitioned among years) was prohibited by the fact that sites were sampled in unequal numbers of years. We justified this pooling on two grounds. First, in every year Michigan and Indiana juncos of each class were significantly heavier than birds of the same class from the southern locations. Therefore, the latitudinal difference in body mass that we report below did not arise out of any tendency to sample northern (or southern) juncos in years when juncos everywhere tended to be heavier (or lighter). Second, the almost uniform absence within a sex-age class of annual variation in wing length at each location suggested to us that juncos at any particular site were similar in lean mass from year to year and that only their fat stores differed. From the many options in SPSS three-way ANOVAs, we selected the classic analysis in which each main effect is assessed separately, adjusting for the effect of every other, before assessing the effects of two-way and then three-way interactions (Nie et al. 1975:415).

Visible fat class data were analyzed by Chi-square. Because these sample sizes were smaller than the others, we combined cases from the southern localities and compared them with those from the combined northern localities.

Environmental influences on body mass of each sex-age class were assessed by standard multiple regression (Nie et al. 1975:336), treating each individual as a case. Snow cover was a dummy variable and was coded 0 for no snow and 1 for snow falling or on the ground.

RESULTS

Total body mass and latitude.—Fig. 1 presents, according to latitude of capture site, the mean body mass of each sex-age class in early winter (N = 1353, all years). As Fig. 1 shows, juncos wintering in Tennessee, South Carolina, and Alabama were of similar mass; north of 36°N (Tennessee), mass increased with latitude. Further, males were considerably heavier than females and adults were slightly heavier than young. Three-way analysis of variance confirms these trends as statistically significant and quantifies the differences as follows (Table 2): after correcting for age and location, males were 1.24 g heavier than females; after correcting for sex and location, adults were only 0.26 g heavier than young; after correcting for sex and age, Michigan juncos were 2.73 g heavier than Alabama juncos. We limited this analysis (and those that follow, except where stated) to early winter because aging was more reliable at that season and because Michigan was sampled only at that time. Late-winter results (see Table 1), however, also indicate a latitudinal difference: Indiana juncos were significantly heavier than those from southern sites (results not shown, three-way ANOVA).

This north–south variation in total body mass (wet weight) obviously arose out of differences in one or more of the components of total body mass, including lean mass, fat, body water, and crop contents; and we now consider how these components may have varied geographically.

Lean body mass, as reflected by wing length.—Wing length is almost certainly not a perfect correlate of lean mass, although it is widely used (e.g., James 1970) as such when fat extraction is impossible. Among female juncos, fat extraction has demonstrated a significant correlation between

TABLE 1

DATES OF CAPTURE, SELECTED ENVIRONMENTAL CONDITIONS[a], AND BODY MASS BY SEX-AGE CLASS DURING EACH CAPTURE EFFORT

Location	Symbol[b]	Dates	Prior temp. (°C)	Immediate temp. (°C)	Day length (h)	Snow	Mean body mass (g)[c]			
							Adult males	Young males	Adult females	Young females
Michigan (42°17′, 85°35′)	a	7–8 Dec. 1976	−5.7	−7.2	10.25	1	21.71 ± .216 (47)	21.33 ± .313 (37)	19.93 ± .377 (13)	20.14 ± .507 (7)
	b	11–13 Dec. 1977	−10.1	−5.5	10.18	1	22.09 ± .306 (28)	21.63 ± .271 (28)	19.93 ± 1.680 (3)	20.58 ± .713 (8)
	c	7–9 Dec. 1978	−1.4	−3.8	10.23	1	21.39 ± .187 (39)	20.94 ± .164 (78)	20.25 ± .495 (12)	19.44 ± .290 (29)
	d	2–4 Jan. 1980	−0.8	−3.5	10.22	1	22.36 ± .282 (28)	22.05 ± .210 (42)	20.40 ± .492 (9)	20.02 ± .441 (13)
	e	3–5 Jan. 1981	−13.8	−9.9	10.25	1	22.90 ± .236 (48)	22.29 ± .163 (55)	21.62 ± .513 (12)	21.32 ± .309 (23)
Indiana (39°10′, 86°32′)	f	26–29 Dec. 1977	1.9	−10.1	10.43	1	20.32 ± .266 (22)	20.42 ± .263 (32)	20.93 ± .888 (3)	18.93 ± .275 (9)
	g	15 Feb. 1978 2, 13, 15 Mar. 1978	1.4	−0.4	12.23	0	21.33 ± .374 (24)	21.51 ± .312 (24)	20.02 ± .572 (5)	20.14 ± .593 (8)
	h	27 Dec. 1978 7 Jan. 1979	0.1	−3.1	10.50	0	18.80 ± .283 (14)	18.78 ± .202 (20)	17.50 ± .513 (3)	17.70 ± .532 (5)
	i	24–26 Feb. 1979	2.8	2.9	12.05	1	21.15 ± .432 (13)	21.19 ± .224 (38)	20.13 ± .319 (7)	20.12 ± .371 (20)
	j	9 Jan 1980	−2.7	−3.1	10.62	1	21.26 ± .278 (13)	20.77 ± .283 (20)	19.31 ± .274 (7)	19.58 ± .258 (11)
Tennessee (36°10′, 86°47′)	k	20–22 Dec. 1978	2.8	8.4	10.95	0	19.40 ± .404 (8)	19.58 ± .238 (13)	18.77 ± .174 (6)	18.09 ± .210 (13)
	l	20–23 Dec. 1979	−2.1	7.5	10.95	0	19.55 ± .391 (8)	19.41 ± .248 (9)	17.37 ± .260 (3)	18.01 ± .231 (12)

TABLE 1
CONTINUED

Location	Symbol[b]	Dates	Prior temp. (°C)	Immediate temp. (°C)	Day length (h)	Snow	Mean body mass (g)			
							Adult males	Young males	Adult females	Young females
	m	2–3 Feb. 1980	−4.9	−7.1	11.47	1	20.16 ± .282 (14)	20.11 ± .373 (11)	18.84 ± .359 (10)	18.09 ± .346 (14)
	n	20–24 Dec. 1980	3.3	−1.4	10.95	0	18.83 ± .420 (13)	19.13 ± .244 (23)	17.68 ± .247 (10)	17.31 ± .274 (27)
S. Carolina (34°41′, 82°50′)	o	14–16 Dec. 1976	7.5	4.7	10.75	0	19.58 ± .171 (31)	19.58 ± .181 (22)	18.41 ± .152 (46)	18.26 ± .223 (21)
	p	19–22 Dec. 1977	11.6	6.0	10.75	0	19.50 ± .187 (27)	19.62 ± .304 (14)	18.28 ± .296 (20)	17.88 ± .434 (12)
	q	5–10 Mar. 1978	1.4	3.8	12.50	0	20.09 ± .214 (36)	19.82 ± .220 (26)	19.06 ± .240 (53)	18.37 ± .192 (46)
	r	14–18 Dec. 1978	1.7	4.4	10.73	0	19.12 ± .222 (30)	18.17 ± .251 (18)	17.45 ± .158 (36)	17.96 ± .216 (24)
	s	15–20 Feb. 1979	4.2	3.6	11.90	1	21.02 ± .256 (28)	19.86 ± .544 (9)	19.42 ± .246 (31)	18.69 ± .423 (13)
	t	13–16 Dec. 1979	6.7	10.7	10.75	0	18.85 ± .195 (24)	18.90 ± .174 (31)	17.72 ± .203 (27)	17.70 ± .147 (28)
Alabama (33°31′, 86°48′)	u	12–13 Dec. 1976	7.8	8.1	10.87	0	18.94 ± .219 (13)	18.68 ± .315 (8)	18.11 ± .213 (21)	18.21 ± .614 (16)
	v	17–18 Dec. 1977	11.9	10.1	10.83	0	19.10 ± .346 (3)	18.22 ± .643 (5)	17.91 ± .178 (8)	17.43 ± .448 (6)
	w	18–19 Feb. 1980	4.4	4.8	11.97	0	20.12 ± .829 (4)	19.53 ± .513 (6)	18.97 ± .205 (15)	18.68 ± .450 (4)
Mississippi (33°27′, 88°47′)	x	15–17 Feb. 1980	2.1	4.5	11.87	0	20.20 ± .502 (7)	21.22 ± .744 (4)	18.74 ± .351 (14)	18.96 ± .670 (5)

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[a] See text for definitions and methods of determining environmental conditions.

[b] Symbols are those used in Fig. 4 and are given to permit cross reference.

[c] Standard error follows mean. Sample size in parentheses.

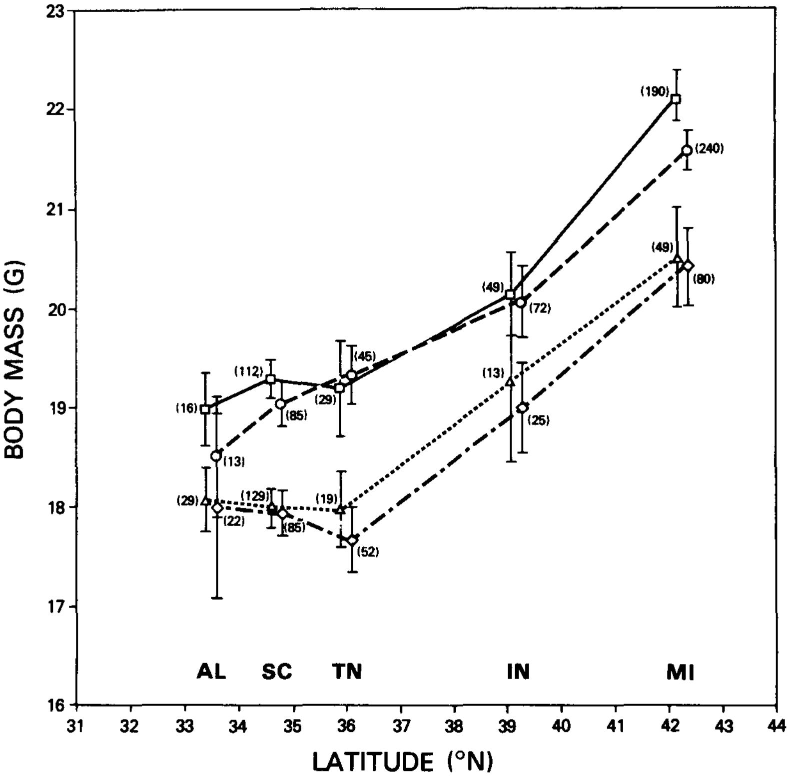

FIG. 1. Body mass of Dark-eyed Juncos in early winter in relation to latitude. Sample sizes appear in parentheses; means (±2 SE) are plotted according to sex-age class: square = adult males, circle = young males, triangle = adult females, angled square = young females. The capture sites are indicated as follows: AL = Alabama, SC = South Carolina, TN = Tennessee, IN = Indiana, MI = Michigan.

lean mass and wing length (Helms et al. 1967), and we have found (unpubl.) a significant positive relationship between wing length and other measures that may correlate with lean mass: tarsal length, tail length, and several bill dimensions. Accordingly, we analyzed early-winter wing length within each sex-age class, from north to south. (Use of wing length was not necessary in early winter, either for the purpose of sexing or of aging.) Fig. 2 and Table 2 show that there were no within-class geographic differences in early winter when all years were combined (N = 1692), and this was also true during each year (results not shown, one-way ANOVA).

The similarity in wing length among juncos of the same sex and age,

TABLE 2
THREE-WAY ANOVA COMPARING BODY MASS AND WING LENGTH IN EARLY WINTER BY SEX, AGE, AND LOCATION[a]

Main effects	Body mass	Wing length
Sex	***	***
Male	850, 0.46 g	1074, 1.60 mm
Female	503, −0.78 g	618, −2.79 mm
Age	***	***
Adult	635, 0.14 g	795, 0.89 mm
Young	718, −0.12 g	897, −0.79 mm
Location	***	NS
Michigan	559, 1.43 g	697, 0.04 mm
Indiana	159, −0.19 g	283, 0.06 mm
Tennessee	145, −1.19 g	177, 0.18 mm
South Carolina	410, −1.21 g	453, −0.13 mm
Alabama	80, −1.30 g	82, −0.18 mm
Interactions		
Sex-age	NS	***
Sex-site	NS	NS
Age-site	NS	NS
Sex-age-site	NS	NS
r^2	0.549	0.834
Grand mean	19.90 g	80.13 mm

[a] Asterisks indicate results of F-tests (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$) for main effects (sex, age, location) and interactions; NS indicates $P > 0.05$. Also given are sample size for each category (e.g., male) separated by a comma from the average deviation in mass of the members of that category from the grand mean (mean of all individuals regardless of category, see bottom line of table) after adjusting for the other main effects. For example, we analyzed body mass of 1353 juncos and the grand mean was 19.9 g; 850 of these were male, and males tended to exceed the grand mean by 0.46 g after accounting statistically for variation in mass attributable to age and capture location. Similar data have been presented for wing length, but because there was a significant sex-age interaction the deviations must be considered only an approximation.

regardless of wintering site, makes it appear highly improbable to us that the demonstrated differences in overall mass were primarily attributable to variation in lean body mass.

Fat stores, as reflected by visible subcutaneous fat.—Fat classes of northern juncos tended to be much higher than those of southern juncos (Fig. 3 and Table 3). We conclude, therefore, that at least some of the greater overall mass of northern juncos was attributable to their carrying more fat, and in most of the remainder of this paper we seek to account for that difference.

Other possible sources of variation.—It is possible that northern juncos

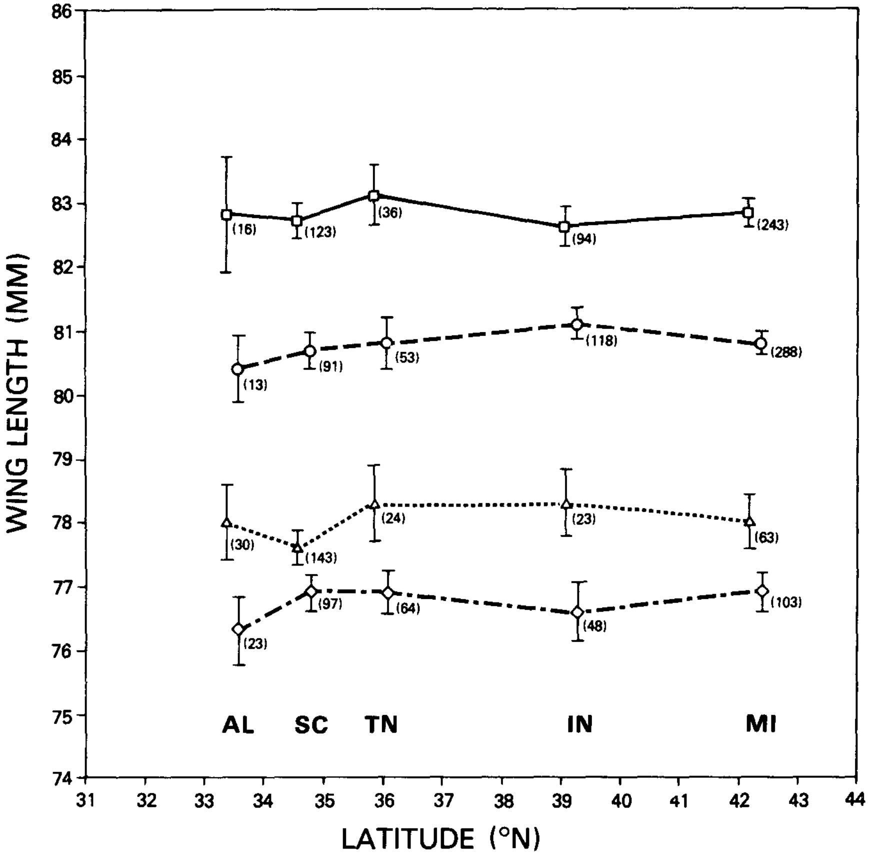

FIG. 2. Wing length of Dark-eyed Juncos in early winter in relation to latitude. See Fig. 1 for meanings of symbols.

carried more body water, and it seems probable that their crop contents were greater. Our bait provided abundant food at all capture sites, but southern juncos may have eaten less frequently and/or consumed less during a single feeding bout. The extent to which these components contributed to the geographic variation in total mass is not known.

Environmental correlates of body mass.—In an effort to explain the north-south variation in fat stores, we regressed (multiple regression) body mass on four environmental and two temporal variables as well as on latitude and wing length. Early- and late-winter data were combined and the sex-age classes analyzed separately. Table 4 presents the results.

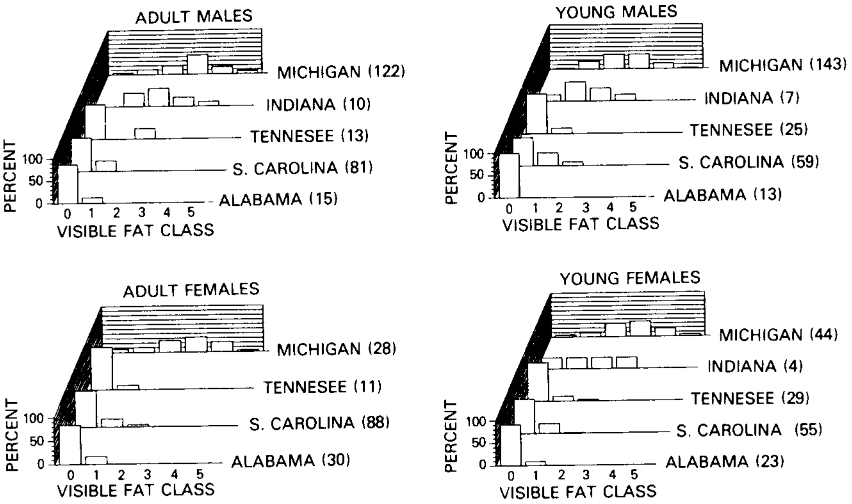

FIG. 3. Frequency distributions of visible fat classes according to location, sex-age classes presented separately. Sample sizes are indicated in parentheses.

Latitude accounted for most of the explained variation. Juncos of each sex-age class were heavier at higher latitudes, and this was true even after controlling statistically for climatic factors often thought to affect seasonal differences in fat stores, i.e., day length, presence or absence of snow, and immediate and prior temperature. Other significant partial regressions were these: (1) Mass increased with day length, i.e., juncos were heavier in late winter. (2) Mass was greater when snow was present. (3) Except in adult females, mass was negatively correlated with air temperature on the days just prior to sampling; except in young females, it was not correlated with air temperature on the days of sampling. (Fig. 4 depicts for one class, adult males, the relationship between mass and prior temperature.) (4) Mass was greater later in the day, as is commonly true (e.g., Helms and Drury 1960). (5) Mass increased with wing length. This may be taken as evidence that wing length is a good indicator of overall lean body size (see above), but other possible interpretations are that longer-winged juncos carry relatively more fat, have more body water, or have fuller crops.

Despite the use of seven independent variables in this regression, considerable variation in body mass was unexplained. Measurement error is partly responsible for this, but unidentified environmental factors may also have been important.

TABLE 3

RELATIVE FREQUENCY OF INDIVIDUALS BELONGING TO VARIOUS VISIBLE FAT CLASSES[a] IN EARLY WINTER, ACCORDING TO LOCATION AND SEX-AGE CLASS; SOUTHERN LOCATIONS (ALABAMA, SOUTH CAROLINA, TENNESSEE) ARE COMBINED AND COMPARED TO NORTHERN LOCATIONS (MICHIGAN AND INDIANA) COMBINED[b]

		Visible fat class						
		0	1	2	3	4	5	median[c]
Adult males	North	5	16	27	55	21	8	2.83
	South	84	21	4	0	0	0	0.14
				χ^2 =	171.23	df = 3		
Young males	North	4	28	49	48	18	3	2.38
	South	72	20	5	0	0	0	0.17
				χ^2 =	163.17	df = 3		
Adult females	North	2	3	7	9	6	1	2.72
	South	103	21	4	1	0	0	0.12
				χ^2 =	101.91	df = 3		
Young females	North	3	5	14	16	8	2	2.63
	South	88	17	2	0	0	0	0.10
				χ^2 =	115.17	df = 3		

[a] Visible fat was classified according to the method of Helms and Drury (1960), slightly modified as described in the text.
[b] Fat classes 0, 1, 2, and 3–5 (last combined) were compared in order to produce acceptable expected values.
[c] Medians were determined by linear interpolation.

DISCUSSION

Our data indicate that (1) junco body size, insofar as it is accurately indicated by wing length, does not vary from north to south during winter; (2) junco body mass does vary, and the larger mass of northern juncos is at least in part attributable to greater fat stores; and (3) the single best predictor of mass, and thus probably of fat stores, is the latitude of the wintering site.

The absence of geographic size (wing length) variation across the winter range of a migratory species is interesting in itself, because many sedentary species in eastern North America exhibit clines in wing length that are closely correlated with climatic variation (James 1970). Similar clines could arise in a migratory species if some mechanism caused individuals to select their wintering sites according to their body sizes. Apparently, juncos have no such mechanism (see also Ketterson and Nolan 1982).

In seeking to account for variation in fat stores, most studies of fattening have focused on temporal fluctuations in fat within and across winters and

TABLE 4

STANDARD MULTIPLE REGRESSION OF BODY MASS ON LATITUDE, WING LENGTH, AND ENVIRONMENTAL VARIABLES, EARLY AND LATE WINTER, ACCORDING TO SEX AND AGE[a]

Variable	b	Partial F, P	r^2 contribution	Simple r	Overall F, df, P
Adult males					
Latitude	0.192	19.97, ***	0.348	0.590	F = 67.56
Wing length	0.170	19.80, ***	0.022	0.154	df = 7,513
Time	0.001	42.26, ***	0.051	0.266	***
Day length	0.307	7.56, **	0.031	−0.210	
Snow	0.817	13.30, ***	0.012	0.587	
Prior temperature	−0.061	14.51, ***	0.014	−0.552	
Immediate temperature	0.022	1.14, NS	0.001	−0.524	
			0.480		
Young males					
Latitude	0.222	24.38, ***	0.321	0.567	F = 56.61
Wing length	0.128	10.43, ***	0.007	0.086	df = 7,561
Time	0.001	23.17, ***	0.024	0.308	***
Day length	0.496	18.94, ***	0.047	−0.164	
Snow	0.633	6.89, **	0.007	0.559	
Prior temperature	−0.047	9.24, **	0.008	−0.478	
Immediate temperature	0.015	0.66, NS	0.000	−0.463	
			0.414		
Adult females					
Latitude	0.195	14.14, ***	0.209	0.458	F = 30.76
Wing length	0.169	16.05, ***	0.036	0.220	df = 7,363
Time	0.001	19.28, ***	0.052	0.255	***
Day length	0.408	13.09, ***	0.051	0.037	
Snow	0.712	10.63, ***	0.022	0.489	
Prior temperature	0.008	0.13, NS	0.000	−0.396	
Immediate temperature	−0.018	0.41, NS	0.001	−0.455	
			0.372		
Young females					
Latitude	0.280	30.68, ***	0.328	0.572	F = 39.13
Wing length	0.233	22.25, ***	0.026	0.155	df = 7,362
Time	0.001	10.78, ***	0.020	0.220	***
Day length	0.379	10.89, ***	0.038	−0.134	
Snow	0.642	6.33, *	0.006	0.529	
Prior temperature	−0.053	6.81, **	0.004	−0.490	
Immediate temperature	0.052	5.62, *	0.009	−0.446	
			0.431		

[a] Levels of significance: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS $P > 0.05$; b = partial regression coefficient; r^2 = coefficient of determination; simple r = Pearson's correlation coefficient.

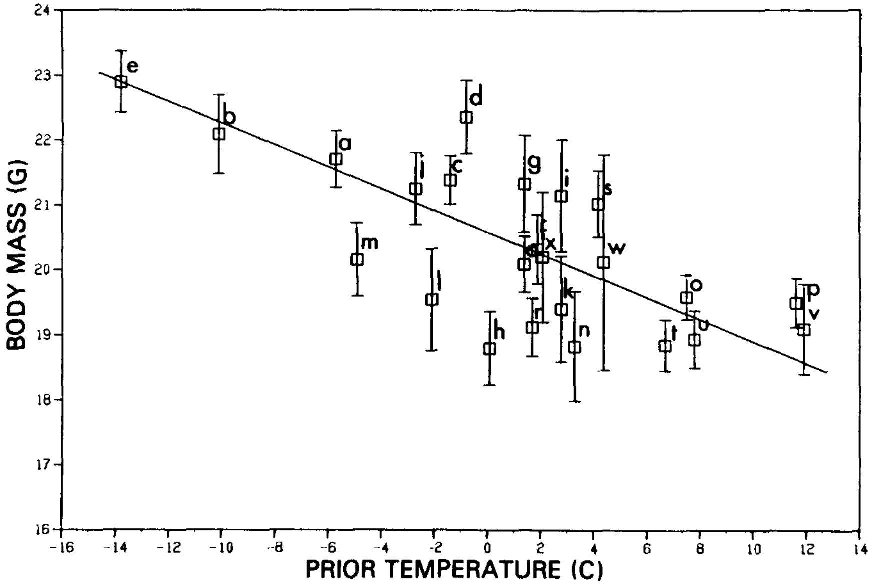

FIG. 4. Body mass of adult males as a function of air temperature. Given is the mean mass (±2 SE) at each sampling event (see Table 1 to match letters with sampling events). The solid line is the least squares regression line of the masses of individual juncos on air temperature prior to sampling (mean temperature during the 3 days prior to sampling).

have sought to correlate these with a variety of environmental variables (e.g., King and Farner 1966, Evans 1969). These studies distinguish between proximate and ultimate causation, i.e., between (1) selective pressures that over evolutionary time have favored individuals that fatten at some dates but not at others and (2) external cues and/or internal rhythms that vary with the season and cause the animal to fatten or not. The discussion that follows makes the same distinction, but our emphasis is on spatial as opposed to temporal variation.

Ultimate cause of fattening.—The ultimate cause of the geographic variation in fat stores that we report is almost certainly climate. Weather is much more likely to restrict the food of northern than of southern juncos. When this happens, the birds can either wait out the period of severe weather, making local movements in search of exposed food, or they can engage in long-distance dispersal that might enable them to reach regions unaffected by the adverse weather. Movements on this latter scale would resemble migration in their energetic demands, and preparation to meet those demands might account for the fatness of northern juncos. However, for two reasons we believe that northern juncos rarely make long-distance winter movements to escape food deprivation. First, analysis of United States Fish and Wildlife Service banding and recovery data reveals little within-winter long-range dispersal (Ketterson and Nolan 1982). Second, with C. M. Rogers, we have transported juncos from Michigan and Tennessee in December and released them in Indiana in January. Most remained at the release site and were recaptured, many after 6 weeks. This suggests to us that the birds may have been physiologically incapable of long movements (see also Rowan 1927); and we believe that it is the strategy of juncos to wait out bad weather at or near the location in which they settle after autumn migration, metabolizing their stored fat in the interim.

In this study, Michigan juncos were approximately 2.7 g heavier than Alabama juncos after correction for sex and age. If we use the rate of overnight weight loss, 0.11 g/h at 4°C, reported for juncos by Ketterson and Nolan (1978) to estimate fasting ability, 2.7 g translates to a 25-h north–south difference. Alternatively, Stuebe and Ketterson's (1982) regression of body mass on fasting endurance [endurance (h) = 5.65 (initial mass [g]) − 74.30] gives Michigan juncos a 14–17-h advantage. Whichever estimate is more nearly correct, the potential advantage of carrying fat in harsh climates seems clear.

Possible advantages of leanness.—The almost uniformly low fat levels of southern juncos may be as interesting as the high levels of their northern counterparts. While it is possible that juncos in the south were lean because food was scarcer there than in the north, we think this very unlikely. First, southern juncos were, like northern, heavier in late winter than in early winter (Table 1), notwithstanding that the food of juncos is largely non-renewing in winter and undergoes depletion with time. Second, recalling that the sex-age classes of juncos differ in relative dominance status and that adult males are the dominant class (Balph 1977, Baker and Fox 1978, Ketterson 1979), we would expect, in the event of food shortage, that adult males would suffer least and therefore would carry the most fat. Contrary to this expectation, Table 3 shows that the median fat classes in early winter in the south were similar for all sex-age classes, suggesting no inequality of access to scarce resources. We therefore believe that southern juncos were lean because it was advantageous to be so.

Leanness might be selected for if cost of locomotion varies with wing loading. If we assume that wing length correlates with wing area and if for a given wing area fat level correlates with wing loading, then, because fat varied with latitude but wing length did not, southern juncos were more lightly loaded than northern (compare Blem 1975); and their locomotory costs were presumably lower (Pennycuick 1975). Lower mass may also improve agility in flight or accelerate take-offs, both factors that might increase the probability of escape from predators. We are not the first to suggest that these and other conjectural pressures might be expected to prevail and counterselect against fattening in environments or at times where fat stores are rarely needed (King 1972, Dugan et al. 1981, Freed 1981, Norberg 1981, Stuebe and Ketterson 1982, for birds; Gyug and Millar 1980, Millar 1981, for mammals).

Proximate causes of fattening.—We consider here the results of our multiple regression analysis and what they may reveal about the cues that regulate fat levels and lead to the north–south difference we observed. Studies of seasonal variation in body mass at single locations have often found air temperature to be a correlate of fattening, but the nature of the relationship has varied. Some investigators have observed negative correlations (e.g., Helms and Drury 1960, King and Farner 1966, Blem 1978, King 1972 for summary); others (Haftorn 1976, Biebach 1977), corelations that shift from negative to positive, or vice versa; and still others (Evans 1969), no correlation at all. In our study, even though low air temperature just prior to sampling was associated with greater mass (and high temperature with lesser mass) when effects of other variables were controlled for, air temperature nevertheless accounted for only a very small part of the observed variation. As for other possible cues, day length (Evans 1969, Knowles 1972, Evans and Smith 1975), snow cover (Haftorn 1976, Vincent and Bédard 1976), and wind speed (Dugan et al. 1981) have been found to be significant correlates of fat levels. Evans (1969) reported that day length on the day 30 days before the one on which fat stores of Yellow Buntings (*Emberiza citrinella*) were measured correlated highly with fat levels, suggesting a proximate cue whose effect, nevertheless, was not immediate. For juncos, we found significant partial correlations between mass and day length and mass and snow cover but, as with temperature, these variables account for very little variation. Evans' finding may suggest that day length, not at the time of sampling but at some earlier time, might explain some of our unaccounted-for variation (see below).

While we recognize that variables found significant in a regression analysis may not be meaningful to the animals under study, the correlations between mass and snowfall and mass and temperature indicate to us that juncos have some limited capacity to respond to short-term weather changes and, other things being equal, that they increase food consumption or decrease energy expenditures when recent temperatures have been cold and snow is on the ground. If this is correct, the ability to augment and deplete fat stores in response to conditions that vary unpredictably and frequently suggests that juncos are highly sensitive to both the advantages and disadvantages of transporting stored fat.

Why did latitude account for most of the explained variation in body mass? We attribute this to the high correlation in the eastern United States between latitude and long-term environmental conditions influencing thermoregulatory demands and food availability. Among these conditions are mean December-February air temperature, the lowest temperature ever recorded, mean annual snowfall, and mean daily minimum air temperature in January (Ketterson and Nolan 1976). When physiological or behavioral events of temperate-zone organisms correlate better with long-term means than with current weather, day length is often proposed as the proximate cue that controls those events (Evans 1969, Vincent and Bédard 1976). If, in fact, juncos fatten to a greater degree in the north because days are shorter there than in the south, we must credit them with the ability to perceive and respond to relatively small differences in length of day. At our sampling site in Michigan the shortest day is 9 h 17 min long, as against 9 h 51 min in Alabama (Nautical Almanac, 1981). Alternatively, it may be that juncos cannot discriminate between day-length differences of this magnitude, but rather that the birds themselves differ from place to place, such that northern juncos respond to days of given lengths by fattening to a greater extent than do southern birds exposed to the same cue. A difference in response to an identical cue would imply genetic differentiation among winter populations; it would also imply some association between the mechanism that controls fattening and the mechanism that controls distance migrated. The absence of geographic size (wing length) clines within sex-age classes is circumstantial evidence that members of any particular breeding population scatter widely in winter, i.e., that winter populations are a mix of breeding populations and not likely to be genetically differentiated from north to south. This question obviously deserves further study (Ketterson and Nolan 1982).

Finally, day length need not be the controlling regulatory variable. Northern birds are exposed earlier in the winter season to conditions that elevate metabolism and they, like some mammals (Selander 1952), may respond to cold (after some delay) by an increase in appetite. The fact that juncos everywhere tended to be heavier in late winter could be explained by supposing a summation effect, with northern juncos experiencing some critical weather variable(s) over a longer period or at a greater intensity than southern juncos.

SUMMARY

Many temperate-zone bird species accumulate fat stores during winter. These stores are commonly assumed to serve as energy reserves for the longer nights, colder temperatures, and increased probability of fasting during periods of snow cover; but little is known about what regulates fat storage at the proximate level. If seasonal fattening is a response to winter climate, then a latitudinal cline in degree of fattening would be expected in many parts of the world.

This paper reports such latitudinal variation in the body mass of Dark-eyed Juncos (*Junco hyemalis*) captured at six locations under a variety of environmental conditions during several winters. Juncos at higher latitudes (Michigan and Indiana) were significantly heavier than those from more southern sites (Tennessee, South Carolina, Alabama, and Mississippi). This was true of young and adult individuals of both sexes and was not a function of latitudinal variation in body size (as measured by wing length). Visible fat stores were also greater at higher latitudes, and we conclude that northern juncos were fatter than their southern counterparts.

Multiple regression of body mass on measures of temperature, day length, and snow cover as well as on wing length, latitude, and hour of day indicates that latitude was by far the best predictor of mass; but all the variables produced significant partial regression coefficients. Thus, juncos were heavier when recent temperatures had been colder, when days were longer, and when snow was present. Additionally, they were heavier if they had longer wings or were caught later in the day.

Two explanations of latitudinal variation in fattening are considered. Northern and southern juncos may represent genetically differentiated populations varying in their regulatory physiology. Alternatively, juncos may simply respond in a graded manner to conditions that vary in their proximate physical environments. Results to date can be taken to support either view.

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