GEOGRAPHIC VARIATION IN WINTER FAT OF DARK-EYED JUNCOS: DISPLACEMENT TO A COMMON ENVIRONMENT[1]

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Abstract. Many small temperate-zone birds fatten in winter and use this reserve when food becomes unavailable. The winter body mass of migratory Dark-eyed Juncos (*Junco hyemalis*) usually is greater where severe weather is more frequent, i.e., at higher latitudes or altitudes. The mechanism responsible for this geographic variation is unknown, and we asked whether geographically separated populations are composed of birds with different capacities or tendencies to fatten. We sampled the lipid index (LI, grams of lipid per gram of lean dry mass) of free-living juncos at three latitudes in two winters and found geographic variation. However, the pattern of variation in LI at the three latitudes was not consistent, either within or between winters.

We also displaced wintering juncos from northern, intermediate, and southern sites and exposed them to a common environment in Indiana. One group of displaced birds was released in natural junco habitat (during three winters), and another was held outdoors in captivity (during two winters). Many released birds remained nearby, and when we recaptured some of them in late winter the LIs of the three geographic subgroups were statistically indistinguishable. It was also indistinguishable from the LI of juncos sampled at that time from the free-living Indiana population. Among the displaced birds that we held captive, we found no differences among the geographic subgroups either in LI or total body mass. In one of the years, late-winter LI and body mass of the captives did not differ from values for the released group or from values of newly caught Indiana juncos, but in the second year values for the captives were lower.

Our results indicate that geographic variation in winter fattening of juncos is not a population-specific trait that persists independently of current environmental information and that it probably reflects a response to local environmental conditions. To our knowledge, this is the first experiment using free-living birds to test the role of the environment in maintaining geographic variation in a life history trait in the nonbreeding period.

Key words: common garden; displacement; geographic variation; junco; lipids; nonbreeding fitness; regulation; winter fattening.

INTRODUCTION

In winter, many bird species at temperate latitudes increase stored body fat (see King 1972, Blem 1976 and, for reviews, Dawson et al. 1983*b*, Blem 1990). Winter fat supplies energy for thermoregulation during long, cold winter nights (Lehikoinen 1987, Webb and Rogers 1988, Rogers and Rogers 1990) and provides an emergency reserve during periods of sudden food shortage, such as occur after snowfall (King 1972, Ketterson and King 1977, Nolan and Ketterson 1983, Rogers 1987, Dawson and Marsh 1989). Fattening varies geographically in some species, the usual pattern being a positive relationship between fat and latitude (Blem 1973, Dick and Pienkowski 1979, Nolan and Ketterson 1983), although there are exceptions (King and Mewaldt 1981, Dawson and Marsh 1986). Further, lipid

reserves at any particular site, at least at higher latitudes, tend to be low after autumn migration and in early winter and to reach a peak in mid- or late-winter (Helms et al. 1967, Evans 1969, Newton 1969, Carey et al. 1978, Blem 1980, Dawson et al. 1983*a*, Lehikoinen 1986, 1987 are examples), although again there are exceptions (e.g., Blem 1981, Mortensen et al. 1985). Thus, both geographic and temporal variation appear to reflect associated variation in nightly thermoregulatory demands and probability of weather-related fasting.

The fat reserve can be viewed as a life history trait that allows bird populations to adjust to winter environmental conditions (Nolan and Ketterson 1983, Lima 1986, Rogers 1987, Houston et al. 1988). The winter environment of interior North America is characterized by highly variable temperature and snowfall. As a result, for small ground-feeding birds, metabolic demands and access to food are unpredictable. Plasticity in life history traits is expected to evolve in such uncertain environments (Bradshaw 1965, Levins 1968, Jain 1979, Caswell 1983, Newman 1988, 1989, Stearns 1989). Therefore geographic differences in fattening may

be attributable to plasticity of behavior and physiology in response to recent and current local environmental conditions. Alternatively, these differences might reflect the operation of past selection on geographically separated winter populations, adapting members of the populations to average environmental conditions at the appropriate latitudes. We report a set of "common garden" experiments designed to distinguish between these hypotheses in the Dark-eyed Junco (*Junco hyemalis*), a small-bodied emberizid finch that exhibits north-to-south variation in the winter fat level.

Nolan and Ketterson (1983) measured winter body mass and visible subcutaneous fat of Dark-eyed Juncos at five locations in the eastern United States and found that both mass and visible fat were greater in the north than in the south. Values varied clinally southward to about latitude 36° N; south of this, variation disappeared (Nolan and Ketterson 1983). Latitude, snow cover, day length, and recent temperature all produced significant partial regression coefficients when related to mass, with latitude accounting for the greatest percentage of variation. Visible fat class, body mass, and lipid index (LI, ratio of dried extractable fat to lean mass) are strongly correlated in juncos (Rogers and Rogers 1990, Rogers 1991).

These relationships are consistent with both of the possibilities presented above. First, fat storage in juncos may be regulated in large measure by the severity of recent weather. Recently experienced day length is also an environmental variable that might be involved in regulation. Because the severity of weather and also day length covary with latitude, the statistical correlations reported by Nolan and Ketterson (1983) could be explained by supposing that latitude is a complex variable summarizing important elements of the individual junco's recent and current environment. The alternative hypothesis is that the association of winter fat stores with latitude is the result of population-level differentiation in the tendency to fatten during winter, i.e., that geographic variation may be independent of environmental factors that vary within the lifetime of the individual bird.

We sampled the early-winter fat reserve of juncos at three latitudes and found geographic variation. We also transported juncos from the northern and the southern locations to the third site (Indiana), which is in the middle of the junco's winter range and approximately halfway between the other two locations. We asked (1) to what extent exposure of displaced juncos to a common environment would abolish their early-winter geographic differences in fat stores and (2) to what extent their late-winter fat stores would resemble those of free-living members of the populations from which we displaced them and also of members of the natural free-living Indiana population. If geographic differences in winter fattening depend upon recently experienced environmental variables, displaced subgroups would converge in their fat reserves and would ap-

proximate the level of the natural population at the Indiana displacement site. If, however, the reported differences in fattening were specific to geographic populations and independent of current local environmental information, individuals from populations whose early-winter LI differed according to latitude would continue to differ after displacement.

METHODS

Study species

Our subjects were young juncos (hatched in the preceding breeding season; aged as described by Ketterson and Nolan 1976, 1982, Nolan and Ketterson 1983) belonging to the eastern migratory race, which moves southward in fall from breeding grounds located primarily in the boreal forests of Canada (Ketterson and Nolan 1976). In eastern North America, the winter range lies between 45° N and 26° N (Ketterson and Nolan 1983a). Males tend to winter north of females and young to winter north of adults of the same sex (Ketterson and Nolan 1976, 1979, 1983a, 1985). Fall migration ends about 1 December (Nolan and Ketterson 1990). Thereafter populations are considered stable until ≈1 March (but see Terrill 1987), when spring migration begins, probably at all latitudes (Ketterson and Nolan 1976). Prenuptial molt is slight (primarily on the chin and throat) or is absent, and spring premigratory fattening in our displaced juncos did not begin until the 3rd wk of March, i.e., too late to affect our results.

Capture and treatment of subjects

All juncos in this study were caught at the three locations in Michigan (MI), Indiana (IN), and Tennessee (TN) where Nolan and Ketterson (1983) reported geographic variation. Subjects are divided among three groups: (1) juncos in natural populations at their chosen winter sites; (2) juncos displaced to Indiana in early winter and released there; (3) juncos displaced to Indiana in early winter and held captive there. The fat reserve in all three groups was measured using a lipid index determined by lipid extraction as described by Rogers (1991). Data were arcsine transformed in accordance with Blem (1984).

Locations, dates of sampling, and numbers of birds sampled from the natural populations are presented in Table 1. Juncos that were displaced also were caught at the times and locations shown in Table 1. In addition, during 1984–1985 we displaced birds from these same three locations on 15–19 December (IN), 20–22 December (MI), and 2–5 January (TN). We immediately transported all displaced birds by automobile to the Indiana University aviary, where we either caged or released them. Dates of release were 19 January 1983, 7–9 January 1984, and 15 January 1985. Each winter, numerous free-living juncos occupy the aviary grounds, and in all winters many displaced–released

TABLE 1. Dates and locations of capture of natural junco populations sampled for LI (grams of lipid per gram lean dry mass)*.

| Winter | Geographic location† | | |
	MI, 42°17′ N	IN, 39°10′ N	TN, 36°10′ N
1982–1983			
Early	15–17 Dec 1982	18–26 Dec 1982	28–31 Dec 1982
Late	19–20 Feb 1983	17–26 Feb 1983	18 Feb 1983
1983–1984			
Early	14–16 Dec 1983	18–22 Dec 1983	29–31 Dec 1983
Late	2 Mar 1984	27–29 Feb 1984	23–25 Feb 1984

* Sample size was 10 birds in all cases, except that in early and late winter 1983-1984 sample size was 6 birds in TN.
† MI = Michigan; IN = Indiana; TN = Tennessee.

birds joined the free-living population. We distributed cracked corn and millet on the grounds and kept food available after snowfalls. Late in winter we recaptured some of the released birds at the aviary and later analyzed their LI. Recapture dates were 26 February and 2 March 1983, 27 February 1984, and 16–17 February 1985. On these same dates in 1983 and 1984, we caught new samples of Indiana juncos in order to compare their LI with that of the displaced birds. Average hour of capture was about the same (near midday) in each winter. On about these same dates in 1983 and 1984, we returned to the locations from which we had taken the displaced birds (Table 1) and caught samples of free-living juncos there; later we analyzed the LI of these samples.

Birds that we held captive after displacement were sacrificed for LI analysis on 2 March 1983 and 1 March 1984. Prior to this we weighed displaced–captive birds every 2–7 d (shortly after dark), because we expected body mass would provide an estimate of stored body fat (Helms et al. 1967). This proved to be true (Rogers and Rogers 1990, Rogers 1991). The large outdoor cages, in which captives could move at will between

an unheated indoor and an outdoor chamber, have been described elsewhere (Ketterson and Nolan 1983b). Cracked corn, millet, water supplemented with vitamins, and branches and cut evergreen trees as roost sites were freely available. In order to facilitate comparisons of body mass, average wing length (a general indicator of overall body size, James 1970) was equalized in the selection of birds to be caged. Male juncos are larger and heavier on average than females (Nolan and Ketterson 1983); therefore when comparing body mass of geographic subgroups we controlled statistically for sexual variation.

RESULTS

LI of juncos at natural winter sites

Among the geographic populations sampled on their home ranges in early winter and again in late winter of 1982–1983 and 1983–1984 (Table 1), mean LI of the subgroups varied from 0.30 to 0.45 in early winter and from 0.41 to 0.56 in late winter (Fig. 1). Geographic variation was significant in both early and late winter of each year. However, the pattern changed seasonally and between winters.

In early winter 1982–1983, the rank order of LI was MI > IN > TN (analysis of variance F test, $P = .026$). A posteriori multiple comparisons (after Sokal and Rohlf 1981) indicated that the Michigan and Indiana subgroups were indistinguishable statistically and differed from the Tennessee subgroup ($P < .05$, Tukey's test). Two months later, in February 1983, the rank order of LI was the same, and the geographic variation was again significant ($P = .003$), but now the Indiana and Tennessee subgroups were alike and were different from the Michigan subgroup ($P < .05$, Fig. 1).

Geographic variation was also significant in early winter 1983–1984 ($P \ll .001$), but the rank order was TN > IN > MI; mean LI varied from 0.32 to 0.64 (Fig. 1). LI in the Michigan and Indiana subgroups did not differ significantly, but both differed from the Tennessee subgroup ($P < .05$). In late February–March 1984, the rank order was IN > MI > TN, the mean LI ranging from 0.28 to 0.53. The difference was significant ($P = .001$); the Michigan and Indiana birds
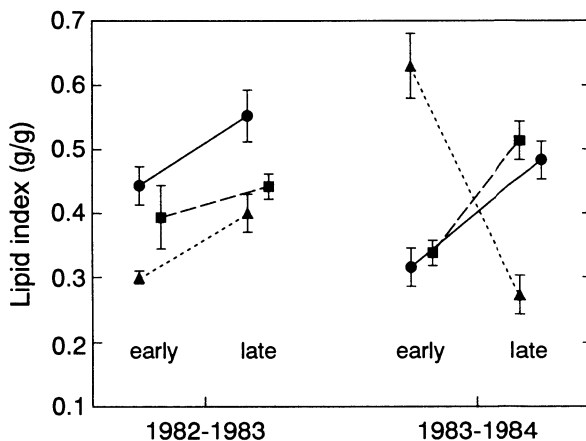

FIG. 1. Lipid index (grams of lipid per gram lean dry mass, $\bar{X} \pm 1$ SE) of natural junco populations in early and late winter, 1982–1983 and 1983–1984. ●, ■, and ▲ represent MI, IN, and TN, respectively. Sample size was 10 birds, except that in Tennessee in early and late winter sample size was 6.

did not differ from one another but did differ significantly from the Tennessee subgroup ($P < .05$, Fig. 1). Tennessee juncos, the fattest subgroup in early winter, were the leanest in late winter.

LI of displaced–released juncos

Separating the late-winter data by capture location and pooling across all 3 yr, mean LI among the released geographic subgroups varied from 0.48 to 0.49 and did not differ among locations ($P = .952$). Analyzing each year separately, LI did not differ significantly according to site of origin ($P > .05$, analysis of covariance with capture time as a linear covariate), but in one year the difference approached significance (1983: $P = .052$; 1984: $P = .304$; 1985: $P = .391$; Fig. 2). There was no consistent rank order of LI among geographic subgroups, and in no winter were the birds from the northern population (Michigan) fattest (Fig. 2).

Mass and LI of captive juncos

On the occasions when we weighed the displaced–captive birds, body mass never differed significantly among geographic subgroups (13 dates 1982–1983, 11 dates 1983–1984; Fig. 3, $P > .05$ in all cases). Similarly, LI in late winter did not differ among subgroups ($P = .247$ and .355 for 1983 and 1984, respectively; Fig. 2). LI of captives in late winter ranged from 0.37 to 0.45 (compare Fig. 1 and Fig. 2) and was slightly less variable than LI of free-living birds sampled at their natural three geographic locations late in the same two winters.

Comparison of displaced juncos with Indiana juncos caught in late winter

In late winter 1982–1983 and 1983–1984, we compared body mass and LI of the pooled displaced–cap-
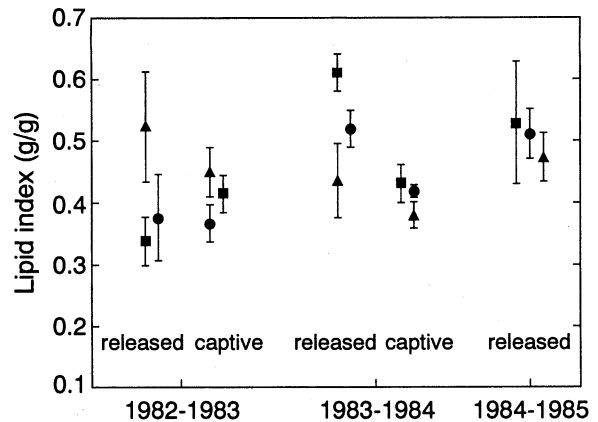

FIG. 2. Lipid index ($\bar{X} \pm 1$ SE) of displaced–released and displaced–captive juncos in late winter. Symbols as in Fig. 1. Sample sizes were as follows: 1982–1983, released MI and IN 5, TN 4 birds; captive, all locations 10 birds; 1983–1984, released MI 2, IN 5, TN 3 birds; captive, all locations 8 birds; 1984–1985, released MI 10, IN 8, and TN 14 birds.

tive birds, the pooled displaced–released birds, and Indiana birds newly caught from the free-living population (Table 2). In 1983 there were no significant differences in either body mass or LI among these groups (Table 2). In 1984, the groups tended to differ in LI ($P = .055$), with captives showing the lowest values (Table 2); in addition, captives had significantly lower body mass than the other two groups.

Pooled analysis of LI of captive and released birds

When we consider the mean LI of all of the displaced–released and displaced–captive subgroups, we

TABLE 2. ANCOVA comparisons* of late-winter lipid index (LI = grams of lipid per gram lean dry mass) and body mass among three groups of juncos. Data shown as means ± SE. N = no. birds.

Group	N	LI	Body mass (g)
1983			
IN: natural population	10	0.45 ± 0.02	19.88 ± 0.39
MI, IN, TN: displaced–released (pooled)	14	0.41 ± 0.04	19.75 ± 0.49
MI, IN, TN: displaced–captive (pooled)	30	0.41 ± 0.02	18.80 ± 0.15

Source of variation	df	P	df	P
Group	2	.182	2	.479
Time of day	1	.554	1	.144
Sex	1	⋯	1	.001
Group × Sex	2	⋯	2	.002

Group	N	LI	Body mass (g)
1984			
IN: natural population	10	0.53 ± 0.03	20.77 ± 0.49
MI, IN, TN: displaced–released (pooled)	10	0.52 ± 0.03	20.40 ± 0.24
MI, IN, TN: displaced–captive (pooled)	24	0.42 ± 0.02	18.80 ± 0.15

Source of variation	df	P	df	P
Group	2	.055	2	.005
Time of day	1	.001	1	.888
Sex	1	⋯	1	.004
Group × Sex	2	⋯	2	.137

* GLM procedure (SAS 1985).

obtain a sample of 15 means (displaced–released subgroups from three locations in three winters and displaced–captive subgroups from three locations in two winters). If we take each mean as a unit of replication (Eberhardt and Thomas 1991) and compare the populations, we find no significant geographic variation in late-winter LI (Kruskal–Wallis one-way analysis of variance, $P = .464$). This analysis is a stronger test of similarity in fat level of the displaced populations than are the analyses presented above, which use individual birds as the unit of replication.

DISCUSSION

It was long assumed that variation in life histories reflects the outcome of natural selection acting to optimize adaptation to local environmental conditions. However, studies of many taxa in uncertain environments have suggested strong environmental influences on life history traits, such that individual organisms undergo phenotypic change as the proximate environment changes (Bradshaw 1965, Levins 1968, Stearns 1976, Jain 1979, Caswell 1983, Brown 1985, Schlichting 1986, 1989, Kaplan 1987, Newman 1988, 1989, Ford and Siegel 1989, Rotenberry and Wiens 1991). It has become apparent that knowledge of plasticity of traits is essential for fuller understanding of life history evolution (Stearns 1989). Thus among birds, James (1983, 1991) has demonstrated experimentally that patterns of geographic variation in morphology of Redwinged Blackbirds (*Agelaius phoeniceus*) have a component that is directly induced by the environment in which the young develop. She has also reported (1991) high, general concordance among a number of bird species in their clinal patterns of geographic variation in size and color of plumage.

LI of juncos at their natural winter sites

Among juncos caught and sacrificed at their natural winter locations in 1982–1983, the north-to-south rank order of LI conformed in both early and late winter to the pattern described by Nolan and Ketterson (1983). That is, body mass and fat varied positively with latitude. Next year, however, in early winter 1983–1984, Tennessee juncos were fattest, whereas in late-winter Indiana birds were fattest; thus, at neither season in 1983–1984 was LI of Michigan birds highest. The difference in the geographic pattern of fattening between 1982–1983 and 1983–1984 is contrary to predictions of the hypothesis of population-level differentiation in energy storage. Since day length was constant between winters but rank order of fat reserves differed, the annual variation also suggests that day length is not the primary environmental cue that juncos use to adjust LI.

LI of displaced–released juncos

Although LI differed geographically early in the two winters in which we analyzed local populations on their chosen wintering grounds, in late winter significant differences were no longer apparent among the displaced–released birds. On the assumption that the displaced birds were representative of their source populations (i.e., assuming that their LI differed geographically at the time they were displaced), the absence of a late-winter geographic difference in their LI suggests that the subgroups became more similar after exposure to a common environment. However, the samples were small, the power of the test was low, and the variation considerable, so the evidence from 1982–1983 is weak. We therefore ask whether the trends of within-winter change might suggest geographic differentiation of populations.

In late winter 1982–1983, the displaced–released birds from Tennessee had the highest LI of the three subgroups. In contrast, among juncos caught late in that same winter at their respective home sites, Tennessee juncos were the leanest (Fig. 1). This comparison of Tennessee birds that were free living with those that we displaced and released shows that Tennessee birds were capable of storing greater energy than they in fact stored when they wintered in Tennessee. Somewhat similarly, late in the same winter (1982–1983), Michigan juncos on their chosen wintering grounds were considerably fatter than Michigan birds displaced to and released in Indiana. Thus, high LI in late winter is not an obligate trait of juncos from Michigan. These observations are inconsistent with the prediction of the hypothesis that fat levels in late winter are determined by differentiation among populations; they suggest instead that recent environment has a strong regulatory effect.

In 1983–1984, the late-winter rank order of the displaced–released subgroups was the same as the late-winter order in the natural populations (IN > MI > TN) (Fig. 1). However, for the natural populations this represents a change from early winter, when their rank order had been TN > IN > MI (Fig. 1). In addition, juncos displaced from Tennessee were considerably fatter than juncos that remained in Tennessee, indicating (as in 1982–1983) that Tennessee juncos were capable of greater lipid storage than they displayed on their natural wintering grounds (compare Fig. 1 and Fig. 2).

In 1984–1985, when we compared displaced–released birds in late winter, the subgroups were very much alike (Fig. 2). This suggests convergence in Indiana, but we have no data from natural populations in that year.

Finally, LI and body mass of the pooled displaced–released juncos and of juncos caught in Indiana in late winters of 1983–1984 and 1984–1985 did not differ (Table 2). This also tends to falsify, perhaps most convincingly, the hypothesis that winter fattening is regulated independently of current local environmental conditions.
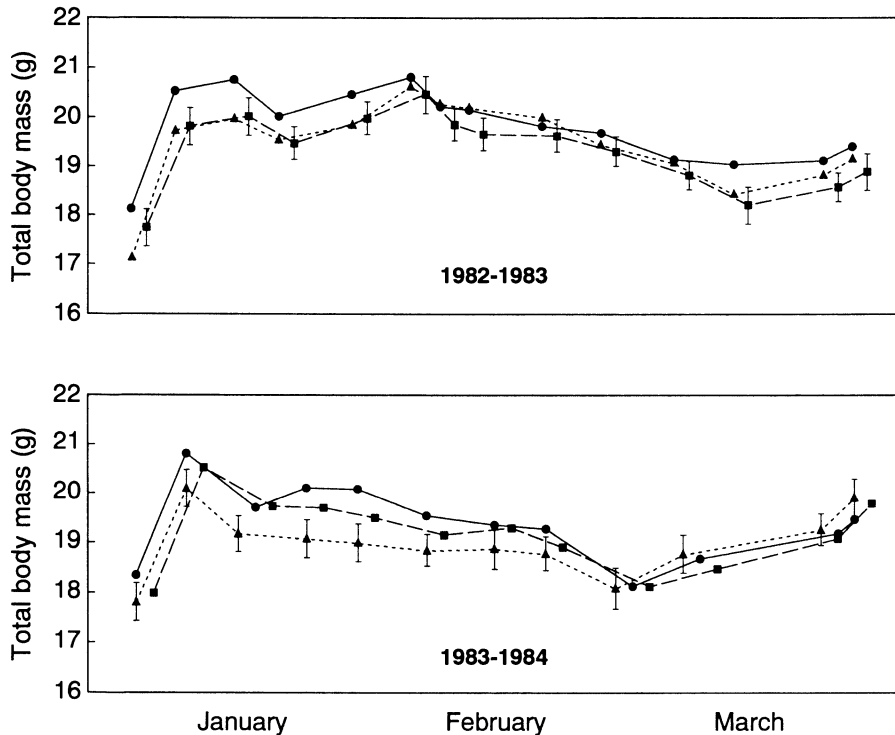
FIG. 3. Total body mass ($\bar{X} \pm 1$ SE) of the displaced–captive juncos in 1982–1983 and 1983–1984. For clarity, only the largest SE is shown. In 1982–1983, sample sizes were 20 birds per geographic subgroup (symbols as in Fig. 1) for the first 11 dates; thereafter they were 10. In 1983–1984, sample sizes were MI 14, IN 18, and TN 12 birds. Sex ratios were at unity in each geographic subgroup in each year.

Body mass and LI of captive juncos

In 1982–1983 and 1983–1984, there was no significant geographic difference in body mass of the displaced–captive juncos on any of the dates on which we weighed them (Fig. 3). In both winters, mass was lowest shortly after the birds were transported and caged, probably because this experience disrupted normal feeding. Soon, however, mass rose to its highest or almost its highest level and was strikingly similar among subgroups; thereafter the subgroups remained similar, even though mean mass per subgroup changed over time (Fig. 3). Thus, the data on mass point to recent environment as a major basis for regulation of fattening. Consistently with this result, LI in late winter did not differ among captive geographic subgroups in either year.

In one of the two years (1983–1984), captives weighed less in late winter and were less fat than either the released birds or the newly caught Indiana birds. This may indicate that the condition of being captive sometimes prevents juncos from regulating fattening normally, as was reported by Helms and Smythe (1969) for American Tree Sparrows (*Spizella arborea*). However, a more likely explanation of this result is that captive juncos did regulate normally and, in response to the fact that abundant food was predictable, deposited less fat than free-living conspecifics (see Ekman

and Hake 1990). We also made food available on the aviary grounds, but, even so, birds living free in Indiana in winter must contend with conditions that make future access to food unpredictable; this fact could cause them to store more energy than captives. In any case, displaced captives, displaced–released birds, and newly caught Indiana juncos all were exposed to the same temperatures. This eliminates temperature as a factor in the difference between the captive and free-living juncos, leaving predictability of resources as a candidate (J. B. Ekman, *personal communication*).

Conclusion

Our results suggest that winter junco populations are alike in their regulation of fattening and that geographic differences are probably caused by response to a recently experienced set of environmental factors. Taken together, our evidence does not support the hypothesis that geographic variation is caused by population-level differences in the regulatory system. All displaced birds shared exposure to the Indiana photoperiod and weather in the weeks preceding sacrifice for analysis of LI. Differences in day length between the northern and the southern sites from which we displaced juncos averaged only 15 min from 1 December to 1 March. For temperate-zone birds, this seems a small difference to account for the observed latitudinal variation in fat-

tening and for the fact that LI of displaced–released and of free-living Indiana juncos were indistinguishable in late winter. Further, the difference in rank order of LI of natural populations differed between 1982–1983 and 1983–1984, when we sampled at the same three locations and on virtually the same dates (Table 1), indicating that fattening is not strongly regulated by photoperiod. Exposure to recent weather, then, seems most likely to be the experience to which the regulatory mechanism reacts. If so, the junco resembles species that fatten in direct response to recent temperature (e.g., Newton 1969, O'Connor 1973, Jenni and Jenni-Eiermann 1987) and differs from those that store winter fat in anticipation of long-term average conditions (King and Mewaldt 1981, Blem and Shelov 1986, Dawson and Marsh 1986). The basis for the junco's responsiveness to current local winter conditions may be its differential migration. A corollary of the fact that young juncos tend to winter north of adults (Ketterson and Nolan 1983a, 1985) is that fidelity to the winter site is low, especially in birds entering the second winter of life (V. Nolan Jr. and E. D. Ketterson, *unpublished manuscript*). Further, banding evidence reveals that when individuals were caught in two different winters, in most cases they had migrated farther southward in the second winter (Ketterson and Nolan 1982). Adaptation to the climate of a particular latitude would not be expected, given such a life history (C. M. Rogers, V. Nolan Jr., and E. D. Ketterson, *unpublished manuscript*).

An additional basis for the absence of population-specific modes of winter fattening may be the fact that most of the winter range of the Dark-eyed Junco lies in the unpredictable continental climate of interior North America (Ketterson and Nolan 1983a), where both temperature and snowfall are highly variable both within and among winters. The geographic variation in winter fattening of juncos supports theory predicting evolution of plasticity in uncertain environments (Caswell 1983). Through such a strategy, birds can maximize probability of survival by avoiding the costs of depositing and carrying unnecessary fat. These costs probably include exposure to predators while feeding (Lima 1986) and, possibly, reduced maneuverability. If weather begins to worsen, fat can be deposited quickly as the probability of forced fasting increases. Our study extends knowledge of life history plasticity to the nonbreeding period, when survival, not reproduction or development, is the fitness variable.

ACKNOWLEDGMENTS

LITERATURE CITED

Blem, C. R. 1973. Geographical variation in the bioenergetics of the House Sparrow. Ornithological Monographs 14:96–121.

——. 1976. Patterns of lipid storage and utilization in birds. American Zoologist 16:671–684.

——. 1980. Multiple regression analyses of mid-winter lipid levels in the House Sparrow, *Passer domesticus.* Pages 1136–1142 *in* R. Nohring, editor. Proceedings of the XVIIth International Ornithological Congress. Verlag der Deutschen Ornithologen-Gesellschaft, Berlin, Germany.

——. 1981. Geographic variation in mid-winter body composition of Starlings. Condor 83:370–376.

——. 1984. Ratios in avian physiology. Auk 101:153–155.

——. 1990. Avian energy storage. Pages 59–113 *in* D. M. Power, editor. Current Ornithology 7. Plenum, New York, New York, USA.

Blem, C. R., and M. H. Shelov. 1986. Multiple regression analyses of mid-winter fasting of the White-throated Sparrow. Canadian Journal of Zoology 64:2405–2411.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics 13:115–155.

Brown, K. M. 1985. Intraspecific variation in a pond snail: the roles of population divergence and phenotypic plasticity. Evolution 39:387–395.

Carey, C., W. R. Dawson, L. C. Maxwell, and J. A. Faulkner. 1978. Seasonal acclimatization to temperature in cardueline finches. II. Changes in body composition and mass in relation to season and acute cold stress. Journal of Comparative Physiology B125:101–113.

Caswell, H. 1983. Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. American Zoologist 23:35–46.

Dawson, W. R., and R. L. Marsh. 1986. Winter fattening in the American Goldfinch and the possible role of temperature in its regulation. Physiological Zoology 59:357–368.

Dawson, W. R., and R. L. Marsh. 1989. Metabolic acclimatization to cold and season in birds. Pages 83–94 *in* C. Bech and R. E. Reinertsen, editors. Physiology of cold adaptation in birds. Plenum, New York, New York, USA.

Dawson, W. R., R. L. Marsh, W. A. Buttemer, and C. Carey. 1983a. Seasonal and geographic variation of cold resistance in House Finches, *Carpodacus mexicanus.* Physiological Zoology 56:353–369.

Dawson, W. R., R. L. Marsh, and M. E. Yacoe. 1983b. Metabolic adjustments of small passerine birds for migration and cold. American Journal of Physiology 245:R755–R767.

Dick, W. J. A., and M. W. Pienkowski. 1979. Autumn and early winter weights of waders in northwest Africa. Ornis Scandinavica 10:117–123.

Eberhardt, L. L., and J. M. Thomas. 1991. Designing environmental field studies. Ecological Monographs 61:53–57.

Ekman, J. B., and M. K. Hake. 1990. Monitoring starvation risk: adjustments of reserves in Greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. Behavioral Ecology 1:62–67.

Evans, P. R. 1969. Winter fat deposition and overnight survival of Yellow Buntings (*Emberiza citrinella*). Journal of Animal Ecology 38:415–423.

Ford, N. B., and R. A. Siegel. 1989. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. Ecology 70:1768–1774.

Helms, C. W., W. H. Aussiker, E. B. Bower, and S. D. Fretwell. 1967. A biometric study of the Slate-colored Junco, *Junco hyemalis.* Condor 69:560–578.

Helms, C. W., and R. B. Smythe. 1969. Variation in major body components of the Tree Sparrow (Spizella arborea) sampled within the winter range. Wilson Bulletin 81:280–292.

Houston, A. S., C. Clark, J. McNamara, and M. Mengel. 1988. Dynamic models in behavioural and evolutionary ecology. Nature 332:29–34.

Jain, S. 1979. Adaptive strategies: polymorphism, plasticity, and homeostasis. Pages 160–187 in O. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven, editors. Topics in plant population biology. Columbia University Press, New York, New York, USA.

James, F. C. 1970. Geographical size variation in birds and its relationship to climate. Ecology 51:365–390.

———. 1983. The environmental component of geographic variation in the size and shape of birds: transplant experiments with blackbirds. Science 221:184–186.

———. 1991. Complementary descriptive and experimental studies of clinal variation in birds. American Zoologist 81:694–706.

Jenni, L., and S. Jenni-Eiermann. 1987. Body weight and energy reserves of Bramblings in winter. Ardea 75:271–284.

Kaplan, R. H. 1987. Developmental plasticity and maternal effects of reproductive characteristics in the frog, Bombina orientalis. Oecologia (Berlin) 71:273–279.

Ketterson, E. D., and J. R. King. 1977. Metabolic and behavioral responses to fasting in the White-crowned Sparrow (Zonotrichia leucophrys gambelii). Physiological Zoology 50:115–129.

Ketterson, E. D., and V. Nolan Jr. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (Junco hyemalis hyemalis). Ecology 57:679–693.

Ketterson, E. D., and V. Nolan Jr. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of Dark-eyed Juncos (Junco hyemalis). Auk 96:532–536.

Ketterson, E. D., and V. Nolan Jr. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analyses of winter populations. Auk 99:243–259.

Ketterson, E. D., and V. Nolan Jr. 1983a. The evolution of differential bird migration. Pages 357–402 in R. F. Johnston, editor. Current Ornithology I. Plenum, New York, New York, USA.

Ketterson, E. D., and V. Nolan Jr. 1983b. Autumnal Zugunruhe and migratory fattening of Dark-eyed Juncos apparently suppressed by detention at the wintering site. Wilson Bulletin 95:628–635.

Ketterson, E. D., and V. Nolan Jr. 1985. Intraspecific variation in avian migration: evolutionary and regulatory aspects. Pages 553–579 in M. A. Rankin, editor. Migration: mechanisms and adaptive significance. University of Texas Contributions in Marine Science Supplement 27.

King, J. R. 1972. Adaptive periodic fat storage in birds. Pages 200–217 in K. H. Voous, editor. Proceedings of the XVth International Ornithological Congress. E. J. Brill, Leiden, The Netherlands.

King, J. R., and L. R. Mewaldt. 1981. Variation in body weight in Gambel's White-crowned Sparrow in winter and spring: latitudinal and photoperiodic correlates. Auk 98:752–764.

Lehikoinen, E. 1986. Winter ecology of passerines: significance of weight and size. Dissertation. University of Turku, Turku, Finland.

———. 1987. Seasonality of the body weight cycle in wintering passerines and its consequences. Ornis Scandinavica 18:216–266.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology 67:366–376.

Mortensen, A., E. S. Mordoy, and A. S. Blix. 1985. Seasonal changes in the body composition of the Norwegian Rock Ptarmigan, Lagopus mutus. Ornis Scandinavica 16:25–28.

Newman, R. A. 1988. Adaptive plasticity in developmental time of Scaphiopus couchii tadpoles in desert ponds. Evolution 42:774–783.

———. 1989. Developmental plasticity of Scaphiopus couchii tadpoles in an unpredictable environment. Ecology 70:1775–1787.

Newton, I. 1969. Winter fattening in the Bullfinch. Physiological Zoology 42:96–107.

Nolan, V., Jr., and E. D. Ketterson. 1983. An analysis of body mass, wing length, and visible fat deposits of Dark-eyed Juncos wintering at different latitudes. Wilson Bulletin 95:603–620.

Nolan, V., Jr., and E. D. Ketterson. 1990. Timing of autumn migration and its relation to winter distribution in Dark-eyed Juncos. Ecology 71:1267–1278.

O'Connor, R. J. 1973. Patterns of weight change in the House Sparrow, Passer domesticus (L.). Pages 111–125 in S. C. Kendeigh and J. Pinowski, editors. Productivity, population dynamics and systematics of granivorous birds. PWN-Polish Scientific Publishers, Warszawa, Poland.

Rogers, C. M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? Ecology 68:1051–1061.

———. 1991. An evaluation of the method of estimating body fat by quantifying visible subcutaneous fat. Journal of Field Ornithology 62:349–356.

Rogers, C. M., and C. J. Rogers. 1990. Seasonal variation in daily mass amplitude and minimum body mass: a test of a recent model. Ornis Scandinavica 21:105–114.

Rotenberry, J. T., and J. A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. Ecology 72:1325–1335.

SAS. 1985. SAS user's guide: statistics. Version 5 edition. SAS Institute, Cary, North Carolina, USA.

Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. Annual Review of Ecology and Systematics 17:667–693.

———. 1989. Phenotypic integration and environmental change. BioScience 9:460–471.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. Freeman, New York, New York, USA.

Stearns, S. C. 1976. Life history tactics: a review of the ideas. Quarterly Review of Biology 51:3–47.

———. 1989. The evolutionary significance of phenotypic plasticity. BioScience 39:436–445.

Terrill, S. B. 1987. Social dominance and migratory restlessness in the Dark-eyed Junco, Junco hyemalis. Behavioral Ecology and Sociobiology 21:1–11.

Webb, D. R., and C. M. Rogers. 1988. Nocturnal energy expenditure of Dark-eyed Juncos roosting in Indiana in winter. Condor 90:107–112.