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## **Winter fattening in the dark-eyed junco: plasticity and possible interaction with migration trade-offs**

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**Abstract** Although fat often supplies the major source of metabolic fuel during winter fasts of birds, this critical life-history trait is little studied by ecologists. In the dark-eyed junco *Junco hyemalis*, we have in a series of studies investigated the extent of plasticity in the winter fat reserve. Earlier (Rogers et al. 1993), we reported (1) a highly variable pattern of geographic variation in the winter fat reserve of junco populations in eastern North America, (2) disappearance of statistically significant interpopulation variation after experimental displacement to a common latitude, and (3) post-displacement temporal variation in the fat reserve. In analyses reported here, recent temperature, recent snowfall (a measure of short-term predictability of resources), season (perhaps reflecting continued exposure to unpredictable resources) and daylength explained spatial variation in the fat store. Recent temperature explained temporal variation in the fat reserves of groups of displaced juncos. These results suggest that plasticity in a life-history trait has evolved in an uncertain winter environment. Through environment-dependent fattening, the costs of fat can be avoided during warm periods and at locations where fat confers little benefit, whereas benefits of fat can be quickly gained if weather conditions become harsh and snowfall might restrict food. Three types of winter fatteners probably exist among birds: responders (fatten in response to the proximate environment), predictors (fatten in anticipation of long-term environmental conditions), and responder-predictors (combination of both types of regulation). Because dark-eyed juncos select different winter latitudes as they age, we hypothesize that the nonbreeding component of the life-history of juncos includes the co-adapted plastic traits of winter

fattening and post-breeding migration. Life-history theory can apparently explain important traits related to fitness in the nonbreeding period.

**Key words** Plasticity · Life history · Migration · Fat · Trade-off

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## Introduction

Life-history theory considers how complexes of traits (e.g., age at first reproduction, offspring size and number) interact to determine fitness (Williams 1966; Stearns 1976; Lessels et al. 1989; Sinervo and Licht 1991). It was long assumed that variation in life histories reflects largely genetic variation, i.e., natural selection acting to adapt individuals to local environmental conditions. However, studies of many taxa in uncertain environments have suggested strong environmental influences on life-history traits; apparently, many organisms can increase fitness by altering their phenotypes as demographic and environmental conditions vary (Bradshaw 1965; Levins 1968; Jain 1979; Caswell 1983; Brown 1985; Schlichting 1986, 1989; Kaplan 1986; Newman 1988; Ford and Siegel 1989; Stearns 1989; Brawn 1991; Rotenberry and Wiens 1991). It has become increasingly apparent that knowledge of plasticity in traits is essential for a complete understanding of life-history evolution.

Most studies of life-history phenomena have focused primarily on events in the reproductive period. However, the life history of many organisms includes one or more lengthy nonbreeding periods, which must be survived in order to reach the breeding season. Selection should favor those traits that maximize the probability of nonbreeding survival (Lima 1986; McNamara 1990; McNamara and Houston 1990; Houston and McNamara 1993). Here we report the results of several tests for phenotypic plasticity in a nonbreeding trait of small birds, the winter fat reserve.

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Among birds, body fat supplies the major source of metabolic fuel during winter fasts, e.g., sudden resource shortages (snowfalls) and prolonged roosting at low environmental temperatures (Rogers 1987; Rogers and Rogers 1990; Rogers and Smith 1993; recently reviewed by Blem 1990). In an earlier study of dark-eyed juncos *Junco hyemalis* in central North America (Rogers et al. 1993), we reported that: (1) the pattern of geographic variation in the winter fat level was highly variable, with a positive relationship between fat and latitude changing to a negative relationship both within and between winters; (2) in a series of experiments, the fat levels of northern- and southern-wintering junco populations displaced to an intermediate latitude became indistinguishable from the fat level of an intermediate-latitude population; and (3) a substantial amount of post-displacement temporal variation in fat occurred, and was similar among displaced populations.

These three findings suggest environmentally-driven variation in this life-history trait which adapts individuals to local winter environmental conditions of temperature and snowfall (Nolan and Ketterson 1983; Lima 1986; Rogers 1987; Houston et al. 1988; Ekman and Hake 1990). Through this mechanism, the costs of fattening [e.g., exposure to predators while feeding (Lima 1986) and reduced maneuverability (Blem 1975)] can be avoided in warm periods, but the benefits (fasting capacity) can be quickly gained by rapid fat deposition as cold and snowy conditions occur. Thus, through plasticity in the uncertain winter environment, an "optimal" amount of winter fat might be maintained at any place in the winter range, and at any time in the winter period. In this companion paper on the dark-eyed junco we present three different analyses designed to identify the environmental factors behind the changing pattern of geographic variation in the fat level, and the apparent convergence and subsequent temporal variation in fat observed among displaced populations. These analyses are therefore of data reported by Rogers et al. (1993).

Post-breeding migration is a second life-history trait in the non-breeding period of many bird species. Therefore a second goal of this report is to consider how winter fattening and postbreeding migration might both be plastic traits that interact to maximize nonbreeding fitness. To attempt this, we review junco migration in eastern North America and discuss the extent to which winter fattening and migration might be co-adapted in the traditional sense of life-history theory (Stearns 1976).

## Methods

Analysis 1: predictors of the fat reserves in natural junco populations

### Sampling natural junco populations

Dark-eyed juncos (members of each sex produced in the preceding breeding season; age and sex determined after Ketterson and Nolan 1976, 1982) were collected in late afternoon from natural winter populations in southern Michigan (MI), southern Indiana

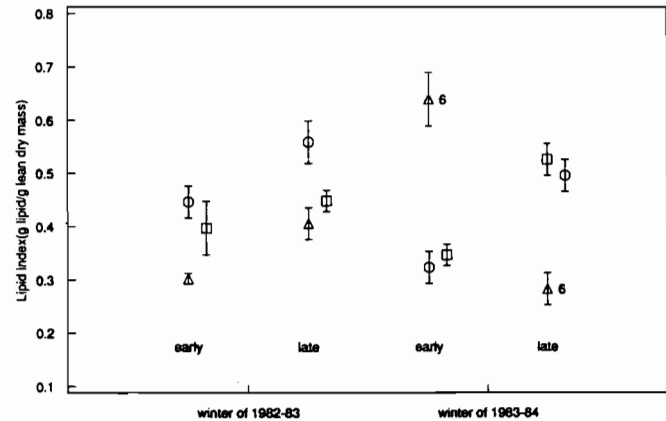


Fig. 1 Lipid index ( $\bar{x} \pm 1$  SE) in natural junco populations in early and late winter; two separate winters are shown (from Rogers et al. 1993). Sample size is 10 except where indicated otherwise. Circles, squares, and triangles represent MI, IN, and TN, respectively

(IN), and central Tennessee (TN) early and late in each of two winters. The lipid index (LI, g lipid/g lean dry mass) of each bird was determined in the laboratory (details concerning sampling and lipid extraction are given by Rogers 1987, 1992). Wing length, a measure of body size in juncos, does not vary with latitude in the MI, IN, and TN populations (Nolan and Ketterson 1983), nor does lean dry mass, a more direct measure of body size (Rogers in prep.); hence body size could not have confounded geographic variation in LI caused by environmental factors (below).

### Multivariate analysis: rationale and structure

Sampling natural junco populations revealed a highly variable pattern of geographic variation. When LI was sampled early and late in each of two winters, LI varied both positively and negatively with latitude between MI and TN [all  $P$ s < 0.05, Fig. 1; this figure is repeated from Rogers et al. (1993) for clarity of presentation]. A correlation and regression analysis was designed to identify environmental factors that might drive the changing pattern of geographic variation. Mean LI on the 20 days that natural populations were sampled was transformed with the angular transformation, weighted for sample size, correlated with a set of environmental variables, and regressed on a representative subset of non-colinear variables, as follows (SAS Institute 1985).

The factor set includes the major environmental factors that vary with time and space in the wintering phase and range of the junco, i.e., recent and long-term temperature, daylength, recent snowfall, and snow cover (Table 1). SEASON and DAYLENGTH were highly correlated in the data set (Pearson  $r = 0.999$ , 2-tailed  $P < 0.0001$ ); hence only SEASON was used in the analysis. However, in this correlation analysis, any interpretation of the effect of one variable (e.g., SEASON) cannot exclude an effect of the alternative variable (e.g., DL; see Discussion).

The correlation matrix relating independent variables revealed frequent multicollinearity, a condition associated with unreliable regression coefficients (Weisberg 1985; Wonnacot and Wonnacot 1985). To eliminate this problem, a representative subset of non-colinear factors (all Pearson  $r < 0.90$ ) was chosen for stepwise regression of LI: MT0C, MT0-10C, MNORMC, SEASON/DL, SC05TOT, TSN, and LAT (Table 1). That colinearity was removed by this process of variable selection was suggested by the regression diagnostics in SAS (procedure REG), which indicated no colinearity in the correlation matrix of selected variables.

**Table 1** Definition of variables entered into the initial correlation analysis of mean LI in winter MI, IN, and TN junco populations (see Methods for subset of these factors included in the weighted multiple regression analysis). Units of variables: daily temperature, °C; temperature normals, °C, where temperature normals are long-term means (1931–1960) with extreme values removed (see below); snow variables, cm; season, number of days since beginning of the wintering phase (1 December, the date all juncos in a given population can be first considered as postmigratory); daylength, h; latitude, °N latitude of trap sites. Temperature data were obtained from U.S. Environmental Data Service Climatological Data 1982–1984 (daily temperatures), and from a U.S. Weather Bureau decennial census, U.S. Weather Bureau (1963) (normals); snowfall data were obtained from Climatological Data and supplemented with on-site field observations made during trap efforts; daylength was calculated as the interval from a.m. civil twilight to p.m. civil twilight

Variable abbreviation	Variable definition
AT0C	mean daily temperature [(minimum + maximum)/2] on trap day
AT1-3C	average of 3 mean daily temperatures occurring on the 3 days before trap day
AT0-10C	average of 11 mean daily temperatures occurring on trap day and the 10 days preceding it
MT0C	minimum daily temperature occurring on trap day
MT1-3C	average of 3 daily temperature minima occurring on the 3 days before trap day
MT0-10C	average of 11 daily temperature minima occurring on trap day and the 10 days preceding it
ANORMC	average of maximum and minimum temperature normals for trap day
MNORMC	minimum temperature normal for trap day
SNO	presence or absence of snowfall on trap day
SNO5	presence or absence of snowfall in the period including trap day and the 5 days preceding it
SC0TOT	total snowfall on trap day
SC05TOT	total snowfall in the period including trap day and the 5 days preceding it
TSN	total snowfall in the period from 1 Dec. through trap day
DL	daylength on trap day
SEASON	number of days after 1 Dec. that trap day occurred
LAT	latitude at which birds were trapped

Analysis 2: predictors of the fat reserves in displaced-released junco populations

#### *Displacement, release, and retrapping*

In the early winters of 1982–1983, 1983–1984, and 1984–1985, MI, IN, and TN juncos trapped on their wintering grounds were displaced to the intermediate latitude (IN), and released into natural junco habitat (Rogers et al. 1993). IN juncos were taken from local IN populations occupying habitat near the release site. Many displaced-released birds remained in the release area and some were retrapped in late winter for determination of LI. Statistical analysis of retrap data showed that MI and TN birds remained at the release site at rates similar to or greater than “displaced” IN juncos. Thus there is no reason to suspect that data from retrapped juncos are biased by differential mortality.

#### *Multivariate analysis*

Of the set of environmental variables considered for natural populations, only temperature differed substantially among the three different winters during which displaced populations were stud-

ied. Therefore a correlation analysis of late-winter LI limited to temperature variables and latitude of winter origin was performed (see Results).

Analysis 3: predictors of the fat reserves in displaced-captive junco populations

#### *Displacement and aviary conditions*

In the winters of 1982–1983 and 1983–1984 (but not 1984–1985), a subset of each displaced junco population was held captive in IN (instead of being released). Captive populations occupied a large aviary together (described in Rogers et al. 1993) and were weighed every several days from the time of flock establishment (mid-January) until late winter (end of March). Temporal variation in mean total body mass on weigh days was used as an indicator of variation in size of the fat reserve (Rogers et al. 1993; see also Ekman and Hake 1990).

#### *Multivariate analysis*

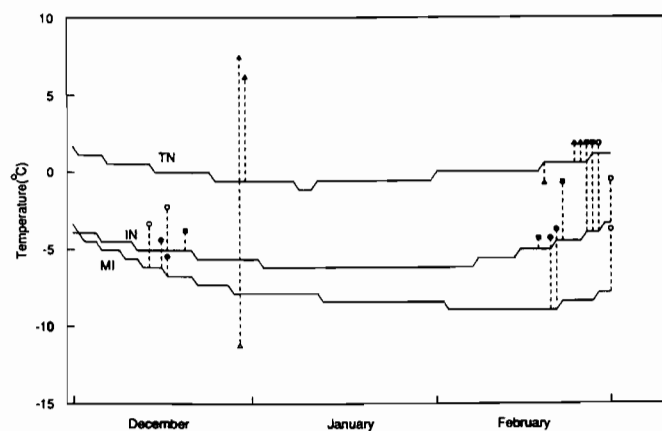
Variation in body mass was correlated with each independent variable in the complete set described above, although only the best correlates are reported because data taken repeatedly from the same individuals are not independent. A “best correlate” is defined as the independent variable that generated the highest Pearson correlation coefficient when all variables were correlated individually with mean body mass and then compared.

## **Results**

Analysis 1: predictors of the fat reserves in natural junco populations

Recent temperature (measured by MT0-10C, the best correlate of LI, see below) departed substantially from long-term temperature normals on the 20 days that natural populations were sampled (Fig. 2). This feature of the data set facilitated statistical isolation of the influences of these factors, because either recent or long-term temperature, but not both, would be likely to emerge as a good predictor of the dependent variable. Temperatures preceding trap days at all three latitudes showed substantial departures from the long-term normals, especially in TN (Fig. 2). Almost all departures were above normal, an important exception being one early winter in TN (Fig. 2).

Of the set of 15 variables in the preliminary correlation analysis, four were significantly correlated with geographic variation in arcsin-transformed LI (Table 2). Of the noncolinear subset of eight variables, recent temperature (MT0-10C), SEASON/DL (recall their high correlation, hence their treatment as one factor), and snow cover (SC0TOT) each explained a significant proportion of the variation in transformed LI, resulting in an  $R^2$  value of 68% (Table 3). As expected from the significance of SEASON/DL, the simple correlation between transformed LI and MT0-10C varied in size and significance from early to late winter (Fig. 3). Recent temperature was a better predictor of transformed LI in early than in late winter.



**Fig. 2** Long-term daily normal temperature (1931–1960) for MI, IN, and TN capture sites (solid lines). Departures of recent temperature from long-term temperature on the 20 days that the natural populations were sampled are indicated by dashed vertical lines and symbols (circles MI, squares IN, triangles TN; open and closed symbols represent the winters of 1982–1983 and 1983–1984, respectively). Recent temperature is represented by the average of the 11 daily minima on capture day and the 10 days preceding capture day, MT0-10C (see Material and methods). This factor was the best correlate of LI detected among the natural junco populations (see Results)

**Table 2** Correlates of LI (treated with the angular transformation) in the pooled natural junco populations (MI, IN, TN), listed in decreasing order of statistical significance. Pearson product-moment correlation coefficients weighted for sample size are given; 2-tailed *P* values are in parentheses

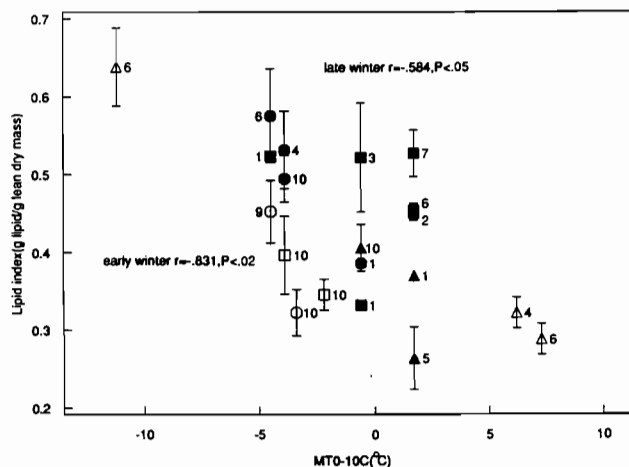
Variable	<i>r</i> ( <i>P</i> )	Variable	<i>r</i> ( <i>P</i> )
MT0-10C	-0.574 (0.008)	AT0C	-0.338 (0.145)
AT0-10C	-0.497 (0.026)	ANORMC	-0.314 (0.178)
MT1-3C	-0.493 (0.027)	MNORMC	-0.285 (0.223)
AT1-3C	-0.461 (0.041)	SC0TOT	0.270 (0.249)
SEASON/DL	0.386 (0.093)	TSN	0.258 (0.271)
SN05	0.369 (0.109)	LAT	0.252 (0.285)
MT0C	-0.345 (0.137)	SC05TOT	-0.178 (0.451)
SN0	0.341 (0.141)		

**Table 3** Results of stepwise multiple regression of LI (treated with the angular transformation) on environmental and latitudinal factors, in the pooled natural junco populations (MI, IN, TN)

Factor	Partial reg. coeff. ( <i>P</i> )	Contrib. to <i>R</i> <sup>2</sup>
MT0-10C	-0.0106 (<0.0001)	33.0
SEASON/DL	0.0011 (<0.0001)	27.5
SC0TOT	0.0186 (0.0166)	7.1
Y intercept = 0.9269		total <i>R</i> <sup>2</sup> = 67.6

#### Analysis 2: predictors of the fat reserves in displaced-released junco populations

Among displaced juncos released in southern IN, the best correlate of transformed LI (weighted for sample



**Fig. 3** Relationship between LI and MT0-10C in natural junco populations, by season. Circles MI, squares IN, triangles TN. Open and closed symbols represent early and late winter, respectively. Points represent mean LI on different winter days ( $n=1$  on 4 days). Sample sizes are adjacent to symbols, with 1 SE indicated when  $n > 1$ . In addition to MT0-10C, snow cover and SEASON/DL each explained a significant proportion of the variation displayed in this figure. Correlation coefficients: early winter  $r = -0.831$ ,  $P < 0.02$ ; late winter  $r = 0.584$ ,  $P < 0.05$

**Table 4** Correlates (Pearson product-moment correlation coefficients) of mean body mass and temperature for the displaced-captive groups, according to geographic origin. The best correlate of the environmental factor set is shown for each year/population combination. *P* values are 2-tailed. 1983:  $n = 13$  weighing dates; 1984:  $n = 11$  weighing dates

1983		1984	
Factor	<i>r</i> ( <i>P</i> )	Factor	<i>r</i> ( <i>P</i> )
Michigan	AT0-10C -0.892 (<0.001)	AT0C	-0.800 (<0.005)
Indiana	AT0-10C -0.871 (<0.001)	AT0C	-0.884 (<0.001)
Tennessee	MT0-10C -0.855 (<0.001)	AT0C	-0.788 (<0.005)

size) was AT0C when data from all three years of displacement were pooled to maximize sample size ( $R = -0.973$ , 2-tailed  $P = 0.0002$ ; recall that displaced-released populations did not differ significantly in fat reserve following displacement).

#### Analysis 3: predictors of the fat reserves in displaced-captive junco populations

Given the lack of independence of body mass data, correlation coefficients for captives are reported for corroborative purposes only. For each displaced population held captive, the best correlate of temporal variation in the fat reserve (estimated by body mass) from mid to late winter in southern IN was always a recent temperature variable, although the specific variable differed within and between winters (Table 4). Long-term temperature

was never a better correlate of mean body mass than was recent temperature. In these correlation analyses, long-term temperature was represented by values for the release site in southern IN. However, results were unchanged when MI, IN, and TN long-term temperature was used instead of long-term IN temperature. In other words, this latter analysis asked whether MI and TN juncos fattened in anticipation of long-term temperature on their chosen wintering sites, despite having been displaced to IN.

## Discussion

### Analyses 1–3 and evolutionary aspects of energy storage in small birds

The winter fat reserve of small birds is critical to their survival of the extensive nonbreeding period. Throughout this time, stored lipid supplies the major source of metabolic fuel during forced fasts brought on by sudden resource shortages, e.g., snow and ice storms (Lehikoinen 1987) and prolonged nocturnal roosting at low temperatures (Blem 1990). The present analyses of data in Rogers et al. (1993) show that recent temperature, snowfall (a measure of resource unpredictability), or both were significant predictors of spatial and/or temporal variation in a measure of the winter fat reserve. Direct experimental evidence supports this suggestion that recent temperature and resource unpredictability are cues for winter fattening in small birds. Rogers (submitted) found that juncos held in an environmental chamber and subjected to low ambient temperature ( $-12^{\circ}\text{C}$ ) had significantly greater ( $P < 0.05$ ) fat reserves than controls held at a higher temperature ( $+20^{\circ}\text{C}$ ). The same result was obtained for song sparrows (*Melospiza melodia*) under the same experimental regime. In addition, Ekman and Hake (1990) showed that greenfinches *Carduelis chloris* exposed to temporally unpredictable resources fattened more than controls with access to highly predictable resources.

An additional significant predictor of fat variation in natural populations was the SEASON variable. However, SEASON was highly correlated with the DL variable, a feature making it impossible to assign causation to either or both factors. Whatever factor(s) caused it, the significance of the SEASON/DL component of the fat reserve is difficult to determine, given its lack of correlation with either long-term temperature or the probability of snowfall in eastern North America (Rogers unpublished data). We suggest two possible explanations. Daylength might directly stimulate winter fattening (Evans 1969) and therefore be partly responsible for convergence among displaced birds. Alternatively, the apparent seasonal influence could represent a fattening response to continued exposure to unpredictable resources as winter progresses (Ekman and Hake 1990). We favor this latter interpretation for the following reasons considered together. Both the natural populations

and captives displayed a regulatory response to recent temperature when exposed to natural daylengths. However, only the natural populations exposed to unpredictable resources over the course of the winter showed an additional SEASON effect; the captives, exposed to highly predictable resources in the experimental aviaries, did not (Rogers unpublished data). A similar effect of season subject to the same interpretation was found in an earlier analysis of body mass in natural junco populations studied at the same sites as those reported here (Nolan and Ketterson 1983).

### Implications for life-history theory

#### *Plasticity in an uncertain environment*

Life-history theory has largely ignored survival in the nonbreeding period, especially energy storage strategies of small birds. However, recent theoretical and empirical investigations have suggested that wintering birds maintain a fat reserve that represents a trade-off between the costs of fattening (predation risk, cost of flight) and its benefits (ability to fast during sudden resource shortages) (Lima 1986; Rogers 1987; Rogers and Smith 1993). Nonbreeding fitness is apparently maximized by fat deposition that minimizes the combined probabilities of mortality from predation and mortality from starvation (Lima 1986; McNamara 1990; McNamara and Houston 1990; Houston and McNamara 1993). Our present data suggest that in the case of the junco, this trade-off is regulated in part by a plastic response to temperature and possibly also to resource predictability. With this strategy, the costs of fat can be avoided during warm periods and at locations where fat confers little benefit, whereas the potential benefit of a fat reserve can be quickly gained if weather conditions become harsh and snowfall might restrict food. Such plasticity in an uncertain environment is consistent with theory predicting its evolution (Bradshaw 1965; Levins 1968; Jain 1979; Caswell 1983; Schlichting 1989).

A review of the literature suggests the evolution of at least three different types of systems regulating the fat storage strategy of small birds in winter (see also Blem 1990). "Responders" appear to exploit local environmental information, and adjust the fat reserve to current conditions of temperature and resource unpredictability (e.g. the house sparrow *Passer domesticus*, Kendeigh et al. 1969; O'Connor 1973; the bullfinch *Pyrrhula pyrrhula*, Newton 1969; the greenfinch, Ekman and Hake 1990; the song sparrow *Melospiza melodia*, Rogers in prep.). Of course, the present study suggests that the dark-eyed junco is a responder. "Responder-predictors" show a similar response to proximate variation in the environment, and in addition deposit a component of the fat reserve in anticipation of harsh winter conditions (e.g., the white-throated sparrow *Zonotrichia albicollis*, Blem and Shelor 1986; several European parid species, Haftorn 1989). The third regulatory type,



"predictors", appears to rely strictly on a regulatory system that oversees fat deposition in anticipation of future conditions (the yellow bunting *Emberiza citrinella*, Evans 1969; the white-crowned sparrow *Z. leucophrys*, King and Mewaldt 1981; the American goldfinch *Carduelis tristis*, Dawson and Marsh 1986).

It is at first puzzling that juncos wait for cold and/or unpredictable environmental conditions before fattening ("responding"). It would seem that it would always be a superior strategy to fatten in anticipation of environmental conditions ("predicting"), because a high fat level would always be ready in the event of environmental extremes. The answer might lie with the main cost of fattening, i.e., predation risk (Blem 1975; Lima 1986; Rogers 1987; Rogers and Smith 1993). Responders might have evolved in highly variable environments (e.g., the continental regions of North America and northern Europe) because it is too costly to deposit a large fat reserve in anticipation of rare environmental extremes of temperature and snowfall. It may be a better strategy to avoid predators at the maximal rate until bad weather is imminent, then store fat to cover the near-certainty of temporarily increased metabolic costs.

Where might we expect the predicting strategy? It should be found in species inhabiting more benign and stable winter environments (e.g., southern North America and the Neotropics), where a small, low-cost fat reserve would cover maximum expected metabolic expenditures. There, the duration of the fasting period and predation risk should be positively related to the fat level. In addition, the predicting strategy can also be expected in species occupying a predictable microhabitat (e.g. the arboreal foraging niche) in northern North America (Dawson and Marsh 1986).

*Energy storage strategy and migration:  
co-adapted life-history traits?*

The capacity of the junco to adjust its energy reserve to fluctuations in winter weather takes on added significance when we consider a second aspect of this bird's natural history. Partial segregation of the age-sex classes in eastern North America is produced each year by differential migration from the breeding grounds in autumn. Analysis of population structure at different latitudes shows that males tend to winter north of females, and, within the sexes, birds hatched in the preceding summer to winter north of older birds (Ketterson and Nolan 1976, 1983; Nolan and Ketterson 1990, 1991). Furthermore, banding records reveal great distances separating the winter sites of some individuals (ages unknown) in successive years. With few exceptions, the site in the second year is south of the earlier site (Ketterson and Nolan 1983, 1985; Nolan and Ketterson 1990).

Differential migration in juncos might reflect differences in the balance of selective pressures on the sex-age classes, such that in the nonbreeding period the fitness of the members of each class is maximized at different

distances from the breeding grounds (Ketterson and Nolan 1983; Rogers et al. 1989). For example, males might winter farther north than females in order to gain the benefits of early territory acquisition, although in so doing they might experience greater winter mortality (Rogers et al. 1991; Arcese et al. 1992) than if they wintered farther south. Other interpretations involving trade-offs in the differential migration of juncos are possible, but the general point is that post-breeding migration appears to be a life-history trait closely related to fitness in the nonbreeding period.

We therefore hypothesize that post-breeding migration and winter fat storage in juncos are co-adapted traits that interact to increase the probability of winter survival. To illustrate, the same individual might find itself in very different physical environments from one winter to the next. A capacity to adjust the fat reserve to avoid unnecessary costs of fat as the bird experiences milder winter weather over its lifetime would clearly be adaptive. Life-history theory might explain diverse, previously unconnected traits of the nonbreeding period of birds.

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