

INTRASPECIFIC AND GEOGRAPHICAL TRENDS IN BODY SIZE OF A DIFFERENTIAL MIGRANT, THE EVENING GROSBEAK

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ABSTRACT.—I examined body-size variation in age and sex classes of the Evening Grosbeak (*Coccothraustes vespertinus*) to test the hypothesis that differential migration in this species can be explained by the body-size hypothesis. This hypothesis proposes that larger-bodied age and sex classes of migratory species should winter farthest north because body size influences the probability of winter survival. From the known winter distribution of age and sex groups (males wintering farther north than females, but no distributional differences between adults and immatures), I predicted that males should be larger-bodied than females, but that there should be no size differences between age classes of either sex. I also predicted that individuals within age and sex classes should increase in size from south to north during winter. Body size was assessed using multivariate analysis of measurements obtained from 1,739 museum specimens of birds collected throughout the winter range and from 73 live-caught birds wintering in southern Alberta. Males were larger-bodied than females, but adult males and females were larger than immatures of the same sex. A positive (but weak) relationship between body size and latitude occurred only in females. I suggest that females, because of their relatively small size, may be most influenced by climatic conditions occurring on the wintering grounds. The physiological implications of body-size variation (cold tolerance and fasting endurance) must be determined before a full assessment of the body-size hypothesis can be made. Received 22 January 1993, accepted 1 July 1993.

IN MANY SPECIES of birds, age and/or sex classes differ in the distance that they migrate from the breeding grounds. Such "differential migration" (Ketterson and Nolan 1983) results in clinal variation in age and sex ratios on the wintering grounds, with males of most species tending to winter closer to the breeding grounds than females (Ketterson and Nolan 1976, Prescott 1992). Patterns of age distribution are less consistent. In some species, adults tend to winter closest to the breeding grounds (Gauthreaux 1978), whereas in others the reverse pattern occurs (Ketterson and Nolan 1982, 1985, Morton 1984, Prescott and Middleton 1990).

Several hypotheses have been proposed to account for the evolution of differential migration. These focus on factors that produce variation in the costs and benefits of migration distance among age and sex classes. Such factors include social interactions (Gauthreaux 1978, 1982), the risk of mortality per unit distance travelled (Ketterson and Nolan 1982), and the

need to arrive on the breeding grounds early in spring (Myers 1981). My study focuses on the body-size hypothesis (Ketterson and Nolan 1983, 1985), which proposes that when age and sex classes differ in overall body size, individuals of these classes should migrate different distances from the breeding grounds because the probability of surviving winter is proportional to body size. Large individuals have a lower surface-area-to-volume ratio than do smaller individuals (Calder 1974). That is, the volume of heat-producing tissue (muscles) increases faster than the surface area of the body (across which heat is lost) as body size increases (Kendeigh 1969, Calder 1974). Large individuals can also store more body fat than small individuals and, because mass-specific metabolic rate declines with body size, fat is catabolized at a slower rate in large-bodied individuals (Kendeigh 1945, Calder 1974). In short, larger individuals (or age and sex classes) should be able to withstand colder temperatures than smaller conspecifics and should be better able to withstand food deprivation. In the Northern Hemisphere, winter temperature typically decreases with increasing latitude, and snowfall (which can periodically cover food supplies and limit their

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availability) increases from south to north (Potter 1965, Bryson and Hare 1974). The body-size hypothesis therefore predicts that, in migratory species, larger-bodied individuals should winter farther north. This argument should apply to the geographic distribution of age and sex classes during winter, as well as to the latitudinal distribution of individuals within each class.

There have been few studies of geographic variation in body size of migratory species during the winter (Zink and Remsen 1986). In both the Townsend's Warbler (*Dendroica townsendi*; Morrison 1983) and Painted Bunting (*Passerina ciris*; Storer 1951), smaller-bodied individuals are reported to winter farthest north. European Starlings (*Sturnus vulgaris*) are largest at mid-latitudes of their winter range (Blem 1981), and Savannah Sparrows (*Passerculus sandwichensis*) show no geographic variation in body size during winter (Rising 1988). Despite a lack of evidence that larger individuals winter farther north among migrants, the body-size hypothesis has been cited frequently as a possible explanation for differential migration in birds (Myers 1981, Ketterson and Nolan 1976, 1983, 1985). Most support for this hypothesis is derived from the observation that the larger-bodied sex or age class tends to winter closest to the breeding grounds (Nichols and Haramis 1980, Sayler and Afton 1981, Dolbeer 1982, Prescott and Middleton 1990, Belthoff and Gauthreaux 1991). This approach offers only weak support for the hypothesis because it fails to distinguish between body-size effects per se and other effects, such as social dominance or the benefits of proximity to the breeding grounds, that may be associated with age and sex differences (Zink and Remsen 1986).

A more rigorous test asks whether trends in body size within age and sex classes are consistent with predictions of the body-size hypothesis. To date, only two studies have addressed body-size variation within age or sex classes of differential migrants during the winter. Nolan and Ketterson (1983) found that, although male Dark-eyed Juncos (*Junco hyemalis*) are larger than females and winter farther north, there are no latitudinal differences in body size within any age or sex class during winter. Conversely, James et al. (1984) found that both male and female Red-winged Blackbirds (*Agelaius phoeniceus*), a species in which the larger-bodied males winter farther north than females, show

an increase in size from south to north during winter (James et al. 1984). Unfortunately, James et al. (1984) apparently sampled both migratory and sedentary populations during the winter and, therefore, it is difficult to distinguish latitudinal trends in morphology for birds of different migratory status. Furthermore, both of these studies (and most others that have considered body size) suffer because "size" was determined from a single morphological measure (wing length), and univariate measures are often poor indicators of overall body size in birds (Rising 1988, Rising and Somers 1989, Freeman and Jackson 1990).

In this paper, I test predictions of the body-size hypothesis as they apply to intraspecific differences in winter range of the Evening Grosbeak (*Coccothraustes vespertinus*). Male Evening Grosbeaks winter farther north than do females, but there are no differences in distribution between age classes of either sex (Prescott 1991). If the body-size hypothesis can account for differential migration in this species, I predict that (1) males should be larger-bodied than females, but (2) adults and immatures of both sexes should be of similar body size. Furthermore, (3) within each age and sex class, larger-bodied individuals should be found farther north during winter. These predictions are tested using a multivariate assessment of body size for individuals collected over a wide geographic area (museum skins), as well for live-caught birds wintering in southern Alberta.

METHODS

Between December 1988 and December 1989, I examined study skins of Evening Grosbeaks contained in 59 North American museum collections (see Acknowledgments). I considered only birds collected in provinces and states east of British Columbia, Montana, Wyoming, Colorado and Arizona (presumably *C. v. vespertinus*; AOU 1957) to eliminate the confounding influence of altitude in western North America, and because the western subspecies (*C. v. brooksi* and *montana*) are less migratory than their eastern counterpart (Balph and Lindahl 1978, Yunick 1983). The location and date of capture were recorded from museum labels. Latitude/longitude coordinates were later assigned (using Anonymous [1966] and regional gazetteers) to specimens for which the county or municipality of collection was recorded. Individuals were aged and sexed using plumage characteristics (Yunick 1977, Pyle et al. 1987). Birds collected during the breeding season (1 June through 31 August) were excluded from my study because molt during this

period could introduce error in wing and tail measurements, and because of difficulties in accurately determining the age of breeding males. The molt from immature to adult plumage occurs at approximately one year of age (Dwight 1900), so males hatched during the previous summer could be designated as either immature or adult, depending on whether the molt had been completed at the time of collection.

Attempts to assign ages to study skins of females were abandoned because soiling and fading of many museum specimens made age criteria difficult to apply. In order to quantify the relative body sizes of adult and immature females, and to verify other age- and sex-specific patterns of body size observed in the museum data, I supplemented museum measurements with similar data from free-living Evening Grosbeaks captured in southern Alberta from December 1989 to March 1990, and from November 1990 to April 1991. Because of possible shrinkage in museum specimens (e.g. Harris 1980, Bjordal 1983), separate analyses were conducted on data from live and museum specimens.

Six external measurements using digital calipers were taken from each bird by a single investigator as follows: unflattened wing chord, bill length (exposed culmen), maximum bill width (width of lower mandible plus rhamphotheca measured at its junction with facial feathers), maximum bill depth (measured from points on midline of upper and lower mandibles at their junctions with forehead and chin feathers), and tarsometatarsus (hereafter "tarsus") length (from joint of tibiotarsal/metatarsal bones to distal edge of last undivided scute). In addition, I measured tail length by inserting a ruler between the middle retrices. To verify that measurements were repeatable over time, 77 museum specimens measured during the first month of the study (December 1988) were remeasured during August and September 1989. At this time, approximately 65% of the available study skins had been examined. Initial and final measurements on the same individuals were compared using a repeated-measures multivariate analysis of variance (MANOVA).

Principal-components analysis (Tabachnick and Fidell 1983) was used to quantify the body size of each bird, where the first component (PC1) was considered to represent a body-size vector if it correlated positively with all univariate measures from which it was derived (Johnston and Selander 1971). I extracted components from the correlation matrix, rather than the variance-covariance matrix, because all variables are weighted equally, and the resulting PC1 should be representative of absolute body size, rather than allometric size (Freeman and Jackson 1990). Component scores on PC1 were computed for all individuals in the data set and were used as a measure of overall body size.

Two methods were used to compare body measurements of age and sex classes. MANOVA was used to compare overall differences in morphology among

age and sex classes. Overall body size was compared between age and sex classes using *t*-tests on PC1 scores. A one-tailed test was used to test the prediction that males should be larger than females. A two-tailed test was used to examine for differences in body size between age classes of males and females. Males of undetermined age were included in the calculation of principal-component scores and in comparisons of sexual differences in body size, but were excluded from comparisons between male age groups.

The prediction that larger individuals should be found farthest north during winter was tested using data from museum specimens collected between 1 January and 15 April. During this period, Evening Grosbeak populations are at the southernmost limit of their migration (Prescott 1991). Individuals were included in this analysis only if latitude/longitude coordinates could be assigned to their collection sites. The data were analyzed in two ways. First, I combined data from all years to test for broad geographic trends in body size. Because the Evening Grosbeak is an irruptive migrant whose winter range changes from year to year (Prescott 1991), this approach might obscure geographic patterns of body size occurring in different years (Rising 1988). Therefore, I also performed separate analyses of the relationship between body size and location of capture for winters in which 15 or more individuals of any age or sex class were collected. For the overall analysis, PC1 scores for each individual were entered as dependent variables in a multiple-regression analysis, with latitude (LAT) and longitude (LONG) as independent variables. I included longitude in the analysis because the tendency for *vespertinus* males to winter north of females is stronger in eastern North America than it is central regions (Prescott 1991). Because of the smaller sample sizes, longitude was not included as an independent variable when considering each year separately. All analyses were performed separately for adult males, immature males, and females. One-tailed tests of significance were used in all cases.

RESULTS

Age and sex differences in morphology.—I examined 1,739 museum specimens (955 male, 784 female). The distribution of samples of known geographical origin ($n = 1,729$) is shown in Figure 1. Of the males, 896 (93.8%) were designated as being either immature or adult.

All univariate measures except tail length were normally distributed in all age and sex groups. Attempts to normalize tail-length measurements by transformations were unsuccessful, so raw values of this variable were retained for all analyses. There was no evidence that any measurements made by the same observer var-

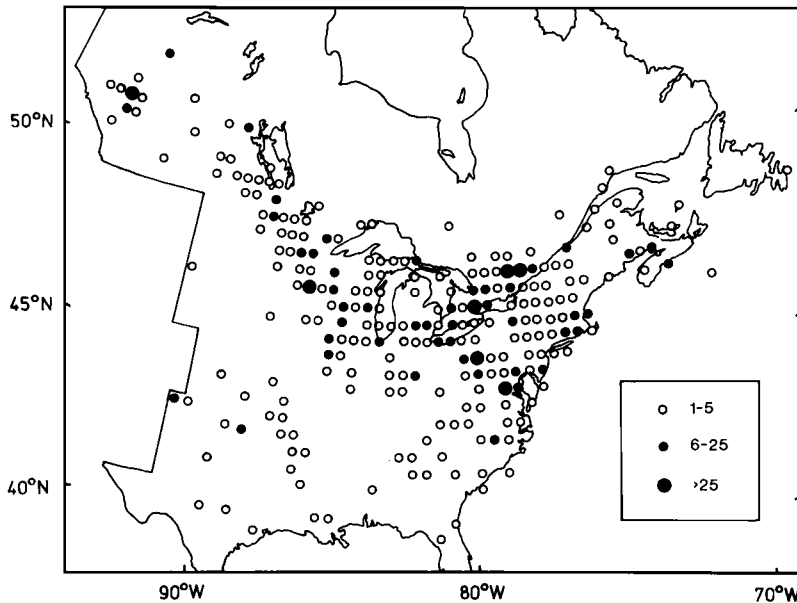


Fig. 1. Geographical origin of Evening Grosbeak study skins used in morphological analyses. Numbers are total specimens in each 1° latitude/longitude block. All specimens collected from 1 September through 31 May.

ied over the study period (repeated-measures MANOVA, $F = 0.7$, $df = 1$ and 73 , $P > 0.6$).

I initially performed PCA separately for each age and sex class to check whether patterns of morphological covariation were similar in each group. In all cases, two components with eigenvalues of more than 1 were extracted (Table 1). Loading patterns were similar among age and sex classes. Therefore, I repeated the analysis and extracted component scores from the entire data set. This procedure again produced two eigenvectors, which accounted for 58.4% of the total variance (Table 1). PC1 (40.0%) corre-

lated positively with all univariate measures and, therefore, was interpreted as representing overall body size. PC2 (18.4%) was characterized by individuals with long wings and tails relative to bill and leg measurements. This component incorporates a shape element, and will not be discussed further.

Univariate measurements and PC1 scores for each age and sex class are given in Table 2. Males were larger than females in all measurements (MANOVA, $F = 77.6$, $df = 6$ and $1,595$, one-tailed $P < 0.0001$), and also had significantly higher PC1 scores ($t = 15.4$, $df = 1,527$,

TABLE 1. Correlations between morphological measurements and principal component scores for study skins of Evening Grosbeaks collected between 1 September and 31 May. In all analyses, only PC1 and PC2 were statistically significant (eigenvalues > 1.0).

Character	Immature males ($n = 368$)		Adult males ($n = 423$)		Females ($n = 691$)		All birds ($n = 1,602$)	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Wing length	0.63	0.53	0.55	0.64	0.60	0.57	0.69	0.49
Bill length	0.63	-0.37	0.64	-0.33	0.61	-0.24	0.62	-0.36
Bill width	0.77	-0.32	0.70	-0.18	0.73	-0.32	0.76	-0.22
Bill depth	0.70	-0.42	0.69	-0.32	0.67	-0.37	0.71	-0.32
Tarsus length	0.49	0.32	0.56	-0.14	0.58	-0.05	0.45	-0.20
Tail length	0.49	0.59	0.34	0.80	0.43	0.75	0.45	0.74
Eigenvalue	2.36	1.15	2.10	1.29	2.24	1.18	2.40	1.10
Percent variation explained	39.4	19.1	35.0	21.6	37.3	19.7	40.0	18.4

TABLE 2. Univariate measurements (mm) and PC1 scores for age and sex classes of the Evening Grosbeak. All data from museum study skins collected from 1 September through 31 May. All *t*-tests between age (two-tailed) and sex (one-tailed) classes are significant ($P < 0.001$) unless otherwise indicated. Values are $\bar{x} \pm SE (n)$.

Character	Immature males	Adult males	All males	All females
Wing length	109.4 \pm 0.1 (410)	111.3 \pm 0.1 (472)	110.4 \pm 0.09 (935)	108.1 \pm 0.1 (753)
Bill length	15.1 \pm 0.03 (403)	15.3 \pm 0.03 (464)	15.2 \pm 0.02 (918)	15.1 \pm 0.03 (738)
Bill width	13.9 \pm 0.02 (409)	14.0 \pm 0.02 (469)	14.0 \pm 0.02 (930)	13.7 \pm 0.02 (752)
Bill depth	14.9 \pm 0.03 (403)	15.0 \pm 0.03 (463)	15.0 \pm 0.02 (916)	14.6 \pm 0.02 (743)
Tarsus length ^{a,b}	20.9 \pm 0.03 (408)	20.9 \pm 0.03 (467)	20.9 \pm 0.02 (928)	21.0 \pm 0.02 (744)
Tail length	62.2 \pm 0.1 (407)	63.0 \pm 0.1 (468)	62.6 \pm 0.09 (927)	61.3 \pm 0.1 (751)
PC1	0.1 \pm 0.07 (393)	0.9 \pm 0.07 (443)	0.5 \pm 0.05 (884)	-0.6 \pm 0.05 (718)

^a Differences between male age classes not significant (two-tailed $P > 0.7$).

^b Difference between sexes significant (one-tailed $P < 0.05$).

one-tailed $P < 0.0001$). Among males, adults were larger than immatures in all univariate measures (MANOVA, $F = 22.2$, $df = 6$ and 829 , two-tailed $P < 0.0001$) except tarsus length ($t = 0.1$, $df = 834$, two-tailed $P > 0.3$), and also had higher PC1 scores ($t = 7.7$, $df = 789$, two-tailed $P < 0.0001$).

Measurements were obtained for 33 male (16 immature and 17 adults) and 40 female (14 immature, 25 adult, 1 unknown age) Evening Grosbeaks wintering in southern Alberta. Complete measurements were obtained for most of these birds. However, knemidokoptiasis ("scaly leg"), which is common in Alberta populations of Evening Grosbeaks (McNicholl 1977), prevented tarsal measurements being taken for three males and five females. All univariate measures were normally distributed, with the exception of bill width in immature females (Shapiro-Wilks test, $W = 0.86$, $P < 0.05$). Transformations did not improve normality, and original values for this variable were retained for all analyses.

Because of the relatively small sample size of live birds, I did not attempt separate principal-components analyses for each age and sex group. When all birds were considered simultaneously, the analysis identified two eigenvectors which summarized 44.7 and 20.9% of the morphological variation, respectively (Table 3). All univariate measures loaded positively on the first component, indicating that PC1 represented an overall size vector. PC2 was interpreted as being a shape vector, being characterized by individuals with relatively short wings and tails.

Males were larger than females when all univariate measurements were considered simultaneously (MANOVA, $F = 5.1$, $df = 6$ and 58 ,

one-tailed $P < 0.001$), but were no larger than females in either wing length ($t = 1.41$, $df = 63$, one-tailed $P > 0.1$) or tail length ($t = 1.69$, $df = 63$, one-tailed $P > 0.1$, Table 4). Males were larger than females along the body size vector (PC1, $t = 11.64$, $df = 63$, one-tailed $P < 0.001$). There were no overall differences in measurements between age classes of males (MANOVA, $F = 2.3$, $df = 6$ and 23 , two-tailed $P > 0.05$; PCA, $t = 0.79$, $df = 28$, two-tailed $P > 0.3$), and the only univariate measurement found to be larger in adults was wing length ($t = 10.4$, $df = 28$, two-tailed $P < 0.01$). MANOVA indicated no overall differences in univariate measurements between age classes of females ($F = 0.25$, $df = 6$ and 27 , two-tailed $P > 0.2$), although adults had longer wings ($t = 4.2$, $df = 32$, two-tailed $P = 0.05$) and deeper bills ($t = 4.41$, $df = 32$, two-tailed $P < 0.05$) than did immatures. PC1 scores were larger for adult females than for immatures (Table 4; $t = 5.25$, $df = 32$, two-tailed $P < 0.05$).

Latitudinal variation in body size.—When all years were combined, there was no evidence within either of the male age groups that larger

TABLE 3. Correlations between principal-component scores and six morphological measures obtained from free-living Evening Grosbeaks wintering in southern Alberta.

Character	PC1	PC2
Wing length	0.38	-0.46
Bill length	0.42	0.15
Bill width	0.50	0.18
Bill depth	0.52	0.18
Tarsus length	0.23	0.57
Tail length	0.33	-0.60
Eigenvalue	2.68	1.25
Percent variation explained	44.7	20.9

TABLE 4. Univariate measures (mm) and PC1 scores calculated from live-caught Evening Grosbeaks in southern Alberta. Values are $\bar{x} \pm \text{SE}$. Tests between age classes are one-tailed *t*; tests between sex classes are two-tailed *t*.

Character	Males		Females		All males (<i>n</i> = 33)	All females (<i>n</i> = 40)
	Immatures (<i>n</i> = 16)	Adults (<i>n</i> = 17)	Immatures (<i>n</i> = 14)	Adults (<i>n</i> = 25)		
Wing length	107.1 ± 0.61	110.1 ± 0.6*	106.5 ± 0.6	108.6 ± 0.6*	108.6 ± 0.5	107.5 ± 0.5
Bill length	15.6 ± 0.21	5.8 ± 0.2	15.2 ± 0.1	15.4 ± 0.1	15.7 ± 0.1	15.4 ± 0.1*
Bill width	14.4 ± 0.11	4.3 ± 0.1	13.8 ± 0.1	14.0 ± 0.1	14.3 ± 0.1	13.9 ± 0.1**
Bill depth	14.9 ± 0.21	4.9 ± 0.2	14.1 ± 0.2	14.5 ± 0.1*	14.9 ± 0.1	14.4 ± 0.1**
Tarsus length ^a	21.1 ± 0.22	0.8 ± 0.2	21.0 ± 0.1	21.2 ± 0.1	21.0 ± 0.1	21.2 ± 0.1
Tail length	64.5 ± 0.66	5.4 ± 0.5	63.2 ± 0.9	63.7 ± 0.8	64.8 ± 0.4	63.4 ± 0.5*
PC1 ^a	0.4 ± 0.3	1.0 ± 0.5	-1.3 ± 0.4	-0.2 ± 0.2*	0.7 ± 0.3	-0.6 ± 0.2**

*, $P < 0.05$, **, $P < 0.01$.

^a Because tarsal measurements could not be obtained for all birds (see text), sample sizes for tarsus length and PC1 were as follows: immature males and adult males, 15; immature females, 13; adult females, 21; all males, 35; all females, 30.

individuals winter farther north (Fig. 2; immatures, $F = 0.58$, $df = 1$ and 219, one-tailed $P > 0.2$; adults, $F = 0.05$, $df = 1$ and 280, one-tailed $P > 0.4$). However, body size increased

from south to north in females (Fig. 2; $F = 2.68$, $df = 1$ and 472, one-tailed $P = 0.05$). In none of the regressions was longitude a significant main or interaction effect ($P > 0.05$). Numbers of specimens were sufficient to analyze geographic trends in body size for adult males in 1886 ($n = 15$) and 1889 ($n = 45$), for immature males in 1889 ($n = 23$) and 1971 ($n = 15$), and for all females in 1889 ($n = 78$), 1961 ($n = 19$), 1968 ($n = 16$), and 1971 ($n = 24$). There was no significant relationship between body size and latitude of capture for any age or sex class in any year (all $P > 0.1$).

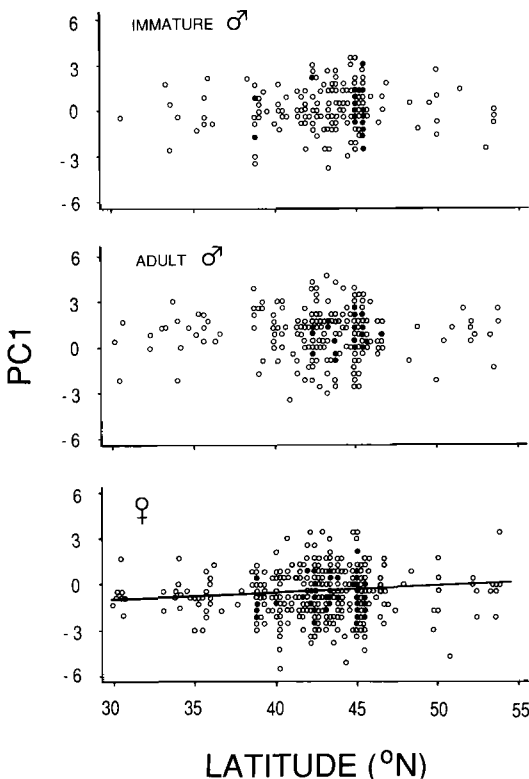


Fig. 2. Relationships between body size (PC1) and wintering latitude for age and sex classes of the Evening Grosbeak. Regression of PC1 on latitude was significant only for females ($Y = -1.91 + 0.03[\text{LAT}]$; $P = 0.05$). Solid circles are points comprising three or more individuals.

DISCUSSION

Analyses of museum specimens from a wide geographic range and of birds from a local population of wintering individuals show that male Evening Grosbeaks are larger-bodied than females. When coupled with the known tendency for males of this species to winter farther north (Prescott 1991), the size difference is consistent with predictions of the body-size hypothesis. Both adult males and females are larger than immatures of the same sex. These differences are contrary to the hypothesis because the latitudinal distributions of age classes in winter are similar (Prescott 1991). For males, this conclusion is based only on the analysis of museum specimens, because populations of live birds wintering in southern Alberta show no age differences in size.

There are two possible reasons why age differences in body size of males were observed in the sample of museum skins, but not in the free-living population. Size differences be-

tween age classes of males may be sufficiently small that they could not be detected from the sample size of live birds obtained in this study. Alternatively, adult and immature males in the Alberta population may not differ in body size. This could result if the local population consists of small adults and large immatures relative to other wintering populations. Whatever the reason for the disagreement between results obtained from live birds and museum specimens, I consider the museum sample to be most representative of specieswide differences, and these data show size differences among age classes of males.

The analysis of geographic variation in body size within age and sex classes also offers conflicting support for the body-size hypothesis. The predicted latitudinal trend in body size was not observed in either age class of males, but larger-bodied females tended to winter farther north than smaller individuals. If the assumption is correct that climatic conditions can influence the choice of wintering latitude by birds of different body size, then males must be sufficiently large that intrasexual differences in size do not confer differential tolerance to winter conditions. Females, however, are smaller-bodied than males of both age classes and may be more influenced by conditions occurring on the wintering grounds. However, if body-size differences alone could produce the observed latitudinal trend in females, then the larger-bodied adults should winter farther north than immatures. This pattern does not occur (Prescott 1991). The observed sexual difference in the relationship between body size and latitude could also result if the variation in body size differed between the sexes. That is, males might be less variable than females in terms of body size, and individual differences in male size might be too small to affect the choice of wintering location. Tests for homogeneity of variances (Ostle and Mensing 1979) showed that this was not the case. PC1 scores for males were no less variable than scores for females (one-tailed tests, museum sample, $F = 1.06$, $df = 884$ and 717 , $P > 0.25$; live birds, $F = 1.26$, $df = 32$ and 39 , $P > 0.2$).

Taken together, my results suggest that sexual differences in winter distribution could result because males are larger than females, but it is not clear whether relative size differences between the sexes are sufficient for males to realize physiological benefits. Comparisons of

body-size distribution within age and sex classes suggest this is unlikely, because only females show a geographic trend in size that is consistent with the body-size hypothesis. To explain adequately the observed patterns of distribution by age and sex classes in terms of the body-size hypothesis, the assumption of physiological advantages to large body size must be verified.

Direct investigation of the relationship between body size and fasting endurance or cold tolerance in birds has been limited (but see Ketterson and King 1977, Ketterson and Nolan 1978, Stuebe and Ketterson 1982, Perry et al. 1988), but evidence from field studies indicates that winter survival is not always related to large size. Directional selection for large body size during severe winters has been observed in Canvasbacks (*Aythya valisineria*; Haramis et al. 1986) and Great Tits (*Parus major*; Lehikoinen 1986), but not in American Black Ducks (*Anas rubripes*; Kremetz et al. 1989). In the House Sparrow (*Passer domesticus*), both the largest and smallest individuals survive better than intermediate-sized birds (Johnston et al. 1972, Johnston and Fleischer 1981, Fleischer and Johnston 1984). In this case, large birds may survive better because of advantages associated with thermoregulation or fasting endurance, or because size confers a high dominance status and priority of access to food. Small individuals might survive well because their food requirements are lower, and they can more easily meet energy demands when food is in short supply. Also, small, subordinate individuals may avoid aggressive encounters, and thereby have more time available for feeding. Intermediate-sized birds gain neither of these advantages and might, therefore, have a low probability of survival when conditions are severe (Johnston and Fleischer 1981, Fleischer and Johnston 1984). Thus, large size need not always be an advantage, and there might be counteracting selection pressures which could eliminate the relationship between body size and latitude predicted for male Evening Grosbeaks.

Even in the absence of physiological advantages to large size, distributional differences between males and females, as well as latitudinal trends in body size of females, could result if size is a determinant of social rank. Numerous studies have shown that social status is positively related to body size in birds (Searcy 1979, Watt 1986, Richner 1989), and large individuals may winter farther north simply because they

are more successful in competition for resources such as food (Ketterson and Nolan 1976). Male grosbeaks are larger than females, and are the socially-dominant sex (Balph and Balph 1976, Bekoff and Scott 1989, Prescott 1992). Nevertheless, body size is not a determinant of social rank in captive flocks of Evening Grosbeaks (Prescott 1992). It remains possible that size may confer advantages in social encounters among free-living individuals, where familiarity among combatants should be less likely than in captive flocks (Balph 1979). If the relationship between social rank and body size can explain geographic patterns of distribution observed here, then such a relationship should occur only among females, because neither age class of males shows latitudinal variation in body size during winter.

The analysis of morphological variation in wintering Evening Grosbeaks provides only weak support, at best, for the body-size hypothesis. Clearly, the physiological implications of intraspecific variation in body size must be understood before the factors responsible for the patterns observed here can be identified.

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