

## GEOGRAPHIC VARIATION IN MID-WINTER BODY COMPOSITION OF STARLINGS

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**ABSTRACT.**—Starlings (*Sturnus vulgaris*) collected during mid-winter from a 2,800-km longitudinal range in the eastern United States showed significant geographic variation in body weight, feather weight, wing length, culmen length, tarsus length, dry weight, lean dry weight, lipid weight and lipid index. Total lipid reserves and indices were greatest at middle latitudes. Starlings from the central part of the study area were significantly larger than those at either northern or southern extremes as measured by wing length, body weight and lean dry weight. Insulation, as measured by weight of body feathers per unit of surface area, increased with isophane, an index of regional temperature, but morphometric measures were generally less interpretable.

Geographic variation within a species generally reflects ecotypic adaptation or phenotypic response to differences in environment. Earlier in this century, the morphometric aspects of such variation received much attention partly because of the ease of measurement, availability of museum specimens, and also because the theme of most research was systematic or taxonomic rather than physiological or ecological. In the past two decades, biologists have increasingly paid attention to the functional and adaptive significance of geographic variation. However, the analyses seldom have provided data useful in the study of the relationships among morphology, physiology and environmental conditions.

To date, studies of the relationships between variation in body composition and environment in endothermic animals are rare, have dealt entirely with sedentary species, and have produced differing results. Hayward (1965), in an analysis of six geographic races of North American deer mice (*Peromyscus*), found large individual and interracial variability in body fat, but discerned no regular interlocality variation in any gross component of body composition either in winter or summer. Blem (1973, 1974), working with North American House Sparrows (*Passer domesticus*), demonstrated regular geographic variation in several body components and insulation, which appeared to be related to mid-winter temperature and adaptive for winter survival. Although numerous studies of seasonal differences in body composition or geographic variation in metabolism are available (e.g., see Hudson and Kimzey 1966, Helms et al. 1967, Barnett 1970), few other data reflect upon geographic variation in body composition or energy reserves.

I studied the mid-winter body composition of a partially migratory species, the Starling (*Sturnus vulgaris*). In eastern North America, individual Starlings may migrate several hundred kilometers along a generally north-south axis, but resident flocks are found throughout the range sampled in the present study (see Kessel 1953). Although migratory individuals cannot be distinguished from non-migrants, I know of no evidence that mid-winter populations are moving great distances (if at all) in response to weather extremes. Therefore my working hypothesis was that interlocality variation at least partially reflects adaptation for survival of mid-winter environment at the collection sites.

### METHODS

One hundred and sixty-eight Starlings were collected late December 1973 to early February 1974 at 10 locations over a 2,800-km longitudinal range (Table 1). All samples were obtained in late afternoon or early evening. The birds were frozen and shipped in dry ice to Richmond, Virginia, where they were weighed to the nearest 0.1 g. Control tests indicated that the weight of freshly collected Starlings did not differ significantly from that obtained after shipping. Wing chord, culmen and tarsus length were measured with calipers to the nearest 0.1 mm. Bill color and neck hackle length (see Kessel 1951) were used to separate first-year birds from adults. Thermal conductance was measured from intact carcasses using Blem's (1974) modification of Herreid and Kessel's (1967) technique. Conductance was calculated both in total gcal/h (calories/bird) and gcal/h·°C per unit "surface area" (where "surface area" is calculated as fat-free weight<sup>0.67</sup>, see Johnson and Cowan 1975). Each bird was then plucked and all body feathers were separated from remiges and rectrices. Feathers were oven-dried for 48 h at 65°C and weighed. The sex of each bird was determined by dissection and the stomach contents removed. The carcass was then chopped into small pieces, refrozen and freeze-dried for 48 h. The dry carcass was weighed and homogenized in a blender. Water content was determined by subtraction. The lipid from one aliquot (8-10 g) of the dry carcass was

TABLE 1. Sites where Starlings were collected in mid-winter for this study.

Location*	°N latitude		Number of birds	
	°Isophane	♂	♀	
Orono, Maine	45.0	51.5	12	4
Huron, Wisconsin	43.5	48.0	14	6
Dundee, Illinois	42.0	46.5	20	8
Dunkirk, (Northern) Ohio	40.5	46.0	7	6
Columbus, (Central) Ohio	40.0	45.5	7	5
New London, Maryland	39.5	45.0	4	2
Richmond, Virginia	37.5	42.0	10	5
Mississippi State, Mississippi	34.5	37.5	19	12
Charleston, South Carolina	33.0	37.0	13	7
Vero Beach, Florida	28.0	32.0	5	2

\* Arranged from north to south.

extracted in a Soxhlet apparatus using a 5:1 petroleum ether:chloroform solution. Another aliquot (8-10 g) was ashed in a muffle furnace at 600°C. Total fat and ash content were then calculated by multiplying the dry weight of the carcass by percent composition of the subsamples. Lipid, ash, and water indices were calculated as the absolute weight of total lipid, ash or water divided by lean dry weight.

RESULTS

Analysis of variance disclosed significant interlocality variation within all of the variables except water index and total ash content (Table 2). The sexes differed significantly in all variables except lipid measurements, ash and water indices, conductance measurements and body feather weight per unit surface area. Male and female birds are analyzed separately for those variables having significant intersexual variation. All variables except water index and conductance values and those involved with body mass (body weight, lean dry weight, wing length and total ash content) differ significantly between age classes (adult vs. first-year). First-year birds were excluded from all analyses of measurements significantly affected by age.

*Sex ratios.* More males than females were collected in the total sample ( $\chi^2 = 16.7$ ,  $P < 0.05$ , Yates correction for continuity performed) and males outnumbered females in all individual samples (Table 1).

*Body size.* Body weights of Starlings increased from lower latitudes up to about 42°N (Table 3, Fig. 1). Measurements of lean dry weight and wing length indicated that this increase was, at least in part, a function of real difference in size and not due to quantity of energy reserve. Females were smaller than males at all localities, but the difference showed no apparent geographic trends. Samples from the two northernmost collection sites had significantly lower body

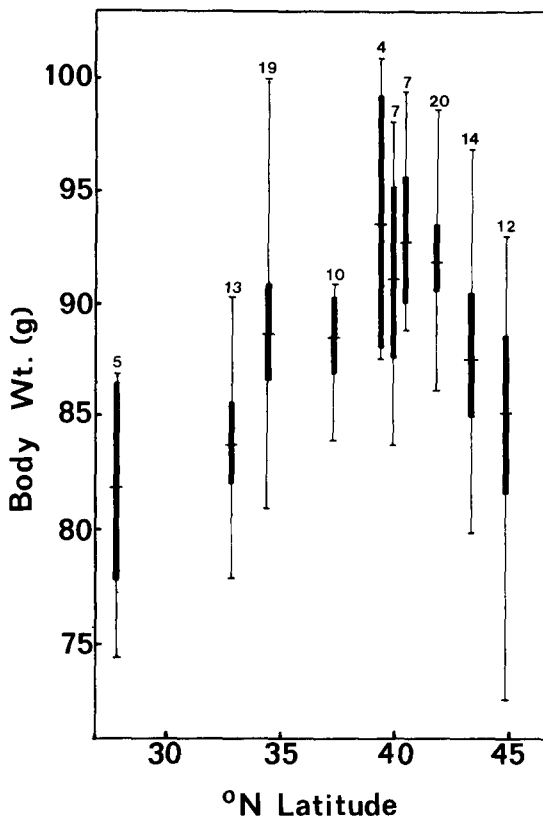


FIGURE 1. Variation in body weight of male Starlings collected in mid-winter at ten localities in the eastern United States. Horizontal bars represent means, vertical bars  $\pm 2$  SE of the mean, and vertical lines the range. Numbers above vertical lines are sample sizes.

weights and lean dry weights than those from the middle of the range. Wing length (WL, in mm) was a significant function of body weight (BW, in g),  $WL = 107.16 +$

TABLE 2. Analysis of variance of the effects of sex, location and age (first-year vs. adult) upon morphology and body composition in Starlings (NS = no significant variation; \* =  $P < 0.05$ ).

	Sex	Location	Age
Body weight	*	*	NS
Wing length	*	*	NS
Culmen length	*	*	*
Tarsus length	*	*	*
Dry weight	*	*	*
Lean dry weight	*	*	NS
Lipid weight	NS	*	*
Lipid index	NS	*	*
Water weight	*	*	*
Water index	NS	NS	NS
Ash weight	*	NS	NS
Ash index	NS	*	*
Body feather weight	*	*	*
Body feather wt./surface area	NS	*	*
Flight feather weight	*	*	*
Conductance (cal/bird)	NS	*	NS
Conductance (cal/surface area)	NS	*	NS

TABLE 3. Measurements of body size in Starlings ( $\bar{x} \pm \text{SE}$ ). See Table 1 for sample sizes.

	Body weight (g)		Lean dry weight (g)		Wing length (mm)	
	♂	♀	♂	♀	♂	♀
Maine	85.2 ± 1.7	82.6 ± 1.9	20.4 ± 0.5	19.2 ± 0.3	125.2 ± 0.8	123.8 ± 1.7
Wisconsin	87.7 ± 1.3	83.8 ± 0.8	20.8 ± 0.4	20.5 ± 0.5	128.4 ± 0.5	125.8 ± 1.0
Illinois	92.0 ± 0.7	88.6 ± 0.9	21.4 ± 0.2	20.5 ± 0.5	128.9 ± 0.5	127.4 ± 0.7
N. Ohio	92.9 ± 1.4	87.3 ± 1.4	21.0 ± 0.2	19.5 ± 0.4	127.9 ± 1.2	126.5 ± 1.0
C. Ohio	91.9 ± 2.2	89.7 ± 4.3	21.0 ± 0.4	20.9 ± 0.9	127.9 ± 1.5	126.8 ± 0.9
Maryland	93.7 ± 2.9	92.8 ± 5.2	21.4 ± 0.6	19.8 ± 0.3	128.0 ± 0.7	124.5 ± 0.5
Virginia	88.5 ± 1.3	84.4 ± 1.6	20.8 ± 0.6	20.0 ± 0.3	127.8 ± 0.7	126.0 ± 1.3
Mississippi	88.7 ± 1.0	83.7 ± 1.9	20.3 ± 0.4	19.5 ± 0.4	128.8 ± 0.5	125.5 ± 0.9
S. Carolina	83.6 ± 0.9	79.9 ± 2.4	19.8 ± 0.3	19.0 ± 0.6	125.9 ± 0.8	124.9 ± 0.9
Florida	82.0 ± 2.2	77.6 ± 2.6	20.2 ± 0.5	19.5 ± 0.3	126.2 ± 1.0	122.5 ± 0.5

0.23 BW,  $r = 0.48$ ; and a slight, but significant, relationship existed between wing length and the cube root of body weight ( $BW^{1/3}$ ),  $WL = 68.16 + 14.00 BW^{1/3}$ ,  $r = 0.37$ . Wing lengths of males in the Maine sample were shorter than those of any other location while females from Maine were larger than only the southernmost sample. Exposed culmen length and tarsus length did not vary regularly in a geographic fashion, although the former tended slightly to be shorter southward. Both culmen and tarsus lengths were larger in males than females (Table 4).

**Lipid weight.** Both lipid weights and indices showed geographic trends that paralleled those of body weight (Table 5), and lipid reserve (g) was a significant function of body weight (lipid =  $-27.40 + 0.42 BW$ ,  $r = 0.77$ ). Lipid reserves were largest in Starlings from the middle of the range although the two northernmost samples had greater weights and indices than the two southernmost samples.

**Ash weight.** Total ash content did not vary geographically, but the sexes differed significantly. Ash index, which shows age and geographic variation, was generally highest at those locations where body mass was smallest.

**Insulation.** Unadjusted weights of body

and flight feathers varied significantly among localities but these data showed no geographic trend. When body feather weights were divided by fat-free body weight expanded to the exponent 0.67 (i.e., calculated on a "surface area" basis), significant interlocality variation resulted which showed a significant regression on isophane (Fig. 2). Isophane (I) is an index of regional temperature calculated from altitude, latitude and longitude of the locality (see Hopkins 1938, Packard 1967, Johnston 1969). The appropriate least-squares equation for this relationship is: feather weight/surface area =  $0.109 + 0.002 I$ ,  $r = 0.57$ . Body feather weights differed significantly between sexes; there was no significant sexual difference in body feather weight divided by surface area.

Significant geographic variation occurred both in conductance/bird and conductance/surface area. No difference was found between sexes or age groups. Conductance (C) was generally lowest in northern populations (Fig. 2) and C in gcal/bird and gcal/surface area were significantly related to isophane as follows: gcal/bird =  $26.267 - 0.217 I$ ,  $r = -0.75$ ; gcal/surface area =  $0.148 - 0.001 I$ ,  $r = -0.81$ .

**Regional temperature regimes.** Because morphometric variables often vary signifi-

TABLE 4. Culmen and tarsus length (mm) in Starlings. First-year birds have been excluded.

Location	Males			Females		
	N	Culmen length	Tarsus length	N	Culmen length	Tarsus length
Maine	12	28.2 ± 0.5	28.9 ± 0.4	4	27.2 ± 0.7	28.6 ± 0.3
Wisconsin	14	27.2 ± 0.3	29.3 ± 0.2	6	26.4 ± 0.4	28.1 ± 0.5
Illinois	13	27.7 ± 0.3	28.2 ± 0.2	—	—	—
N. Ohio	6	27.4 ± 0.4	29.4 ± 0.3	—	—	—
C. Ohio	4	27.1 ± 0.7	28.8 ± 0.3	—	—	—
Maryland	4	26.9 ± 0.7	28.6 ± 0.5	2	25.5 ± 0.4	26.5 ± 1.3
Virginia	6	26.0 ± 0.2	28.6 ± 0.4	4	25.8 ± 0.1	28.9 ± 0.4
Mississippi	14	26.5 ± 0.3	29.6 ± 0.2	2	25.4 ± 0.1	29.5 ± 0.1
South Carolina	13	25.8 ± 0.3	28.4 ± 0.2	7	25.3 ± 0.7	28.6 ± 0.3
Florida	5	27.4 ± 0.4	29.0 ± 0.4	2	25.1 ± 0.4	28.6 ± 0.4

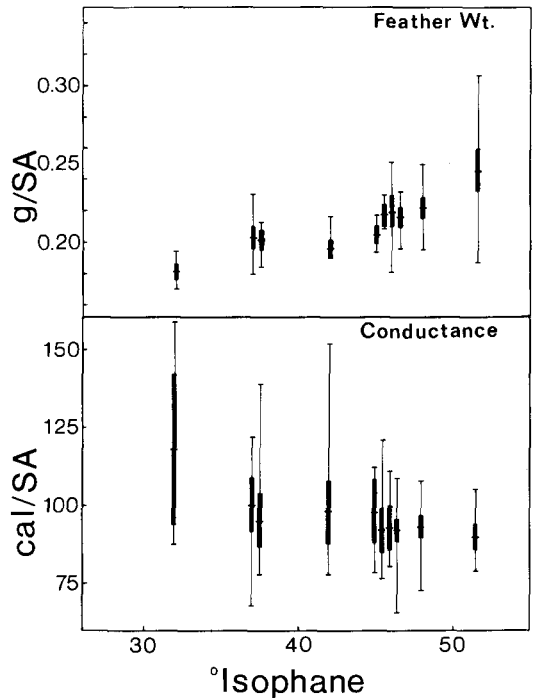
TABLE 5. Lipid weights and indices in Starlings.

Location	N	Lipid weight (g)	Lipid index
Maine	16	6.5 ± 0.4	0.322 ± 0.020
Wisconsin	20	8.3 ± 0.5	0.402 ± 0.028
Illinois	13	12.3 ± 0.6	0.577 ± 0.032
N. Ohio	6	12.4 ± 0.9	0.589 ± 0.039
C. Ohio	4	10.8 ± 1.5	0.512 ± 0.075
Maryland	6	10.1 ± 1.6	0.486 ± 0.082
Virginia	10	10.3 ± 0.5	0.520 ± 0.045
Mississippi	16	11.5 ± 0.6	0.558 ± 0.029
South Carolina	20	5.4 ± 0.3	0.275 ± 0.012
Florida	7	3.2 ± 0.3	0.162 ± 0.014

cantly with regional temperatures, all variables that demonstrated significant geographic variation were tested for relationships to maximum (Max) and minimum (Min) temperature extremes, mean monthly January (Jan.) and July wet-bulb temperatures (°C) and photoperiod (hours of light). Only males were included in the analyses except where there were no significant differences between sexes or age classes; the sample sizes were not large enough to test females or age classes alone. Most compositional variables showed significant simple correlations with environmental variables (Table 6). These correlations were not generally high, but this is not surprising given the curvilinear relationship between body size and isophane and the fact that most compositional variables are correlated with body weight. Multiple regression (see Power 1969, Blem 1976a) was used in order to determine which variables contributed significantly to the prediction of dependent variables. The results of such analysis should be interpreted as suggesting probable factors related to the dependent variable, but not necessarily as causal factors in the phenomenon tested. There is no assurance that all biologically important independent variables have been included. If other variables are added to subsequent models, one may find that the precision of prediction is increased and that independent variables previously thought

 TABLE 6. Correlation coefficients for relationships between body composition of male Starlings and daylength (h) and temperatures (°C) at collection sites (\* = arcsine transformed). All coefficients are significant at the 5% ( $P < 0.05$ ) level.

	Mean January	Mean July	Maximum	Minimum	Isophane	Daylength
Body weight (g)	-0.42	-0.36	0.42	-0.46	0.48	-0.40
Lean dry weight (g)	-0.32	-0.32	0.31	-0.34	0.35	-0.32
Lipid (g)	-0.59	-0.51	0.56	-0.61	0.63	-0.56
Percent lipid*	-0.62	-0.54	0.59	-0.63	0.65	-0.59
Percent water*	0.37	0.40	-0.32	0.34	-0.34	0.38
Percent ash*	0.63	0.56	-0.62	0.64	-0.65	0.61


 FIGURE 2. Body feather weight (g) and conductance (gcal) as a function of surface area (SA) in Starlings. Horizontal bars represent means; vertical lines are  $\pm 1$  SE.

to be important are now less important or even nonsignificant.

In the present instance, mean body weight was a significant function of minimum extreme temperature and photoperiod as follows:  $BW = -0.86 \text{ Min} + 16.53 \text{ Photoperiod} - 100.61$ . The coefficient of determination ( $R^2 = 0.43$ ) was relatively low, but significant. A similar relationship occurred between wing length and maximum temperature extremes ( $R^2 = 0.32$ ):  $WL = 0.40 \text{ Max} + 110.01$ . Lean dry weight was not significantly related to any of the climatic variables. Culmen length was related to January and maximum temperatures ( $R^2 = 0.49$ ):  $\text{Culmen (mm)} = -0.11 \text{ Jan.} - 0.26 \text{ Max} + 37.50$ . Tarsus length did not demonstrate any significant relationship with any measurement of temperature or climatic regime.

Both total lipid and lipid index were related significantly to January and July mean temperatures: Lipid =  $-0.67 \text{ Jan.} + 1.79 \text{ July} - 33.47$  ( $R^2 = 0.63$ ), lipid index =  $-0.03 \text{ Jan.} + 0.09 \text{ July} - 1.59$  ( $R^2 = 0.65$ ). The relationship of lipid measurements to both maximum and minimum temperature extremes should not be taken literally since all temperature variables are highly correlated, but it seems likely that obesity should be related closely to extreme conditions rather than averages. Measurements of insulation were the most highly correlated with temperature variables of any of the carcass components tested. Feather weight per unit surface area (FSA, g) was related to minimum and maximum temperatures:  $\text{FSA} = -0.002 \text{ Min} - 0.003 \text{ Max} + 0.296$ ,  $R^2 = 0.80$  and conductance/surface area (C, gcal) was related to maximum extreme and mean January and July temperatures:  $\text{C} = 0.002 \text{ Max} + 0.003 \text{ Jan.} - 0.005 \text{ July} + 0.129$ ,  $R^2 = 0.97$ .

## DISCUSSION

Following its introduction to New York City from Europe in 1890–1891, the Starling has spread throughout the continental United States, much of Canada and northern Mexico. Although some populations are migratory, the Starling is a permanent resident within its normal breeding range in North America (Kessel 1953, Burt and Giltz 1966). Young of the year often occur south of the hatching site during their first year, but the composition of the migratory portion of Starling populations is not easily characterized. Both North American and European studies indicate that although first- and second-year birds are more likely to migrate, some individuals in all age categories regularly migrate (Kessel 1953). The percentage of migratory Starlings may vary geographically. At some sites not included in the present study, 100% of the population migrates. At other locations this figure may be as low as 3%. In general, the smallest proportion of migratory Starlings seems to occur in the eastern half of the United States, particularly the Atlantic Seaboard, the Northeast and the Lake States (Kessel 1953). The direction of migration is variable but appears to be mostly north–south or northeast–southeast/southwest (Kalmbach 1932, Thomas 1934, Kessel 1953, Burt and Giltz 1966, Bordner et al. 1968). In general, most of the birds classified as adults in the present study and collected at northern sites were probably residents, while first-year birds at all sites and adults at southern sites could well have

been migrants (Kessel 1953, Davis 1960), particularly because they were collected from flocks (Kessel 1957).

Fall migration occurs from late September through November and spring migration from mid-February through March (Kessel 1953); therefore, the samples collected for the present study involve birds that were winter residents rather than transients. Assuming that the adult birds were regular migrants or winter residents, their body composition should reflect adaptation to the environmental regime of the wintering grounds, although other factors acting at breeding sites may partially obscure this adaptation. At the least, one might assume that these samples consist of resident birds adjusted to local climate plus migratory individuals which were wintering at localities to which they were well adjusted. It is therefore possible that the apparent curvilinear nature of the relationship between wing length or body weight and isophane is the result of mixed resident-migratory flocks. If northern, migratory Starlings are larger than sedentary individuals and southern populations, then migration of northern birds to the middle of the range could produce a rough curvilinear relationship between size variables and isophane. Larger samples perhaps would exhibit bimodal size distributions at middle latitudes.

It is important to note that significant interlocality variation does occur that is at least partially attributable to isophane, and therefore to some climatic variable or variables. Thermal conductance and weight of feathers per unit surface area, for example, are functions of isophane as found previously in House Sparrows (Blem 1974). However, variation in size is certainly more complex than portrayed in the present paper. James (1970) demonstrated that isophetetic lines for wing length, which show northward increases, are irregular in areas such as the Mississippi River valley and around the Appalachian Mountains. It would be difficult to analyze sufficient Starling carcasses to detect such variation, but the present paper offers sufficient data to indicate that there has been significant adaptation of insulation to climate.

Wing length generally is considered to be the most valid indicator of body size in birds of any of the morphometric characters (see James 1970). Nevertheless, the reliability of this measurement in the prediction of "real weight" (i.e., fat-free weight or other weights more highly correlated with metabolism) or its relationships to other measure-

ments of bird size have received little attention. As Whitford (1979) pointed out, the ratio of wing length to body weight may not always be statistically significant except within limited samples or a limited range of temperature and/or altitude. In the present analyses, wing length has a low ( $r = 0.40$ ) but significant correlation with body weight. The correlation between wing length and fat-free weight ( $r = 0.37$ ) is also significant as is the correlation between lean dry weight and wing length ( $r = 0.37$ ). If females are excluded from the analyses, the correlation coefficients are 0.62, 0.49 and 0.40, respectively. It therefore appears that wing length is more closely correlated with live weight than other variables that might be expected to vary with metabolism (see Whitford 1979).

Morphometric data must be combined with estimates of energy expenditure in order to evaluate the significance of geographic variation. Data suitable for estimating the metabolic requirements of Starlings are generally incomplete. Measurements of respiratory rates or utilization of metabolized energy have been completed in single studies for only parts of the temperature range or are not directly applicable (see Brenner 1965, Johnson and Cowan 1975, Lustick and Adams 1977). Assembling data from these sources, I have generated an equation that predicts standard metabolism of Starlings as a function of ambient temperature ( $T_a$ , °C):  $\text{kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1} = 0.0148T_a + 0.7694$  ( $r = -0.96$ ,  $N = 6$ ). Inserting appropriate mid-winter (mean January) temperatures in this equation, minimal energy requirements of Starlings (of appropriate weight) may be predicted for each of the collection sites and compared with energy reserves. Fat reserves may be converted to caloric terms by multiplying grams of fat by 9.0 kcal (approximate caloric equivalent; see Blem 1976b). The ratio of kcal fat/minimal energy requirement then indicates the relative amount of energy reserve possessed by each bird. Figure 3 indicates that this ratio is highest in the middle geographic localities. It is possible that extreme low temperatures prevent northern Starlings from attaining the energy surplus possible in mid-range (as in House Sparrows; see Blem 1973), and that southern populations need not accumulate large reserves. Starlings use man-made microclimate at northern sites in a manner that saves energy, including roosting in buildings and resting on warm chimneys during daylight hours. These activities seem to occur less frequently southward, in-

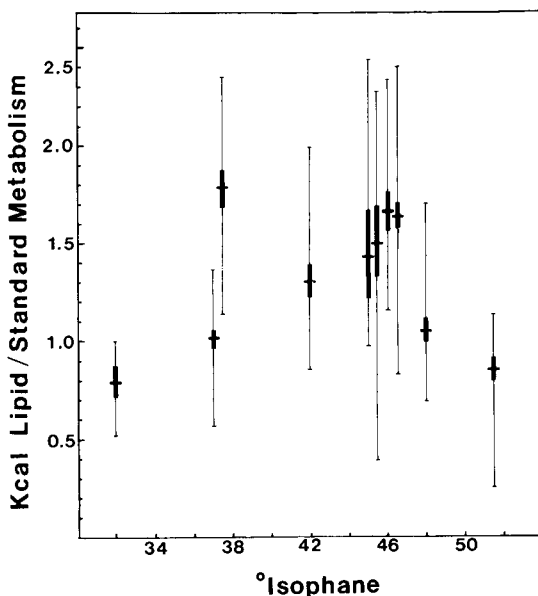


FIGURE 3. Ratios of early evening lipid reserve to minimal daily energy expenditure in Starlings. Horizontal bars represent means; vertical lines are  $\pm 1$  SE.

dicating that accumulation of daily energy needs may not be difficult.

Several workers have suggested that geographic variation in size of homeotherms is of no adaptive value with regard to physics of heat exchange or energy economy (James 1970, McNab 1971). I am not convinced that this is totally true, for several reasons: (1) lower critical temperatures at least theoretically should decrease with increased size (Kendeigh 1969, 1970), (2) real or potential insulation of birds increases with size (Kendeigh 1970, Blem 1974), and (3) increased size may provide an energetic advantage in terms of the ability of the bird to capture, store and carry energy (Blem 1975, Ketterson and Nolan 1976). The present study says little about point (1), but indicates that something other than size increase is involved in changes in insulation. There is no significant relationship between weight and conductance at any single location or over the entire range. Major weight-related adaptation may include only (3); lipid increases significantly both with body weight ( $r = 0.77$ ) and with dry weight ( $r = 0.96$ ).

In summary, Starlings in the eastern United States appear to show geographic variation in morphology and body composition that is at least partially related to climatic regimes. Obviously, environmental factors effective during the reproductive season may also play a role in bringing about this variation and should be examined in future studies.

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## LITERATURE CITED

- BARNETT, L. B. 1970. Seasonal changes in temperature acclimatization of the House Sparrow, *Passer domesticus*. Comp. Biochem. Physiol. 33:559-578.
- BLEM, C. R. 1973. Geographic variation in the bioenergetics of the House Sparrow. Ornithol. Monogr. 14:96-121.
- BLEM, C. R. 1974. Geographic variation of thermal conductance in the House Sparrow, *Passer domesticus*. Comp. Biochem. Physiol. 47A:101-108.
- BLEM, C. R. 1975. Geographic variation in wing-loading of the House Sparrow. Wilson Bull. 87:543-549.
- BLEM, C. R. 1976a. Efficiency of energy utilization of the House Sparrow, *Passer domesticus*. Oecologia 25:257-264.
- BLEM, C. R. 1976b. Patterns of lipid storage and utilization in birds. Am. Zool. 16:671-684.
- BORDNER, D. L., M. WOOD, AND D. E. DAVIS. 1968. Geographical distribution of starlings banded at State College, Pennsylvania. Bird-Banding 39:117-122.
- BRENNER, F. J. 1965. Metabolism and survival time of group starlings at various temperatures. Wilson Bull. 77:388-395.
- BURT, H. E., AND M. GILTZ. 1966. Recoveries of starlings banded at Columbus, Ohio. Bird-Banding 37:267-273.
- DAVIS, D. E. 1960. Comments on the migration of starlings in Eastern United States. Bird-Banding 31:216-219.
- HAYWARD, J. S. 1965. The gross body composition of six geographic races of *Peromyscus*. Can. J. Zool. 43:297-303.
- HELMS, C. W., W. H. AUSSIKER, E. B. BOWER, AND S. D. FRETWELL. 1967. A biometric study of major body components of the Slate-colored Junco, *Junco hyemalis*. Condor 69:560-578.
- HERREID, C. R., II, AND B. KESSEL. 1967. Thermal conductance in birds and mammals. Comp. Biochem. Physiol. 21:405-414.
- HOPKINS, A. D. 1938. Bioclimatics—A science of life and climate relations. U.S. Dep. Agric. Misc. Publ. 280:1-188.
- HUDSON, J. W., AND S. L. KIMZEY. 1966. Temperature regulation and metabolic rhythms in populations of the House Sparrow, *Passer domesticus*. Comp. Biochem. Physiol. 17:203-217.
- JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51:365-390.
- JOHNSON, S. R., AND I. MCT. COWAN. 1975. The energy cycle and thermal tolerance of the Starlings (Aves, Sturnidae) in North America. Can. J. Zool. 53:55-68.
- JOHNSTON, R. F. 1969. Character variation and adaptation in European sparrows. Syst. Zool. 18:206-231.
- KALMBACH, E. R. 1932. Winter Starling roosts of Washington. Wilson Bull. 44:65-75.
- KENDEIGH, S. C. 1969. Tolerance of cold and Bergmann's Rule. Auk 86:13-25.
- KENDEIGH, S. C. 1970. Energy requirements for existence in relation to size of bird. Condor 72:60-65.
- KESSEL, B. 1951. Criteria for sexing and aging European Starlings (*Sturnus vulgaris*). Bird-Banding 22:16-23.
- KESSEL, B. 1953. Distribution and migration of the European Starling in North America. Condor 55:49-67.
- KESSEL, B. 1957. A study of the breeding biology of the European Starling (*Sturnus vulgaris* L.) in North America. Am. Midl. Nat. 58:257-331.
- KETTERSON, E. D., AND V. NOLAN, JR. 1976. Geographic variation and its climatic correlates in the sex ratios of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). Ecology 57:679-693.
- LUSTICK, S., AND J. ADAMS. 1977. Seasonal variation in the effects of wetting on the energetics and survival of starlings (*Sturnus vulgaris*). Comp. Biochem. Physiol. 56A:173-177.
- MCNAB, B. K. 1971. On the ecological significance of Bergmann's Rule. Ecology 52:845-854.
- PACKARD, G. C. 1967. House Sparrows: evolution of populations from the Great Plains and Colorado Rockies. Syst. Zool. 16:73-89.
- POWER, D. M. 1969. Evolutionary implications of wing and size variation in the Red-winged Blackbird in relation to geographical and climatic factors: a multiple regression analysis. Syst. Zool. 18:363-373.
- THOMAS, E. S. 1934. A study of starlings banded at Columbus, Ohio. Bird-Banding 5:118-128.
- WHITFORD, P. C. 1979. An explanation of altitudinal deviations from Bergmann's Rule as applied to birds. Biologist 61:1-10.

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