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Author(s): Frances C. James
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GEOGRAPHIC SIZE VARIATION IN BIRDS AND ITS RELATIONSHIP TO CLIMATE[1]

FRANCES C. JAMES
Department of Zoology, University of Arkansas, Fayetteville 72701

Abstract. There is a high degree of concordance among the patterns of geographic size variation in birds in the eastern and central United States. This is demonstrated for 12 species by assuming that wing length measurements are an indicator of body size on the intraspecific level, and by arranging the data in the form of a grid of means of wing lengths for sample areas. Maps giving isophenetic lines for wing length indicate gradually increasing size clines northward and westward from Florida in the Hairy Woodpecker (*Dendrocopos villosus*), Downy Woodpecker (*Dendrocopos pubescens*), Blue Jay (*Cyanocitta cristata*), Carolina Chickadee (*Parus carolinensis*), White-breasted Nuthatch (*Sitta carolinensis*), and Eastern Meadowlark (*Sturnella magna*). In each case there is a trend for larger (or longer-winged) birds to extend southward in the Appalachian Mountains and for smaller (or shorter-winged) birds to extend northward in the Mississippi River valley. Maps made by a computer and automatic plotter using contour intervals of 0.5 mm of mean wing length for the Downy Woodpecker, for male White-breasted Nuthatches, and for female Blue Jays show that, in addition to the pattern just mentioned, relatively longer-winged birds extend southward in the interior highlands of Arkansas, and relatively shorter-winged birds extend northward up other river valleys. These subtle relationships between intraspecific size variation and topographic features suggest that the link between the two phenomena may be precise adaptations to even minor climatic gradients. The relationship between these findings and the subspecies concept is discussed.

Correlation coefficients for the pattern of variation in the Downy Woodpecker with seasonal and annual wet-bulb temperature, vapor pressure, and absolute humidity were all either equal to or higher than correlations with dry-bulb temperature. Since these variables reflect the combined effects of temperature and humidity, the obvious indication is that size variation is more closely related to this combination than to temperature alone. Additional correlations using the mean wing length data for seven other species confirmed that wet-bulb temperature patterns are more closely related to bird size than either dry-bulb temperature patterns or latitude. These relationships can be expressed numerically as regressions of mean wing length on either annual wet-bulb temperature or mean annual total heat per pound of air. Since increased evaporation at high altitudes and in arid areas accentuates the depression of a wet-bulb thermometer, my hypothesis may partially account for several cases of size variation in birds cited by others as disturbing exceptions to Bergmann's ecogeographic rule. Sections of a translation of Bergmann's paper published in 1847 are given. The biological mechanisms by which these relationships are maintained are unknown, and the wide range of tolerance by birds to diurnal and seasonal temperature variations tends to mask them. If the well-established inverse relationship between weight and metabolic rate per gram of homeotherms is operative on the intraspecific level, the relationships can be discussed in terms of avenues of heat loss and of energy budget equations.

In the eastern and central United States most of the species of birds that vary in size geographically are larger northward. Although the variation is believed to be clinal, it is descriptively organized in the American Ornithologists' Union Check-List of North American Birds (1957) by the recognition of northern and southern subspecies. The boundaries between the subspecies suggest an S-shaped modification of the cline, whereby larger birds are expected slightly farther south in the Appalachian Mountains and smaller birds are expected slightly farther north in the Mississippi Valley. The validity of this modification originally proposed by Baird (1859 in Mengel 1965) has been questioned recently by Mengel (loc. cit.), who recommended that it be tested with modern statistical procedures. Although there is evidence that bird size increases with altitude in high mountain ranges elsewhere (Rand 1936, Traylor 1950, and others), this has not been clearly demonstrated for the Appalachians. In fact the current view is that the degree of topographic variation in this area is too small for one to expect correlations with size variation in birds.

Using a large series (more than 4,000 specimens representing 12 common species, Table 1) from a broad geographic area, and subjecting the data to statistical techniques, I have found very precise interspecific concordance in the patterns of size variation. Increasing size clines northward and westward from Florida are modified in some very subtle ways by factors related to even less pro-

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TABLE 1. List of the species considered giving the period when the specimens were taken, and the tables and figures where the results are presented

Species		Period	Sex	Data in table	Map in figure
Red-shouldered Hawk	*Buteo lineatus*	April-August	M	5	–
Sparrow Hawk	*Falco sparverius*	May-August	M,F	5	–
Screech Owl	*Otus asio*	All year	M,F	4	–
Common Nighthawk	*Chordeiles minor*	May-August 15	M,F	5	–
Yellow-shafted Flicker	*Colaptes auratus*	April-August (May-August N of 37° Lat.)	M,F	5	–
Hairy Woodpecker	*Dendrocopos villosus*	April-August	M	4,5	9
			F	4,5	9,10
Downy Woodpecker	*Dendrocopos pubescens*	All year	M,F	4	1,2,3
Blue Jay	*Cyanocitta cristata*	April-August (April 15-August N of 37° Lat.)	M	4	6
			F	4	7
Carolina Chickadee	*Parus carolinensis*	All year	M	4,5	8
			F	4,5	8
White-breasted Nuthatch	*Sitta carolinensis*	All year	M	4	4
			F	4	5
Robin	*Turdus migratorius*	March 15-August	M	4	–
Eastern Meadowlark	*Sturnella magna*	April-August	M	4,5	11,12
			F	5	11

nounced topographic features than the Appalachians and the Mississippi Valley. This prompted an analysis of the relationship between climatic gradients and geographic size variation, and a review of the question of Bergmann's ecogeographic rule.

METHODS AND ARRANGEMENT OF DATA

The problem of analyzing and describing geographic variation is very difficult. One of the requirements is an unbiased arrangement of the data into a two-dimensional system. The methods used here satisfy that requirement.

The least variable and most valid indicator of body size for intraspecific comparisons in birds is generally considered to be wing length (Lanyon 1960, Selander and Johnston 1967, and others). Increase in wing length represents increase in length of skeletal components as well as in length of feathers (Calhoun 1947), and it parallels increase in fat-free body weight (Connell, Odum, and Kale 1960). Tail length, tarsal length, and a variety of other measurements are also allometrically related to body size (Power 1968); but since these measurements do not add information to the wing length-body size relationship they were excluded from consideration here. A discussion and analysis of the reliability of wing length as a predictor of weight is given in a later section.

Using specimens of the 12 species listed in Table 1, the chord of the wing was measured to the nearest millimeter. Extreme care was taken to exclude juveniles and birds that showed feather wear or molt. The specimens are in the collections of the United States National Museum, the American Museum of Natural History, the Chicago Natural History Museum, and the Universities of Arkansas, Kansas, and Oklahoma. The University of Arkansas collection was supplemented by collections made by the writer in various sections of Arkansas in 1965 and 1966; these were preserved by the freeze-dry method and then were degreased in a Branson Cub degreaser.

Several precautions were taken to minimize the within-locality variation due to sex, age, or season. For the species that are migratory, only specimens taken in the breeding season were used (Table 1). Sign tests on size differences between sexes, made by comparing pairs by locality (Siegel 1956) indicated that there was a significant size difference between the sexes in all of the species except the Hairy Woodpecker, Downy Woodpecker, Yellow-shafted Flicker, and Common Nighthawk (Table 2). In the last three species the sexes were pooled for analysis.

Since more data were available for the Downy Woodpecker than for any other species, these measurements were subjected to two additional tests to find whether there might be within-locality differences due to age (immature versus adult plumage), season (due to the condition of molt or possibly some southward movement of larger northern birds in winter), or sex (Table 3). Sex and age differences among 55 birds from Lawrence, Kansas, collected between September and March were subjected to a two-way analysis of variance. There were no significant differences in wing length due to sex or age ($\alpha = 0.05$). Sex and seasonal differences among 23 birds from Ft. Lee, New Jersey, were subjected to a two-way analysis of variance and also

TABLE 2. Results of two-tailed sign tests (Siegel 1956) to determine whether there are significant size differences between the sexes at single localities

Species	Number of pairs whose differences show a sign N	Number of fewer signs x	Probability of occurrence by chance	Conclusion
Screech Owl	25	4	.002**	Females larger
Common Nighthawk	15	7	.500	Sexes similar
Yellow-shafted Flicker	7	3	.500	Sexes similar
Hairy Woodpecker	12	4	.388	Sexes similar
Downy Woodpecker	25	12	.500	Sexes similar
Blue Jay	25	6	.007**	Males larger
Carolina Chickadee	22	2	.002**	Males larger
White-breasted Nuthatch	25	2	.001**	Males larger
Robin	21	6	.039*	Males larger
Eastern Meadowlark	24	2	.001**	Males larger

*Significant at 0.05
**Significant at 0.01

TABLE 3. Sex, age, and seasonal differences in wing lengths of Downy Woodpeckers at two localities

Locality	Category	Size of sample	Mean	Standard deviation	Probability of a larger F-ratio by chance		
					Sex	Age	Interaction
Lawrence, Kansas (55 birds taken September to March)	Adult male	21	91.9	2.00	0.28	0.08	0.74
	Adult female	12	92.4	2.01			
	Immature male	12	92.8	1.85			
	Immature female	10	93.5	1.89			
					Sex	Season	Interaction
Ft. Lee, New Jersey (23 adults)	Male, April–August	3	94.7	1.53	0.41	0.37	0.32
	Female, April–August	5	92.8	2.75			
	Male, September–March	9	94.5	1.46			
	Female, September–March	6	94.4	2.01			

were not significant ($\alpha = 0.05$). It was concluded that these sources of possible variation were not affecting the data at hand in a way that would obscure an overall pattern of geographic size variation. For subsequent calculations involving the Downy Woodpecker, the sex, season, and age classes were pooled into a single analysis. This is in agreement with Mengel (1965: 303–304) who found no statistically significant sex or seasonal differences in the wing lengths of 72 Downy Woodpeckers taken in Kentucky. The possibility that some interlocality differences in sexual dimorphism exist is supported by a subsequent analysis of wing lengths of Downy Woodpeckers taken in mist nets near Pittsburgh, Pennsylvania (see section The Adaptive Significance of Geographic Size Variation).

Taking the suggestion of Edgren (1961) that a good unbiased method for arranging the data would seem to be the use of a grid, I tried two ways of organizing the measurements. First, points where even-numbered latitude and longitude lines intersect on a map were chosen as arbitrary centers of circular samples. Each circle had a radius of 100 miles and all the birds collected within a circle were considered as one sampling unit. Circles were placed so that a minimum number would be needed to cover the specimens. This gave a grid of 101 partly overlapping circles (Table 4) such as is shown for the Downy Woodpecker in Figure 1. Birds collected at localities where circles overlap were treated as pertaining to each circle. Mean wing lengths for these circular samples, when plotted on a map, present an unbiased, two-dimensional, moving average of size variation.

The second method was to obtain mean wing lengths by states (Table 5) and to plot these on a map. By interpolation, isophenes (lines connecting points of equal value for a phenetic character) can be drawn to show the pattern of variation. An example showing isophenes made by interpolations between means of circular samples is shown in Figure 2, examples made by inter-

TABLE 4. Mean wing lengths for circular areas, each having a radius of 100 miles and a center at a point where even-numbered latitude and longitude lines cross. Standard deviations are given for the Downy Woodpecker. (Sample sizes are in parentheses)

No. of means	Screech Owl M (83) 17	Screech Owl F (70) 16	Hairy Woodpecker M (64) 17	Hairy Woodpecker F (111) 26	Downy Woodpecker M,F (1038) 76	Downy Woodpecker standard deviations 64	Blue Jay M (363) 51	Blue Jay F (175) 30	Carolina Chickadee M (174) 22	Carolina Chickadee F (110) 19	White-breasted Nuthatch M (470) 42	White-breasted Nuthatch F (284) 32	Robin M (124) 14	Eastern Meadowlark M (152) 26
Lat.-Long														
26-80					86.1 (6)	1.4								111.3 (3)
26-82					86.6 (5)	0.8								111.0 (3)
26-96														116.8 (4)
26-98														116.8 (4)
28-80											85.7 (3)			
28-82					87.3 (12)	1.6	124.4 (5)	123.0 (3)			85.6 (9)	85.7 (3)		
30-82					87.5 (5)	0.8	125.0 (4)				85.8 (6)	88.3 (4)		
30-84				112.3 (3)	88.5 (1)									
30-86					88.8 (3)									
30-88					89.0 (9)	2.0	126.0 (4)		57.8 (6)			87.0 (3)		116.7 (3)
30-90	143.5 (2)	146.7 (3)		112.0 (4)	87.2 (28)	2.3	125.0 (10)		59.2 (25)	56.8 (13)				115.4 (5)
30-92	147.7 (3)	151.0 (4)		112.0 (3)	87.0 (13)	2.3			59.6 (11)	57.9 (8)				110.6 (9)
30-94					88.0 (2)				60.0 (9)	60.5 (4)				110.5 (2)
30-96					87.7 (3)				60.9 (8)	60.3 (6)				
30-98									61.7 (3)	61.1 (11)				
32-80					87.2 (17)	1.8	126.6 (5)	123.7 (6)			86.5 (12)			
32-82					87.4 (19)	2.1	127.3 (4)	124.4 (5)			86.7 (7)			
32-84				112.3 (3)	89.3 (7)	3.0								
32-86				109.7 (3)	90.3 (6)	2.2	128.5 (4)	126.4 (5)						116.7 (3)
32-88					89.4 (4)	1.3	127.3 (3)							115.7 (3)
32-90							128.3 (3)		61.0 (6)					
32-92					88.9 (6)	1.8	128.3 (3)		61.2 (5)	58.0 (4)				
32-94					87.7 (3)				60.3 (3)	58.0 (3)				
32-96	159.0 (2)				87.0 (1)					56.5 (2)				
32-98	159.0 (2)				91.0 (2)				64.0 (3)					
32-100					91.0 (2)									
32-110												90.7 (6)		
34-78					89.8 (10)	3.0	127.5 (4)							
34-80					89.4 (25)	3.0	126.3 (4)				87.3 (12)	87.3 (6)		
34-82					90.4 (41)	2.2	127.6 (14)	127.8 (8)			88.9 (10)	88.5 (6)		112.7 (3)
34-84			115.0 (3)		91.3 (34)	1.8	128.7 (10)	127.0 (7)			88.4 (20)	87.0 (9)		114.2 (5)
34-86				111.3 (3)	91.2 (19)	2.1	129.7 (9)	124.5 (6)			87.8 (14)	86.7 (3)		117.5 (4)
34-88				111.5 (2)	90.3 (11)	1.9	130.4 (7)	123.3 (4)	62.3 (3)		88.9 (10)			117.7 (3)
34-90		152.0 (2)	117.5 (2)	115.7 (3)	89.6 (7)	2.1	129.3 (4)		61.5 (6)	60.7 (4)	88.0 (3)			114.9 (9)
34-92	153.0 (5)	152.5 (6)	117.5 (2)	116.0 (3)	90.1 (10)	2.7	128.7 (3)		60.2 (4)	59.5 (4)				114.9 (9)
34-94	153.0 (5)	150.5 (4)	114.0 (2)	114.5 (2)	90.2 (15)	3.0	130.7 (3)		64.1 (7)	61.0 (10)	87.0 (4)			115.9 (7)
34-96	159.0 (2)		118.3 (8)	114.0 (2)	90.5 (10)	2.9			64.3 (10)	60.0 (3)	87.0 (8)			115.2 (6)
34-98			116.8 (6)	115.8 (10)	89.9 (8)	2.1			64.0 (4)	60.0 (4)	86.4 (5)		128.0 (12)	116.4 (5)
34-100			117.0 (2)	118.0 (5)	90.1 (6)	2.4	130.3 (3)							
36-76					90.3 (20)	1.6					87.7 (3)			
36-78					90.8 (17)	1.4					87.3 (4)			
36-80					92.2 (19)	1.6					89.1 (7)			
36-82			117.5 (2)	117.5 (2)	92.5 (37)	2.0	129.1 (14)	129.8 (10)			89.4 (12)	87.5 (6)	130.0 (5)	
36-84			115.6 (7)	113.7 (6)	92.4 (38)	2.3	129.7 (14)	129.8 (5)			89.3 (22)	86.7 (13)		
36-86			113.7 (3)		91.7 (22)	1.7	129.5 (6)				88.7 (9)	87.3 (3)		118.0 (3)
36-88				113.0 (4)	91.3 (26)	1.7	129.5 (11)		62.0 (10)	59.0 (4)	88.7 (11)			116.8 (5)
36-90			116.0 (2)	114.2 (4)	90.5 (17)	2.3	128.9 (7)		61.3 (10)	60.9 (7)		88.7 (3)	128.0 (4)	115.9 (13)
36-92			116.0 (1)						62.0 (3)	61.3 (4)			127.0 (6)	115.5 (13)
36-94		155.5 (4)	116.0 (2)	115.5 (8)	91.5 (17)	3.3		128.5 (4)	63.5 (20)	61.9 (14)	88.7 (24)	87.5 (13)	127.0 (14)	115.3 (18)
36-96		158.0 (3)	118.5 (6)	116.0 (9)	91.1 (25)	3.0			63.8 (11)	63.0 (2)	88.0 (10)	88.0 (4)	128.0 (13)	114.7 (6)

TABLE 4.—Continued

No. of means	Screech Owl M (83) 17	Screech Owl F (70) 16	Hairy Woodpecker M (64) 17	Hairy Woodpecker F (111) 26	Downy Woodpecker M,F (1038) 76	Downy Woodpecker standard deviations 64	Blue Jay M (363) 51	Blue Jay F (175) 30	Carolina Chickadee M (174) 22	Carolina Chickadee F (110) 19	White-breasted Nuthatch M (470) 42	White-breasted Nuthatch F (284) 32	Robin M (124) 14	Eastern Meadowlark M (152) 26
36-98	161.0 (2)	159.0 (2)	118.3 ,6)	117.4 (12)	90.8 (16)	1.8	130.6 (5)		66.0 (7)	62.7 (3)			129.0 (14)	
36-100			118.5 (4)	118.9 (9)	92.4 (7)	1.9	130.2 (5)	127.7 (3)						
36-102			126.7 (6)	122.5 (2)	94.6 (3)			127.0 (3)					131.0 (4)	
36-106												89.0 (9)		
36-108												88.8 (9)		
36-110												87.0 (3)		
38-76					92.0 (57)	2.2	132.0 (14)	127.8 (5)			89.6 (25)	88.0 (22)		
38-78					92.4 (55)	2.2	132.2 (15)	127.8 (5)			89.5 (25)	88.0 (16)		
38-80					93.6 (24)	2.3	133.7 (6)				89.9 (7)	88.7 (3)		
38-82					93.3 (26)	2.2	132.0 (5)	123.7 (3)			90.2 (9)	88.0 (6)		
38-84					92.4 (23)	1.9	131.0 (3)				89.6 (10)	87.4 (5)		
38-86					92.2 (27)	2.2	129.5 (8)				88.2 (5)			
38-88	151.2 (6)	156.5 (4)		112.3 (3)	92.0 (22)	2.1	128.4 (20)	122.1 (8)			88.7 (7)	86.0 (3)		114.3 (4)
38-90		155.5 (2)			90.5 (5)	2.0								
38-94	158.1 (11)	160.4 (11)			92.4 (61)	2.1	131.6 (12)	130.0 (10)			89.8 (21)	86.8 (11)	129.0 (7)	
38-96	158.9 (12)	160.3 (12)			92.3 (61)	2.1	131.7 (12)	130.3 (14)			89.5 (24)	86.9 (18)	131.0 (12)	
38-98	160.5 (4)	162.8 (4)		120.0 (2)			130.8 (4)	128.3 (3)						
38-100	161.0 (2)						130.1 (7)	129.0 (6)						
38-102	163.0 (2)			122.5 (2)			134.5 (4)	129.2 (6)						
38-106													136.0 (5)	
40-74					93.7 (36)	2.3	130.3 (4)	127.0 (3)			89.3 (12)	88.1 (8)		
40-76					92.7 (36)	2.1	133.6 (11)	126.4 (5)			89.4 (26)	88.0 (26)		
40-78					92.8 (35)	2.0	134.1 (11)	128.3 (3)			89.5 (23)	88.2 (26)		
40-80					94.4 (11)	2.1	134.0 (4)				90.0 (5)	88.7 (3)		
40-82				118.0 (2)	93.5 (10)	1.6								
40-84					93.8 (6)	1.0								
40-86					92.2 (10)	1.1								
40-88	152.2 (5)	159.0 (3)			91.7 (13)	2.2	127.5 (8)	123.3 (7)						
40-90		158.7 (3)												
40-92		158.7 (3)												
40-94	158.4 (9)				92.4 (61)	2.1	131.6 (12)	130.6 (9)			89.8 (3)	86.7 (9)	128.0 (4)	
40-96	158.4 (9)						131.7 (12)	130.1 (12)			89.9 (21)	86.8 (17)	131.0 (12)	
40-100							136.6 (5)							
40-102							136.8 (6)							
40-104											90.7 (3)			
42-70					94.5 (5)	0.9								
42-72					94.1 (12)	1.3	131.3 (4)				89.8 (4)			
42-74					93.5 (46)	2.1	130.5 (6)	126.5 (4)			89.4 (12)	88.0 (8)		
42-76					92.7 (9)	2.0								
42-78					93.2 (3)									
42-80					93.8 (3)									
42-88					92.8 (3)			129.7 (3)						
42-90					93.2 (5)	2.6								
44-72					92.5 (10)	2.3								
44-74					92.8 (12)	2.3								
44-78											92.0 (3)			
44-88					96.1 (7)	2.0								
44-104													136.0 (12)	
46-98							133.0 (2)							

FIG. 1. A grid of circular areas, each 100 miles in radius, superimposed over dots representing localities where Downy Woodpeckers considered in this study were collected.

polations between means for states are shown in Figures 8, 9, and 11.

In addition, for those species for which there were adequate data, maps were made by an automatic Electronics Associates Inc. plotter. Robert E. South supervised this project which employed the geological information system of retrieval and data display. This involved a series of approximately 10 programs designed originally to analyze company data for the Sinclair Oil Corporation at its Tulsa Research Center. Contour plotting as employed here involves successive interpolations between adjacent points, rather than simultaneous consideration of all points (trend surface analysis). This method is used commonly by geographers to make topographic maps and by geologists to plot strata. Surface approximations for contour intervals of 0.5 mm of wing length were achieved by this method (Figs. 3 through 7, 10 and 12). Data for these figures were the means of the circular samples (Table 4).

PATTERNS OF SIZE VARIATION

More data were available for the Downy Woodpecker than for the other birds, so the most thorough analysis is for this species. Discussions for the others will be presented in the order of the amount of data available.

Downy Woodpecker

There is a 10-mm difference in mean wing length, ranging from 86.1 to 96.1 between birds in southern Florida and northern Wisconsin (Fig. 2). For any particular longitude the variation shows a steady increase from south to north. There is definitely a trend for larger birds to extend farther south in the Appalachian Mountains than in the Mississippi Valley or the Atlantic coastal sector. The woodpeckers increase in size toward the western states and there is a pocket of relatively large birds extending along the coast of New England. When the political state outlines are considered, it is clear that the variation

TABLE 5. Mean wing lengths by states. (Sample sizes are in parentheses)

	Red-sh Hk M (26)	Sparrow Hk M (19)	Sparrow Hk F (31)	C. Nightk M & F (52)	Y-sh. Flicker M & F (86)	Hairy Wdpkr M (121)	Hairy Wdpkr F (90)	C. Chickdee M (259)	C. Chickdee F (242)	E. Mdlk M (109)	E. Mdlk F (49)
Ala.	310 (1)	178 (2)	193 (2)	187 (12)		113 (9)	110 (5)	61 (12)	58 (3)	117 (4)	104 (3)
Ariz.		182 (3)	187 (4)	195 (2)							
Ark.	318 (3)		188 (3)	190 (4)	152 (4)	117 (5)	115 (9)	63 (24)	62 (22)	116 (34)	111 (7)
Colo.		185 (1)	201 (3)			132 (5)	128 (3)				
Fla.	292 (10)	178 (2)	181 (3)	186 (5)	145 (12)			60 (23)	57 (14)	111 (5)	99 (3)
Ga.		178 (2)	190 (1)		153 (6)	115 (11)	112 (5)	61 (4)	59 (44)	115 (8)	
Ill.	314 (1)	183 (2)	192 (2)			114 (6)	111 (2)	64 (3)	63 (5)	116 (7)	105 (5)
Ind.	313 (1)								61 (4)		
Kan.					153 (22)	118 (3)	118 (3)	65 (8)	62 (5)		
Ky.	312 (2)				154 (3)	114 (2)	114 (3)			116 (3)	
La.	304 (1)	176 (1)		187 (7)				60 (23)	57 (20)	111 (11)	97 (3)
Md.			188 (2)			119 (2)	116 (2)	62 (10)	59 (9)		
Mass.	315 (1)										
Mich.						123 (2)	122 (2)				
Miss.		168 (1)	181 (3)	183 (12)		112 (5)		60 (15)		115 (4)	100 (1)
Mo.	318 (1)					114 (2)	116 (1)		57 (1)		
Mont.		187 (5)	199 (4)								
Nebr.											
N.J.			191 (2)								
N.M.				195 (4)							
N.Y.	319 (1)		190 (2)			119 (3)	118 (6)				
N.C.	318 (1)				151 (11)	118 (7)	115 (5)	62 (26)	59 (29)	117 (6)	106 (4)
Ohio								64 (4)			
Okla.						120 (24)	118 (24)	66 (24)	62 (7)	115 (9)	116 (1)
S.C.				185 (2)	149 (13)	114 (11)	111 (8)	61 (19)	59 (14)	115 (9)	109 (4)
Tenn.	311 (1)				152 (15)	117 (10)	113 (10)	62 (14)	61 (11)	115 (4)	105 (8)
Tex.				177 (2)				62 (19)	61 (21)	117 (5)	105 (4)
Va.	312 (1)			195 (2)		116 (6)		63 (16)	60 (17)		111 (6)
W.Va.	321 (1)					117 (8)	115 (2)	62 (15)	60 (16)		

within a single state is merely a fraction of a complex pattern.

From the same data (Table 4) a computer and automatic plotter were able to achieve isophenetic lines for a contour interval of 0.5 mm, which show further refinements of the pattern of variation (Fig. 3). As before, the primary cline increases northward and westward from Florida and this is modified by a southerly extension of larger birds in the Appalachian Mountains and a northerly extension of smaller birds in the Mississippi Valley. In addition, several more minor effects are apparent. There is a second southward extension of larger birds in southern Missouri, eastern Oklahoma and western Arkansas that corresponds to the interior highlands of the Ozark Plateau and the Ouachita Mountains. This is also evident in Figure 2. In addition to the extension of smaller birds slightly farther north in the Mississippi River Valley, similar effects can be seen in the valleys of the Ohio River, the Red River between Oklahoma and Texas, and even up Chesapeake Bay. Larger birds extend southward down the lower peninsula of Michigan. Along the east coast from New Jersey to Massachusetts mean wing lengths do not vary. On the other hand, the sharpest gradient in the pattern for the entire area is in Texas, and it corresponds to the sharpest ecological gradient.

Although these maps give the overall pattern of average size variation, they do not indicate intralocality variance. For instance, the Florida birds might cluster tightly around their mean, whereas the Wisconsin birds might range from 86 to 106 mm still having a mean wing length of 96 mm. Or there might be a zone within the area under consideration where there is an increase in overall variance. To discover whether this was the case, the standard deviations of 67 samples (Table 4) were subjected to Bartlett's test for homogeneity of variance. Bartlett's test statistic was 91.08 with 66 degrees of freedom. The probability of a larger chi-square statistic by chance was less than 0.023, so it was concluded that the variances were heterogeneous ($\alpha = 0.05$). When the various sample standard deviations were plotted on a map, there was no pattern to their distribution. To test whether the heterogeneity was caused by the fact that some sample circles had crossed more complex parts of the isophene pattern than others, the same test was run again using the standard deviations of birds collected between two isophenetic lines (Figure 2) as sampling units. For these 10 groups the test statistic was 7.99, and since $Pr(\chi^2(9) \geqq 7.99) = 0.534$, it

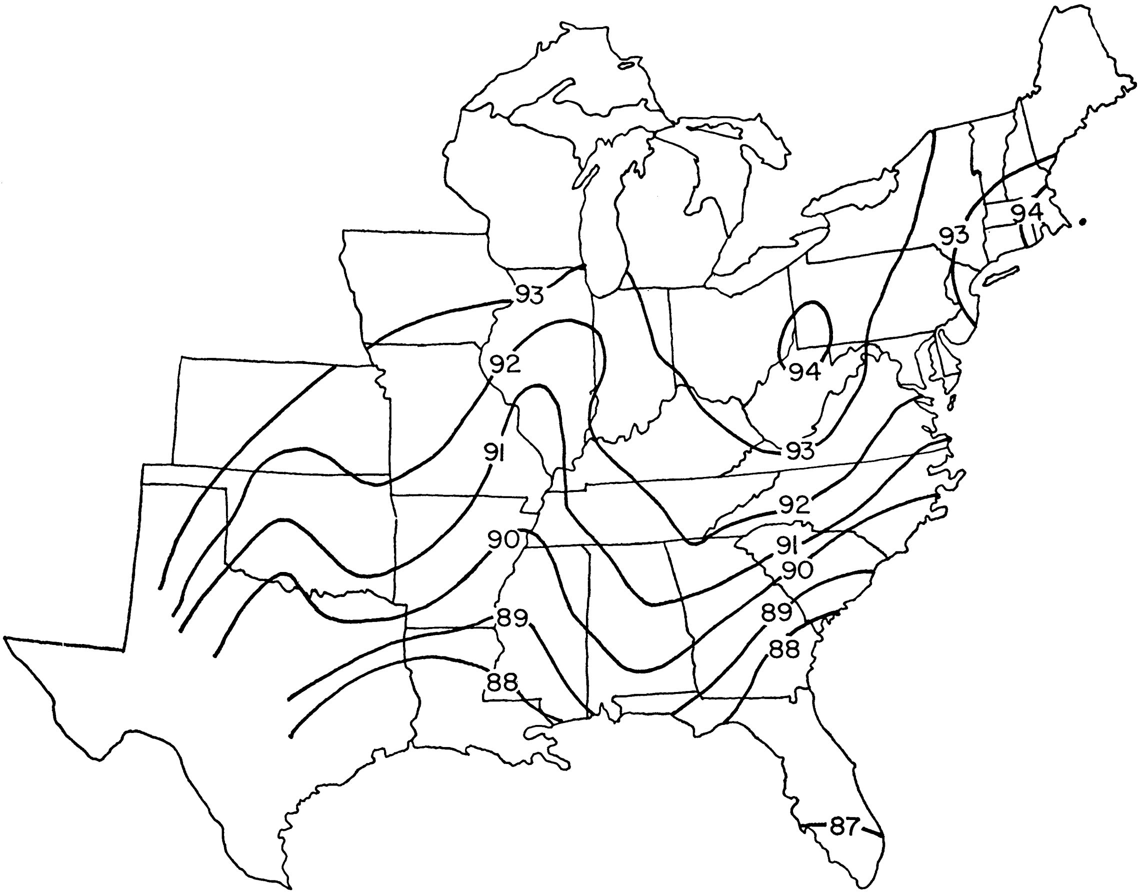

FIG. 2. Isophenes for wing length in the Downy Woodpecker (contour interval, 1 mm; data in Table 4).

was concluded that there were no significant differences among the 10 variances. This further supports the validity of the lines and answers the question of homogeneity of variance in the affirmative.

White-breasted Nuthatch

The size of both male and female White-breasted Nuthatches increases northward and westward from Florida throughout the eastern and central states (Table 4, Figs. 4 and 5). In the male, larger birds extend farther south in a region roughly corresponding to the mountainous area from western Pennsylvania to Alabama and smaller birds extend farther north in the basins of the Mississippi and Ohio Rivers (Fig. 4). In the female, there is but a 3-mm difference between wing lengths of birds in central Florida and in northern Ohio. Note that the sequence of sizes from 89 mm in Ohio toward 91 mm in southern New Mexico dips to 86–87 mm in the region of the Ohio and Mississippi River Valleys (Fig. 5). The interlocality size variation in this species is of small magnitude. It is more pronounced in the male than in the female. In the southeastern states the sexes appear to be identical in size, whereas the mean wing lengths of males are approximately 2 mm longer than those of females in Oklahoma, Missouri, Illinois, Ohio and Indiana. The variation in wing length is clinal and complex.

Blue Jay

The size of Blue Jays increases northward and westward from Florida in both sexes (Figs. 6 and 7, Table 4). In males, larger birds extend farther south in a region from southern New York to Alabama and again in the interior highlands of western Arkansas and eastern Oklahoma. There is a strong westerly clinal increase west of the Mississippi River. The trend for birds to be smaller in the center of the country is sufficiently strong that birds in the vicinity of Lake Michigan are equal in size to those on the northern coast of the Gulf of Mexico. Another westward-increasing cline in the mid-Atlantic states is evidently related to the fact that mean wing lengths for coastal localities from Delaware to Long Island are the same.

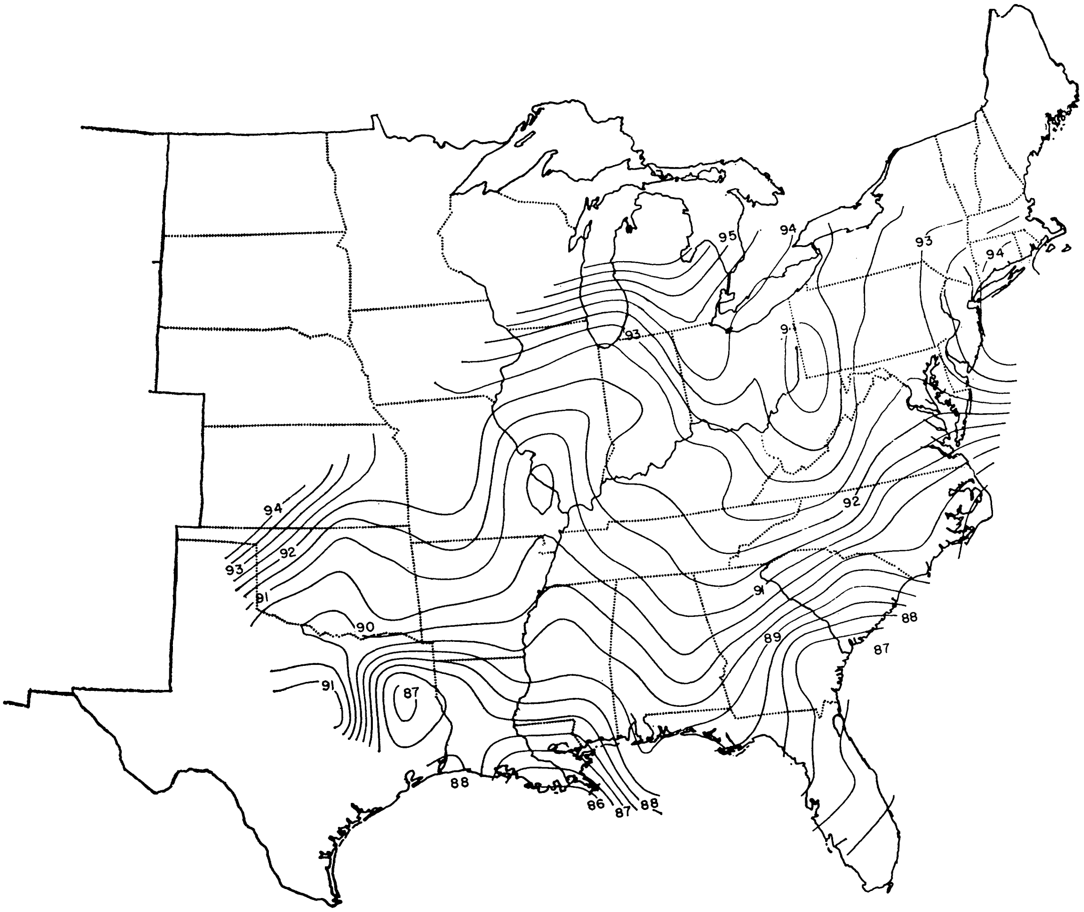

FIG. 3. Isophenes for wing length in the Downy Woodpecker (contour interval, 0.5 mm; data in Table 4).

In females (Fig. 7), the same pattern can be seen, except that the extreme northward extension of smaller birds occurs in the Ohio River Valley in southern Indiana and Ohio, rather than in southeastern Wisconsin and northwestern Illinois as with the males. This exception to the parallel patterns of variation results in an unusually great difference in mean wing length between the sexes in central southern Ohio. This may be an artifact in the data, for that particular section was represented by very few specimens. However, the mean wing lengths of five males and three females taken within 100 miles of lat.-long. 38–82 were 132.0 and 123.7 respectively.

Carolina Chickadee

Figure 8 gives isophenetic lines for mean wing length of Carolina Chickadees made by interpolations between means for 19 states (Table 5). In both sexes there is an increasing size cline northward and westward from Florida modified by a southward extension of relatively large birds in the southern Appalachians and a northward extension of relatively small birds in the valley of the Mississippi River. The patterns of variation of the two sexes are virtually identical, with mean wing lengths of males being consistently 2 mm longer than those of females. Lunk (1952) made the interesting observation that the increasing cline northward is continued through the range of the sibling species *Parus atricapillus* in the northern states.

Hairy Woodpecker

Isophenetic lines for mean wing length in the Hairy Woodpecker were made by interpolations between means for 18 states (Fig. 9, Table 5). Although the sign test (Table 2) indicated that the sexes were not significantly different in size, data for males and females were plotted separately in order to see whether the patterns of geographic variation varied. Obviously they do not, and the pattern for both sexes is similar to those of all species discussed thus far. There is an increasing size cline northward and westward from Florida modified by a southward extension of larger

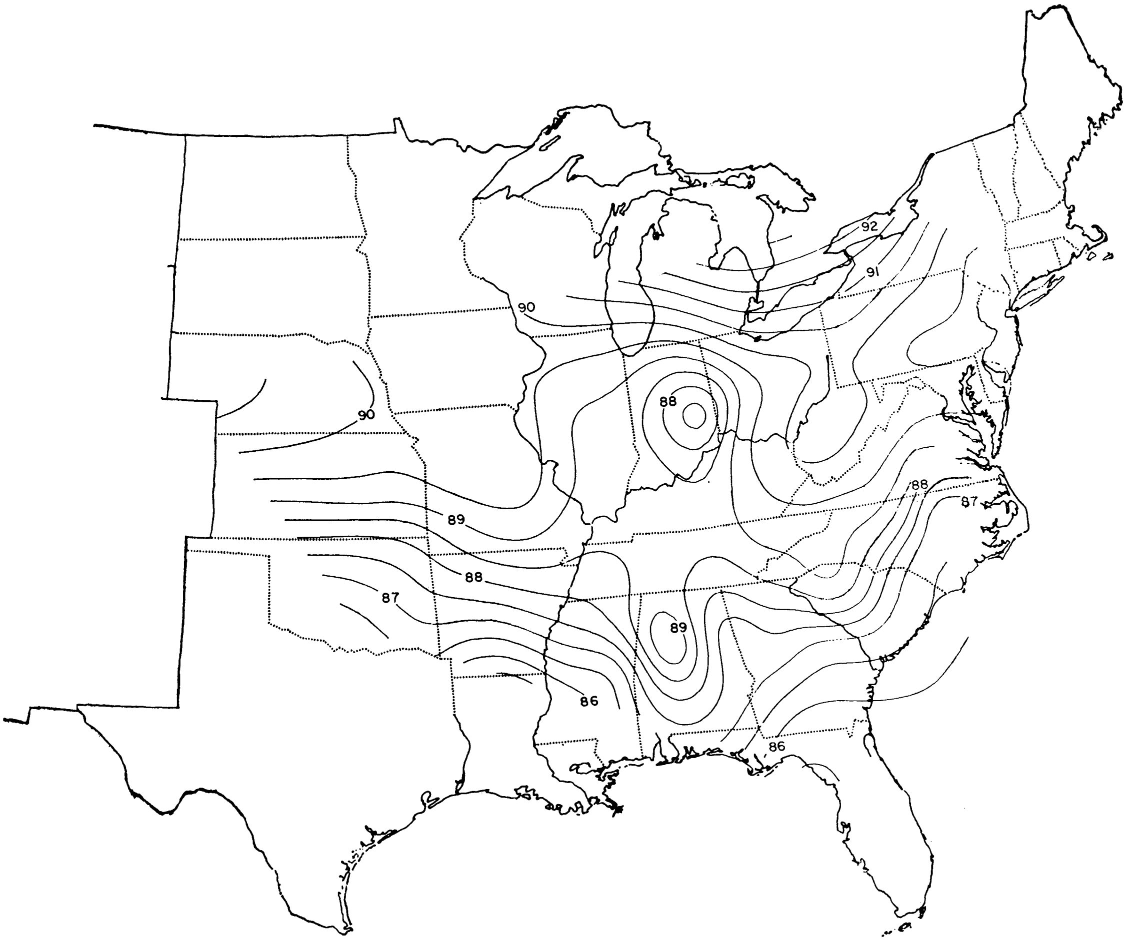

FIG. 4. Isophenes for wing length in male White-breasted Nuthatches (contour interval, 0.5 mm; data in Table 4).

birds in the Appalachians and a northward extension of smaller birds in the valleys of the Mississippi and Ohio Rivers. The pattern of the contour intervals of 0.5 mm for the wing lengths of female Hairy Woodpeckers reemphasizes that there is a trend for birds to be smaller west of the Appalachians and then larger again west of the Mississippi Valley (Fig. 10, Table 4). There seems to be a southeastward extension of larger females from the Ozark Mountains of northwestern Arkansas into the lower part of the valley of the Mississippi River.

Eastern Meadowlark

This open-country species has the same pattern of geographic size variation as the previous five species discussed (Fig. 11, Table 5). Although wing lengths of males average longer than those for females throughout the area considered, the patterns are nearly identical. An additional map giving the variation in males with a smaller contour interval emphasizes the sharp gradient toward very small birds in southern Louisiana and eastern Texas (Fig. 12, Table 4).

Six additional species

Red-shouldered Hawk.—A small series of 26 males taken from April to August demonstrates that wing lengths increase clinally northward and westward from Florida (Table 5).

Sparrow Hawk.—There is a wide range of individual variation in this species, particularly in the females. An arrangement of 19 males and 31 females taken between May and August shows only that the smallest males occur in the Gulf states as expected (Table 5).

Screech Owl.—A consideration of 83 males and 70 females arranged by means for circular areas of 100 miles radius (Table 4) shows an orderly size cline that increases northwestward.

Common Nighthawk.—Fifty-two nighthawks taken from May through August 15 were arranged

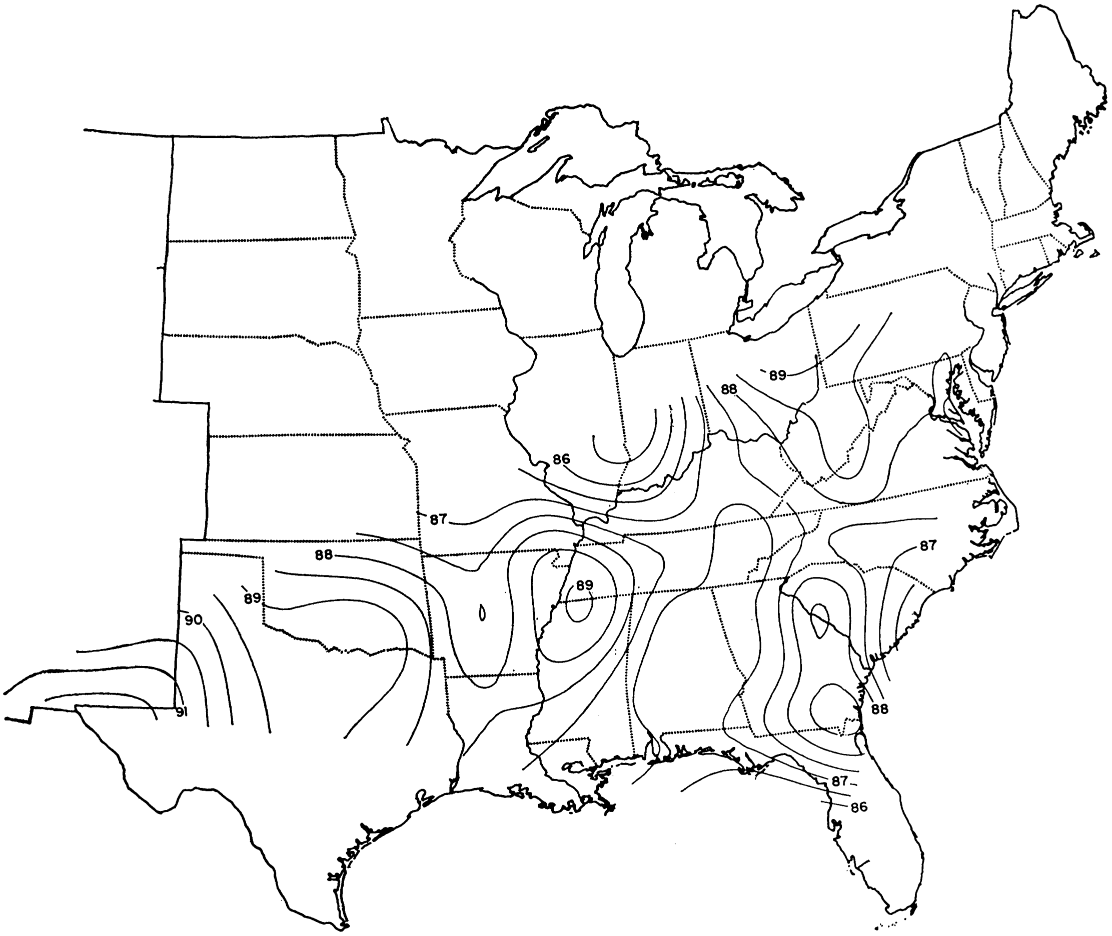

FIG. 5. Isophenes for wing length in female White-breasted Nuthatches (contour interval, 0.5 mm; data in Table 4).

by mean wing lengths for states (Table 5). This demonstrates a gradually increasing size cline northward and westward throughout the area considered.

Yellow-shafted Flicker.—Wing lengths of 86 birds taken in the breeding season, arranged into means for states (Table 5), show a gradually increasing size cline northward. The only sharp gradient in the cline in the area considered is in southern Florida.

Robin.—Wing lengths of 124 males taken from March 14 through August were arranged by circles. These show a size increase northwestward from the Gulf coast and a sharper increase westward beginning at the 100th meridian (Table 4).

Interspecific concordance in size variation

Means of wing length measurements of the 12 species considered show regular clines increasing gradually northward and westward from Florida through the eastern and central states. Maps giving isophenetic lines show complex patterns with a high degree of concordant interspecific variation. In each case there is a trend for larger birds to extend southward in the Appalachian Mountains and for smaller birds to extend northward in the Mississippi River valley. For five species, a computer and automatic plotter were used to make maps having contour intervals of 0.5 mm for wing length. These maps for the Downy Woodpecker, the male White-breasted Nuthatch and the female Blue Jay show that, in addition to the pattern just mentioned, relatively longer-winged birds extend southward in the interior highlands of Arkansas, and relatively shorter-winged birds extend northward up several river valleys. This precise but subtle relationship between intraspecific size variation and topography will be discussed in a later section. The complex nature of continuously changing geographic variation is a warning against the dangers of stating mean measurements as if they were consistent within the boundaries of a

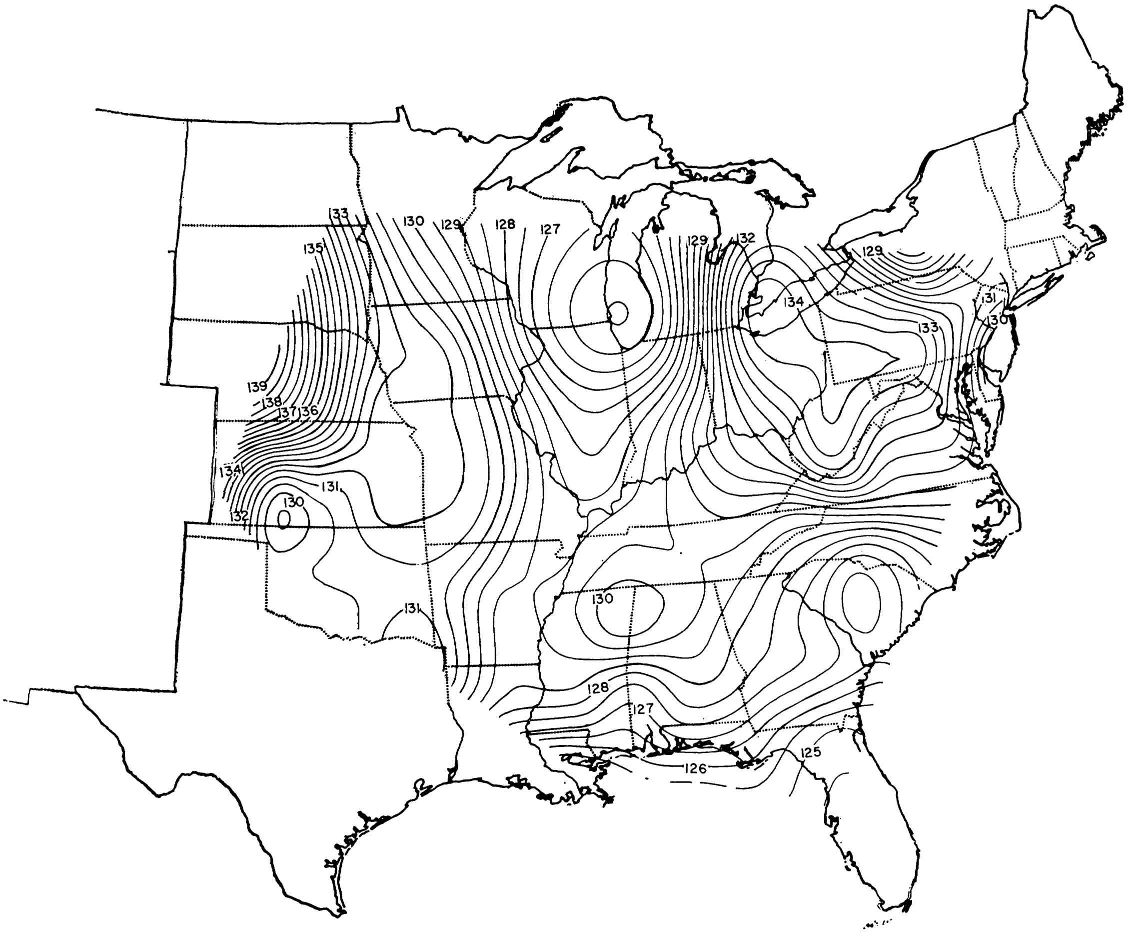

FIG. 6. Isophenes for wing length in male Blue Jays (contour interval, 0.5 mm; data in Table 4).

state or the range of a subspecies. Equally risky is the common practice of comparing mean measurements between two areas using a *t* test, unless it can be shown that the variances are homogeneous.

THE SUBSPECIES CONCEPT AND CLINES

Although the primary goal of this paper was to make an unbiased analysis of size variation, the results bear indirectly on the subspecies concept and the usefulness of the subspecies as a taxon. The varying opinions and current dissatisfaction of many systematists with the present status of this matter are well documented in the pages of the journal *Systematic Zoology*. Even those authors who defend the trinominal system as a useful tool for classification (regardless of its relation to biologic units in nature) feel that it has been misused (Doutt 1955, Edwards 1954, Mayr 1954, Tilden 1961). The major objection expressed by the opponents of the subspecies is that the trinominal system forces the biologist to make arbitrary decisions that frequently distort the real nature of the variation and bias subsequent analysis (Wilson and Brown 1953, Brown and Wilson 1954, Burt 1954, Gillham 1956, Hagmeier 1958, Owen 1963).

Most of the thorough studies of geographic variation show that independent characters vary discordantly in space (Gillham 1956, Wilson and Brown 1953) and time (Doutt 1955, Packard 1967), and also that single-character variation tends to be clinal (Sibley 1954, and others). It appears that many boundaries between subspecies are the result either of dividing a cline for one character and assuming that the other characters vary concordantly, or of multiplying the error by dividing two or more discordant clines (Gillham 1956). Despite the many differences in viewpoint among systematists on the subject of the subspecies concept, there is widespread agreement that breaking up smooth clines is inadvisable.

Suggestions for alternatives to the subspecies as a unit offer only slight improvement. Wilson

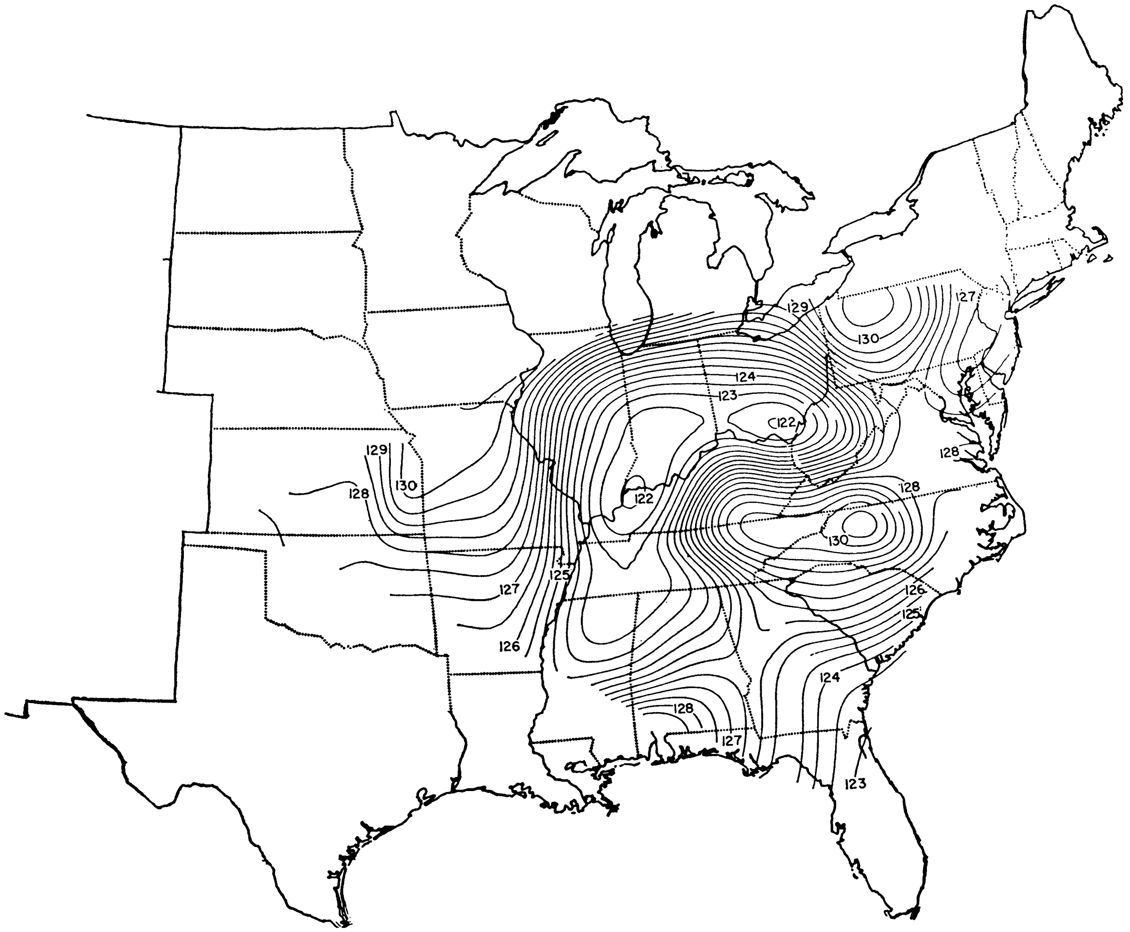

FIG. 7. Isophenes for wing length in female Blue Jays (contour interval, 0.5 mm; data in Table 4).

and Brown (1953) would give only vernacular geographic designations for localities; Doutt (1955) would add the date. Edwards would recognize only allopatric populations as subspecies and call sympatric populations morphs. Burt (1954) recommends maps and Pimentel (1958) graphs. Lidicker (1962) suggests a mathematical procedure for determining the relative degrees of differentiation between populations. None of these methods would permit a unified description of discordant patterns of variation in space and time.

All 12 of the species considered here are currently regarded as divisible into northern and southern subspecies in the eastern United States (AOU Check-List of North American Birds 1957), and in each case the primary criteria for the divisions have been that size increases northward. The fact that the boundaries between the described subspecies reflect the actual pattern of variation is a credit to the work of the early taxonomists. Color criteria such as concordant increasing paleness in the Downy Woodpecker and in the White-breasted Nuthatch or nonconcordant increasing paleness westward in the Blue Jay and in the Carolina Chickadee were also used. But the fact that the variation in both size and color is entirely clinal was acknowledged from the first (Ridgway 1914: 203, Mengel 1965: 129). The present study is limited to an analysis of one character, but the probability that the inclusion of other characters would have verified the usefulness of the present subspecific divisions is not high.

The question of a method of designating clines is simpler than the one of designating geographic variation as a whole. By considering one character at a time an n-dimensional problem is reduced to a two-dimensional geographic problem (or three if you consider time). Huxley (1939, 1942) suggested transforming the data to a scale of 0–100, plotting it on a map, and connecting points of equal value by isophenetic lines. It is similar to the system used here, except that I believe the actual measurements are more meaningful than a scale. Sibley (1954) expressed the need for some numerical way to designate clines. Ideally the

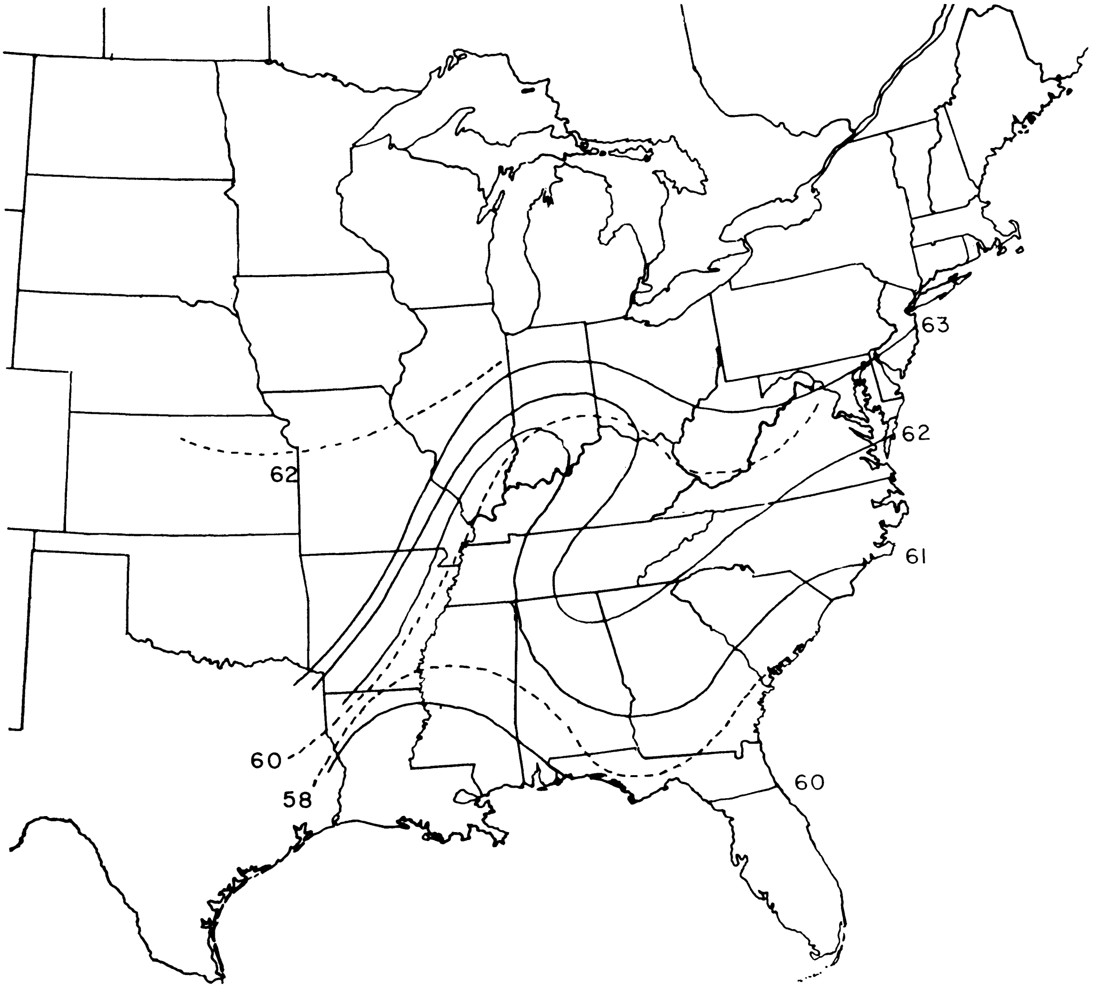

FIG. 8. Isophenes for wing length in the Carolina Chickadee. Unbroken lines are for males, broken lines for females (contour interval, 2 mm; data in Table 5).

variation should be expressed as a numerical function of those factors in the environment to which it is most highly related. An attempt toward that end is made in the next section. If one of the goals of systematics is to "detect evolution at work" (Huxley 1939), this approach might lead in the right direction.

CORRELATIONS WITH CLIMATIC GRADIENTS

Thus far it has been shown that the interspecific concordance in geographic size variation in the birds considered here is more precise than is generally recognized. In addition, the common pattern of variation can be related to latitude and topography to an unexpected degree. This suggests that the link between these two phenomena might be very precise morphologic adaptation to climatic gradients.

Values for a series of climatic variables were obtained by plotting weather station data on a map and interpolating to the centers of the sample circles used for wing length data. Mean noon dry-bulb and wet-bulb temperature data were taken from Summer Weather Data (1939). Mean vapor pressure, vapor pressure deficit, and absolute humidity values were computed by combining i) dry-bulb temperature and relative humidity readings from the Climatic Maps of the United States (U.S. Dept. of Commerce, Wash., D.C.), ii) Tables 4 and 5 in Psychrometric Notes and Tables (Torok 1935), and iii) A Table of Vapor Pressure Deficits (Murphy, T. C., Duke Univ., mimeographed). Estimates of actual annual evapotranspiration were obtained from Publications in Climatology (C. W. Thornthwaite Assoc. 1964, Vol. 17, No. 3). Tables for computing the mean total of the sensible plus latent heat per pound of air are in Psychrometric Notes and Tables (Torok 1935).

Separate correlation coefficients were obtained

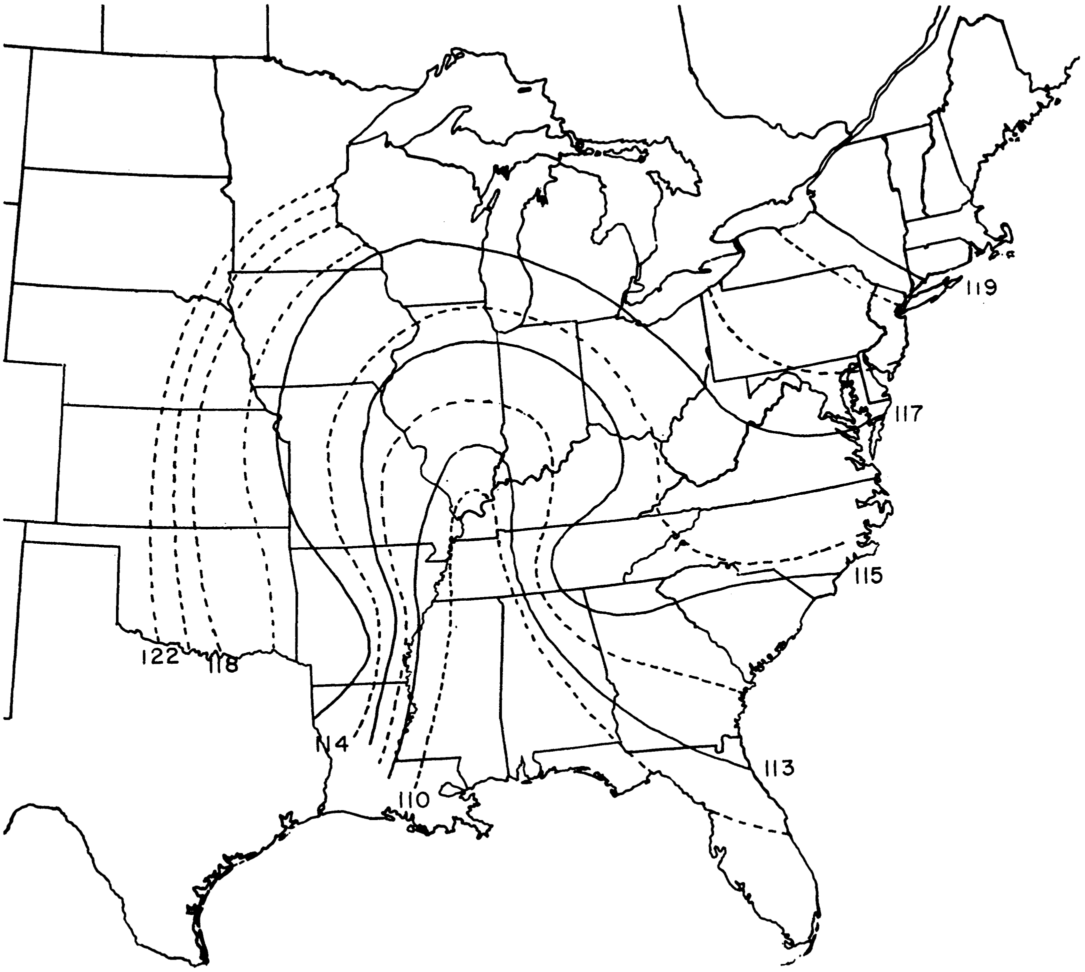

FIG. 9. Isophenes for wing length in the Hairy Woodpecker. Unbroken lines are for males, broken lines for females (contour interval, 2 mm; data in Table 5).

between patterns of size variation and patterns of climatic variation. Since the climatic variables are highly interrelated, and since the birds can obviously not react to them except in combination, this method was preferred to a multiple regression analysis in which the interpretation of partial regression coefficients is made difficult by the fact that they express a hypothetical situation in which other variables are held constant.

Highly significant negative correlations (*r*) were obtained between the wing length of Downy Woodpeckers and the climatic variables tested (Table 6). The close relationship between the patterns of variation of mean seasonal or mean annual dry-bulb temperatures and the pattern of size variation would have been predicted by Bergmann's ecogeographic rule. Correlation coefficients for seasonal and annual maximum and minimum dry-bulb temperatures were not significantly different from these coefficients for the means (data not given). Note particularly in Table 6 that in the Downy Woodpecker the *r* values between wing length and seasonal or annual wet-bulb temperature, vapor pressure, and absolute humidity are all either equal to or higher than correlations with dry-bulb temperature. These last three variables reflect the combined effects of temperature and humidity. The obvious indication is that the size of Downy Woodpeckers is more highly related to the combined effects of temperature and humidity than to dry-bulb temperature alone.

Plant ecologists use several statistics which combine temperature and humidity to interpret relationships between plant growth, plant distribution, and climate. Two of these, annual vapor pressure deficit and actual annual evapotranspiration, were tested here to see whether they are related to the complex pattern of size variation in the Downy Woodpecker. The correlation coefficients for annual vapor pressure deficit and actual evapo-

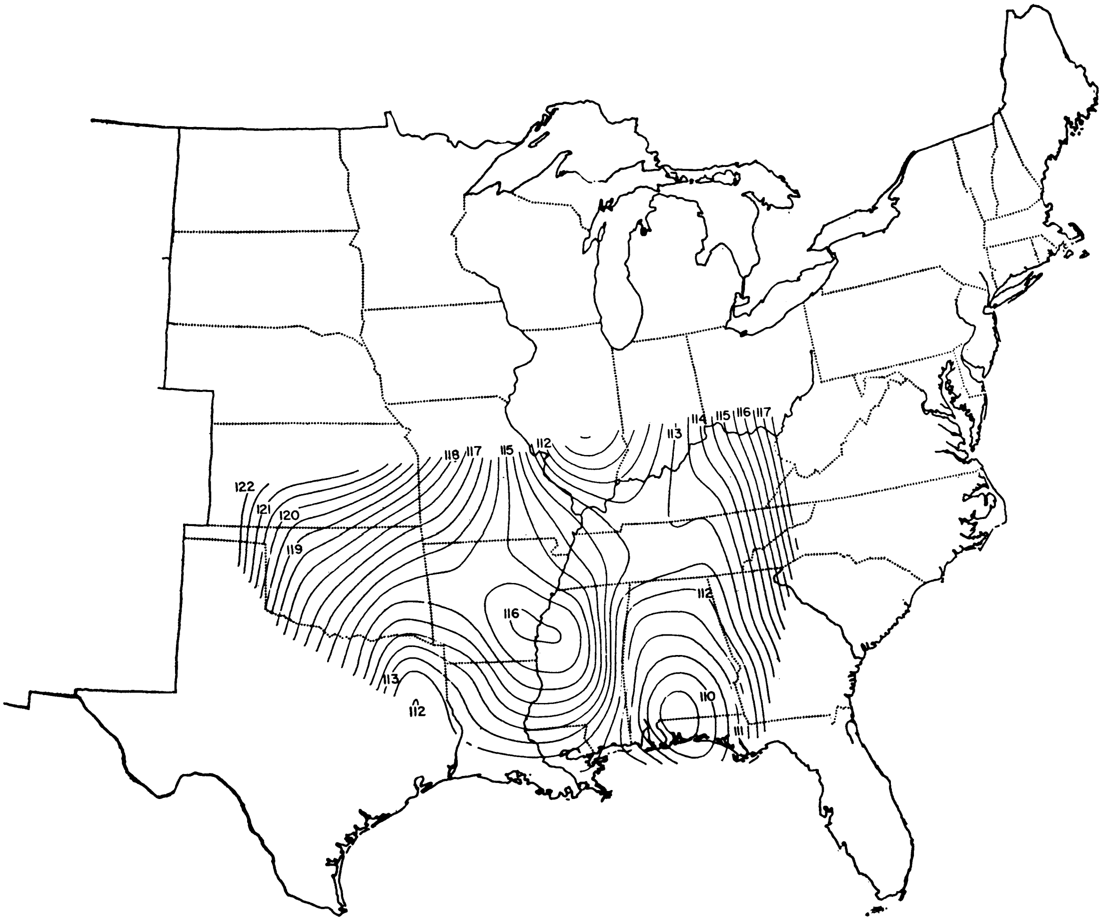

FIG. 10. Isophenes for wing length in female Hairy Woodpeckers (contour interval, 0.5 mm; data in Table 4).

TABLE 6. Correlation coefficients (r) for mean Downy Woodpecker wing length compared with climatic variables and with latitude

	Dry-bulb temperature	Wet-bulb temperature	Vapor pressure	Vapor pressure deficit	Absolute humidity
January	−.858	−.864	−.859 (n=51)	−.772	−.889
April	−.843	−.921	−.928	−.619	−.932
July	−.573	−.882	−.823	−.193 (ns)	−.813
October	−.881	−.921	−.863	−.639	−.899
Summer	−.717	−.903			
Winter	−.872	−.890			
Annual	−.860	−.915	−.893	−.735	−.921
Actual annual evapotranspiration			−.838		
Annual total heat of the air			−.901 (n=75)		
Latitude			−.889		

All correlation coefficients are highly significant at $\alpha=0.01$, except July vapor pressure deficit.
N=76, except as indicated.

transpiration with wing length are lower than the other correlations, although they are still significantly different from zero. One of the assumptions in their usefulness as ecological parameters is that the evaporative surfaces of the organism have the same temperature as the air (Chang 1968). Since this is rarely true for homeothermic organisms, both vapor pressure deficit and actual evapotranspiration are less appropriate than the other variables considered.

Additional correlations (Table 7) between the mean wing lengths of seven other species (Table 4) indicate that wet-bulb temperature is consistently more closely related to bird size than either

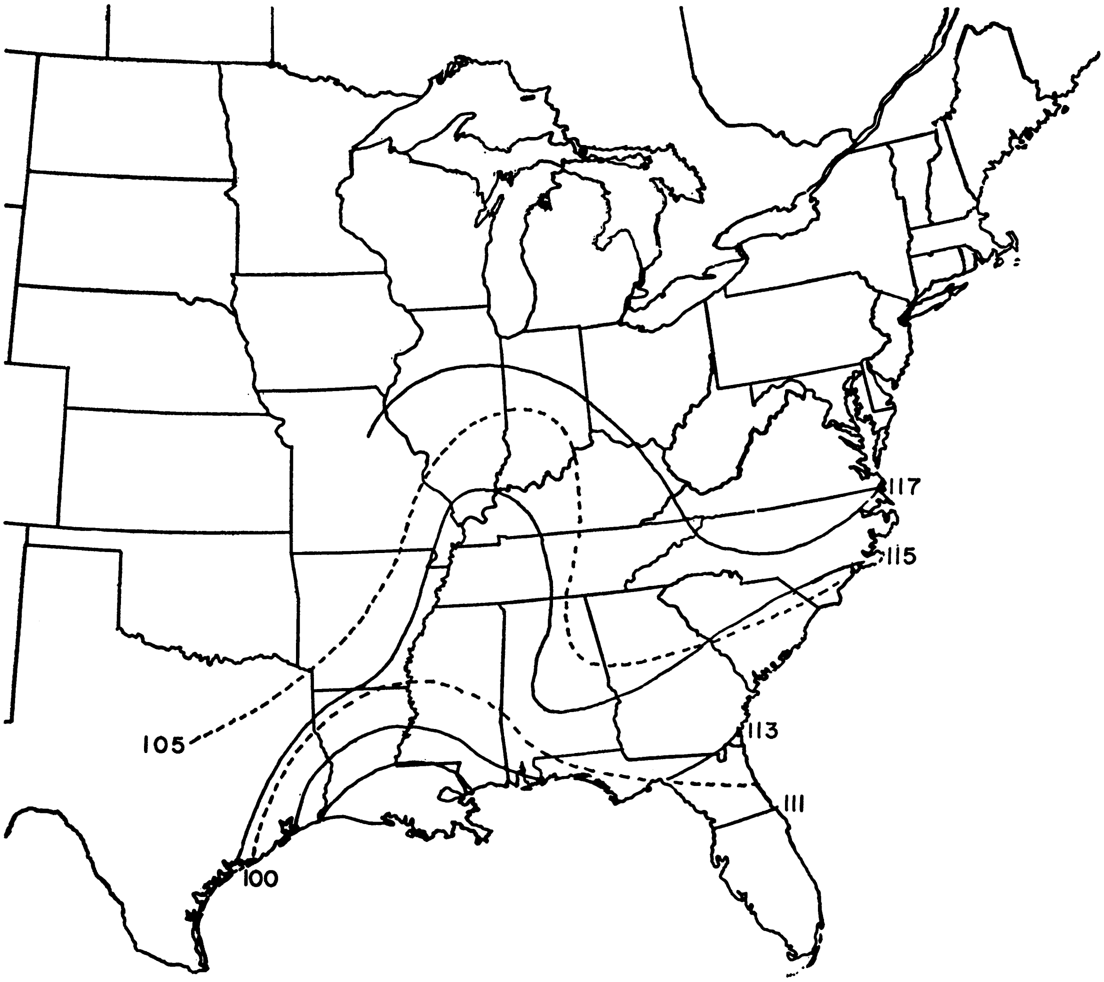

FIG. 11. Isophenes for wing length in the Eastern Meadowlark. Unbroken lines are for males (contour interval, 2 mm), broken lines for females (contour interval, 5 mm). Data in Table 5.

dry-bulb temperature or latitude. For 84 comparisons between correlation coefficients of mean bird wing length and seasonal or annual dry-bulb and wet-bulb temperature, the correlations with wet-bulb temperature are higher in 79 cases. The probability of this happening by chance is less than 0.0001 (sign test in Siegel 1956: 68–75). The differences between the dry and wet-bulb temperatures are greatest in the summer and least in the winter. This might account for Rensch's hypothesis that natural selection for size is greater during the period of winter minimum temperatures (Rensch 1939, and others). But even at this season (note January and winter in Tables 6 and 7) the correlations are higher with wet-bulb temperature than with dry-bulb temperature. The first four species in Table 7 are permanent residents, yet there are no consistent major differences between the wet-bulb temperature correlations for January wet-bulb temperature and annual wet-bulb temperature. The highest correlations for the Screech Owls and the Chickadees are in January. If one takes the position that the periods having the highest correlations represent critical periods of the year for these species, one should note also the r values for April for male Hairy Woodpeckers, July for females, summer for Carolina Chickadees, and July for female White-breasted Nuthatches and male Robins. In general all these species are either permanent resident birds or short-distance migrants. For all, except female White-breasted Nuthatches, which show very little geographic variation in size in the area considered, annual wet-bulb temperature is a good predictor of wing length, which is in turn a function of size. Linear regressions of mean wing length on mean annual wet-bulb temperature are given for nine species in Table 8.

An alternate way of expressing these same relationships would be in terms of the mean annual

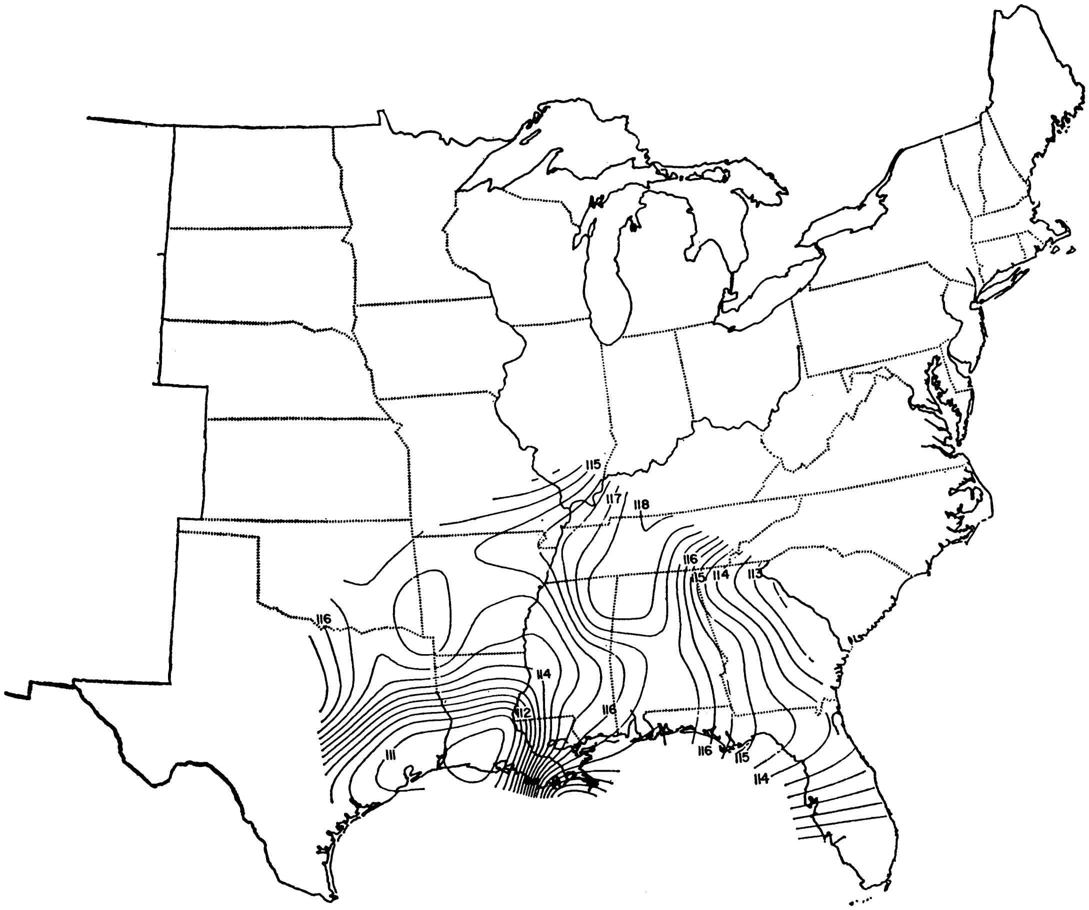

FIG. 12. Isophenes for wing length in male Eastern Meadowlarks (contour interval, 0.5 mm; data in Table 4).

total heat per pound of air. Wet-bulb temperature depends on the sum of the sensible heat (dry-bulb or thermometer heat) and the latent heat of the water vapor. It is a good indicator of the total heat of the air (Torok 1935). To demonstrate this relationship a linear regression was calculated between the mean wing length of Downy Woodpeckers (Table 4) and the mean annual total heat of the air (Fig. 13). The two variables are highly correlated ($r = -0.90$, $n = 75$, $\alpha = .001$). For a mean annual increase of 1 BTU per pound of air, mean Downy Woodpecker wing lengths decrease by an estimated 0.46 mm.

In summary, the complex parallel patterns of size variation demonstrated in the maps are highly correlated with climatic gradients that are combinations of the effects of temperature and humidity. All have one extreme in the southeast from which there is clinal variation northward and westward. Even the secondary modifications of these clines that can be seen in the similarities between the wing length patterns and topography are more precisely related to wet-bulb temperature than to dry-bulb temperature patterns.

THE ADAPTIVE SIGNIFICANCE OF GEOGRAPHIC SIZE VARIATION

In the opinion of many physiological ecologists, intraspecific geographic size variation in homeotherms has no adaptive value with regard to the temperature economy of the organism. Scholander (1955, 1956), Irving (1964) and others have shown that alterations in the insulative properties of the skin, fur, or feathers, and in behavior, permit a wide range of tolerance to temperature variations, far in excess of any advantage that might be gained by a small change in body mass.

Nevertheless, there is also evidence that increased mass does confer some physiological advantages to the tolerance of cold. For 31 species of birds Herreid and Kessel (1967) determined that larger birds have relatively heavier plumage and more effective heat insulation than smaller birds. And Kendeigh (1969) states that "Increased size appears of obvious physiological ad-

TABLE 7. Correlation coefficients (r) for the mean wing length of seven species of birds (Table 4) with mean seasonal and annual dry-bulb and wet-bulb temperature, and also with latitude

		SO (M)	SO (F)	HW (M)	HW (F)	CC (M)	CC (F)	WN (M)	WN (F)	R (M)	EM (M)	BJ (M)	BJ (F)
Sample Size		17	16	17	26	22	19	42	32	14	26	51	30
Latitude		.517*	.840**	.194	.608**	.648**	.565*	.881**	.067	.639*	.344	.768**	.437*
Jan.	Dry	-.674**	-.883**	-.535*	-.717**	-.760**	-.581**	-.837**	-.120	-.463	-.459*	-.759**	-.491**
	Wet	-.723**	-.892**	-.625**	-.781**	-.800**	-.574*	-.828**	-.201	-.754**	-.476*	-.776**	-.520**
Apr.	Dry	-.410	-.746**	-.051	-.521**	-.342	-.500*	-.846**	-.143	-.678**	-.331	-.719**	-.322
	Wet	-.605*	-.826**	-.751**	-.772**	-.668**	-.506*	-.883**	-.356**	-.748**	-.417*	-.780**	-.395*
Jul.	Dry	.657**	.159	.165	.230	.696**	.235	-.612**	-.151	-.429	.287	-.285*	.038
	Wet	-.690**	-.820**	-.624**	-.847**	-.779**	-.486**	-.802**	-.531**	-.923**	-.268	-.795**	-.453*
Oct.	Dry	-.491*	-.806**	-.101	-.566**	-.507*	-.502*	-.894**	-.002	-.691**	-.361	-.739**	-.418*
	Wet	-.646**	-.855**	-.467	-.741**	-.654**	-.478*	-.896**	-.424*	-.898**	-.416*	-.803**	-.531**
Sum.	Dry	.035	-.331	.117	-.096	.420	-.036	-.423**	.005	-.651*	-.172	-.503**	-.096
	Wet	-.632**	-.765**	-.435	-.814**	-.623**	-.623**	-.597**	-.323	-.835**	-.379	-.814**	-.529**
Win.	Dry	-.559*	-.812**	.032	-.568**	-.655**	-.560*	-.868**	-.099	-.560*	-.456*	-.753**	-.432*
	Wet	-.668**	-.822**	-.535*	-.722**	-.704**	-.469*	-.863**	-.219	-.768**	-.472*	-.790**	-.469**
Ann.	Dry	-.566*	-.780**	-.389	-.615**	-.505*	-.538*	-.877**	.120	-.713**	-.400*	-.757**	-.444*
	Wet	-.685**	-.866**	-.618**	-.794**	-.737**	-.545*	-.889**	-.319	-.899**	-.426*	-.813**	-.522**

*Significant at $\alpha=0.05$
**Significant at $\alpha=0.01$

TABLE 8. Linear regressions of mean wing length (Y) on mean annual wet-bulb temperature (X)

Species	Sex	Regression formula
Screech Owl	M	$Y=196.11-0.73X$
	F	$Y=200.55-0.80X$
Hairy Woodpecker	M	$Y=163.15-0.83X$
	F	$Y=149.81-0.61X$
Downy Woodpecker	M,F	$Y=108.96-0.32X$
Carolina Chickadee	M	$Y=86.26-0.41X$
	F	$Y=76.14-0.27X$
White-breasted Nuthatch	M	$Y=101.09-0.23X$
Robin	M	$Y=164.82-0.67X$
Eastern Meadowlark	M	$Y=126.20-0.19X$
Mourning Dove	M	$Y=152.53-0.16X$
Blue Jay	M	$Y=151.57-0.39X$
	F	$Y=140.94-0.26X$

Wing length data in Table 4.
Correlation coefficients, sample size, and significance levels in Tables 6 and 7.

vantage for tolerating cold in several ways: 1) reduction in relative amount of energy required for existence, 2) lower metabolic stress per degree drop in temperature, 3) extension of zone of thermoneutrality to a lower critical ambient temperature, and 4) lower extreme limits of tolerance."

Although the studies mentioned are based on interspecific differences, there is no reason to belive that they do not also apply to intraspecific differences (Kleiber 1961: Kendeigh 1969). Thus, the possibility remains that, in addition to the thermoregulatory adaptations of homeotherms to diurnal and seasonal temperature variations, there is a tendency toward an optimum mass at each particular climate. For those species that vary in size geographically, both phenomena may operate at the same time.

For a bird under normal conditions to maintain a constant temperature there must be an equilibrium between the heat production and the various avenues of heat loss. The dissipation of heat occurs primarily by radiation, conduction, convection and evaporative cooling. King and Farner (1964) represent this relationship as

$$Q_p = Q_l = q_c + q_r + q_e$$

where Q_p is the rate of heat production, Q_l the rate of heat loss, q_c the rate of loss by conduction and convection, q_r the rate of loss by radiation, and q_e the rate of loss by evaporation. They suggest that this relationship can be approximated by a combination of several physical laws as

$$Q_p = Q_l = \underset{(1)}{as\dot{v}\beta(p_s - p_e)} + \underset{(2)}{a\theta(t_s - t_e)}$$

where a is the heat transfer constant, s the area of the evaporating surfaces of the respiratory system, $\dot{v}$ the ventilation volume rate, β a proportionality constant, p_s the water vapor pressure at the evaporating surfaces, p_e the vapor pressure of inhaled environmental air, θ an empirically derived coefficient based on insulation (resistance to heat flow), t_s the temperature of the body surface, and t_e the temperature of the radiating surfaces of the environment. Of the two elements on the right side of the equation the first (1) measures the

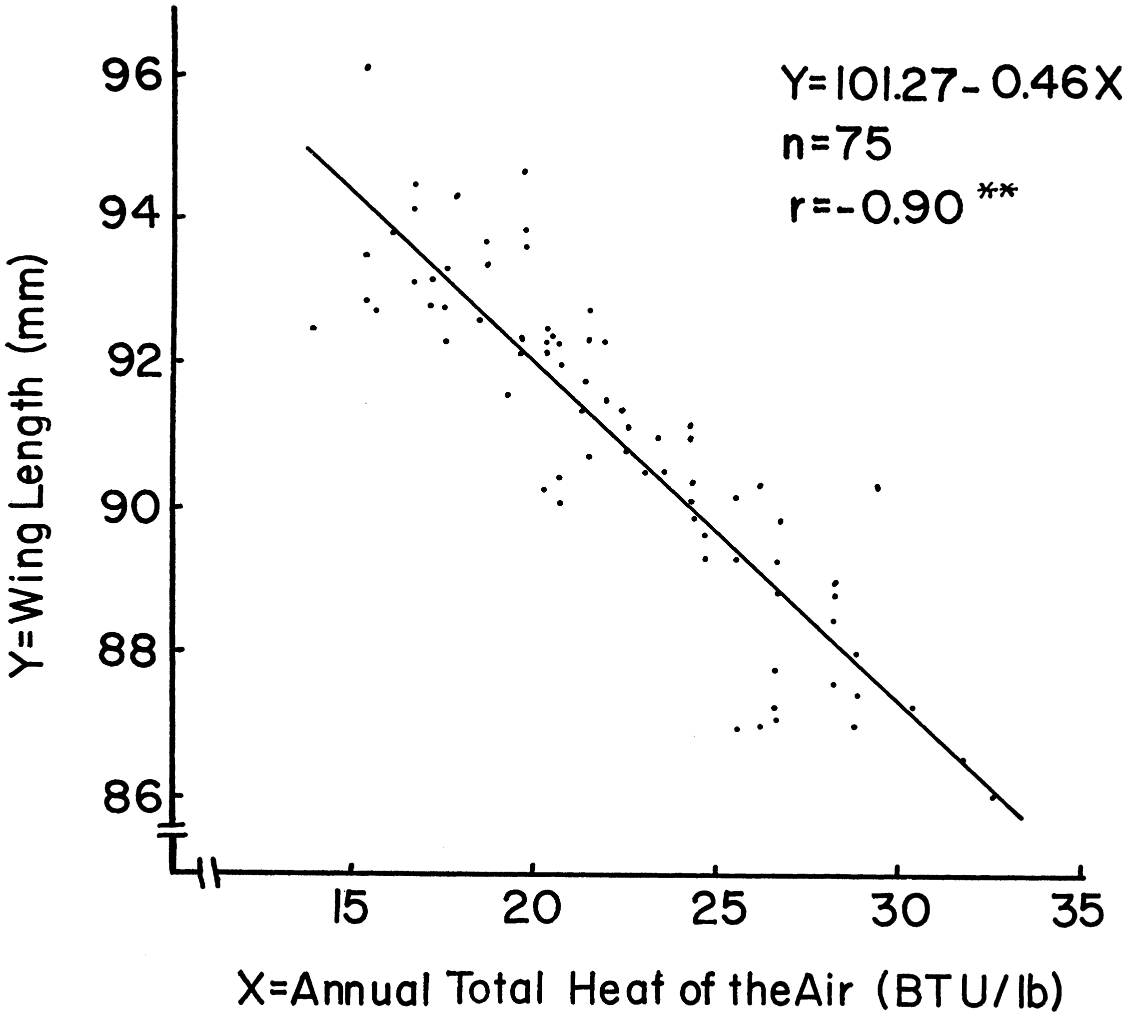

FIG. 13. Simple linear regression of Downy Woodpecker wing length on mean annual total heat per pound of air.

evaporative heat loss, and the second (2) is the Newtonian cooling model which approximates the rate of heat loss (or gain) due to the combined effects of conduction, convection and radiation. Adjustments to environmental changes in vapor pressure (p_e) and temperature (t_e) may be accomplished by compensatory alterations in the ventilation volume rate ($\dot{v}$) of the first element, or in certain insulative properties (θ) of the second element such as changes in cutaneous blood flow, arrangement of feathers, posture, etc. As environmental temperature approaches body surface temperature, the possible heat dissipation by convection, conduction and radiation (2) is reduced, and the bird can maintain normal body temperature only by increasing the rate of loss by evaporation (1) or by decreasing its rate of heat production (Q_p).

For the purposes of discussion, consider whether this equation could relate also to intraspecific geographic size variation and its relationship to climate. The environmental influences on the thermal equilibrium of the organism can be generally represented as the mean dry-bulb temperature and the mean vapor pressure. Could there be a tendency toward an optimum body mass (an element of θ) that is adapted to the overall temperature and moisture conditions of the environment? If so, one would expect the smallest mass (lowest weight, shortest wing length, highest heat conductance) in a hot, humid climate, for this is where the restrictions on heat loss by both elements of the equation are at their maximum. An optimum size in a cool humid climate would be larger since heat loss by convection, conduction and radiation (2) would be facilitated by the increased difference between the body surface temperature and the ambient temperature ($t_s - t_e$). An optimum size in a hot dry climate would also be larger, since heat loss by evaporation (1) would be facilitated by the increased difference between the water vapor pressure of the evaporating surfaces and the vapor pressure of the inspired air ($p_s - p_e$). These predictions are supported by the empirical observations of this study. Of the 12 species considered, each has its smallest size (shortest wing length and presumably lowest weight) in the hot humid southeast; each shows regularly increasing size clines toward the cool humid northeastern states and toward the hot dry southwestern states. The degree of interspecific concordance in this pattern is very high. The fact that the pattern is precisely related to even minor variation in those climatic variables that combine the conditions of temperature and moisture is reflected in secondary correlations with latitude and topography. If the inverse relationship between the weight and metabolic rate of homeotherms is also operative at the intraspecific level, then it can at last be recognized as adaptive.

Taking the Downy Woodpecker as an example, an attempt was made to summarize these proposed relationships between geographic size variation, metabolic rate, and climate. One serious problem with this endeavor is that weight data for birds are considered to be only moderately reliable as a predictor of size (mass). Variable fat levels and water content can cause diurnal or seasonal weight changes that obscure the basic condition. Nevertheless, for the weights of 171 Downy Woodpeckers taken in mist nets near Pittsburgh, Pennsylvania, a two-way analysis of variance of sex and seasonal effects showed neither to be significant (Table 9). For these same birds a two-way analysis of variance of sex and seasonal effects on the wing length data showed both to be significant (Table 9). The fact that earlier analyses showed no statistically significant differences between sexes or seasons at two other localities (Table 3) indicates interlocality variation at least with regard to sexual dimorphism. The seasonal differences in the Pittsburgh data are probably due largely to feather wear. However, adjusting the wing lengths for sex or season using covariance analysis did not improve the power of the wing length data to predict weight.

Since there is no reason to expect the relationship between weight and wing length to be linear, a descriptive model must employ either logarithms or a power function. Using the model

$$W = a + \beta[\log_{10}(Y)]$$

where W = weight (g), a and β are population parameters to be estimated empirically, and Y is wing length (mm), the following relationship holds for the data set mentioned above:

$$W = -41.06 + 34.41[\log_{10}(Y)]$$

See also Figure 14.

Or, substituting an allometric equation similar to the one recommended by Zar (1968),

$$W = a + Y^{\beta},$$

the relationship is

$$W = -0.88 + Y^{0.731}$$

Recent calculations of the relationship between standard metabolism (M, in kcal/bird-day) and body weight (W, in kg), using a log-log approximation (Lasiewski and Dawson 1967), predict that

$$M = 78.3W^{0.723}$$

By fitting a power function to the same data, Zar (1968) found nearly the same relationship,

$$M = 76.7W^{0.741}$$

Thus, in the case of the Downy Woodpecker and presumably the other species in this study, wing length can be used to predict weight, weight can be used to predict metabolic rate, and there ap-

Table 9. Sex and seasonal differences in weights (g) and wing lengths (mm) of 171 Downy Woodpeckers taken in mist nets near Pittsburgh, Pennsylvania

		Weight (g)						Wing Length (mm)				
Sex	Season	Size of sample	Mean	SD	Probability of a larger F-ratio by chance			Mean	SD	Probability of a larger F-ratio by chance		
					Sex	Season	Interaction			Sex	Season	Interaction
M	Jan.-Mar.	7	26.6	1.37	0.515	0.279	0.534	92.6	2.49	0.000**	0.006**	0.913
M	Apr.-Jun.	29	26.6	1.69				93.5	2.12			
M	Jul.-Sep.	20	26.5	1.71				93.1	2.52			
M	Oct.-Dec.	35	27.2	2.08				94.5	2.83			
F	Jan.-Mar.	17	27.0	1.46				94.1	2.44			
F	Apr.-Jun.	14	27.4	1.65				94.7	2.41			
F	Jul.-Sep.	15	26.4	1.38				95.1	2.70			
F	Oct.-Dec.	34	27.1	1.57				96.0	2.35			

**Significant at 0.01

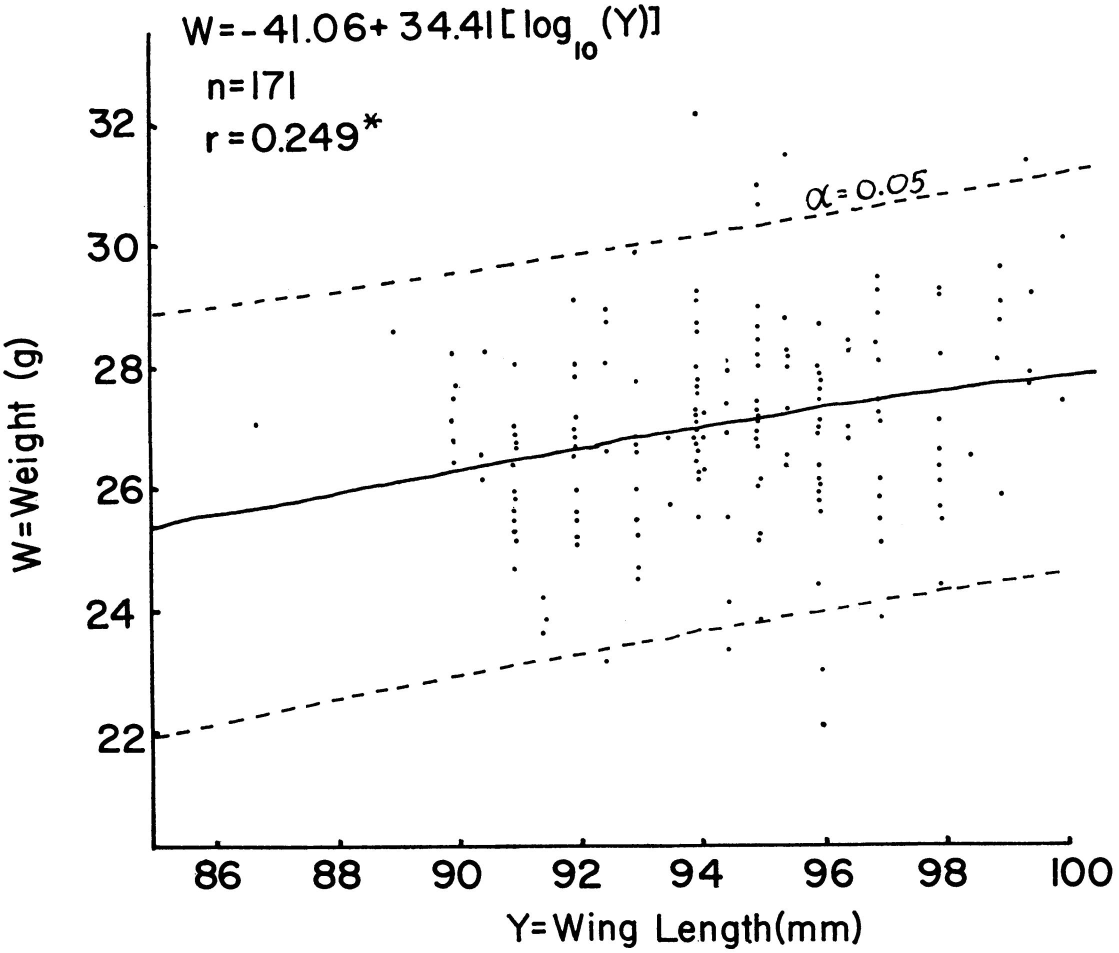

FIG. 14. Simple linear regression of Downy Woodpecker weight on wing length.

pears to be a tendency for the birds to have an optimum weight (and metabolic rate) that is correlated very precisely with the temperature and moisture conditions of the climate. These relationships can be summarized by mathematical expressions that relate wing length to mean annual wet-bulb temperature or to mean annual total heat per pound of air. The high degree of concordance between size, metabolic rate, and these climatic variables does not necessarily imply any direct causal relationship. The possibility remains that the climatic variables affect the vegetation or the insect food supply which in turn affect size and metabolic rate. On the other hand, the relationships are consistent among the species considered, even though they occupy a variety of habitats and vary in their feeding habits.

BERGMANN'S ECOGEOGRAPHIC RULE

The best known of the ecogeographical generalizations describing parallels between morphological variation and climatic gradients is Bergmann's ecogeographic rule, which as presently defined by Mayr (1963) states that "races from cooler climates tend to be larger in species of warm-blooded vertebrates than races of the same species living in warmer climates." Mayr adds that the rule is independent of any physiological interpretation of the selective advantages of larger size in cooler climates, that it applies only or mainly to intraspecific variation, and that it is convincingly supported by the high percentage of cases in which it holds true. His definition evades the challenge of physiological ecologists to the classical interpretation of Bergmann's rule, that larger animals withstand cold better because of a reduced surface to volume ratio. Nevertheless, Bergmann's paper (1847) was entitled "Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse" and he clearly intended to demonstrate a relationship between the temperature budget of the organism and the temperature of its environment.

With the help of Margaret Middel, a German graduate student at the University of Arkansas in

1968–69, I was able to translate a major part of this important paper. Since it has been frequently misinterpreted, I am offering some sections of the translation in the appendix.

The following is a short summary of the three major points in Bergmann's paper:

1. The constant temperature of homeothermic organisms is maintained by a balance between the production of warmth within the volume of an animal and the loss of warmth from its surface.
2. The limitation of the ratio of its body surface to its volume is one of the factors that determines its size.
3. When other factors are constant, the smaller *species* in a *genus* will occur in a warmer climate.

Clearly the present interpretation of the rule is a great modification of Bergmann's concept. Nevertheless, subsequent evidence has demonstrated many examples of size increases in cooler climates on the intraspecific level, and there is conflicting evidence as to whether large size confers a physiological advantage in a colder climate. Although Mayr's definition considerably modifies Bergmann's original message, it fits our present knowledge of intraspecific size variation and has usefulness as an ecogeographic principle. Perhaps the solution would be to call the rule the "Neo-Bergmannian Rule" in the same sense that we now have neo-Darwinian selection and neo-Mendelian genetics. Bergmann deserves credit for some perceptive observations about geographic variation and about biophysics. In fact, the relationship between intraspecific size variation and climatic gradients appears to be far more precise than is suggested by any definition proposed thus far.

The results of this study generally support Bergmann's original message. In addition they indicate that intraspecific size variation is more highly related to a combination of climatic variables than to dry-bulb temperature patterns. If these relationships are found to hold true for other homeotherms in other areas, it may be possible to reformulate Bergmann's Rule as:

> Intraspecific size variation in homeotherms is related to a combination of climatic variables that includes temperature and moisture. Small size is associated with hot humid conditions, larger size with cooler or drier conditions.

This is merely an empirical observation. It was first expressed by Hamilton (1958, 1961) and more recently by James (1968) and Power (1969). The extent to which these relationships are genetic and the biological mechanism by which they are maintained are questions for the future. For a recent review of current hypotheses on the latter topic see Rosenzweig (1968).

COMPARISONS WITH OTHER STUDIES

It was Julian Huxley (1939, 1942:206) who proposed the term *cline* for continuous character variation in animals and predicted that this type of variation would be found to be "much commoner than is generally supposed." At approximately the same time several other workers summarized parallel continuous size variation in species of birds (Rensch 1934, 1939; Meise 1938; Rand 1936; and others) and subsequent work has borne out Huxley's prediction (see particularly Sibley 1954; Snow 1954, 1958). These examples of concordant interspecific size variation are generally attributed to Bergmann's ecogeographic rule. Evidence that the precision of the relationship between size and climate may be higher than is suggested by the current interpretation of the rule may be found in studies of the House Sparrow (Calhoun 1947; Johnston 1969a, b; Johnston and Selander 1964; Packard 1967), the Great Tit (Van Balen 1967), the Wood Rat (Brown and Lee 1969), and the 12 species considered here.

Several investigators have attempted to analyze size variation in a way that would discover the extent of the exceptions to the rule and/or what particular factors of the temperature of an area are most highly related to body size. Comparisons between some of the results of these studies and those of the present work can be interpreted as supporting my hypothesis that geographic size variation in birds is closely related to the combined effects of several climatic variables.

Rensch (1939) reported almost perfect agreement between isotherms for the coldest month and the sizes of corvids and picids, and concluded that selection in temperate regions is by winter minimum temperature. With certain exceptions, Snow (1954) found a similar relationship for palearctic members of the genus *Parus*. He discusses an interesting modification of Bergmann's rule which he designates as the "latitude effect." Wing lengths tend to be greater in populations from the mountains of southern Europe and northwestern Africa than in more northerly lowland populations, even though all have the same winter minimum temperatures. This "departure from expected clinal variation" (Snow, loc. cit.) could be accounted for by a consideration of temperature as modified by evaporation, for as Visher (1924:58) points out "whenever temperatures at higher altitudes are equal to those at low altitudes, the rate of evaporation tends to increase with altitude." The increased evaporation at high altitudes would make wet-bulb temperatures lower there than at the more northerly latitudes. The same interpretation could account for Moreau's (1957) positive correlation between the wing length of African *Zosterops* and altitude, independent of air temperature.

Another modification of Bergmann's rule was suggested by Hamilton (1958) after he found that in three species in the genus *Vireo,* and in several other species including the Downy Woodpecker, wing lengths tend to be greater in hot arid regions and smaller in hot humid regions. He noted the findings of Bartholomew and Dawson (1953) which compare several desert species and show that under controlled conditions the respiratory water loss decreases per unit of body weight with increased size. Small birds expire relatively more moisture and would be at an advantage in humid areas where the saturation deficit was less (Hamilton 1958). Later Hamilton modified these conclusions about the "aridity effect" (Hamilton 1961) in favor of the effects of relative humidity. In nature this phenomenon would be countered by the increased evaporation due to the increased vapor pressure gradient between the respiratory surfaces of the bird and the dry air of the desert. Could this also be an adaptation to the conditions of high latitudes and altitudes as well as arid conditions? Could this factor be operative on the intraspecific level? I believe so. Since the capacity of air to hold moisture decreases with decreasing temperature, cold air is exceedingly dry. When cold dry air comes in contact with a moist warm respiratory surface, the air is warmed by contact and becomes *relatively* even drier. For a homeothermic organism, cold air as well as hot dry air causes increased evaporation (Visher 1924: 57, 63). It appears that Snow's "latitude effect," Hamilton's "aridity" or "relative humidity effect" and the voluminous literature relating the size of homeotherms to latitude and/or altitude may all be part of one complex phenomenon, a precise relationship between mean body size and the combined effects of temperature, moisture, and possibly other climatic variables. Environmental variables that are a function of both temperature and moisture conditions (such as wet-bulb temperature, vapor pressure, and absolute humidity) have patterns of variation that include highest values in the southeast and lower values northward (colder) and westward (drier). These are negatively correlated with the patterns of intraspecific size variation in birds. Kittredge (1938) found that this same pattern is correlated with forest types and with their growth rates.

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Appendix

The following are excerpts from a translation of Carl Bergmann's classic paper, "Ueber die Verhältnisse der Wärmeökomie der Thiere zu ihrer Grösse," published in 1847:

p. 600 "For the degree of warmth to which it is possible for an animal to rise above its environment, the ratio of its surface is naturally of great importance."

p. 601 "The *surface* is the site of the loss of warmth. Its value, together with the characteristics of the surface (covering with hair, etc.), the difference between the temperature of the animal and the surrounding medium (air or water) determines the loss of warmth.

"On the other hand, the *volume* of the animal may be regarded as a measure of the possible creation of warmth. To be sure the creation of warmth in the same volume is different at different times.

"Now the cubic content of objects and the extension of their surface does decrease or increase according to the same ratios. Animals need to create less warmth in relationship to their size the larger they are, in order to get a rise in temperature above that of the surroundings."

p. 629 "We are going to consider the distribution of smaller and larger homeotherms over the earth's surface and in the sea, in order to see how far the effects of our rule are suggested in this distribution, or in how far the results of the rule can not be seen because of the richness of modifications."

p. 648 "Although it is not as clear as we would like, it is obvious that on the whole the larger *species* live farther north and the smaller ones farther south."

p. 630 "Even for a plant the determination of the conditions of climate is more than the temperature and humidity of the region in which it exists. It is the distribution of warmth through the seasons and through the times of the day. Continental climate and shore climate, stronger or weaker radiation of warmth during the night, whether the sky is clear or cloudy,—all of this is of the greatest importance, even though by different values of these elements the mean temperature can be the same.

"The conditions of climate for the animals are not that easy to state. It is necessary to observe animals in their way of life, to determine the ratio of the dissipation of warmth under which they are living during the year. If animals are exposed to the sun or to the warmer times of the day, or if they are exposed more to the cooler hours,—whether they avoid the effects of winter coldness by building burrows,—these matters make the same climate different for different animals."

p. 637 "We see the possibility of very different sizes of homeothermic animals in the same climate, conditioned by the variety of factors of the creation of warmth and the factors of the dissipation of warmth.

"The breadth of these modifications has to decrease, the more similar the animals are to each other in their organization."

p. 638 "If we could find two species of animals which would only differ from each other with respect to size, all these modifications would be excluded. The geographical distribution of the two species would have to be determined by their size. The smaller species must demand a warmer climate, the larger a colder climate. If there are *genera* in which the species differ only in size, the smaller species would demand a warmer climate, to the exact extent of the size difference. If the species differ in other ways, the regularity of the geographic distribution would be modified accordingly."

p. 677 "It seems paradoxical that the effects of the same rule in *races* of animals are not very apparent. Is it not to be expected that races which should be more similar to each other in their organization than the species of a genus, should be more dependent on their size ratios in their distribution than the latter? This sounds obvious."