

ECOGEOGRAPHIC VARIATION IN THE AMERICAN ROBIN (*TURDUS MIGRATORIUS*)

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ABSTRACT.—From analysis of external measurements of 949 museum study skins of American Robins (*Turdus migratorius*) taken in the breeding season throughout North America, we estimated the extent of geographic variation in size, shape, and color of plumage on the basis of 39 ecoregions. After we defined seven univariate size and six scale-free shape variables, we studied their variation and the extent of their allometric covariation. Because wing length is highly correlated with six other reasonable measures of general size but is simple and easy to visualize, we used wing length as a measure of general size.

The smallest robins occur in the warm, humid eastern United States, and the largest occur in the high, cool, and dry Rocky Mountains, northern Great Plains, and northern deserts. Wing shape changes allometrically with size, becoming more pointed in larger birds, but wing shape in the Arctic is more pointed than would be predicted by this trend. Another exception to the allometric covariation of size and shape is that leg length as a proportion of general size is small in Mexico and large in the cool, humid forests along the Pacific coast. Robins in the cool maritime forests of Newfoundland have unusually long tarsi. This variation in leg length is accompanied by variation from pale plumage in Mexico, especially in Baja California, to dark plumage in Newfoundland. Bill length covaries with general size, except that robins with the longest bills occur in the isolated population in the mountains of southern Baja California.

Univariate correlations among size and shape variables are useful for study of the complex nature of geographic variation in the robin, but graphic presentations of the results in maps and bivariate graphs are even more informative. They allow comparisons between specific aspects of morphometric variation, and they allow the identification of extreme cases.

To understand the relationship among geographic variation in robins, climatic variation, and altitude, we analyzed correlations among these variables. The eight climate variables are mean noon dry- and wet-bulb temperature and relative and absolute humidity for April and for July. In the United States, the general size of robins varies not with dry-bulb temperature, as predicted by Mayr's definition of Bergmann's Rule, but with variables that are a function of both dry-bulb temperature and the evaporative power of the air. Multiple regression analysis using climate and altitude as predictors of the general size of robins shows that July absolute humidity alone has exceptionally high predictive power. When general size is viewed on a psychrometric chart in which ecoregions are located on the basis of their July climate, the relationships are clarified.

The plumage of the robin is darkest not in the most humid regions, which are in the southeastern United States, as would be predicted by the most common definition of Gloger's Rule, but in cool areas where the percent saturation of the air is high.

These trends of geographic variation in size and color are concordant with those reported in many other species. Whether parallelism among unrelated species in their patterns of geographic variation and its high correspondence with gradients in the physical environment are evidence of natural selection, either by physical factors or indirectly by their covariates, is unknown. Received 25 September 1989, accepted 23 August 1990.

OUR PRIMARY objective in this paper is to describe major geographic patterns in size, shape,

and color of the plumage of the American Robin (*Turdus migratorius*) for all of North America. Size variables and shape variables are defined a priori, so their covariation can be assessed and exceptions noted. Because we are interested in ecological correlates of the variation, we organ-

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ize the data by ecoregions. We demonstrate climatic variation within the United States on a psychrometric chart that gives the relationships between measures of temperature and humidity. Then we show the pattern of size variation in robins in this space. We discuss the generality of correlations between the physical environment and character variation in the robin in the context of ecogeographic rules.

Bergmann's Rule, once an important explanatory theory in evolutionary biology, has been losing support (Zink and Remsen 1986). This thesis was that birds and mammals have an optimal ratio of size to surface area that is a function of their thermal balance with the physical environment. As evidence Bergmann noted that larger members of a genus, with their larger ratios of size to surface area, usually live in colder climates. This argument has been debated by physiologists (Scholander 1955, Ken-deigh 1969, McNab 1971, Calder and King 1974), but systematists have often found substantial empirical support for Bergmann's rule at the intraspecific level (Mayr 1970), often by regressing size on latitude, altitude, or isophene (e.g. Packard 1967, Johnston 1969).

James (1968, 1970) and Power (1969) showed that the relationship between intraspecific size variation and climate is stronger if the effects of temperature and humidity are considered together. James (1970), who found extensive parallelism in geographic size variation in 12 species of birds in the eastern and central United States, suggested that Bergmann's physiological argument might still be valid in this context. Small size would be an advantage in a warm, humid environment because a large ratio of respiratory surface area to body size would facilitate heat loss. Larger birds would be expected in higher, or cooler, or drier environments. A combination of high, dry, and cool conditions would favor the largest size. Grinnell (1910), Boyce (1979), and Murphy (1985) have pointed out that variance in climatic variables is higher in cool and dry areas than it is in warm and humid areas. Rather than dismiss as overly simplistic the hypothesis that intraspecific patterns of size variation in birds may be thermal adaptations (Zink and Remsen 1986), we prefer to examine relationships between size variation and climate in more detail.

Our analyses for the robin are explicitly correlative. Causes other than physiological adaptations could account for geographic varia-

tion. In birds these include (1) the various covariates of geographic variation in the physical environment (e.g. microhabitat, diet), (2) the influence of cryptic color on survival (Bowers 1960), (3) character displacement (Grant 1987), (4) isolation and other historical factors (Endler 1982, Cracraft 1985, Lande 1985), (5) distance and chance (Schnell and Selander 1981), and (6) nongenetically based developmental plasticity (James 1983, Slagsvold and Lifjeld 1985). However, if unrelated species that differ in life history are found to exhibit parallelism in character variation, causes 1-5 are less parsimonious explanations than is 6. The argument that either environmentally induced physiological responses or genetically based adaptations to either the physical environment or its correlates are a direct cause is strengthened.

METHODS

Morphometric data and analysis.—Aldrich measured 949 museum study skins of adult robins collected in Mexico, the United States, and Canada. The measurements, made to the nearest 0.1 mm, are as follows: wing length (WL), from the bend of the folded wing to the tip of the longest primary feather; wing tip (WT), from the end of the longest secondary of the folded wing to the tip of the longest primary; tail length (TL), from the insertion of the two central rectrices to the end of the longest rectrix; culmen (CU), bill length from the depression between the cranium and the maxilla to the tip of the maxilla; maxilla height (MA), depth of upper bill at the distal end of the depression around the nostril; tarsus length (TS), from the posterior aspect of the junction of the tibiotarsus and the tarsometatarsus to the junction with the middle toe (anterior aspect); and middle toe (TO), from the junction with the distal end of the tarsometatarsus to the proximal end of the claw. Measurement error was not evaluated and probably contributes to variation in the data.

In addition to the seven measurements, which we call size variables, we used six dimensionless (scale-free) shape variables in the analysis. These were wing tip/wing length (WT/WL), tail length/wing length (TL/WL), culmen/wing length (CU/WL), culmen/maxilla height (CU/MA), tarsus/wing length (TS/WL), and tarsus/toe (TS/TO). All of these shape variables have potential functional significance: WT/WL for flight, CU/MA for manipulation of food, TS/TO for ground locomotion and foraging, and TL/WL, CU/WL, and TS/WL for tail length, bill length, and leg size as their proportions of general size (as measured by wing length) for a bird that forages on the ground in parkland habitat. The shape variables describe various aspects of the shape of the bird, and their geo-

graphic variation is of at least as much relevance to fitness in different environments as are size variables.

Our statistical comparisons use lognormal assumptions (Mosimann and James 1979, Mosimann and Malley 1979). Our shape variables (ratios) are expressed as differences between logs and studied directly. The ratio WT/WL becomes $\log WT - \log WL$. (See Mosimann and James (1979: fig. 3) for a demonstration that the consequences of assuming a lognormal distribution with data such as ours are small.)

In several cases, we use median wing length as a general size variable. It is highly positively correlated with six other reasonable but more complex measures of size. In the morphometric analysis we examine correlations among size variables and shape variables. The patterns of allometric covariation are given in bivariate plots. The slope of the pattern of data in these plots can indicate associations between scale-free ratios or proportions and size. They allow visual comparisons of patterns of geographic variation in particular aspects of size, shape, and sexual dimorphism. We do not treat the variables as statistically independent. In fact, the associations that result from their lack of independence are of particular interest. Virtually all morphometric data sets exhibit shape variation, and we think it can advantageously be studied directly.

Our specimens were taken during the breeding season from May through August, inclusive. All available specimens that did not show excessive wear were used. In most areas of the United States, robins have young in the nest in May (James and Shugart 1974). Although a few birds may still be arriving in northern Ungava in the second week of May (Bent 1949), even at the arctic tree line most birds have arrived at their breeding grounds by early May. Late summer specimens in highly worn or fresh autumn plumage were omitted. In autumn, robins in most areas of the breeding range migrate to regions where large flocks congregate at sources of abundant food. Studies of banded robins show a strong tendency for birds to return to their natal areas in the breeding season (Eiserer 1976).

Specimens were pooled across years by ecoregions (Table 1), according to a modification of the ecoregion sections and provinces of Bailey (1976, 1981, 1983). Bailey's classification is based on regions of fairly uniform dominant vegetation, climate, and soil type (Kuchler 1964). These regions vary in size. We subdivided the Arctic Tundra in eastern and western sections and the Boreal Forest into Middle Boreal and Newfoundland. We do not assume a priori that character variation in robins is homogeneous within ecoregions or that the ecoregions somehow determine the magnitude of character variation. However, character variation in birds is known to be more highly differentiated in western than in eastern North America (Miller 1956). In the West, short distances separate areas that are highly distinct ecologically.

For our comparisons, pooling by ecoregions, which are sensitive to ecological differentiation, is preferable to pooling by other methods.

If character variation were a direct function of distance, then variance would be higher in larger ecoregions. However, for the 13 ecoregions for which we have ≥ 20 male specimens, the Spearman rank correlation of variance in male wing length with ecoregion area is negative ($r = -0.21$, NS). Although Zink (1985) and Dickerman (1985) have objected to the use of ecoregions as study units (e.g. by Aldrich 1984), we see no circularity to pooling data by vegetational features and climate when the goal is to examine the relationship of environmental variation to avian character variation.

Some large areas of the breeding range of the robin in central Canada and in the central and southwestern United States are not represented in our samples (blank areas in Figs. 1, 2, 3, 5), but most of North America is covered. We assume that most phenotypic variation is encompassed and that our results are unbiased by omissions. We summarize patterns for important size and shape characters in computer-generated maps and bivariate graphs.

Because some of our sample sizes are as low as four (Table 1), when we use these samples we use medians to estimate their central tendency. For a sample size of four, the probability from the binomial distribution that the true median lies between the extreme values is 87.5%; for a sample of six, 97%. We give median values for all size and shape variables for both sexes (Appendix 1). In Table 2, which is based on samples that have 10 or more specimens per group, we use parametric methods.

Variation in color of plumage.—To score main directions of geographic variation in plumage, we assigned increasing values to color of breast (1–5), color of back (1–4), and amount of white spotting on the tail (1–4). This procedure was carried out for 8 groups of specimens from ecoregions inhabited by 8 of the 9 currently recognized subspecies of robins (Table 4). Color categories were based on the Munsell Book of Color (Anonymous 1929–1942). Although fading and wear can affect color comparisons, we doubt that these factors would confound the effects of geographic variation. Molt occurs after the breeding season. To have assigned freshly molted birds taken in autumn migration or winter to their regions of origin would have been highly subjective.

Climate.—A psychrometric chart (Fig. 8a) was constructed according to an example in Zimmerman and Lavine (1964). It expresses the relationship between temperature and moisture relations in a graph in which the variables are dry-bulb temperature, wet-bulb temperature, and relative and absolute humidity. *Wet-bulb temperature* is the dry-bulb temperature, measured by an ordinary thermometer, depressed by the evaporative power of the air. *Absolute humidity* is the amount of water vapor in a unit of dry air. *Relative*

TABLE 1. Ecoregions, general geographic areas, and sample sizes of specimens of the American Robin (see Fig. 1). Ecoregions are based on the categories of Bailey (1976, 1981, 1983).

Ecoregion	Sample size		Bailey code	General geographic area
	Male	Female		
1 Arctic Tundra (E)	4	—	1211	(1-4) Arctic tundra, east to west, Laborador to
2 Arctic Tundra (W)	16	7	1212	Alaska, including Brooks Range, Alaska
3 Brooks Range	12	6	M1210	
4 Bering Tundra	13	—	1240	
5 Yukon forest	16	9	1320	(5-8) Boreal forest, west to east, Alaska to
6 Yukon-Stikine Plateau	30	10	P1330	Newfoundland
7 Middle Boreal	33	7	1332	
8 Newfoundland Boreal	17	12	1331	
9 Laurentian Forest (Maritime)	5	—	2115	(9-12) Northern hardwood forest
10 Laurentian Forest (New England)	4	—	2113	
11 Laurentian Forest (N.Y.-Wis.)	4	—	2113	
12 Appalachian Oak Forest	50	49	2214	
13 Mixed Mesophytic Forest	9	8	2211	(13-14) Eastern deciduous forest, eastern
14 S.E. Mixed Forest	23	12	2320	Virginia and eastern Tennessee south to Louisiana
15 Tallgrass Prairie (E)	—	6	2531	(15-16) Midwest, tallgrass prairie, western
16 Tallgrass Prairie (W)	41	10	2532	Minnesota to eastern North and South Dakota
17 Shortgrass Prairie (E)	—	6	3112	(17-20) Northern Great Plains, east to west,
18 Shortgrass Prairie (W)	14	6	3111	western Dakotas to eastern Montana and
19 Wyoming Basin (N)	4	—	A3141	Wyoming, east of the Rocky Mountains,
20 Wyoming Basin (S)	6	—	A3142	including Wyoming basins
21 Fraser-Nehaco Plateau	20	9	P2120	(21-25) Rocky Mountain forests, northern
22 Columbia Forest (W)	9	7	M2111	Rocky Mountains of British Columbia south
23 Columbia Forest (E)	11	7	M2112	to southern Idaho and Utah, intermountain
24 Oregon Rockies	29	9	M3111	plateau
25 Montana Rockies	5	6	M3112	
26 Palouse Grassland	10	6	3120	(26-28) Northern desert and Palouse grassland
27 Sagebrush-Wheatgrass	22	5	3131	of eastern Washington and western Idaho
28 Ponderosa Scrub	—	5	3135	south to Nevada and western Utah
29 Alaska Coast	20	13	M2416	(29-34) Pacific forests of Alaska coast south to
30 Sitka Spruce-Cedar-Hemlock	28	31	M2411	middle California including coastal and
31 Cascades (Silver and Douglas Fir)	18	8	M2415	Cascade Mountains
32 Willamette-Puget forest	8	6	2410	
33 California Mixed Evergreen	4	4	M2414	
34 Redwood Forest	4	7	M2412	
35 Sierra Forest	23	18	M2610	(35-36) Sierra Nevada Mountains and south-
36 California Chaparral	12	11	M2620	western California chaparral
37 Baja California*	36	16	M3210	(37-39) Isolated Mexican mountain forest of
38 Sierra Madre Occidental	11	8	M3150	extreme southern Baja California and
39 Sierra Madre del Sur	35	19	M412	mountain forests of western and southwestern Mexico
	606	343		

* This population was treated as a separate species, *Turdus confinis*, until 1983 (AOU 1983).

humidity is the percent saturation of the air. Our climatic data (Appendix 2) consist of mean noon April and July values for 21 ecoregions in the United States, in most cases interpolated from cities to central places in ecoregions for which we have more than 10 male specimens of robins. Because there are only 16 such ecoregions for female robins and the sexes are highly concordant in their geographic variation, we based

our analysis on males. Comparable climatic data for Canada and Mexico were not available to us.

RESULTS

The ecoregions in Figure 1 are identified in Table 1. Although ecoregions differ greatly in

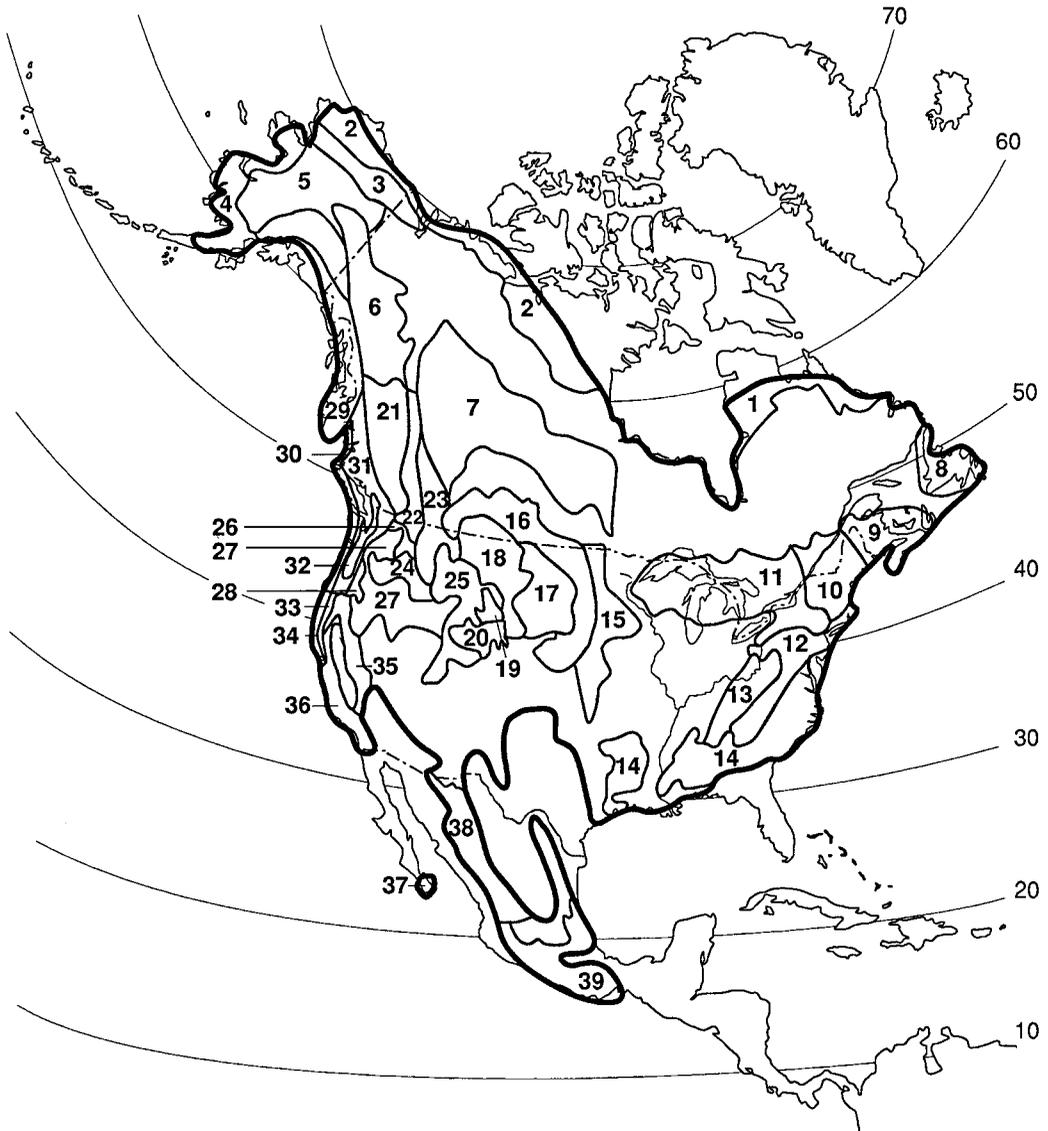


Fig. 1. The breeding range of the American Robin, showing 39 ecoregions. The names of the ecoregions and their general geographic areas are given in Table 1.

size, for the 11 ecoregions with 10 or more specimens of each sex, we found that each of the 7 size and 6 shape variables exhibits significant geographic variation (Table 2). The variance components (first and third columns of numbers in Table 2) permit comparisons between variation among and variation within ecoregions for each variable. The highest F -ratios are for leg length (TS), bill length (CU), and wing length (WL). Two scale-free shape variables

(CU/WL and TS/TO) exhibit a higher degree of geographic variation than do the other shape variables, although all have P -values less than $\alpha = 0.05$. The F -values by character are roughly similar between the sexes.

For the 29 ecoregions for which we have data for both sexes, the sexes have similar correlations among medians of size and shape variables (Table 3). Allometric correlations between size and shape variables show, for example, that

TABLE 2. Tests of geographic variation in the size and shape of the American Robin. The significance of among-ecoregion variation is tested by separate one-way analyses of variance for size and shape variables for 298 males and 179 females for the 11 ecoregions* for which $n \geq 10$ for both sexes. All F -ratios are significant at $\alpha = 0.01$ except log (culmen/maxilla height) in females, which is significant at 0.03. Variance components $\times 10^{-4}$ yields the actual variance estimates. Tests of differences between the sexes in median values of each variable are given in the last column. All significance values were multiplied by the number of simultaneous tests ($n = 13$, the Bonferroni criterion, see Harris 1985).

	Code	Tests of geographic variation				Sexual dimorphism
		Male ($n = 298$)		Female ($n = 179$)		Significance of two-tailed t-tests and sign of average male minus female difference
		Variance components (among/within)	F	Variance components (among/within)	F	
Size variables						
Log wing length	WL	16/1	11.8	23/2	14.0	0.01 (+)
Log wing tip	WT	151/18	8.2	141/14	10.0	0.07 (+)
Log tail length	TL	17/3	5.4	22/3	6.4	0.01 (+)
Log culmen	CU	73/4	18.4	59/3	21.0	NS
Log maxilla height	MA	29/7	4.2	38/7	5.3	NS
Log tarsal length	TS	58/3	21.2	36/2	14.9	NS
Log middle toe	TO	32/6	5.3	15/4	3.5	0.01 (+)
Shape variables						
Log (wing tip/wing length)	WT/WL	87/17	5.3	63/11	5.9	NS
Log (tail length/wing length)	TL/WL	10/1	7.5	7/2	4.1	NS
Log (culmen/maxilla height)	CU/MA	46/8	5.7	17/8	2.1	NS
Log (culmen/wing length)	CU/WL	58/5	12.5	44/4	11.8	0.01 (-)
Log (tarsal length/wing length)	TS/WL	42/3	12.1	20/3	7.9	NS
Log (tarsal length/middle toe)	TS/TO	30/7	4.3	15/5	3.2	0.01 (-)

* The 11 ecoregions are 6, 8, 12, 14, 16, 29, 30, 35-37, and 39.

in both sexes, as wing tip (WT) increases, the shape of the wing becomes more pointed (WT/WL becomes higher).

In both sexes, proportional tarsal length (TS/WL) increases with tarsal length, and proportional bill length (CU/MA and CU/WL) in-

creases with bill length. The correlations also show a negative allometric relationship between foot size (TO) and hind limb proportions (TS/TO). Robins in populations that have large feet tend to have proportionately even larger legs. These complex relationships could be an-

TABLE 3. Pearson product moment correlations (r) among median values of log size variables and log shape variables for 29 ecoregions with data for both sexes. Only values ≥ 0.5 or ≤ -0.5 are given. Males first, females second. Spearman rank correlations (r_s) with color of breast (MBR) and back (MBA) are given for males.

	WL	WT	TL	CU	MA	TS	TO	TS/WL	TS/TO
WT/WL	0.5/	1.0/0.9							
TL/WL			/0.6						
CU/MA				0.6/0.6	-0.5/			-0.5/	
CU/WL				0.7/0.8			/-0.5		
TS/WL				/-0.5		0.6/0.7			
TS/TO	/0.5					/0.6	-0.6/-0.5		
MBR	-0.9	-0.7	-0.8	-0.6		-0.8		0.5	-0.6
MBA						-0.5			

TABLE 4. Pearson product-moment correlation matrix among various measures of general size for males ($n = 36$ ecoregions, see Appendix). The variables are as follows: median wing length (A), the sum of the medians of the 7 size variables (B), the sum of the ranks of the medians of the 7 size variables (C), the geometric mean of the 7 size variables (D), the sum of the ranks of the geometric means of the 7 size variables (E), principal component 1 of the variance-covariance matrix of the size variables (F), principal component 1 of the correlation matrix of the size variables (G), and log wing length (H).

	A	B	C	D	E	F	G
A							
B	0.96						
C	0.86	0.93					
D	0.86	0.95	0.97				
E	0.81	0.87	0.96	0.92			
F	0.82	0.89	0.78	0.88	0.76		
G	0.91	0.97	0.98	0.98	0.92	0.82	
H	1.00	0.96	0.86	0.87	0.80	0.82	0.91

alyzed by multivariate analysis, but that would not reveal these specific aspects of geographic variation in the size and shape of robins.

Sexual dimorphism.—Within ecoregions, males have longer wing length, tail length, and toe length (Table 2, last column) than females. However, tarsal length and bill size and shape do not differ between the sexes within ecoregions, nor do wing shape (WT/WL), proportional tail length (TL/WL), or proportional leg length (TS/WL). We did not analyze geographic variation in sexual dimorphism.

Wing length as a measure of general size and ratio of wing tip to wing length as wing shape.—General size can be quantified in various ways. A correlation matrix (Table 4) among 8 reasonable choices of a criterion for general size that could be used in comparisons among ecoregions shows high correlations among all of them. Because of the high correlations of all measures with wing length (column A), we chose to use wing length. It is a single character that is easy to visualize, and it shows highly significant geographic differentiation (Table 2). There is no reason to prefer a multivariate measure like the scores of principal components (F or G). We do not have sufficient data for weight to make similar comparisons.

The pattern of geographic variation in the general size (wing length) of male robins is illustrated on a map of North America (Fig. 2).

Relatively small birds occur in the eastern United States and along the Pacific coast, whereas large birds occur in the central section of the Rocky Mountains and in the adjacent northern Great Plains. In addition, large males occur in the Sierra Madre Occidental of Mexico. The size of robins increases with latitude in eastern North America, but not in western North America. A similar map for wing shape measured as wing tip/wing length (Fig. 3) shows that males in most areas of eastern North America have more rounded wings (lower values of WT/WL) than do males in the West. In addition to the trend for larger birds to have more pointed wings, male robins in Newfoundland and elsewhere in the far north have exceptionally pointed wings. Geographic variation in the wing shape of male robins in Mexico is equal to that of all of North America.

The allometric relationship between wing length and wing shape (wing tip/wing length) can be compared visually (Figs. 2 and 3) or graphically where these variables are plotted for each sex (Fig. 4: a and b). We do not have data from each ecoregion for each sex. Ecoregions at the periphery of the data (Fig. 4) are identified in Table 1. Small robins with rounded wings occur in the east (11–14, lower left side of Fig. 4: a and b). Large birds with more pointed wings occur in the central Rocky Mountains (e.g. 24, 25), northern deserts (26–28), northern Great Plains (19, 20), and Mexican mountains (38). Robins of the more southern Pacific forests (32, 34) are smaller (i.e. have shorter wings) than other robins in western North America. Populations in the Arctic Tundra (1, 3) have exceptionally pointed wings for their size. These relationships are generally the same in both sexes.

Leg size (tarsus) and proportional leg size (tarsus/wing length).—A map of median tarsal length by ecoregion (Fig. 5) for males shows a different geographic pattern from the maps for wing length and wing shape (Figs. 2 and 3). The extremes of leg size are between the short-legged birds in Mexico, especially in lower Baja California, and the long-legged birds in Newfoundland. Note also (Fig. 5) the long tarsi of robins in the northern Pacific forests compared with the short tarsi of robins in the northern deserts of the Great Basin.

The relationship between leg size (tarsus) and leg size as a proportion of general size (tarsus/wing length) is given in Figure 6. The positive

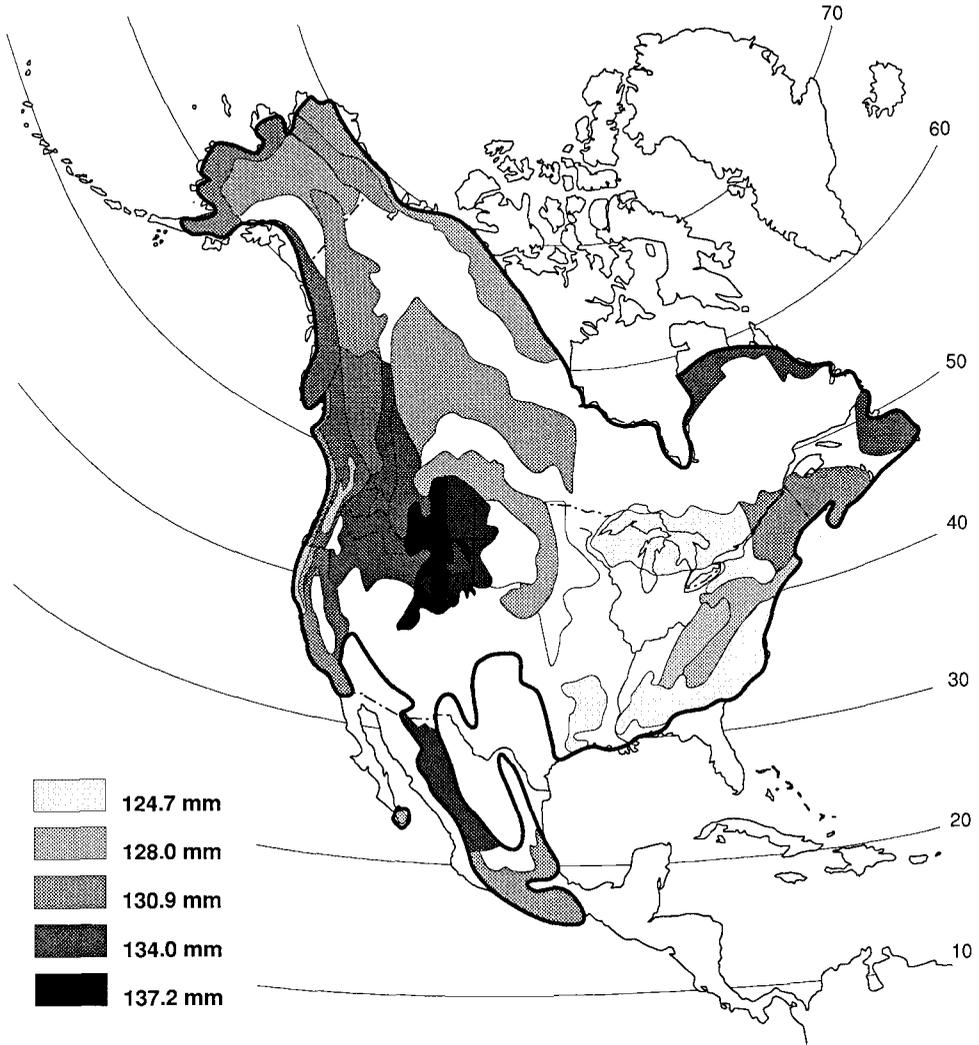


Fig. 2. A computer-generated map giving the median wing length of male robins in 36 ecoregions. Map with shading increments of 1.5% was made with Adobe Illustrator program; legend gives extremes, quartile values, and their corresponding shading. There are no data for white areas.

slope on the graph indicates allometric covariation of leg size and proportional leg size. This relationship was evident in the significant correlation between TS and TS/WL in both sexes (Table 3), but in Figure 6 it can be examined in more detail. Populations with long legs also have proportionately long legs. In males the extremes of proportional leg length (vertical axis) are in the Laurentian (11) and Pacific coastal forests (30, 32, 34). Both sexes in the humid eastern deciduous forest (13, 14) also have high values on this axis, and robins in Mexico (37,

38, 39) have exceptionally low values. Our samples do not include specimens from Arizona or New Mexico, so we do not know whether the robins there are intermediate in proportional leg length between those of Mexican birds and those of birds in more northern areas. In the East the tarsus is especially long in Newfoundland (8). Large values other than for Newfoundland are all associated with birds in the west. Although tarsal length shows highly statistically significant geographic variation in both sexes (high *F*-values in Table 2), its major geo-

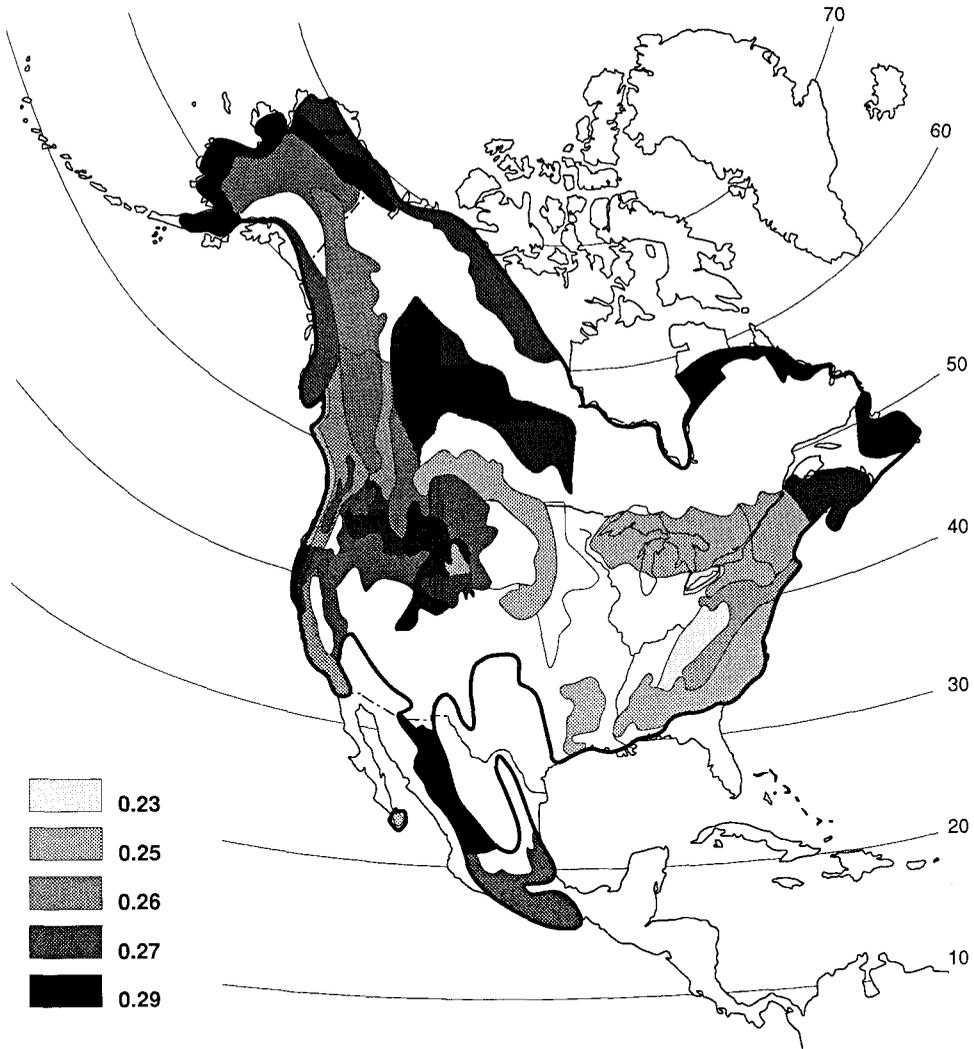


Fig. 3. Map of median values of wing tip/wing length for 36 ecoregions for male robins. There are no data for white areas.

graphic pattern of differentiation is not the same as the general trend in size. Neither tarsal length nor proportional tarsal length exhibits significant sexual dimorphism within ecoregions (compare distribution of data along axes in Fig. 6 [a and b], and see Table 2). This differs from Figure 4 (a and b), which shows sexual dimorphism on one axis (wing length) but not on the other.

Bill length (culmen) and bill shape (culmen/maxilla).—The bivariate plots of bill length (culmen) and bill shape (culmen/maxilla, Fig. 7: a and b), except for one outlying point (37), show that geographic variation in median bill length

is less than 2.5 mm and that the sexes are alike in bill length (see Table 2, last column, as well). Even so, the sequence of the ecoregions along the horizontal axis (Fig. 7) varies positively with the general size of robins, from eastern deciduous (13, 14) to northern hardwood (12) and boreal (5–7) forests in the east, and from Pacific forests (30, 34) to the Rocky Mountains (23, 25) in the west. The very long bills of the robins in Baja California (37) and the short bills of robins in the Yukon forest (5) are exceptions. Again, these extremes are apparent in both sexes.

Variation in plumage.—Eight of the nine sub-

species of *T. migratorius* are represented in our ecoregion samples (Table 5). Their original designations were based on plumage color, the extent of white spotting on the outer tail feathers, and morphometric differences. The extreme color phenotypes are in southwestern (subspecies *confinis*, ecoregion 37) and northeastern (subspecies *nigrideus*, ecoregion 8) North America. Very pale birds with small white tail spots occur in Baja California (subspecies *confinis*, 37), and very dark birds with large white tail spots occur in Newfoundland (*nigrideus*, 8). Within the United States, robins in the high, dry Rocky Mountains, grassland, and desert region (ecoregions 17–28, subspecies *propinquus*) are paler than robins elsewhere. When the entire geographic range is considered, some of the morphometric extremes are also extremes of color. The palest birds, in southern Baja California, also have very short legs and exceptionally long bills. The very dark birds, in Newfoundland, have exceptionally long legs. This association of leg length and color is not the same as the major geographic trend of variation in general size, wing length, and wing shape. The size and wing shape of male robins have extremes in the southeastern and north-central United States. The extremes of leg length and color are in Baja California and Newfoundland. Note that the color of the breast in males (MBR) is negatively correlated with most size variables within the United States and positively correlated with TS/WL, whereas the color of the back is negatively related to TS/TO (Table 3).

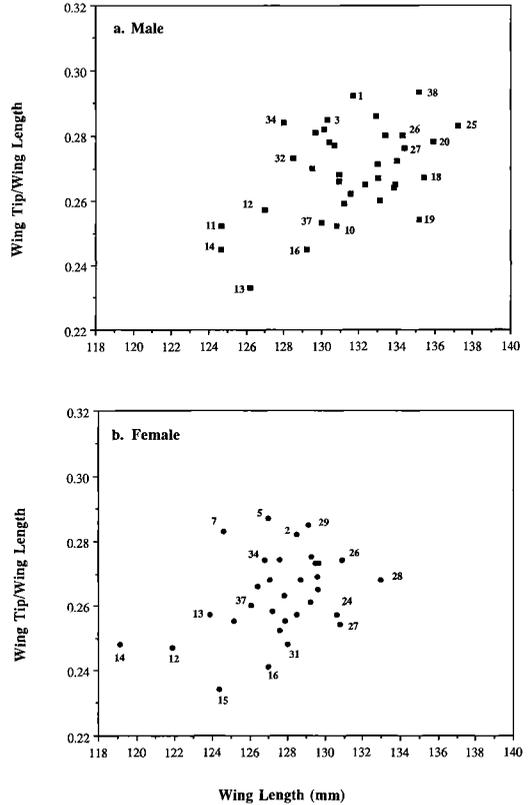


Fig. 4. The relationship between size (median wing length) and wing shape (ratio of wing tip to wing length) for males (a) and females (b). Numbers at the periphery of the distribution are for ecoregions identified in Table 1.

TABLE 5. Geographic variation in the color of the plumage of male robins based on reference to charts in the Munsell Book of Color (Anonymous 1929–1942).

Ecoregions	Subspecies	Color of breast ^a (BR)	Color of back ^b (BA)	Sum	White spots in tail ^c
37	<i>confinis</i>	1	1	2	2
17–28, 38	<i>propinquus</i>	3	2	5	3
39	<i>phillipsi</i>	3	3	6	2
29–34	<i>caurinus</i>	4	2	6	2
35–36	<i>aleucus</i>	4	2	6	1
1–7, 9–12, 15–16	<i>migratorius</i>	4	3	7	4
13, 14	<i>achrusterus</i>	5	2	7	4
8	<i>nigrideus</i>	5	4	9	4

^a #1 Yellow-red Yellow (10.0), value 8, chroma 6; #3 Yellow-red (5.0), value 5, chroma 8; #4 (5.0) 5/6; #5 (5.0) 4/6. Because *confinis* has a much paler breast than all other subspecies, there are no #2s for color of breast. Categories #3–5 show increasingly dark rust color of breast.

^b Pale gray backs of all populations of robins are closest to the reference color Reddish Yellow (2.5Y) and chroma 2. They vary only in value. From light to dark they are #1, 6; #2, 5; #3, 4; #4, 3.

^c #1 is very reduced white spots, #4 is extensive white spots on the outer tail features, #2 and #3 are intermediate.

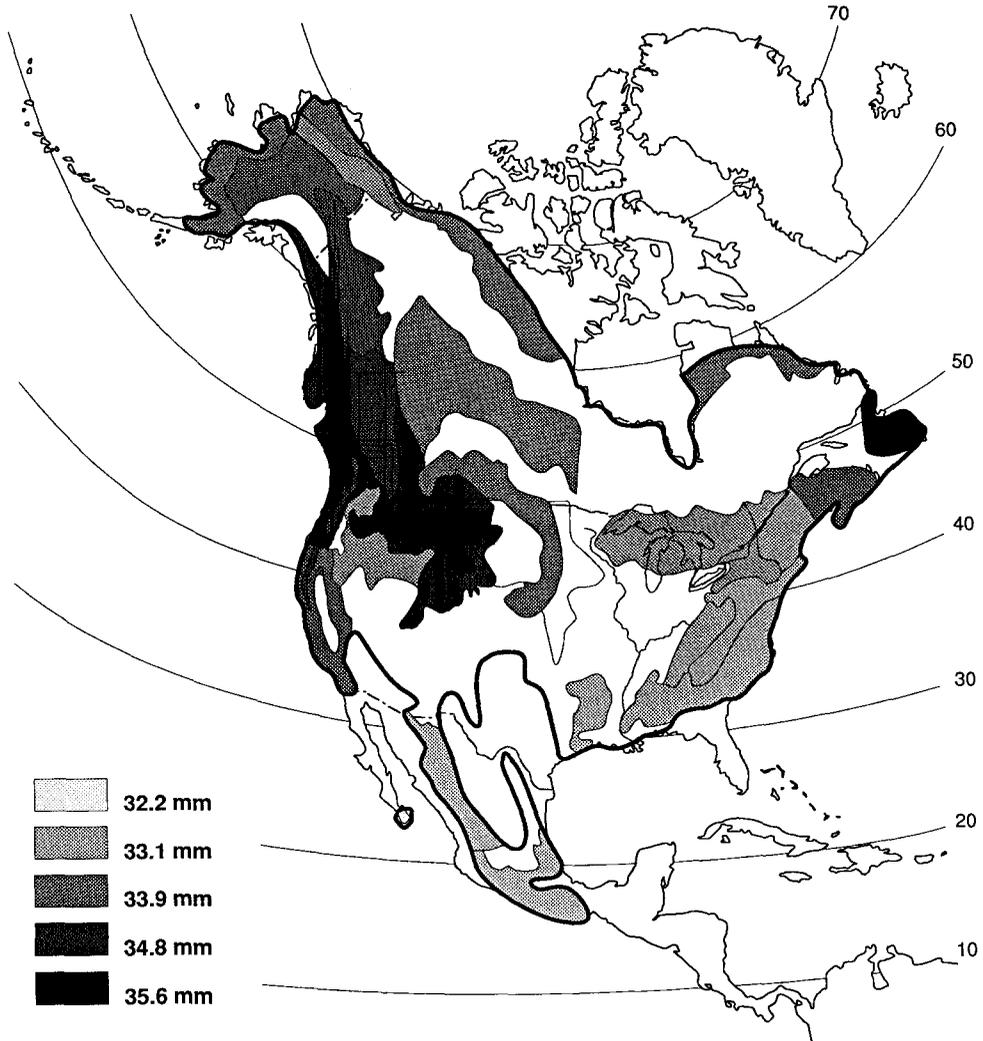


Fig. 5. Map of median values of tarsal length for 36 ecoregions for male robins. There are no data for white areas.

Psychrometry.—For 21 ecoregions in the United States, we explored the relationships among climate, altitude, and character variation in the robin by using mean noon April and July dry-bulb and wet-bulb temperatures (ADBT, JDBT, AWBT, JWBT) and relative and absolute humidities (AAH, JAH, ARH, JRH) (Appendix 2). The period April to July spans the period when robins are on their breeding grounds. Spearman rank correlations between these eight climate variables and size variables for male robins are negative (Table 6). In both sexes the variables that are a function of both temperature and hu-

midity (WBT, AH, RH) are better predictors of all size variables than are dry-bulb temperatures. The best overall predictor is July absolute humidity (JAH) (11 entries). Altitude is an excellent predictor, but it is not better than JAH. All subsets multiple regression found only one combination of these nine variables that was a better predictor of general size (WL) in male robins than was JAH alone (JAH, $r^2 = 0.701$; all nine variables, adjusted $r^2 = 0.717$, a negligible improvement). Although we do not know the mechanism that underlies these relationships of size and climate, climatic variables that are

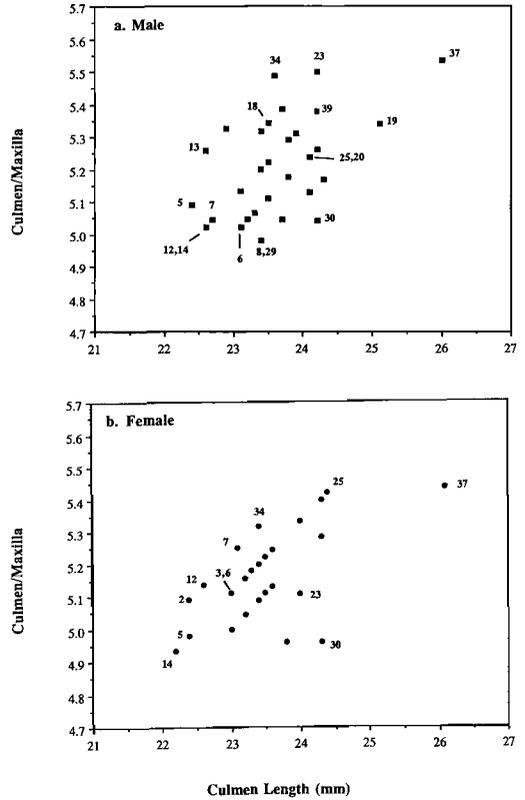
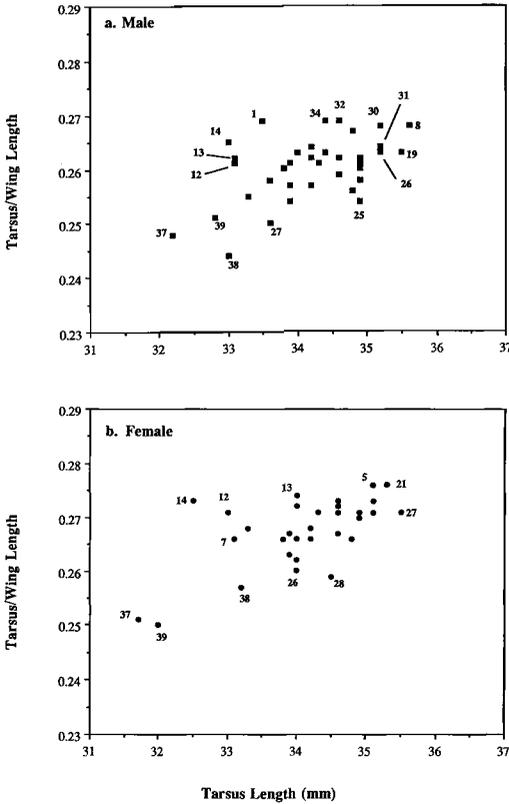


Fig. 6. The relationship between leg size as estimated by tarsal length and proportional leg size (ratio of tarsal length to general size as estimated by wing length) for males (a) and females (b). Numbers are for ecoregions identified in Table 1.

Fig. 7. The relationship of bill size as estimated by bill length (culmen) to bill shape (ratio of bill length to maxilla height for males (a) and females (b). Numbers are for ecoregions identified in Table 1.

a function of the amount of moisture in the air during the breeding season can have high predictive value for size variation in robins, at least within the United States.

Psychrometry is the study of the properties of air and water vapor mixtures at atmospheric pressure (Zimmerman and Lavine 1964). A psychrometric graph permits the reading of absolute humidity and relative humidity from values for dry-bulb and wet-bulb temperature (Fig. 8a). We have located 21 ecoregions in the United States on a psychrometric graph on the basis of their July mean noon climate (Fig. 8b). Data were interpolated from major weather stations to the centers of ecoregions. Eastern regions (dark circles) are higher on the vertical scale (indicating higher absolute humidity) than are western regions. The high correlation between the general size of male robins and July absolute

humidity ($r_s = -0.8$, Table 6), in spite of the complex geographic pattern of size variation (Fig. 2), can be expressed as a simple function of July absolute humidity (see sizes of circles in Fig. 8b). We do not think that July has special significance. A further analysis should include May and June, and data for Canada and Mexico should be included.

The strictly Bergmannian prediction of a strong negative relationship between size and dry-bulb temperature is not fulfilled. The inclusion of the western localities has confounded the negative relationship in the east (Fig. 8b), but wet-bulb temperature, absolute humidity, and relative humidity are all closely related to size for the entire United States (Table 6).

The data for darkness of plumage (Table 5) cannot be analyzed thoroughly with our climate data for the United States because the ex-

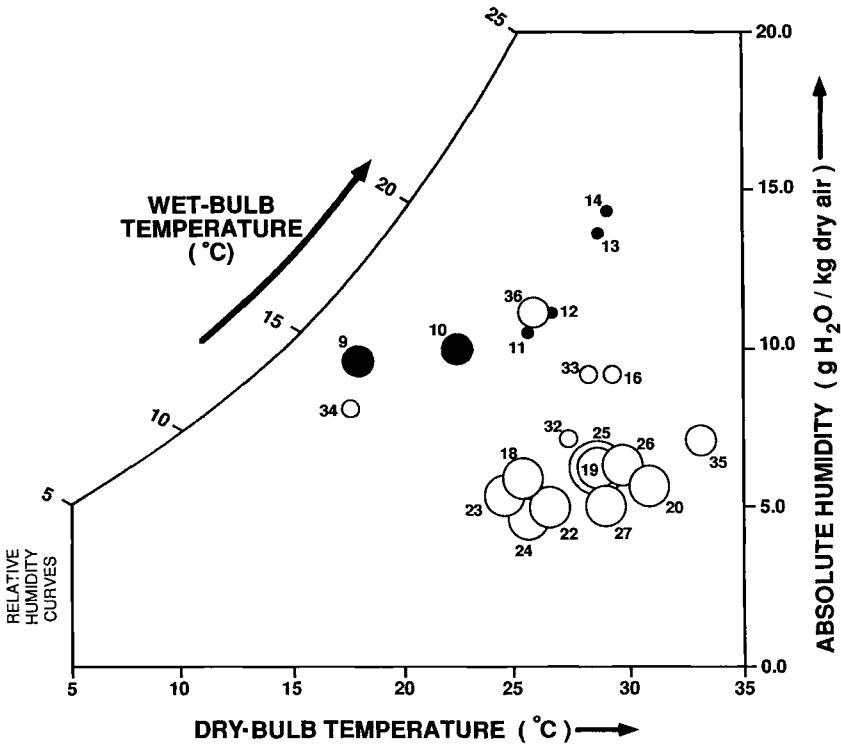
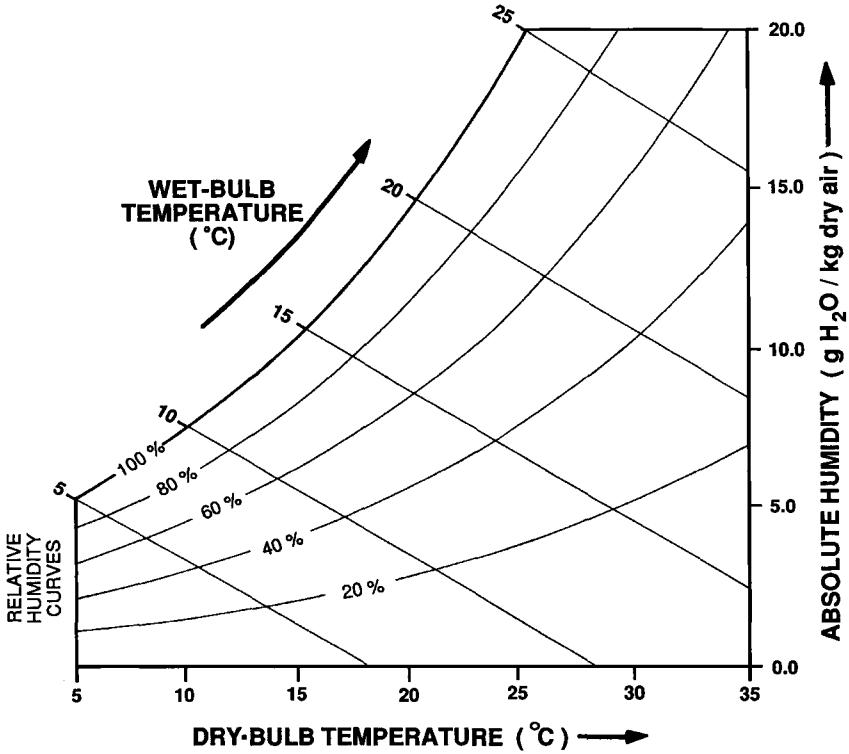


TABLE 6. Relationship of size variables and color of robins to climate and altitude. Spearman rank correlations (r_s) between size variables and climate variables by ecoregions in the United States for males ($n = 21$, first) and females ($n = 16$, second). Size and color (MBR and MBA) variables are as in Tables 2 and 3. Climate variables are April dry-bulb temperature (ADBT), April wet-bulb temperature (AWBT), July wet-bulb temperature (JWBT), April absolute humidity (AAH), July absolute humidity (JAH), April relative humidity (ARH), and July relative humidity (JRH). The highest values tend to be for July absolute humidity. The last 3 lines give correlations with 7 categories of altitude (ALT), 4 of male breast color (MBR), and 4 of male back color (MBA) (Table 5). Only correlations of absolute value ≥ 0.5 are given. None of the correlations with July dry-bulb temperature (JDBT) were this high, so JDBT was omitted.

	WL	WT	TL	CU	MX	TS	TO
ADBT							-0.5/
AWBT				/-0.5			-0.7/
JWBT	-0.6/-0.5	-0.7/-0.6	-0.5/-0.5	-0.6/-0.6		-0.6/-0.7	
AAH	-0.6/		-0.6/-0.5	/-0.7			-0.5/
JAH	-0.8/-0.7	-0.7/-0.5	-0.7/-0.7	-0.6/-0.7	/-0.5	-0.7/-0.7	
ARH	-0.8/-0.7		-0.7/-0.8	/-0.6		-0.5/-0.5	
JRH	-0.7/-0.8	-0.5/-0.5	-0.7/-0.6	-0.5/-0.6		-0.5/-0.6	
ALT	0.7/0.6	0.5/	0.6/0.5	0.6/0.6	/0.6	0.6/0.7	
MBR	-0.9/	-0.7/	-0.8/	-0.6/		-0.8/	
MBA						-0.5/	

treme values of color occur in Canada and Mexico. Even so, it is clear (Tables 5 and 6) that robins with pale breasts occur in dry highlands (ecoregions 17-28 and 37-39), and dark ones occur in both warm humid areas (13-14) and cool areas where the relative humidity is high (8). A detailed psychrometric analysis of these relationships is clearly needed. Within the United States, color of the breast in males is positively related to TS/WL ($r_s = 0.51$), a relationship that pertains to robins throughout their range (Fig. 6a), but the negative correlation between color and tarsus in the U.S. (Table 3) does not pertain to robins throughout their range.

DISCUSSION

The use of ratios in morphometric work has been challenged by Atchley et al. (1976) and Atchley and Anderson (1978). They believed that the opportunities for misuse were so high that they recommended that ratios be avoided in all analysis of biological data. This was an overreaction. Misuse is possible, of course, but

log-transformed ratios have been important to allometric studies for many years (e.g. Huxley 1932). Mosimann (1970, 1975a, 1975b, 1988) and Hills (1978) have shown that, when the data can be considered to be approximately lognormally distributed, analysis of ratios as differences between logarithms are not only proper but allow insightful comparisons about size and shape relationships. In our data for the robin, the correlation between wing length and log wing length is 0.99 (Table 4), so wing length and log wing length can be used interchangeably to indicate size. Note also that correlations of log ratios between dependent variables and their denominator need not be negative (WT/WL with WL in Table 3, and see Mosimann 1975a). The correlations of log ratios and log size (Table 3) represent geographic variation in allometric relationships between aspects of shape and size. Mosimann and James (1979), Darroch and Mosimann (1985), and Boecklen (1989) extend this type of analysis to multivariate cases. We think that the direct study of geographic variation in shape either by uni-

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Fig. 8. The relationship between size variation in male robins and variation in climate in July in the United States. Fig. 8a is a psychrometric chart, which shows the relationship between dry- and wet-bulb temperature and relative and absolute humidity; Fig. 8b gives size variation (median wing length) in male robins in five size classes of circles for 21 ecoregions located by their mean noon values of the climate variables. Ecoregions in the east have dark circles.

variate analysis or by multivariate analysis is important. For robins we showed that dimensionless shape variables show significant geographic variation.

Although the magnitude of variation in the American Robin is only moderate, its geographic pattern of variation in size and color is similar to that of many other species that exhibit more variation (James 1991). This supports observations of Grinnell (1924), Rensch (1936, 1938), Mayr (1963, 1970), and others, who documented parallelisms among species in continental patterns of geographic variation that correspond to gradients in the physical environment. Further assessment of the extent of parallelism and convergence in size and color of plumage among species that occupy the same physiographic areas but that differ in history and ecology (microhabitat, diet, predators) could explore further the likelihood that the trends are adaptations (genetic or nongenetic) to trends in the physical environment. Differences in the phenology of the breeding season of different species should be taken into account (James and Shugart 1974). As cases accumulate, it might be possible to evaluate the effects of other factors such as character displacement, isolation, historical factors, or distance. Lack of concordance in patterns of variation among species would suggest that they may be due to chance. The extent of covariance between genetically and nongenetically based variation could be studied by means of manipulative experiments (James 1983).

Striking regularities have been found previously between geographic patterns of size variation in birds in the eastern and central United States and patterns of variation in climatic variables such as wet-bulb temperature, vapor pressure, and absolute humidity, all of which are combined functions of dry-bulb temperature and the percent saturation of the air (James 1970). The present study shows that these relationships are still present in the male robin when western states are included, even though a negative relationship between size and dry-bulb temperature is not evident in the west. High absolute humidity is associated with smaller size, low absolute humidity with larger size, regardless of dry-bulb temperature (Fig. 8b). Because we have data for climate for only 16 ecoregions for female robins, we present the analysis only for males. We show (Table 3) that some size and shape variables exhibit sexual

dimorphism within ecoregions and some do not. Sexes also covary geographically (Figs. 4, 6, and 7).

The primary correlate between size variation in the American Robin and the physical environment is its negative relationship with absolute humidity, the amount of moisture in the air. Because cool air cannot hold as much moisture as warm air, this negative relationship between size and moisture is sometimes also a function of dry-bulb temperature, latitude, or altitude. Other cases in which birds have been found to be larger in drier as opposed to colder climates (Grinnell 1904; Ripley 1950; Hamilton 1958, 1961; Aldrich 1968, 1984; Power 1969, 1970) have usually been counted as exceptions to Bergmann's Rule. For the robin, if the area under study includes regions that are warm and dry, significant correlations between size and dry-bulb temperature, latitude, or altitude are less probable than are correlations with absolute humidity. Rather than continuing to tally exceptions (Zink and Remsen 1986), it would be more useful to improve Bergmann's model by examining heat exchange between organisms and their physical environment. For examples of approaches in biophysical ecology, see Tracy (1972), Porter et al. (1973), Calder and King (1974), Rosenberg (1974), Walsberg and King (1978).

In contrast, Zink and Remsen (1986) recently found substantial support for Gloger's Rule, defined as the expectation that plumages of birds are darker in more humid environments. A refinement of this rule that might account for even more variation in the darkness of plumage would be to distinguish among pigments and between relative and absolute humidity. Indeed, according to Mayr (1963), Gloger's (1833) original paper discussed this matter, and Grinnell (1910) noted that avian plumages are dark in areas where the average percent saturation of the air is high, and plumages are pale in dry areas with cloudless skies. In the American Robin, the plumage is darkest in Newfoundland. This is not the area of highest absolute humidity.

The fact that pale short-legged robins occur in Baja California and dark long-legged robins occur in Newfoundland suggests color adaptations for background matching and morphometric adaptations for ground foraging according to the amount of organic matter in the soil. However, agents of selection cannot be deter-

mined from data of this type. Grinnell (1924) thought that local variation represented adaptations to food, cover, and animal associates, which were in turn controlled by physical factors. It is equally reasonable to argue that local variation represents physiological adaptations to the physical environment. Such adaptations could cause parallel geographic patterns of character variation in the size, shape, and color of birds, which must then find appropriate food and cover.

Many species of birds have more pointed wings in drier parts of their geographic ranges (Davis 1951, Pitelka 1951, Savile 1957, Grant 1966, Newton 1967, Aldrich 1984) and in migratory populations (Grinnell 1910, but see Rensch 1938). Variation in the robin is consistent with both of these observations. In our samples, male robins (but not females) in the Sierra Madre Occidental of western Mexico have wings just as pointed as are those of the highly migratory arctic populations. This observation needs further study. The more pointed wings of birds in high dry areas is allometrically related to size variation. However, robins in the Arctic, which migrate thousands of miles, have more pointed wings than would be expected for their sizes, considering the overall variation in the species.

It is tempting to invoke natural selection as a causal agent for the origin and maintenance of patterns of geographic variation in the robin, but this is not justified by current information. The magnitude of the variation in relation to the size of the area studied is small. The extremes of median wing length in males by ecoregion for all of North America are <13 mm apart, tarsus <4 mm, and culmen <4 mm.

The conventional model that accounts for clines in character variation is that genetically based variations in size, shape, and color are associated with fitness and that natural selection produces optimal phenotypes that vary in subtle but predictable ways across the geographic range of a species. We know that even slight differences can be associated with survival (Nice 1937), and biologists have yet to propose any other model to account for adaptation. To the extent that species with different phylogenetic relationships and life histories show concordant patterns of variation in size and color, the case that they represent physiological adaptations to the physical environment or its correlates is strengthened.

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APPENDIX 1. Median measurements (mm) of seven size and six shape variables for male robins and for female robins by ecoregion (see Table 1). Morphometric variables are identified in Table 2.

Ecoregion	WL	WT	TL	CU	MA	TS	TO	WT/WL	TL/WL	CU/MA	CU/WL	TS/WL	TS/TO
Males													
1	133.4	37.3	96.9	23.4	4.4	33.9	22.2	0.280	0.726	5.318	0.175	0.254	1.527
2	129.7	36.4	100.3	23.1	4.5	33.9	20.9	0.281	0.773	5.133	0.178	0.261	1.622
3	130.3	37.1	97.1	23.1	4.5	33.6	22.4	0.285	0.745	5.133	0.177	0.258	1.500
4	131.7	38.5	99.5	23.2	4.6	33.9	21.4	0.292	0.756	5.043	0.176	0.257	1.584
5	129.5	35.0	97.2	22.4	4.4	34.2	21.6	0.270	0.751	5.091	0.173	0.264	1.583
6	130.9	35.1	98.5	23.1	4.6	34.4	21.1	0.268	0.752	5.022	0.176	0.263	1.630
7	130.1	36.7	97.8	22.7	4.5	33.8	21.3	0.282	0.752	5.044	0.174	0.260	1.587
8	132.9	38.0	99.7	23.4	4.7	35.6	21.7	0.286	0.750	4.979	0.176	0.268	1.641
9	130.7	36.2	98.5	23.7	4.7	34.2	21.7	0.277	0.754	5.043	0.181	0.262	1.576
10	130.8	32.9	101.2	23.7	4.4	33.3	22.5	0.252	0.774	5.386	0.181	0.255	1.480
11	124.7	31.4	93.0	22.9	4.3	33.5	21.8	0.252	0.746	5.326	0.184	0.269	1.537
12	127.0	32.6	96.4	22.6	4.5	33.1	21.2	0.257	0.759	5.022	0.178	0.261	1.561
13	126.2	29.4	95.3	22.6	4.3	33.1	20.5	0.233	0.755	5.256	0.179	0.262	1.615
14	124.7	30.5	94.6	22.6	4.5	33.0	20.7	0.245	0.759	5.022	0.181	0.265	1.594
15													
16	129.2	31.7	98.6	23.3	4.6	34.0	21.1	0.245	0.763	5.065	0.180	0.263	1.611
17													
18	135.4	36.2	101.4	23.5	4.4	34.9	21.5	0.267	0.749	5.341	0.174	0.258	1.623
19	135.2	34.3	100.5	25.1	4.7	35.5	22.7	0.254	0.743	5.340	0.186	0.263	1.564
20	135.9	37.8	101.9	24.1	4.6	34.8	21.2	0.278	0.750	5.239	0.177	0.256	1.642
21	132.3	35.1	98.8	23.8	4.6	34.6	20.7	0.265	0.747	5.174	0.180	0.262	1.671
22	133.8	35.3	100.0	23.5	4.6	34.6	22.2	0.264	0.747	5.109	0.176	0.259	1.559
23	133.9	35.5	99.6	24.2	4.4	34.9	21.2	0.265	0.744	5.500	0.181	0.261	1.646
24	134.3	37.6	101.0	24.2	4.6	34.9	20.7	0.280	0.752	5.261	0.180	0.260	1.686
25	137.2	38.8	105.8	24.1	4.6	34.9	21.7	0.283	0.771	5.239	0.176	0.254	1.608
26	134.0	36.4	101.2	23.8	4.6	35.2	21.5	0.272	0.755	5.174	0.178	0.263	1.637
27	134.4	37.1	101.2	23.6	4.3	33.6	21.1	0.276	0.753	5.488	0.176	0.250	1.592
28													
29	133.0	35.5	97.6	23.4	4.7	34.9	21.3	0.267	0.734	4.979	0.176	0.262	1.638
30	131.2	34.0	99.6	24.2	4.8	35.2	21.5	0.259	0.759	5.042	0.184	0.268	1.637
31	133.1	34.6	101.5	24.1	4.7	35.2	21.2	0.260	0.763	5.128	0.181	0.264	1.660
32	128.5	35.1	95.6	24.3	4.7	34.6	21.8	0.273	0.744	5.170	0.189	0.269	1.587
33	130.4	36.3	97.9	23.4	4.5	34.8	20.2	0.278	0.751	5.200	0.179	0.267	1.723
34	128.0	36.4	95.5	23.6	4.3	34.4	21.4	0.284	0.746	5.488	0.184	0.269	1.607
35	133.0	36.0	99.2	23.9	4.5	34.2	21.0	0.271	0.746	5.311	0.180	0.257	1.629
36	131.5	34.4	99.1	23.5	4.5	34.3	21.0	0.262	0.754	5.222	0.179	0.261	1.633
37	130.0	32.9	100.2	26.0	4.7	32.2	20.8	0.253	0.771	5.532	0.200	0.248	1.548
38	135.2	39.6	98.4	23.8	4.5	33.0	19.5	0.293	0.728	5.289	0.176	0.244	1.692
39	130.9	34.8	96.4	24.2	4.5	32.8	19.9	0.266	0.736	5.378	0.185	0.251	1.648
Females													
1													
2	128.5	36.3	97.7	22.4	4.4	34.2	20.5	0.282	0.760	5.091	0.174	0.266	1.668
3	125.2	31.9	96.3	23.0	4.5	34.0	21.8	0.255	0.769	5.111	0.184	0.272	1.560
4													
5	127.0	36.5	95.6	22.4	4.5	35.1	20.7	0.287	0.753	4.978	0.176	0.276	1.696
6	128.7	34.5	98.2	23.0	4.5	34.9	20.4	0.268	0.763	5.111	0.179	0.271	1.711
7	124.6	35.2	93.2	23.1	4.4	33.1	21.2	0.283	0.748	5.250	0.185	0.266	1.561
8	129.3	35.6	97.9	23.2	4.6	34.9	21.4	0.275	0.757	5.043	0.179	0.270	1.631
9													
10													
11													
12	121.9	30.1	91.2	22.6	4.4	33.0	20.1	0.247	0.748	5.136	0.185	0.271	1.642
13	123.9	31.8	91.2	23.6	4.5	34.0	20.5	0.257	0.736	5.244	0.190	0.274	1.659
14	119.1	29.5	90.6	22.2	4.5	32.5	19.7	0.248	0.761	4.933	0.186	0.273	1.650
15	124.4	29.1	93.0	23.0	4.6	33.3	21.5	0.234	0.748	5.000	0.185	0.268	1.549
16	127.0	30.6	96.0	23.4	4.5	33.8	20.7	0.241	0.756	5.200	0.184	0.266	1.633
17	129.7	35.4	96.7	23.4	4.5	34.0	20.4	0.273	0.746	5.200	0.180	0.262	1.667
18	127.6	34.9	96.4	24.3	4.6	34.2	20.7	0.274	0.755	5.283	0.190	0.268	1.652
19													
20													
21	127.9	32.6	96.2	23.4	4.5	35.3	21.0	0.255	0.752	5.200	0.183	0.276	1.681
22	128.5	33.0	96.3	23.8	4.8	35.1	20.3	0.257	0.749	4.958	0.185	0.273	1.729
23	127.1	34.1	93.4	24.0	4.7	34.6	21.0	0.268	0.735	5.106	0.189	0.272	1.648
24	130.6	33.6	99.3	23.6	4.5	34.8	20.0	0.257	0.760	5.244	0.181	0.266	1.740
25	129.5	35.4	98.8	24.4	4.5	35.1	19.8	0.273	0.763	5.422	0.188	0.271	1.773
26	130.9	35.9	95.5	23.4	4.5	34.0	20.3	0.274	0.730	5.200	0.179	0.260	1.675

