GEOGRAPHIC VARIATION IN THE SURFACE/VOLUME RATIO OF THE BILL OF RED-WINGED BLACKBIRDS IN RELATION TO CERTAIN GEOGRAPHIC AND CLIMATIC FACTORS

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Much circumstantial and experimental evidence exists to relate logically intraspecific and interspecific variation in bill morphology with functional adaptations in diet and feeding behavior (e.g., Beecher 1951; Pitelka 1951; Betts 1955; Morris 1955; Hinde 1959; Bowman 1961; Kear 1962; Myton and Ficken 1967). Although geographic variation in bill shape and size is often explained in this way, it is also important to consider the fact that more than one environmental factor may exert a selective influence on a given character, and that multiple environmental factors may therefore be responsible for the pattern of geographic variation. The present analysis considers one aspect of bill morphology, the surface/volume ratio (s/v), of Red-winged Blackbirds (*Agelaius phoeniceus*) from central North America and examines geographic variation in this character in relation to eight geographic and climatic factors. The results suggest that variation is the consequence of natural selection by more than one factor and also show what appears to be a previously unrecorded relationship between bill s/v and minimum temperature during the breeding season.

Earlier (Power 1970), geographic variation in bill length, bill depth, lower bill width, and upper bill width was examined statistically with over 50 samples of males and 48 samples of females, all of breeding season birds, from throughout central North America. The study area (fig. 1) includes the prairie provinces of Canada and most of the Great Plains states of the United States. In both sexes, bills are longest in the northwestern and central Canadian plains and parts of the northern U.S., become shorter in the central plains and states of Wyoming and Colorado, and are long again in the southeastern plains, including Iowa, eastern Oklahoma, Illinois, and Missouri. Bills are thickest in Northwest Territories and northern Alberta, are slightly thinner through central Canada and the northern and western plains of the U.S., become gradually thinner through the central plains, and are thinnest in the southeastern plains states.

The present study examines geographic variation in bill s/v in relation to longitude, latitude, altitude, mean temperature during the breeding season (May to July), April minimum temperature, July maximum temperature, July wet-bulb temperature, and total precipitation during the breeding season. The purpose was to determine if statistical relationships exist between the character and the environmental variables and if these would point to logical arguments concerning the adaptive significance of geographic variation in bill morphology. Only breeding season samples and breeding season locality data were used since specific wintering areas of birds from specific breeding sites are largely unknown.

Considering the likelihood of the significance of more than one environmental factor and the fact that the eight environmental factors are intercorrelated to various degrees, a multiple regression analysis was used to estimate the amount of variation in bill s/v accounted for by the simultaneous effect of all of the environmental factors, and to estimate the degree of statistical relationship between bill s/v and a single environmental variable while variation accounted for by the remaining environmental factors included in the test is held constant. In this way multiple regression analysis takes into account the existence of correlations among the environmental factors and is thereby a more powerful technique than would be a series of simple linear regression analyses.

MATERIALS AND METHODS

Data were gathered for 51 locality samples of males and 48 locality samples of females from throughout the study area (fig. 1). Bill length was measured from the tip of the bill to the base at the fronto-nasal hinge. Bill height was measured from the exposed portion of the mandibular rami on the lower mandible to the highest point at the top of the culmen on the upper bill. And lower bill width was taken at the widest part of the base of the bill across the mandibular rami. For males sample sizes ranged from 10 to 58 with a median of 16, and for females sample sizes ranged from 5 to 29 with a median of 13. Only adult specimens were used for males, since first-year

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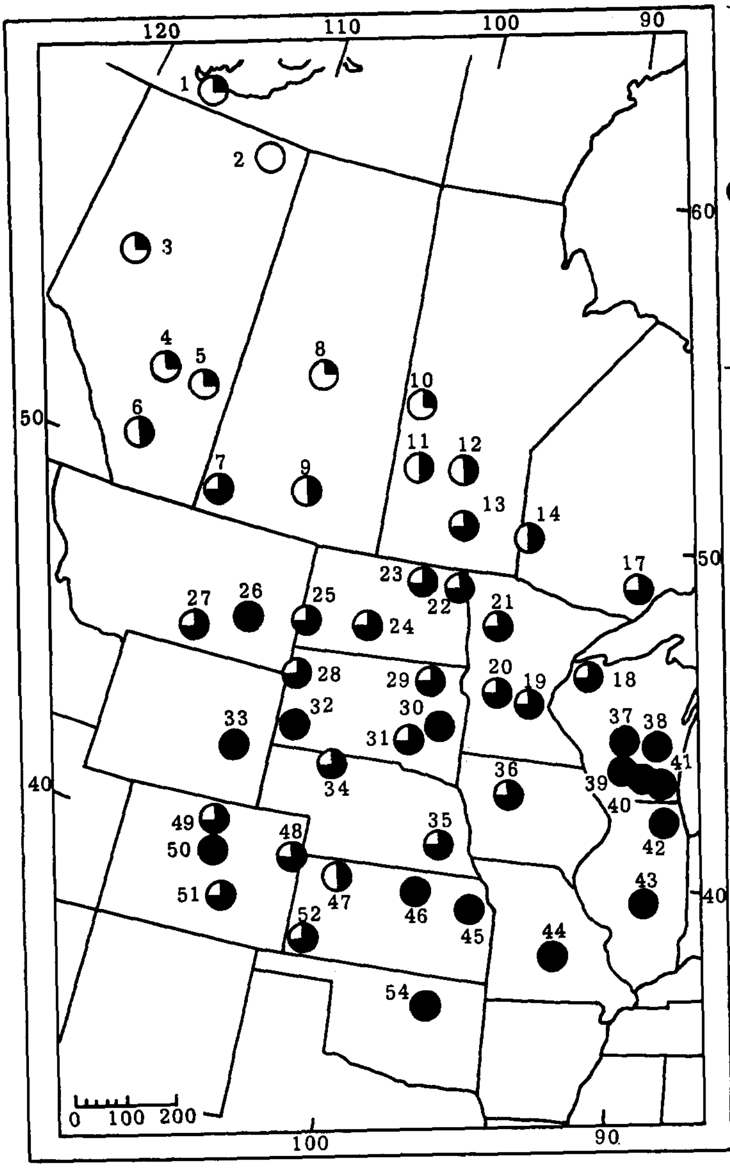

40	.7208	.0164	(13)
54	.7197	.0253	(13)
38	.7179	.0174	(58)
42	.7154	.0189	(13)
37	.7146	.0199	(39)
26	.7145	.0268	(9)
39	.7143	.0175	(30)
41	.7134	.0134	(23)
44	.7132	.0293	(14)
43	.7123	.0197	(13)
50	.7108	.0217	(15)
45	.7100	.0220	(25)
32	.7092	.0181	(16)
46	.7085	.0241	(12)
30	.7084	.0189	(15)
33	.7069	.0213	(20)
19	.7060	.0159	(13)
21	.7052	.0178	(14)
20	.7035	.0145	(14)
18	.7031	.0184	(13)
51	.7028	.0222	(19)
49	.7014	.0202	(10)
25	.7014	.0217	(18)
23	.7013	.0266	(20)
48	.7012	.0298	(18)
52	.6995	.0180	(9)
27	.6993	.0206	(21)
22	.6985	.0246	(26)
34	.6981	.0175	(15)
35	.6977	.0242	(14)
36	.6976	.0178	(15)
29	.6970	.0178	(15)
28	.6955	.0238	(23)
7	.6955	.0207	(34)
24	.6951	.0171	(15)
31	.6945	.0178	(14)
13	.6939	.0137	(10)
17	.6939	.0230	(15)
47	.6901	.0216	(11)
14	.6886	.0240	(10)
11	.6862	.0297	(8)
12	.6840	.0181	(9)
9	.6819	.0181	(30)
6	.6792	.0146	(25)
8	.6772	.0230	(17)
4	.6680	.0161	(31)
10	.6675	.0195	(15)
5	.6669	.0197	(7)
3	.6667	.0191	(18)
1	.6656	.0234	(13)
2	.6488	.0109	(9)

FIGURE 1. Geographic variation of bill surface/volume ratio in male central North American Red-winged Blackbirds. From left to right the columns of numbers are locality number, mean, standard deviation, and sample size. Lines to the right of the columns of numbers delimit maximal non-significant ($P < 0.05$) subsets of samples resulting from STP test on ranked means. Variously shaded circles show division of the range of means into fifths and serve to summarize the pattern of geographic variation.

males average slightly shorter bills than adults (Power 1970). For females adult and first-year specimens were combined since no significant or consistent differences were found between age classes for these characters. For each specimen the bill surface area (s) and volume (v) were calculated, using formulae for the surface area and volume of one-half of a cone with an elliptical cross-section, as follows:

$$s \doteq \frac{\pi l}{2}\sqrt{\frac{w^2+h^2}{2}} + w\sqrt{l^2-h^2},$$

$$v = \frac{\pi w h}{6}\sqrt{l^2-h^2},$$

where l is bill length, w is one-half of the lower bill width, and h is bill height. The surface/volume ratio is then simply calculated as s/v. The formula for s is approximate, whereas that for v is exact. When h is considerably smaller than l (it was not in the present case), it is possible to replace $\sqrt{l^2-h^2}$ in the formulae by l, or, better, by $l - [h^2/(2l)]$, with little loss in accuracy. If the cross-section of the bill is parabolic rather than elliptical the formulae are

$$s \doteq \frac{l\sqrt{w^2+4h^2}}{2} + \frac{lw^2}{4h}\log_e\left(\frac{2h}{w}+\sqrt{\left(\frac{2h}{w}\right)^2+1}\right) + w\sqrt{l^2-h^2}$$

and

$$v = \tfrac{2}{3} w h\sqrt{l^2-h^2}.$$

If $w = h$ (i.e., the lower bill width is equal to twice the bill height) then the ellipse becomes a circle and

TABLE 1. Standard partial regression coefficients of bill surface/volume ratio of Red-winged Blackbirds on certain geographic and climatic factors, with and without wing length as an adjustment for body size.

	Without wing length as an independent variable		With wing length as an independent variable	
	Males	Females	Males	Females
Longitude	–0.203	–0.410*	–0.178	–0.464*
Latitude	–1.243***	–0.579	–1.368***	–0.565
Altitude	–0.007	0.253	–0.060	0.180
Mean temp.	–0.543	–0.451	–0.576	–0.388
Minimum temp.	0.496*	0.479*	0.443*	0.264
Maximum temp.	–0.564	–0.093	–0.510	0.112
Wet-bulb temp.	0.445	0.398	0.263	0.128
Precipitation	–0.321*	–0.223	–0.349*	–0.259
Wing length			–0.192	–0.262*

* $0.01 < P < 0.05$; *** $P < 0.001$

the surface/volume ratio is approximately given by $5/w$.

To test for significance or non-significance of differences among sub-samples of localities, Gabriel's (Gabriel and Sokal 1969) sums of squares simultaneous test procedure (STP) based on ranked means was carried out. The use of multiple regression analysis in studies of geographic variation has been discussed earlier (Power 1969). Methods may be found in most advanced statistics texts.

RESULTS

Geographic variation. Patterns of geographic variation in bill s/v are summarized in figures 1 and 2. The large amount of overlap among non-significant subsets indicates the smoothly clinal pattern of variation. The pattern of geographic variation is thus a gradual increase from northwest to southeast. Geographic variation is similar for the sexes. Using locality means of bill s/v, the correlation coefficient between males and females is 0.885 ($P < 0.01$).

Multiple regression analysis. For each sex, sample means for bill s/v were treated as the dependent variable and locality values for the eight geographic and climatic factors were considered as independent variables in a multiple regression analysis. The multiple correlation coefficients, indicating the correlation between s/v and all geographic and climatic factors simultaneously, are 0.911 for males and 0.920 for females. Both are highly significant ($P < 0.005$). The partial regression coefficients of the multiple regression analysis indicate the regression of bill s/v on each environmental factor while the effect of all other factors is held constant. Thus, for example, a significant regression on latitude is independent of temperature if temperature is included as an independent variable in the analysis. The *standard* partial regression coefficients are simply based on standardized data (i.e., mean = 0; standard deviation = 1) for all variables and are free of scaling effects. Standard partial regression coefficients for mean bill s/v on eight geographic and climatic factors are given in table 1. For males there are significant partial regression coefficients on latitude, April minimum temperature, and breeding season precipitation. The coefficients show a tendency for decrease in bill s/v with an increase in latitude, an increase in s/v with an increase in minimum temperature, and a decrease in s/v with an increase in precipitation. For females there are significant partial regressions on longitude and minimum temperature. These indicate a tendency for a decrease in bill s/v with an increase in longitude and, as with males, an increase in s/v with an increase in minimum temperature.

To determine if the relationships are of bill s/v as a function of body size, locality means for wing length were introduced as an additional independent variable (table 1). Weight would be the best indicator of size, but weight data were available for only a few locality samples. Wing length appears to be a satisfactory indicator of size for comparisons among localities. For ten samples of males the correlation coefficient between mean cube root of body weight and mean wing length was 0.874 ($P < 0.01$). For seven samples of females a correlation coefficient similarly calculated was 0.915 ($P < 0.01$). The partial regression coefficients for males are again significant on latitude, minimum temperature, and precipitation. For females the only significant coefficient that remains is that with longitude. The significant coefficient on wing length indicates that as body size increases the bill s/v decreases, and that part of the geographic variation in bill s/v is a function of body size. Further, much of the variation accounted for by minimum temperature appears to be size dependent in females.

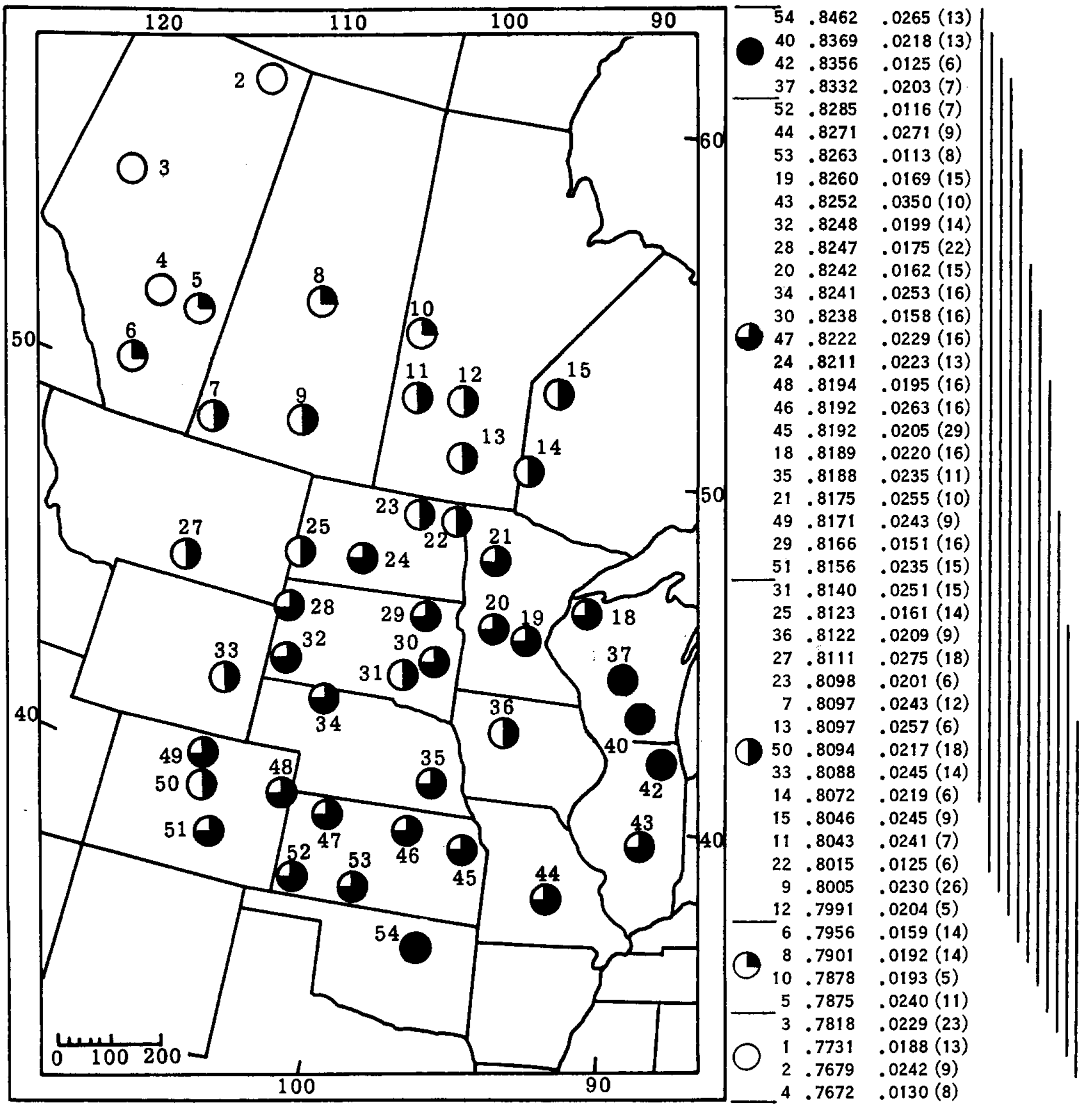

FIGURE 2. Geographic variation of bill surface/volume ratio in female central North American Red-winged Blackbirds. See legend for figure 1.

A significant partial regression may be graphed in a simple two-dimensional diagram. To do this for bill s/v on April minimum temperature for the first set of coefficients (i.e., those without wing length as an independent variable), variation in the character must be adjusted for variation that is accounted for by all factors other than minimum temperature that are included in the analysis (for procedure, see Power 1969). The adjusted character regressed on minimum temperature will then have a slope that is the corresponding partial regression coefficient. Results of this procedure are given in figure 3. There is an obvious trend of increase in bill s/v with an increase in minimum temperature. It should be noted that the slopes (b) given in the equations ($Y = a + bX$) of the diagrams are of a different magnitude than those given in table 1. The values in the figure are the partial regression coefficients and the values in the table are the *standard* partial regression coefficients (i.e., based on standardized data). The trends, of course, remain the same.

DISCUSSION

A larger surface/volume ratio generally indicates a thinner bill, while a smaller s/v generally indicates a thicker, more robust bill. It is difficult to explain in terms of natural selection the relationship between bill s/v and latitude and precipitation, as seen for males, and longitude, as seen for females. Presumably, certain aspects of the diet are highly

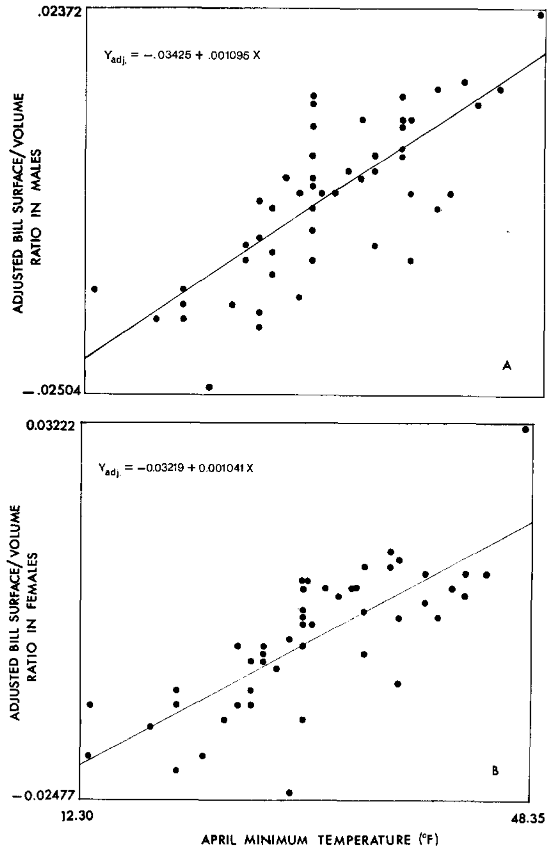

FIGURE 3. Partial regression of adjusted bill surface/volume ratio on April minimum temperature for male (A) and female (B) Red-winged Blackbirds.

correlated with longitude, latitude, and precipitation. The significant partial regression coefficients on these variables may then indicate appropriate functional adaptations of the bill relating to food habits and feeding behavior. In addition, it is not surprising to find dissimilarities between males and females in the pattern of significance of the coefficients. The lack of similarity may be related to dietary variation due to size dimorphism and behavioral differences. For example, the larger bill in males suggests that males consume larger insects and are capable of extracting and crushing larger and harder seeds. In addition, females, rather than males, have the sole responsibility of feeding the young, the diet of which is almost totally insects (Beal 1910).

The occurrence of significant, positive partial regression coefficients on April minimum temperature suggests that geographic variation in the bill is partly a result of selection by low temperatures encountered on the breeding grounds. It also suggests that low winter temperatures might also exert a selective influence. Since the underlying bone structure of the bill is highly vascular, the bill may be an avenue for a small amount of heat loss. A reduction in the surface area per unit of volume in the bill may reduce heat loss at low ambient temperatures and may thereby be of survival value in colder areas. A change in the surface/volume ratio of the bill in evolutionary response to cold ambient temperatures would seem to increase thermoregulatory efficiency by only a trivial amount. However, as Mayr (1956) points out, the existence of more important thermoregulatory devices does not eliminate any selective advantage for a less important device. Theoretically, a thin bill (with a high s/v) may also facilitate heat loss at high temperatures. However, the absence of significant negative partial regression coefficients with July maximum temperature or July wet-bulb temperature indicates that high ambient temperature is not an important factor.

It appears then that part of the geographic variation of bill size and shape in central North American Red-winged Blackbirds is a function of diet, and part may be a manifestation of Allen's ecogeographic rule, namely, that in polytypic species of endotherms, extensions of the body tend to be larger (or have a higher surface/volume ratio) in the warmer parts of the range and shorter (or have a lower surface/volume ratio) in cooler parts.

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