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Complementary Descriptive and Experimental Studies of Clinal Variation in Birds[1]

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Synopsis. In this paper I argue that the general concordance among species of birds in their clinal (gradual) patterns of geographic variation in size and color of plumage is so high that the primary regulatory process must be physiological adaptation to climate or its correlates. Size variation in the American Robin, a widespread species that shows the pattern of clinal variation typical in North American passerines, can be well predicted by measures of summer climate that include the effects of both temperature and humidity. July mean noon absolute humidity is a good predictor of size variation in the robin within the United States. Geographic variation in the color of the plumage of the robin, which involves interactions among several pigments, is independent of its size variation but in accord with color variation in other species. Both Bergmann's and Gloger's ecogeographic rules are important empirical models for which the physiological basis needs further study. To establish that functional differences are subject to natural selection requires showing that geographic differences have a genetic basis and that these differences are related to the survival and reproduction of individuals at different localities.

Laboratory and field experiments with Red-winged Blackbirds show that environmentally induced effects on development probably contribute to clines in measurements of adults in this species. Further work is needed to clarify the generality of the relationship between clinal variation and environmentally induced variation and to determine the functional significance of clines and their relationship to survival and reproduction in different localities. Environmental plasticity itself is geographically variable. It may have a genetic basis and be an object of selection.

Introduction

I will discuss the study of evolution in birds by focussing on clines, the gradual changes in character variation that occur within species across broad geographic areas. I will refer to variation in size, shape, and color of plumage. One of my objectives is to demonstrate the complementarity of descriptive and experimental research in this area, and another is to emphasize the importance of all of the different types of investigation to a full understanding of geographic differentiation.

When comparisons are among related species, it is tempting to consider each one as representing an optimal design. Descriptive studies of related species have shown repeatedly that small differences in their size and shape are correlated with differences in their behavior and life history (Bock, 1966; see James, 1982, and Leisler and Winkler, 1985, for reviews of the avian literature). When such comparisons are used as a basis for experimental studies in functional morphology (*e.g.*, by Leisler and Thaler, 1982), very small morphological differences between species can be shown to be functionally important. However, so many interdependent variables have to be balanced in the total phenotype that in no case can we say for certain that optimal design has been achieved (Schmidt-Nielson, 1984, pp. 211–212). Nor can we say with confidence that natural selection has been the dominant force that has caused morphological differences among species (Gould and Lewontin, 1979). Similarly, demonstration of functional differences among phenotypes from different populations of the same species is not necessarily evidence of adaptation.

Among the possible causes of genetic differences among populations within species are natural selection, historic or phylogenetic causes, gene flow, and genetic drift. Each of these processes leads to specific predictions about patterns of geographic variation. The importance of natural selection

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would be supported if clinal variation could be predicted by rates of reproduction and survival among genotypes at different localities. The importance of historical events would be supported if patterns of geographic variation could be predicted on the basis of biogeographical factors like the relative sizes of geographic ranges (*e.g.*, the taxon cycle of Ricklefs and Cox, 1972). If gene flow were important, there would be higher levels of geographic differentiation in species with less gene flow, that is, shorter modal distances between sites of birth or hatching and breeding. Tests of these predictions would gain strength if predictions were upheld in independent cases of many different species.

If the same pattern of geographic variation is found to occur repeatedly in many species that differ in their ecology, history, and dispersal distance, these causes of genetic differentiation become less likely as important causal agents of regional differentiation. In addition, genetic drift could be eliminated as an important causal factor because agreement among species is improbable if the mechanism is driven by chance (Coyne and Beecham, 1987).

The first step in the investigation of processes that cause geographic differentiation should be the description of similarities and differences in patterns of variation in the characters of interest over the entire geographic ranges of many species. This analysis should include description of the environmental correlates of the patterns of geographic variation in the organisms. Then experiments should be designed and conducted to detect functional differences among representative samples of the geographic variants. Differences must be defined precisely and their covariation analyzed in relation to function. This step should include study of the relationship between functional differences and the reproduction and survival of different genotypes.

After the patterns of geographic variation are known, their functional significance evaluated, and its relationship to fitness determined, we need to determine how the traits are inherited and how they are genetically coupled in their between-locality differences. Only then are we ready to study how natural selection, gene flow, and genetic drift may be contributing to the pattern of variation. This step should determine the relative contributions of genetic differences and environmental plasticity (environmentally induced variation) to geographic differentiation.

Not many species are amenable to all of the types of investigation listed above, so the single researcher is unlikely to get beyond the stage of the blind man feeling part of the elephant. The first step requires a large sampling effort and carefully planned comparisons with regional environmental variation. Size and shape should be defined precisely and studied both separately and together. Both univariate and multivariate methods are available (Mosimann and James, 1979; Darroch and Mosimann, 1985). Even if experiments can demonstrate functional differences in mortality and physiology, the determination of their genetic basis and differences in fitness can be difficult. The final studies involve population genetics and the experimental study of norms of reaction, the ways in which genotypes vary in their responses to environments. In the next sections I give examples of work in each of these areas in ornithology.

DESCRIPTIVE ANALYSIS OF CLINES IN THE SIZE AND COLOR OF BIRDS AND THEIR ENVIRONMENTAL CORRELATES

Any definition of size has to be somewhat subjective, depending upon the organism and the problem (Mosimann and James, 1979). In this paper I use the traditional statistic of wing length as an intraspecific measure. Early work demonstrated that geographic variation in the shapes of the wings and bills of birds exists (Rensch, 1929, 1934), but a bird that has a longer wing is likely to be larger in other dimensions (James, 1970). I define shape in terms of ratios and proportions. The color variation to be discussed is not the patterns of discrete variation seen in wing bars and eye rings, but rather the degree of melanism and carotenism in the body feathers (Buckley, 1987).

As bird populations have become established in their present geographic ranges, clinal differentiation in size and color has developed. Demonstration that this differentiation occurs in a fairly short time has come from study of the House Sparrow, *Passer domesticus.* In less than 50 years, beginning when it was introduced into the eastern United States from England in 1852, it developed geographic variation in size and color (Johnston and Selander, 1964; Gould and Johnston, 1972, Fig. 3; see also Baker, 1980). Today it is small along the central California coast, in Florida, and in southeastern Mexico. Increasing clines from these areas have their extremes of large size on the Mexican Plateau and in the Rocky Mountains and northern Great Plains.

Some species of birds do not exhibit geographic variation in size. In others, like the Northern Cardinal, *Cardinalis cardinalis* (Ridgway, 1901), variation is slight. In the case of the Red-winged Blackbird, *Agelaius phoeniceus,* the wing length and weight of adult males in the populations with the smallest individuals (108 mm, 57 g) are only 78% and 76% of those in the populations with the largest ones (138 mm, 75 g; James and NeSmith, 1988). Redwings in the breeding season are smallest in Florida and along the Gulf of Mexico in Central America and largest on the Mexican Plateau and the northern Great Plains of Canada (Power, 1970; James and NeSmith, 1988).

Aldrich and James (1991) have just completed an analysis of clinal variation in the size and shape of another widespread North American species, the American Robin, *Turdus migratorius.* Although the degree of its geographic differentiation is only moderate (range of median wing length in males, 125–137 mm), its pattern of size variation is similar to that of the House Sparrow and the Red-winged Blackbird. In the United States, robins, as measured by wing length or any of a number of other measures, are small in the southeastern United States and along the central California coast and large in the Rocky Mountains and the associated high plains (Fig. 1)

To what extent do patterns of geographic variation in the sizes of passerine birds agree with the pattern found in the House Sparrow, the Red-winged Blackbird, and the American Robin? To answer this question, I drew a random sample of 75 species of passerines from the 263 species listed in the classic work of Ridgway (1901, 1902, 1904, 1907) as having subspecies (substantial geographic variation) in the taxonomy of the day. Of these, 22 had at least two subspecies that occurred north of Mexico, but one was the robin. For each species for which there were data for areas where I had data for the robin, I calculated the Spearman rank correlation between its size variation and that of the robin (Table 1). The fact that 19 of 21 correlations were positive means that, among the passerines in North and Middle America (over 1,000 species), those that exhibit size variation in the United States and Canada show a striking concordance in their geographic pattern. Further support comes from study of 12 common species of birds in the eastern and central United States (James, 1970). In that study, the concordance in size variation among several species was so high that topographic features such as the Appalachian Mountains and the Mississippi Valley could be detected in patterns of variation in wing length.

What is the relationship between clinal size variation in birds and variation in the environment? If the evolution of size variation were primarily the result of natural selection due to competition for resources (character displacement, Grant, 1972, 1975; Dayan *et al.,* in press; predators competing for prey, McNab, 1971; Rosenzweig, 1966; see discussion by Ralls and Harvey, 1985), geographic variation in size should be related to variation in the sizes of the competing species and to geographic variation in the sets of species that coexist. If the dominant agent of selection were characteristics of food, or its distribution in relation to the structure of the habitat, geographic variation should be related to these factors. Species that differ in their competitors, use of resources, history, and dispersal distances would not be expected to have the same pattern of geographic variation in size. Because there is concordance among species in their pattern of size variation, we have to look for a common cause.

BERGMANN'S RULE

Trends in size variation in birds and mammals are conventionally attributed to

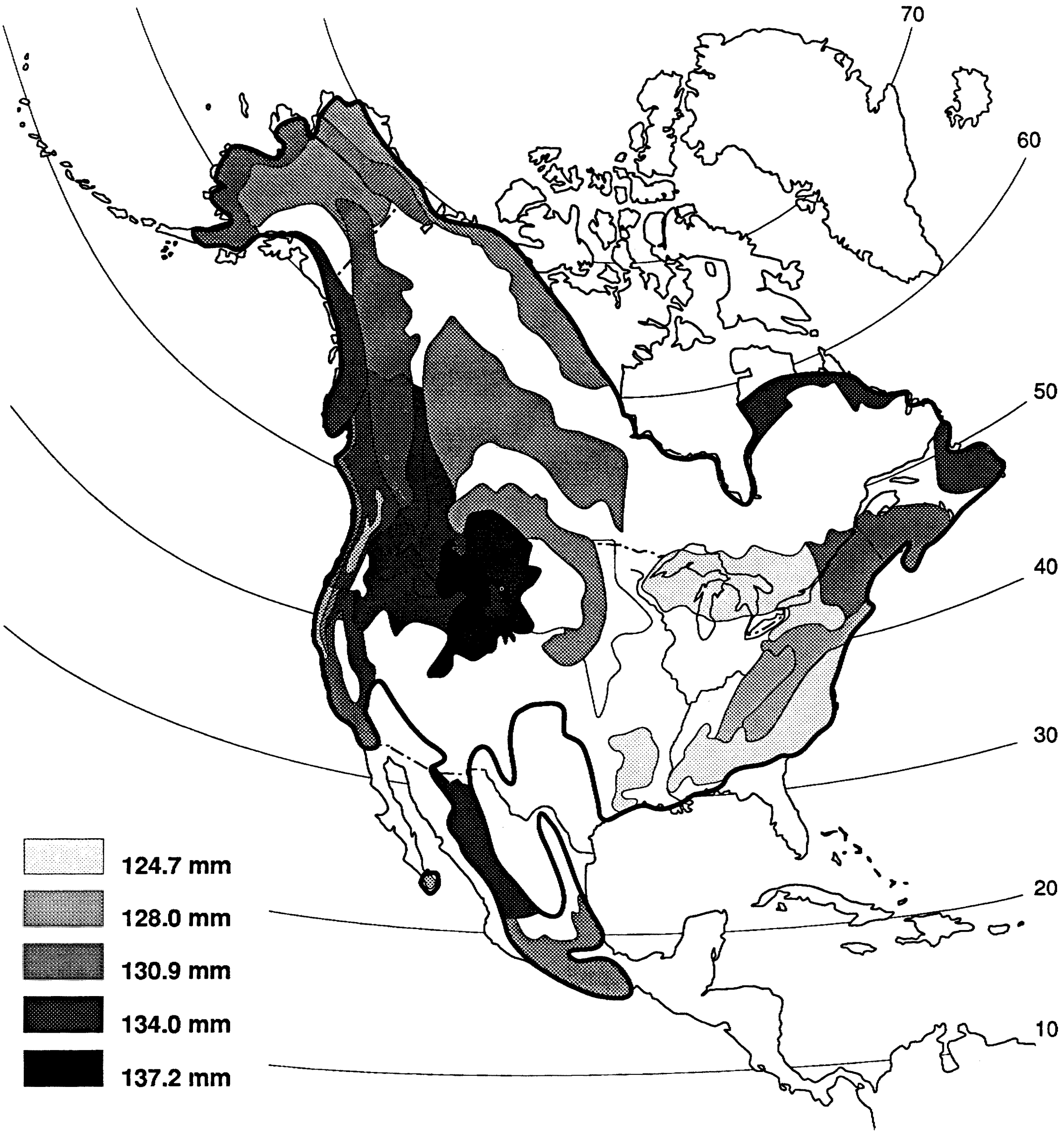

FIG. 1. The size of the American Robin, *Turdus migratorius* (median wing length of males), in the breeding season in 36 ecoregions of North and Central America (from Aldrich and James, 1991). The outline of the breeding range of the robin is given by a dark line. There are no data for the white areas.

Bergmann's (1847) rule. His thesis was that species of birds and mammals that occupy colder areas are larger than are their congeners in warmer areas. He interpreted this phenomenon as conferring a thermal advantage, given the similar design of the species being compared, because the lower surface area to volume ratio of the larger animal should help it retain heat. Mayr (1956; 1963, pp. 318–325) revised the rule to apply only to races within species. He noted the major exception that many widespread Eurasian and North American species of birds are largest, not in the coldest parts of their geographic ranges, but rather in the highlands of the semiarid tropics (Iran, Atlas Mountains, Mexican highlands). He dropped the argument about thermal adaptation, which had been challenged by physiologists (Scholander, 1955). In a recent survey of the literature on intraspecific variation in birds, Zink and Remsen (1986) used the criterion of larger size at higher latitudes and altitudes to determine the generality of Bergmann's rule. It is not clear from their paper how these variable were combined. They found many exceptions to the predictions of their model and concluded that Bergmann's rule is not very useful.

James (1970) argued that a Neo-Bergmannian model based on the negative relationship between size in birds and either wet-bulb temperature, vapor pressure, or absolute humidity (all measures sensitive to both temperature and moisture) could account for the various exceptions to Bergmann's rule that had been described by others.

Wet-bulb temperature is the dry-bulb temperature decreased by the evaporative power of the air. In climatic variation, as wet-bulb temperature increases, its variance decreases (Boyce, 1979; Murphy, 1985). Absolute humidity is the amount of moisture in a given unit of air. Although the relationship between size variation in birds and these two climatic variables in the breeding season is merely correlative, its generality is strongly suggestive of a common physiological adaptation. Absolute humidity nearly determines an animal's ability to unload heat by evaporation. Any organism having a constant design will be able to unload heat more easily if it has a higher ratio of respiratory surface to body size.

James (1970) showed that the new model was also consistent with aspects of Bergmann's original interpretations about thermal economy. Small size is usually associated with regions of warm humid climate and larger size with increasingly cooler and drier regions (Hamilton, 1961). To the extent that climate is cooler and drier at higher altitudes and latitudes, and because cool air cannot hold much moisture, clines of increasing size with increasing altitude and latitude support this interpretation. The proposed model also accounts for the fact that size tends to increase in arid regions independently of latitude and altitude and that widespread species tend to be largest in areas that are high, cool, and dry.

TABLE 1. *The extent of concordance in patterns of size variation in North American passerine birds was tested by application of a sign test to 21 Spearman rank correlations between ranks of size (average wing length of males) of subspecies with ranks of size for the American Robin in the same areas. Data for subspecies were taken from Ridgway (1901, 1902, 1904, 1907) and for the robin from Aldrich and James (1991). The species to be compared with the robin were randomly selected from the North American passerines that exhibit geographic variation. The probability of obtaining so many as 19 positive correlations out of 21 by chance is 0.00011.*

Species	No. of subspecies	Spearman Rank Correlation
1. *Eremophila alpestris*	10	.57
2. *Hirundo pyrrhonota*	2	−1.0
3. *Cyanocitta stelleri*	5	.7
4. *Corvus brachyrhynchos*	2	1.0
5. *Parus inornatus*	4	.95
6. *Cistothorus palustris*	7	.96
7. *Catharus ustulatus*	2	1.0
8. *Sialia mexicana*	2	1.0
9. *Toxostoma curvirostre*	2	1.0
10. *Vireo gilvus*	2	−1.0
11. *Dendroica petechia*	3	.88
12. *Icteria virens*	2	1.0
13. *Quiscalus quiscula*	3	.5
14. *Icterus cuculatus*	2	1.0
15. *Leucosticta arctoa*	4	1.0
16. *Carduelis tristis*	3	.5
17. *Carpodacus purpureus*	2	1.0
18. *Spizella socialis*	2	1.0
19. *Spizella pusilla*	2	1.0
20. *Zonotrichia leucophrys*	2	1.0
21. *Pipilo erythrophthalmus*	6	.33

In summary, there is a remarkably consistent pattern of intraspecific size variation in breeding populations of North American birds. If in fact it represents an adaptive response, Bergmann's original rationale of thermal economy, reinterpreted in terms of temperature and moisture rather than temperature alone, still stands as a parsimonious explanation.

Aldrich and James (1991) suggest the possibility of a further refinement. They show, for the robin within the United States, that mean noon absolute humidity in summer is more highly correlated with size variation than is wet-bulb temperature ($r_s = -0.79$, $P = 0.0004$, *versus* $r_s = -0.59$, $P = 0.008$) and also that the percent saturation of the air in summer (relative humidity) may be a better predictor of color variation than is absolute humidity. These relationships can be summarized on a chart that has dry-bulb temperature, wet-bulb temperature, and absolute humidity as axes (Fig. 2a). Differences in the summer climate among physiographic regions of the United States can be shown in this graphic space. The smallest birds are in the Eastern Deciduous Forest (highest absolute humidity) and the largest ones are in the Rocky Mountains and Northern Deserts (lowest absolute humidity) (Fig. 2b). This analysis does not include Canada and Mexico, nor does it take into the account the phenology of the breeding season. It may have to be modified when new data become available. The extremes of color variation in the robin are not in the same places as the extremes of size variation. They are the pale birds in Baja California of Mexico and the dark birds of the cool wet forests of Newfoundland.

GLOGER'S RULE

Gloger's rule is acknowledged to be a valid generalization about clines of melanism in birds and mammals. It is usually stated as the observation that they tend to have darker feathers and fur in areas of higher humidity (*e.g.,* Zink and Remsen, 1986). The general association of dark color and more humid climate applies to beetles, flies, and butterflies as well as to homeothermic vertebrates (Mayr, 1963). Gloger's original paper (Gloger, 1833), cited by Mayr (1963), was just about birds, and it discussed differences between the darkness of rusty and gray pigments in dry and wet cold areas as well as hot humid areas. An observation offered by Grinnell (1910), and one that is supported by color variation in the robin, is that birds are darker where the percent saturation of the air (relative humidity) is highest. The interactions among different melanins and among melanins and carotenoids as related to geographic variation in climatic factors are poorly known (Buckley, 1987).

Nevertheless, as with size variation, birds that have vastly different competitors, diets, history, and levels of gene flow show widespread concordance in patterns of color variation (Zink and Remsen, 1986). Again, the most likely cause is common physiological adaptation or its correlates.

EXPERIMENTS TO STUDY FUNCTIONAL DIFFERENCES AMONG GEOGRAPHIC VARIANTS AND THEIR DIFFERENCES IN FITNESS

Because it is impossible to establish causes from survey data (Sokal, 1978), other types of work are required. The first question is whether differences in size and color are related to functional differences in different environments.

With regard to size differences, comparisons among species have shown that, although insulation affects thermal balance in birds (Scholander, 1955), the cost of thermoregulation increases as body size decreases (Kendeigh, 1969) and that smaller size increases rates of evaporative water loss (Hamilton, 1961). These same relationships are likely to hold at the intraspecific level, but they need to be tested. To the extent that theoretical predictions based on dimensional considerations are upheld, the idea that intraspecific size variation in birds confers physiological advantages in terms of thermal economy will be empirically supported.

The degree of melanism in animals is known to be correlated with physiological effects (Ford, 1975) and can be related to fitness. For example, Murton *et al.* (1973) showed that, within a population, darker-plumaged rock doves (*Columba livia*) breed earlier and are favored in areas that support longer breeding seasons. Dark Arctic Skuas (*Stercorarius parasiticus*) breed at an older age and have larger territories than do lighter ones (O'Donald, 1983). Even so, the functional significance of clines of color variation within species is less clear (Hamilton, 1973, p. 105; Butcher and Rohwer, 1989). A common argument is that color is an object of selection because it confers crypticity from predators (Hamilton, 1961; Zink and Remsen, 1986; Greenberg and Droege, 1990) or by predators (Rohwer and Paulson, 1987). Butcher and Rohwer (1989) review the literature on the role of sexual selection and conspicuous coloration in communication in birds. Experiments are needed to determine the extent to which the color of the plumage in birds is functionally related to physiological advantage and to crypticity.

Concordant patterns of intraspecific size and color variation in birds, even if they are shown to have functional significance and to have a genetic basis, need not represent adaptations (Snyder and Weathers, 1975; Stearns, 1977; Smith-Gill, 1983). Both size and color may be carried as correlates of life history traits unrelated to physiology or crypticity but subject to selection (Boag and van Noordwijk, 1987).

THE POPULATION GENETICS OF CLINAL VARIATION

Even if birds did not display clines of size and color, we would expect their variation to have a genetic basis and to be inherited as Mendelian traits controlled by several genes (Buckley, 1987). There is variability in nearly all traits in any wild species, and "a genetic component of such variability is found whenever looked for within local populations and among different ones" (Wright, 1978, p. 365).

Given the fact that clinal variation in size and color is in accord with environmental variation, and not merely an effect of geographic distance, it is most likely to be maintained by natural selection. However, bird species that exhibit more geographic differentiation do not necessarily have more genetic differentiation (Corbin, 1987; Evans, 1987; Barrowclough and Johnson, 1988). Apparently, clinal aspects of genetic differentiation are not well sampled either by electrophoresis or by polymorphism of mtDNA (Ball *et al.*, 1988). Because of their high levels of gene flow relative to other vertebrate groups (Rockwell and Barrowclough, 1987), the mechanism that maintains clines in birds must be a powerful one.

The data on inheritance of traits that vary geographically are better for rodents (Bowen, 1968; Sumner, 1932) than for birds. An example of the type of complexities that arise involves the inheritance of pigments. Of the four types of melanic pigments, blackish eumelanin and brownish phaeomelanin are the most common. When eumelanin is lost, the remaining phaeomelanin produces a warm brown color; loss of phaeomelanin produces gray (Buckley, 1987).

How would we test for mechanisms maintaining clines of color and size in birds? In addition to data on variation in the characters of interest, it would require data on survival rates or reproductive success (*e.g.*, clutch size, fledging success, subsequent survival) measures of gene flow between populations, and the construction of models that could be compared and tested (Slatkin, 1985). Within-locality studies do not address the question of mechanisms that maintain between-locality differences (Boag and van Noordwijk, 1987; Price and Boag, 1987).

THE CONTRIBUTION OF ENVIRONMENTAL PLASTICITY

Laboratory experiments on the extent of environmentally induced phenotypic variation in vertebrates other than birds have shown temperature effects on the size of frogs (Blouin, 1989) and the size and shape of swine (Heath, 1983). Diet during development can affect the head shape of cichlid fishes (Meyer, 1987) and the muscle activity of centrarchids (Wainwright and Lauder, 1986). Berven *et al.* (1979) showed that, although adults of the green frog *Rana clamitans* are larger in the mountains of Virginia than they are in the lowlands of Maryland, montane tadpoles metamorphose at a smaller size than do lowland tadpoles when both are reared at cold temperatures. There is a single temperature for each population at which development of tadpoles is fastest

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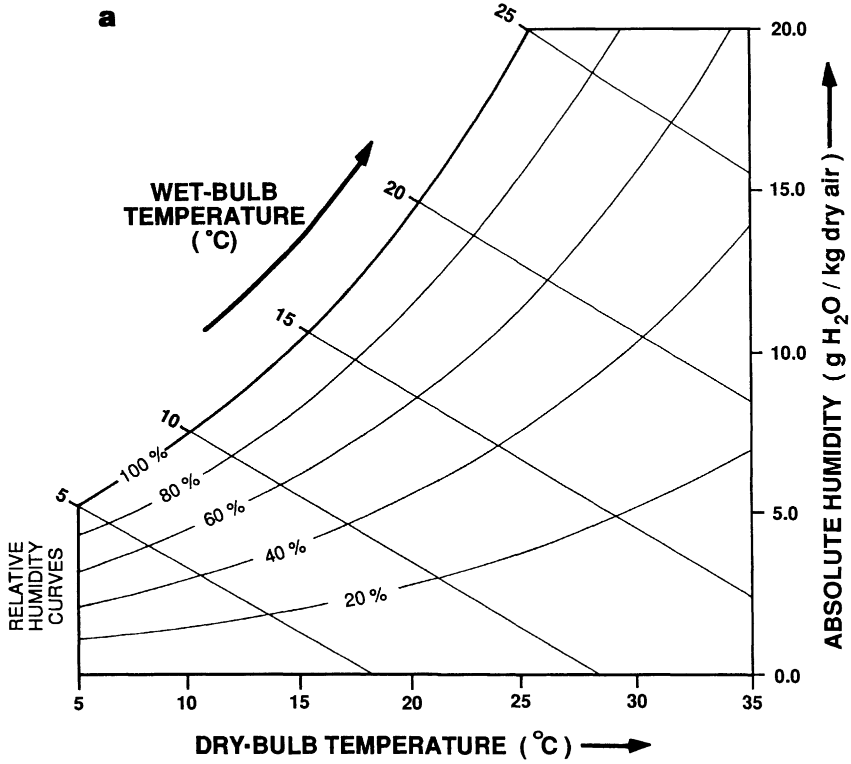
FIG. 2. The relationship between size variation in robins and variation in climate in July in the United States. a. Psychrometric chart, which shows the relationship between dry- and wet-bulb temperature and relative and absolute humidity. b. Size variation (median wing length) in male robins in five size classes of circles for 21 ecoregions located by the mean noon values of their climate variables: 9–12 Northern hardwood forest, 13–14 Eastern deciduous forests, 16 Tallgrass prairie, 18–20 Northern Great Plains, 22–25 Rocky Mountain forests, 26–27 Palouse grassland and northern desert, 32–33 Northern Pacific forests, 34 Coastal redwood forests of central California, 35 Sierra Nevada Mountains, 36 California chaparral. Ecoregions in the east have dark circles. From Aldrich and James (1991).


a
WET-BULB TEMPERATURE (°C)
5
10
15
20
25
100 %
80 %
60 %
40 %
20 %
RELATIVE HUMIDITY CURVES
0.0
5.0
10.0
15.0
20.0
ABSOLUTE HUMIDITY (g H_2O / kg dry air)
5
10
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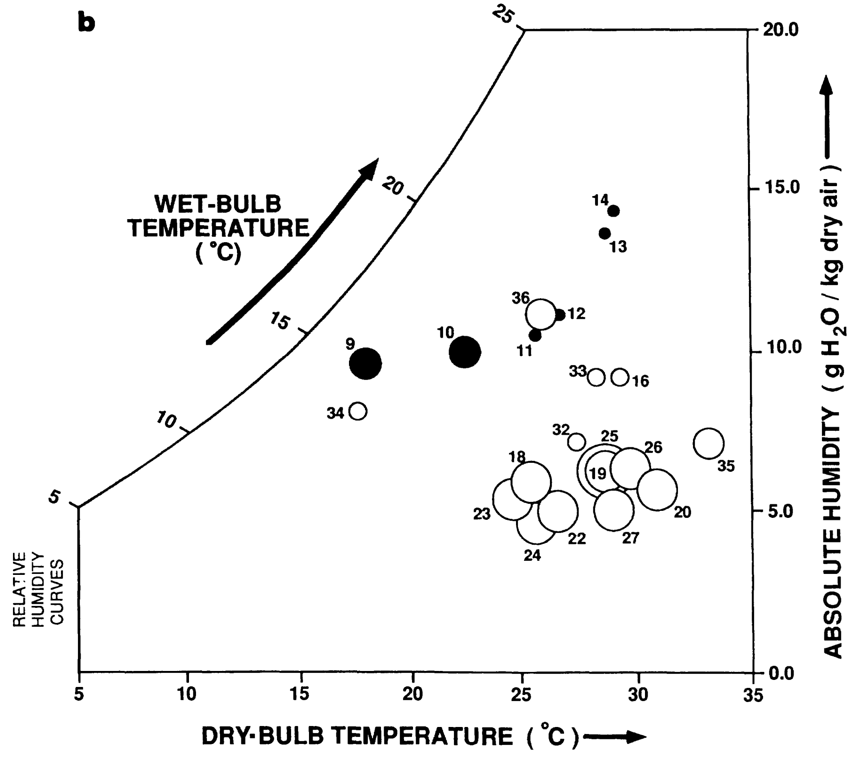
20
25
30
35
DRY-BULB TEMPERATURE (°C)


b
WET-BULB TEMPERATURE (°C)
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RELATIVE HUMIDITY CURVES
0.0
5.0
10.0
15.0
20.0
ABSOLUTE HUMIDITY (g H_2O / kg dry air)
5
10
15
20
25
30
35
DRY-BULB TEMPERATURE (°C)

and size at metamorphosis is smallest. This nonlinear developmental response of genotypes to sets of environmental conditions is probably an important general phenomenon (Levins, 1969), one that is not efficiently handled by conventional methods of analysis of variance (Lewontin, 1974; Gupta and Lewontin, 1982).

NeSmith (1985) conducted an experiment in the laboratory to discover whether the physical environment might be a direct cause of environmentally induced effects on the shape of developing Red-winged Blackbirds within a locality. She randomly assigned 4-day-old siblings from our population in Tallahassee, Florida, to one of three environmental chambers: (a) cold, (b) hot and humid, (c) hot and dry. At 20 days of age, most of the birds in the cold chamber had proportionately shorter bills than did their sibs in the other chambers (Fig. 3). This result shows that the development of the bill is susceptible to the temperature of the rearing environment. Because the effect was not seen in every sib group, it also shows that there may be genetic variation within populations in their susceptibility to environmentally induced effects.

The way to reveal the full potential of genotypes to respond to natural environments, and to see the contribution of nongenetic variation to clines, is to conduct transplant experiments in which individuals are exchanged among localities. The classic experiments of this type were conducted with altitudinal forms of the plant *Potentilla glandulosa* (Clausen *et al.,* 1940, 1948). These experiments showed that each altitudinal form of the plant developed a unique set of phenotypes in the various environments. My students and I have studied geographic variation in the size and shape of the Red-winged Blackbird in a similar fashion.

We transplanted eggs between nests in northern and southern Florida. In another experiment, eggs were transplanted from nests in Colorado to nests in Minnesota. The experimental nestlings were measured daily as they were being reared by wild foster mothers in the nonnative locality. Control birds developed from eggs kept in an incubator and then placed in foster nests in their native locality. There were statistically significant differences in the shapes of nestlings in the control and the experimental groups, indicating that some proportion of the regional differences in nestling shape was nongenetic in origin (James, 1983). Also, the degree of plasticity was not the same in all populations. When this experiment was repeated in Mexico (James and NeSmith, 1988), the bill and the toe were the measures that were most susceptible to environmental modification. The size of the nestlings, as defined by weight, was not affected by the experiment. Apparently, the genetically determined appetites of the nestlings and their efficiency at processing food determined their weight gain, even though they were being reared in a locality where native

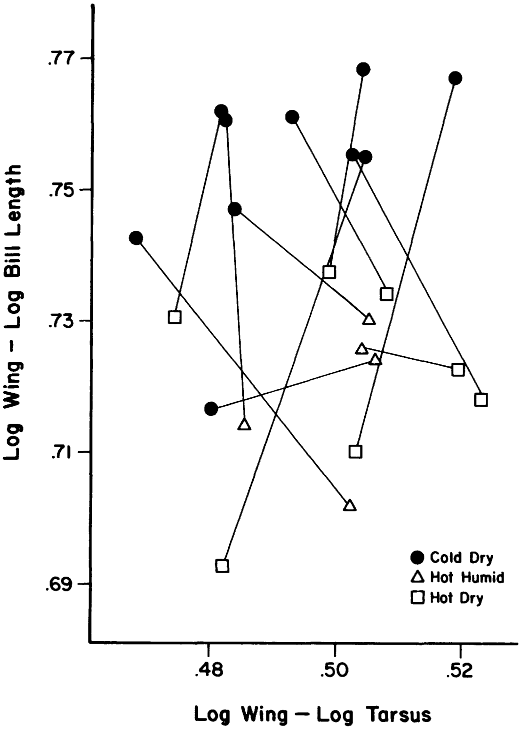

FIG. 3. The shapes of 20-day-old Red-winged Blackbirds in 11 sibling groups. Birds had been randomly assigned to environmental chambers at 4 days of age and then hand reared. Values are plotted for the two sibs that showed extreme values of log wing minus log bill length, which is equivalent to wing length divided by bill length or proportional bill length. In 9 of 11 pairs of sibs, the birds reared in the cold dry chamber had proportionately shorter bills (modified from NeSmith, 1985).

birds developed differently. We did not study the environmental plasticity of variation in juvenile plumage.

In 1987 we performed a reciprocal transplant experiment with redwing eggs between Tallahassee and Greeley, Colorado. Just before the birds were ready to fledge, at 8 or 9 days of age, we took them into captivity. By this age, the growth of the tarsus is already complete, but the wing length, bill length, and bill depth are only about half of their adult values. Among females the measurements of Florida birds reared in Colorado were smaller than were those of control birds in Florida, and Colorado birds reared in Florida were larger than were control birds in Colorado. Growth in measurements was retarded by transplantation to Colorado and accelerated by transplantation to Florida. Again, the weights of the birds were not affected by the experiment. Some differences in measurements between control and transplanted groups of birds were maintained for the next few weeks after fledging, so environmentally induced differences in dimensions of the redwing can persist into the adult phenotype.

PLASTICITY AS AN OBJECT OF SELECTION

The traditional view of the functional morphologist has been that phenotypic correlations between form and function represent adaptations that are the result of natural selection; the traditional view of the population geneticist has been that evolution primarily involves changes in gene frequency buffered, but not enhanced, by phenotypic plasticity and environmental heterogeneity. Neither view focusses sufficiently on the possibility that environmental plasticity itself may be an object of selection (Stearns, 1983; Schlichting, 1986; Sultan, 1987). We have a tendency to consider morphometric traits to be the object of evolution, just because we can measure them relatively easily. This is like looking for the lost keys under the lamppost. The more elusive ability of a single genotype to produce more than one form, physiological state, or behavior in different environments needs more attention (Bateson, 1988; West-Eberhard, 1989). In plants, phenotypic plasticity itself is known to respond to selection (Bradshaw, 1965), and adaptation can be achieved by an environmentally induced response. The point is that regional differences in environmentally induced responses may not only have a genetic basis; they may have selective value.

These ideas, although not new (Schmalhausen, 1949; Marshall and Jain, 1968; Waddington, 1975), are promising ways to expand our concept of apparent adaptation at the intraspecific level. Nongenetic behavioral (Plotkin, 1988) or developmental (Caswell, 1983) responses are likely to be the first responses of an organism to a new habitat, a new food source, or new physical conditions. Animals that make the appropriate adjustments are likely to leave more offspring. In other words genetically based geographic variation in responses to environments could affect demography, which in turn could affect the genetics of populations (Stearns, 1983; Patton and Brylski, 1987; Wcislo, 1989). Our experiments with Red-winged Blackbirds suggest that the proportions of the bird, especially of the bill, are more susceptible to developmental modifications than is size. If this result is general, then developmental responses to the physical environment may provide genetically based variation in the shape of the trophic apparatus, which is then susceptible to various other selective pressures. Color of plumage is generally regarded as not susceptible to environmental modification, but a recent study by Slagsvold and Lifjeld (1985) suggests that exceptions occur.

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