SOME SIZE GRADIENTS IN NORTH AMERICAN BIRDS

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In 1871, J. A. Allen wrote that increase in size with increase in latitude was so well known for the birds of eastern North America that any further demonstration of it was unnecessary. Hamilton, in 1958, writes that he can find little evidence for the application of Bergmann's rule (wing length and presumably body size being greater in colder climates) within New World species. Obviously these two statements need to be harmonized!

HISTORICAL NOTE

There has been a great deal of work done on correlating patterns of geographical variation in size of birds since J. A. Allen wrote. The situation has been found to be much more complex than a simple increase in size with a decrease in temperature.

Allen was writing in the infancy of the study of geographical variation. He was attempting to codify it by the use of a subspecies concept, and also to codify it by formulating rules outside the use of the subspecies concept. This was the pioneer stage.

A second stage was reached in regard to subspecies when the concept was accepted and an attempt was made to indicate all geographical variation by subspecies names. A third stage is being reached with the realization that every even moderately separated population probably differs from every other, and that to name as a subspecies every one that can be shown to be different in some way would stultify the concept and render it completely useless. Subspecies names as used by many taxonomists now indicate only some of the more obvious geographical variants.

Indeed some students of geographical variation are groping for a more useful way to indicate geographical variation than using taxonomic nomenclature. A system of numbers or letters, in effect a formula, has been suggested, and has actually been used in analyzing variation in some species. But until human mentality will use latitude 40° 42′ N; longitude 74° W for Manhattan Island, instead of saying New York City, subspecies names will not be entirely superseded by formulae.

Concepts of zoogeographical rules, which deal with the same material in part as do subspecies, are in somewhat the same situation as subspecies concepts. They have passed through the same phases: (a) being established, (b) attempts made to cram all observed variation into them, (c) the realization that environmental factors are so complex and interacting that our "rules" can hope to outline only parts of the more obvious correlations. The dissatisfaction with "rules" is part of the same dissatisfaction with subspecies, and the solutions of both are bound up together. The fact that "rules" for the character gradients are less sharply defined, especially in the allocation of single specimens, has delayed their re-evaluation. The most important step has been the generalization of Huxley in pointing out that a more general, neutral term, cline, can be used for any character gradient without attaching an interpretation to it. Certain apparent exceptions are characterized as stepped clines, and it is realized that while one cline in one character may have a certain geographical pattern, another character may show a different pattern.

CLIMATE AND GEOGRAPHY

That northern localities have colder temperatures than more southern ones is only partly true. It is true in general for the United States east of the Rocky Mountains, with average annual temperatures in southern Florida of 75° F., and Texas of 70° F., and in northern Maine of 40° F. and central North Dakota of 40° F., and a rather regular decrease from south to north in between (excepting the small area of the Alleghanies). However, while the isothermal lines in this area run more or less east and west, the case is different in the Rockies and west to the Pacific Coast. Here many of the isothermal lines have a north-south trend, and areas in both Montana on the Canadian border, and in northern New Mexico (600 miles farther from the north pole than Maine) have 40° F. as the average annual temperature.

That is, in the eastern United States (except for the Alleghanies), latitude is a good guide to temperature; in the west it is a very poor one. (U.S. Dept. of Agri., 1941, p. 703, with different facets of the climate mapped on following pages.)

Rainfall gives a somewhat similar picture, with rainfall decreasing from 60 inches on the Gulf of Mexico to 30–40 inches in the northeast United States; much of western North America and northeastern Canada have less than 20 inches. However, the picture near the Pacific Coast is complicated.

SIZE

The word size continually appears in discussing some character gradients. In the present state of the study of geographical variation in birds, the use of the word size has not the necessary precision. In more popular writing it has its place, where it may mean wing length, total length, weight, or apparent bulk. But in more technical papers it should be replaced by the measurement which is actually meant. Allen equated wing length with weight, and this assumption is still common. While it is valid in some cases, it is not always true. If accepted for samples of birds of the same species from distant areas with widely different environments, there is danger of falling into grievous error.

The available data on weights are poor, incomplete, and scattered. One is tempted to apologize when using them. But there are some data available, and it is better to use them than to depend entirely on speculation for data when discussing weight variation and its implications.

SIZE AND GEOGRAPHY

The wing length of a species may remain fairly uniform over a wide area, as is well shown by the Ruffed Grouse (*Bonasa umbellus*), which ranges from northern Georgia to Nova Scotia and west to Alaska and northern California. The species breaks up into 12 races, based mainly on color, yet the average wing length of subspecies varies only from 178 (once) and 181 to 186 mm. (Aldrich and Friedmann, 1943).

However, variation in wing length is sometimes considerable, and we look for parallel variation in different species and hope to find this correlated with environmental factors. Even if such correlations are real, we can hardly expect the same set of factors to be operative over the whole of North America, with its wide range of environments. They vary from subtropical in southern Florida, forests and prairies of the lowlands and hills of the eastern and central part of the country, arctic barrens of the north, and the deserts, scrubs and forests of the mountains and valleys of the western part of the continent. Consequently I have presented the data by geographical areas within which some consistency is evident or to be expected. While I have confined myself largely to cases where both wing length and weight are available, I have also kept in mind that there is a greater body of data on wing length alone, which may be indicative and at least points the way to further investigation.

Ideally, size should be compared with habits and the local environmental conditions of the populations, and at various times of year, as well as geography. But in this paper I am correlating size with geography, and mentioning a few of the possibly correlated environmental factors of the breeding ranges.

WING, WEIGHT, AND GEOGRAPHY

One aspect of this is one of the most widely quoted ecological rules, often stated as: Within a species, birds from higher latitudes are larger. It seems to have application, but is by no means the whole story, its applicability varying in different parts of the continent. Another aspect which may be important is the relatively lighter weight of some western populations of widespread species. As might be expected, there are exceptions to both generalizations.

Eastern North America.—Increase in wing length and weight with increase in latitude is shown by ten species as follows:

(a) nine species in eastern United States, eight of them listed in Table 1, and the United States population of the Sandhill Crane (Table 2) ; and

TABLE 1

COMPARISON OF WING LENGTHS AND WEIGHTS OF GEOGRAPHICALLY SEPARATED BIRDS

Species and Location	Wing Length (mm.)		Weight (grams)	
	♂	♀	♂	♀
Hairy Woodpecker (*Dendrocopos villosus*)				
Southeastern United States	113	112	(1) 58	(2) 50
Northeastern United States	120	119	(11) 73	(12) 63
Downy Woodpecker (*Dendrocopos pubescens*)				
Southeastern United States	88	88	(1) 23	(4) 21
Northeastern United States	94	94	(23) 26	(19) 28
Carolina Chickadee (*Parus carolinensis*)				
Southeastern United States	59	55	(5) 9	(4) 8
Northeastern United States	64	61	(13) 10	(24) 9
Tufted Titmouse (*Parus bicolor*)				
Southeastern United States	77	76	(5) 20	(2) 18
Northeastern United States	80	77	(17) 22	(12) 20
Blue Jay (*Cyanocitta cristata*)				
Southeastern United States	126	121	(4) 78	(6) 71
Northeastern United States	137	134	(10) 88	(7) 86
Red-winged Blackbird (*Agelaius phoeniceus*)				
Southeastern United States	112	92	—	(4) 35
Northeastern United States	120	98	—	(7) 43
Common Grackle (*Quiscalus quiscula*)				
Southeastern United States	133	119	(8) 108	(6) 79
Northeastern United States	144	126	(23) 120	(9) 101
Cardinal (*Richmondena cardinalis*)				
Southeastern United States	90	84	(4) 37	(1) 32
			(7) 39	(10) 38
Northeastern United States	94	90	(16) 45	(13) 42
			(30) 43	(10) 44

The data on weight are from Amadon, 1944; Hartman, 1955; and Norris and Johnston, 1958; the data on wing length from standard taxonomic sources. Averages only are given. Numbers in parentheses are numbers of specimens.

TABLE 2

COMPARISON OF WING LENGTHS AND WEIGHTS OF SPECIES NESTING ON THE ARCTIC BARRENS

Species and Location	Wing Length (mm.)		Weight (lbs.)	
Canada Goose (*Branta canadensis*)				
Mid continent	410–550		6 –18	
Arctic barrens	350–480		4 – 5	
Snow Goose (*Chen hyperborea*)				
No. Alaska to So. Baffin Island	387–450		4 – 6½	
No. Baffin Island to No. Greenland	425–485		5½–10½	
	♂	♀	♂	♀
Sandhill Crane (*Grus canadensis*)				
Florida, etc.	501	477	(3) 10	(1) 8¼
Mid continent, etc.	539	533	(7) 11⅞	(4) 9½
Arctic barrens, etc.	468	447	(11) 9 13/16	(10) 8 13/16

Data from Delacour (1954) and Walkinshaw (1949). Numbers in parentheses are numbers of specimens.

TABLE 3

COMPARISON OF WING LENGTHS AND WEIGHTS OF BIRDS FROM THREE WIDELY SEPARATED AREAS IN THE UNITED STATES

Species and Location	Wing Length (mm.)		Weight (grams)	
	♂	♀	♂	♀
Hairy Woodpecker (*Dendrocopos villosus*)				
Southeastern United States	113	112	(1) 58	(2) 50
Northeastern United States	120	119	(11) 73	(12) 63
Western United States (Nevada)	133	131	(1) 74	(3) 61
Downy Woodpecker (*Dendrocopos pubescens*)				
Southeastern United States	88	88	(1) 23	(4) 21
Northeastern United States	94	94	(23) 26	(19) 28
Western United States (Nevada)	99	100	(6) 26	(2) 25
White-breasted Nuthatch (*Sitta carolinensis*)				
Southeastern United States	87	85	—	—
Northeastern United States	90	88	(20) 20	(21) 20
Western United States (Nevada)	90	88	(5) 16	(2) 16
Loggerhead Shrike (*Lanius ludovicianus*)				
Southeastern United States	98	97	(12) 48	(6) 47
Western United States	99	98	(20) 48	(14) 50
Lower California	101	—	(7) 45	—
Rufous-sided Towhee (*Pipilo erythrophthalmus*)				
Florida	80	76	(11) 44	(4) 36
Georgia, etc.	85–87	80–83	(11) 45	(6) 44
Northeastern States	87	83	(44) 41	(10) 38
California (Hastings)	87		(13) 38	

Data on weight from Linsdale (1936), Miller (1931), Hartman (1955), Norris and Johnston (1958), and Davis (1957). Wing length is from standard taxonomic sources. Numbers in parentheses are numbers of specimens.

(b) one species, the Snow Goose, of the Arctic barrens (Table 2).

Exceptions to this are three in number, as follows:

(a) the Rufous-sided Towhee of the Eastern United States, which is longer-winged but lighter in weight in the Northeast (Table 3); and

(b) the Canada Goose and the mid-continent and northern populations of the Sandhill Crane (Table 2).

For comparison, Chapman (1912) listed 27 species which had longer-winged northern subspecies in eastern North America, and seven with shorter-winged northern subspecies.

Western North America.—Both environmental factors and geographical variation in the mountainous western part of the continent are complex.

As one might expect, the detailed studies of jays by Pitelka (1951), shrikes by Miller (1931), juncos by Miller (1941), and nuthatches by Norris (1958), indicate that latitude and size variation do not correlate well.

Eastern and Western United States.—In Table 3, I have listed five species in which populations from the western United States are relatively lighter in weight, compared with wing length, than populations from the eastern United

TABLE 4
COMPARISON OF WING LENGTHS AND WEIGHTS BY SUBSPECIES

Subspecies and Location	Wing Length (mm.)		Weight (grams)	
	♂	♀	♂	♀
Warbling Vireo				
(*Vireo gilvus swainsoni*) (Nevada)	67	66	(10) 11	(10) 11
(*V. g. gilvus*) (Kansas on migration)	73	70	(12) 15	(5) 16
Solitary Vireo				
(*Vireo solitarius cassinii*) (Nevada)	72	72	(8) 15	(6) 14
(*V. s. solitarius*) (Maine)	75	—	(5) 16	(5) 16
Scrub Jay (♂ only)				
(*Aphelocoma coerulescens*)				
Florida	115	—	(2) 78	—
12 western subspecies	118–143	—	79–125	—

Data from Linsdale (1936), Hartman (1955), Tordoff and Mengel (1956), and Pitelka (1951). Numbers in parentheses are numbers of specimens.

States. In two of these (Downy and Hairy Woodpecker), the wing length of the western birds is greater, but the weight is about the same. In two others (nuthatch and towhee), the wing is the same but the weight is less in the west; in the shrike the Lower California bird has a lighter weight.

In two species of vireos (Table 4), the wing length and the weight are both less in the two western populations.

In the Scrub Jay (Table 4) the Florida population is both shorter-winged and lighter in weight than any of the western populations.

That is, for eight species, one is a case of smaller wing and lighter weight in the east; two are cases of smaller wings and lighter weight in the west, and five are cases in which the western populations are relatively lighter-bodied.

WING LENGTH CORRELATIONS

There are other cases of greater wing length at both higher and lower latitudes in the eastern part of North America, and of birds with larger wings in the west and southwest, but I have no weight data. However, there are two other categories which I want to mention in regard to variation in wing length, as similar correlations may be found in weight variation.

Wing Length and Altitudes.—There seem to be no clearly demonstrated altitudinal subspecies in North America. The mountain subspecies, of which we have a number, are latitudinal representatives as well.

Marshall (1957: 57–58), in his studies of Arizona birds, has shown that what have been considered altitudinal subspecies there are capable of another interpretation, i.e., a latitudinal one.

This does not mean, however, that there is no evidence for increase in wing length with increase in altitude in the New World, as has been stated by some

TABLE 5

WING LENGTHS OF TWO GROUPS OF VIREOS ON CARIBBEAN ISLANDS

	VIREO OLIVACEUS Superspecies	VIREO GRISEUS Superspecies
	Wing, male only 67–82 mm.*	Wing, male only 55–66 mm.*
Bahamas	80	64
Florida Keys	80	—
Tortugas	—	63
Old Providence	—	61
Cozumel	—	62
Grand Cayman	74	—
Cuba	—	56
Jamaica	—	58
Hispaniola	83	—
Puerto Rico	—	65
St. Kitts	80	—

Data from Hamilton (1958).
*Range in averages of continental populations.

authors. Traylor (1950) has presented good evidence for this type of geographical variation in birds in the mountains of Bolivia.

Wing Length Irregularity in the West Indies.—The data Hamilton (1958) gives for two West Indian vireos, *V. olivaceus* (superspecies) and *V. griseus* (superspecies), are very interesting as indicating no obvious pattern to the variation in wing length. Not latitude, longitude, size of island, humidity, or temperature seem to fit the pattern of variation. As only one of the 11 islands concerned has both species, it seems that interspecific competition is not concerned. On the Bahamas where both occur, in each case a large but not the largest race of each species occurs.

Hamilton (1958: 334) says that *Vireo olivaceus* and *V. griseus* show the tendency for insular populations to have "greater wing length and relatively longer bill length (see Murphy, 1938)."

A survey of the tabular material on wing length, Table 5, does not support this aspect of the statement, nor does Murphy (1938) discuss wing length, in the paper cited.

Rather, these island vireos seem to be cases of the irregularity which is conspicuous in island populations. Similar irregular variation may account for some of the variation in series of continental populations.

CHARACTER GRADIENTS

Characters sometimes change gradually, giving a cline. The measurements for the Hairy Woodpecker for the eastern United States (Table 6) is a good illustration of a character gradient or cline.

But the term cline, and especially stepped cline, is often used when the

TABLE 6

CLINE IN WING LENGTH FROM NORTH TO SOUTH

Species and Location	Wing Length (mm.)	
	♂	♀
Hairy Woodpecker (*Dendrocopos villosus*)		
Maine and New Brunswick	125–129	123
New York and Pennsylvania	119–122	116–120
Maryland and District of Columbia	119	—
Virginia	117–118	118
North Carolina	119	115
South Carolina	116	113
Georgia	113	113
Florida	113	111

Data from Ridgway (1914:202–203).

characters are uniform over a considerable area, then suddenly change to another. These cause one to wonder if some other than environmental factors may not be at work. The towhees (Table 3) are a case in point, in which the wing from New England to Georgia averages about 87 mm.; in Florida it averages 80 mm. (males only), and it is especially interesting that the change in weight does not occur in the same place as does that in wing length.

Another case is that of the Carolina Wren in which the wing length of the male averages 62 mm. in the peninsula of Florida, but only 60 mm. from northern Florida to New England (Lowery, 1940). In such cases, the question arises if the terms character gradient or cline are properly used for the whole geographical range, when such a small proportion of it actually shows a cline.

SPECIES SHOWING TWO TYPES OF VARIATION

I have wing and weight data on three species which, depending on the area the samples come from, show two types of variation. The Downy and Hairy Woodpeckers show increase in wing length and weight from south to north in eastern North America, but are relatively lighter in weight in the western part of the country (Table 3). Two types of change with latitude are shown by the Sandhill Crane. The southern birds (Florida) are medium in wing and weight; the mid-continent birds are large (increase in size with latitude); the northern birds are smallest (decrease in size with latitude), see Table 2.

DISCUSSION OF CORRELATIONS

The above correlations are based on facts. That the geographical factors are the direct, causal factors is improbable. Rather, the causal factors are probably correlated with the geography.

The following correlations are to be considered here, though others, such as interspecific competition and migration, could play a part:

Temperature.—The classical increase in size, both wing length and weight, in colder parts of the species range, is evident in eastern North America; 10 cases of positive correlation; three cases of exceptions.

Aridity Effect.—This, as Hamilton (1958: 320–327) proposed it, has no factual basis whatever. On the basis of longer wing length of populations from the western part of North America, he postulated a greater body weight, and then discussed the physiology of greater weight in more arid regions. But, he had no weights. Outside the vireos, he presented wing lengths for only four species: Downy Woodpecker, White-breasted Nuthatch, Loggerhead Shrike, and Cardinal. Of these, I have presented weights as well as wing lengths for the first three, and the western birds are not heavier than eastern populations, though their wing lengths are indeed longer in two cases, and all three are relatively lighter in weight.

Habitat Effect.—Both Miller (1931: 102–105) and Pitelka (1951: 366) have suggested that where the interstices of the habitat are smaller, one would expect birds to fly less and to be smaller-winged, with heavier bodies; openness of habitat may correlate with more space in which the bird may fly, and greater need for flight, and result in birds being longer-winged, or relatively longer-winged. I have pointed out elsewhere (Rand, 1961) that between species, the birds that fly most are relatively longer-winged and lighter in weight. In the present paper I have given data on several species in which this may apply to western populations.

Randomness of Variation (Lack of correlations).—In the complexity of adaptations, one would expect some birds to adapt in other ways than by size. They have to be some size, and they may exist in spite of their precise size.

SUMMARY AND CONCLUSIONS

The complexity of variations and the factors that bring them about are so great that we are fortunate in being able to see partial correlations over limited areas, and being able to use subspecies names and ecological rules to codify part of our knowledge.

The only effect for which there is evidence enough to be convincing is that decreasing temperature correlates with larger wing and weight (this is in accord with Bergmann's rule), and this only in eastern North America.

Suggestive is the evidence that relatively longer-winged (or lighter-bodied) western representatives of birds may occur in the more open habitats there (which last may be correlated with aridity), where more flying is involved in the daily life of the bird.

This points up the fact that wing length is not always an indicator of body weight within a species, especially when birds from quite different environmental conditions are compared.

More than one factor could be in operation at one time, working in different directions, canceling or modifying each other.

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NEW LIFE MEMBER

Jayson A. Walker, of Waterloo, New York, has been an active member of the Society since 1949. He is especially interested in the banding and photographing of birds, but is also interested in the study of flowering plants, reptiles, and amphibians. Mr. Walker is also a member of the AOU, Federation of New York State Bird Clubs, and the Eastern Bird Banding Association. We welcome him as a new life member of the Wilson Ornithological Society.