GEOGRAPHIC VARIATION OF THE RED-COCKADED WOODPECKER

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The Red-cockaded Woodpecker (*Picoides borealis*) is an endemic resident of mature pine and pine-oak forest habitats in the southeastern United States. Various aspects of its geographic variation, sexual dimorphism, and ecology have been discussed by Davis (1965), Ligon (1968), Short (1970), and Morse (1972). Populations of the species have declined in recent years because of habitat disturbance and it is considered endangered (Jackson 1971a, U.S.D.I. 1973). As a result there has been discussion of reintroductions in areas where the species has been extirpated but where seemingly suitable habitat has been reestablished (Jackson et al. 1976); an understanding of the Red-cockaded Woodpecker's geographic variation is thus particularly desirable at present.

Long considered monotypic taxonomically, the species was divided into two subspecies when Wetmore (1941) separated the somewhat smaller birds of southern peninsular Florida under the name of *P. b. hylonomus*. Mengel (1965:308) noted that the Red-cockaded Woodpeckers of the Cumberland Plateau of Kentucky averaged larger than those of much of the Coastal Plain and Piedmont Plateau by about the same amount that *P. b. hylonomus* was smaller, and later measured most (more than 500) of the specimens in North American museum collections. An analysis of these measurements follows.

MATERIALS AND METHODS

After eliminating obviously worn or damaged individuals, we examined 266 adult males and 164 females collected throughout the range of the species from November through April (most worn and badly soiled specimens were taken May–September and many early autumn specimens are in molt). No geographic variation in color or pattern was perceptible to us. Culmen, wing, and tail length of each specimen were measured by Mengel to the nearest millimeter using dividers and a rule. Measurements were taken as follows:

- culmen length: from the base, or the angle of the frontonasal hinge, to the tip of the rhamphotheca.
- wing length: the chord of the folded wing from the wrist to the tip of the longest primary.
- tail length: from the notch between the points of emergence of the central rectrices to the tip of the longest rectrix.

In analyzing these data we grouped the specimens into 24 samples (Table 1), of which 18 consist of specimens collected within circles of 130 km in diameter. Few specimens exist from the western parts of the range, however, so the two samples from west of the Mississippi River include much larger areas.

We then did analyses of variance, sum of squares simultaneous test procedures (SS-STP), and three linear regression analyses on the sets of data for each character. These calculations were carried out on a GE 625 computer at the University of Kansas Computation Center using UNIVAR, a univariate statistical program (Power 1970). Independent variables used in the regression analyses include mean January temperature, mean July temperature, and mean annual precipitation. Environmental data were taken from U.S.D.A. (1941).

The geographic center of the set of specimen localities for each of the 24 samples was used as a data point for plotting the isophenes of characters. These isolines of variation were generated by SYMAP, a computer mapping program which generates isolines by a flowing vector system and interpolates into areas lacking data (Lieth and Radford 1971).

RESULTS

Basic statistics for the three characters for each locality are presented in Table 2. While there is significant variation among the samples in culmen length within sexes ($P \leq 0.05$), the variation is slight and appears geographically random. Comparison of the variance of the culmen lengths of all males with that of all females indicates that this character is significantly more variable in females ($P \leq 0.01$). The mean culmen length of all males is approximately 0.8 mm longer than that of all females, a difference that is highly significant by any of several conservative tests ($P \leq 0.001$ by Student's t-test, 428 df, $t = 8.48$). There were no significant regressions of any of the climatic variables with variation in culmen length.

Analyses of variance of wing and tail length of males versus females indicated no significant sexual dimorphism in either of these characters, so the sexes were pooled in subsequent tests.

Geographic variation in both characters is highly significant ($P \leq 0.001$) and is approximately parallel. In general, variation is clinal from northwest to southeast (Fig. 1) with the largest birds occurring in Kentucky and the smallest in Florida. Smaller birds occur farther north along the Atlantic coast than else-

TABLE 1. Red-cockaded Woodpecker specimen sample localities.

Locality Letter	Locality
A	SE Oklahoma, central and northern Arkansas, south central Missouri
B	SE Texas, west and northern Louisiana
C	65 km radius of Picayune, Pearl River Co., Ms.
D	65 km radius of McLellen, Santa Rosa Co., Fla.
E	65 km radius of Mountain Hill, Harris Co., Ga. and 65 km radius of Montgomery, Montgomery Co., Ala.
F	65 km radius of Amsterdam, Decatur Co., Ga.; 65 km radius of Port St. Joe, Gulf Co., Fla.; and 65 km radius of Mystic, Irwin Co., Ga.
G	65 km radius of Rockwood, Roane Co., Tn.
H	65 km radius of Somerset, Pulaski Co., Ky.
I	65 km radius of Stapleton, Glasscock Co., Ga.
J	65 km radius of Monticello, Fairfield Co., S.C. and 65 km radius of McColl, Marlboro Co., S.C.
K	65 km radius of Bolivia, Brunswick Co., N. C. and 65 km radius of Askin, Craven Co., N.C.
L	65 km radius of Cross, Berkeley Co., S.C.
M	65 km radius of Richmond Hill, Chatham Co., Ga.
N	65 km radius of Hillard, Nassau Co., Fla.
O	65 km radius of Obrien, Suwannee Co., Fla.
P	65 km radius of Bunnell, Flagler Co., Fla.
Q	65 km radius of 16 km SW of Cedar Key, Levy Co., Fla.
R	65 km radius of Cape Kennedy, Brevard Co., Fla.
S	65 km radius of Clermont, Lake Co., Fla.
T	65 km radius of Indian Rocks Beach, Pinellas Co., Fla.
U	65 km radius of Sebring, Highlands Co., Fla.
V	65 km radius of Jupiter, Palm Beach Co., Fla.
W	65 km radius of Bonita Springs, Lee Co., Fla.
X	65 km radius of Miami, Dade Co., Fla.

where. Birds in southern Alabama, southwestern Georgia, and the Florida panhandle appear to have longer wings than those from adjacent areas. Non-significant subsets of these localities as determined by SS-STP are depicted for wing length in Figure 2.

A significant negative regression of variation exists in both wing and tail length with mean January and mean July temperature. The strongest regression is that of wing length with mean January temperature (Fig. 3).

DISCUSSION

SEXUAL VARIATION, CULMEN LENGTH

Previous literature on this point is somewhat contradictory. Ligon reported (1968:207–208) that a difference of 0.42 mm in mean culmen lengths of 29 males and 20 females (S.D. 0.69 and 0.57 respectively) was not significant. In fact, a Student's t-test shows these values to be significant ($.02 < P < .05$, df = 47). This error resulted from an oversight on Ligon's part (J.D. Ligon, pers. comm.). (His males also displayed greater variability than females, but see below.) Morse (1972:409) found no differences, while Davis (1965:567), relying on measurements of 21 males and 17 females given by Ridgway (1914:270) noted that bills of males averaged 5% longer than those of females, the least dimorphism, incidentally, of eight species of *Picoides* discussed. As noted, our sample of 266 males and 164 females from throughout the range shows the culmen of males to average 22.6 ± .05 (S.E.) and that of females 21.8 mm ± .08, the difference being highly significant ($P < .001$), while the variability of males is very significantly *less* ($P < .001$, coefficient of variation 3.9 ± .17 compared with 4.4 ± .24).

SEXUAL VARIATION IN LENGTH OF WING AND TAIL

As with other workers on this species, we found no significant differences in the wing length of males and females.

Davis (1965:565), relying on measurements of Ridgway's (1914:270), reported no sexual difference in tail length, but Short (1970:87) reported a significant difference ($P = 0.01$, Student's t-test) in tail length between samples of 38 females and 47 males collected December–March from southern Florida and between samples of 32 females and 31 males from north of Florida. Respective measurements reported were: 75.68 versus 74.14 (difference, 1.54) and 77.43 versus 75.99 (difference, 1.44).

As indicated above (Table 2) our larger series, independently measured (and presumably including most of the same specimens) fails to show such a difference, which led us to a second check of part of our sample. In 70 females (mean, 73.27 mm) and 102 males (73.36) taken November through April in southern and central peninsular Florida, no significant difference, again, was found, nor did elimination of November- and April-taken specimens affect the results. (We discovered, however, that omission or duplication of one measurement from either series without appropriate adjustment of N was sufficient to generate a "significant" difference in this statistic.)

For the present, it would seem best not to base biological speculations (as did Short 1970 and Jackson 1971b) upon any postulated sexual difference in tail length in this species.

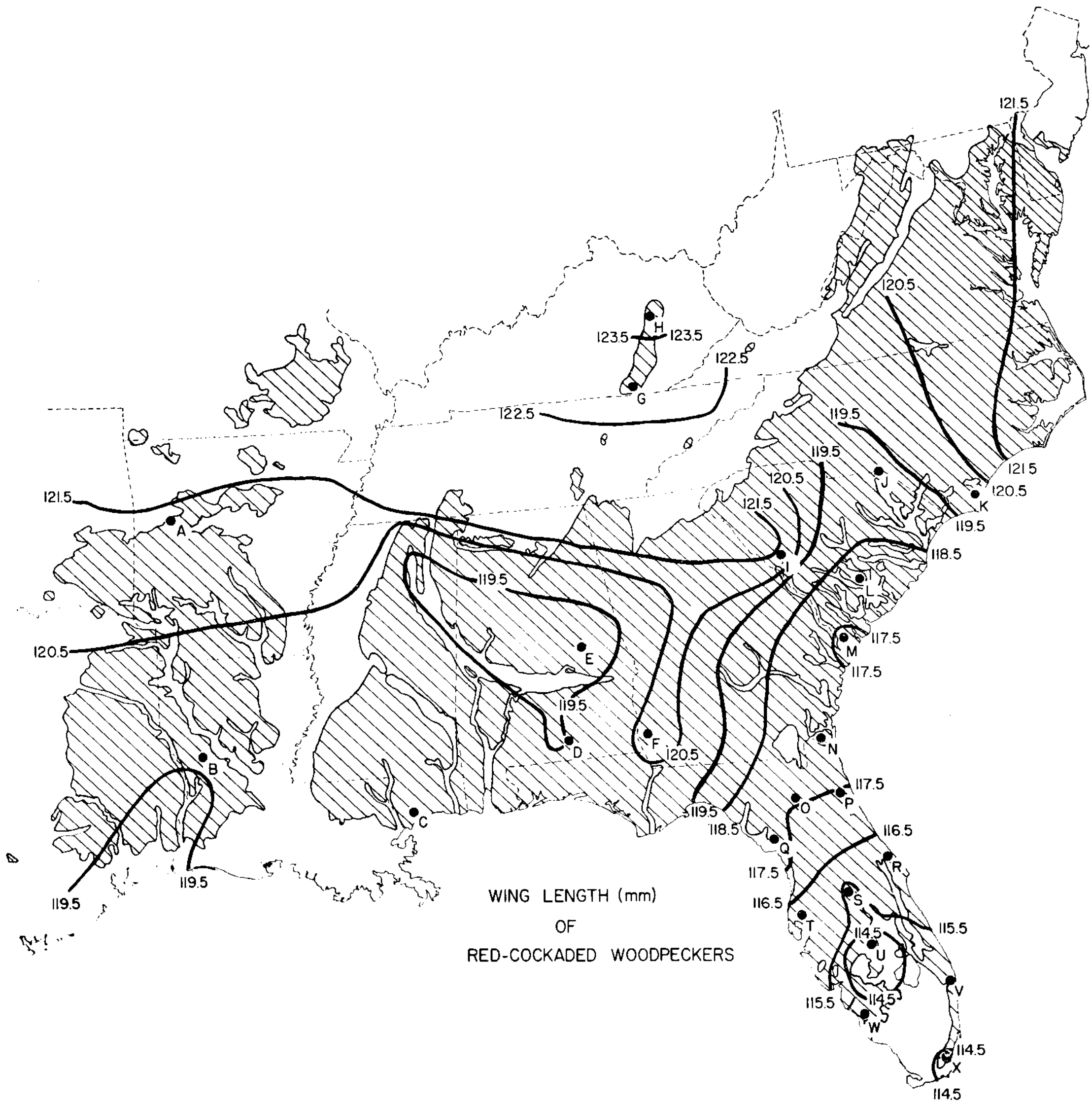

FIGURE 1. Isolines of variation in wing length of Red-cockaded Woodpeckers produced by SYMAP and superimposed on a potential range map of the species. The hatched area includes regions of potential suitable habitat for Red-cockaded Woodpeckers (pine and pine-hardwood forest) indicated on Kuchler's (1964) vegetation map. See text for discussion of possible errors in the isolines shown.

Over-all, sexual dimorphism in the Red-cockaded Woodpecker is the least found among several comparable woodpeckers (Davis 1965:567), a matter of considerable interest but beyond the scope of this paper.

GEOGRAPHIC VARIATION

Except for sexual variation in length of bill, and intrapopulation variation in size (which is evidently independent of sex), variation in this species is mainly or entirely geographic and the principal variable is size.

Overall size in birds is probably best expressed by fat-free body weight taken at a standard time in the daily activity cycle, but this is a difficult measurement to obtain for wild birds in quantities appropriate for large-scale geographical studies. Ornithologists generally have accepted wing length as a reasonable index of size. Other measurements, such as length of tail or tarsus, are comparable indicators of size in normally-proportioned species, but are usually more variable, hence less useful in comparisons between populations (excellent summary in James 1970).

Weights obtained from wild Red-cockaded Woodpeckers are probably fairly accurate indicators of absolute size, since this species, in common with non-migratory woodpeckers

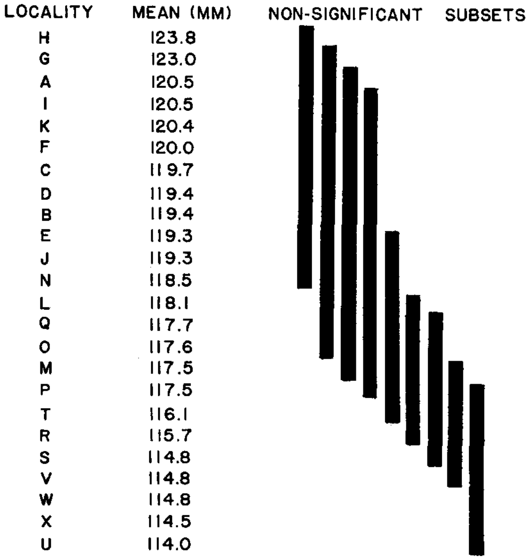

FIGURE 2. Subsets of specimen localities which do not differ significantly from one another; wing length.

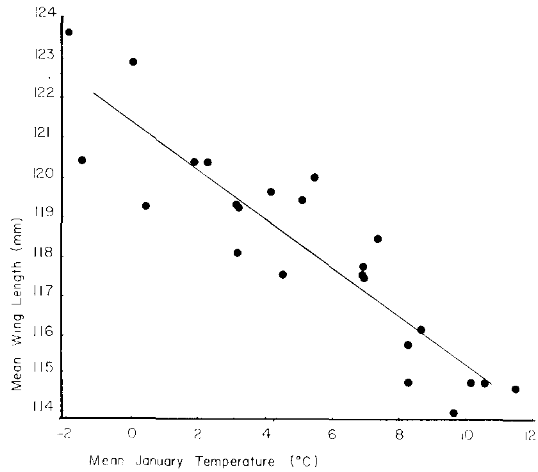

FIGURE 3. Regression of mean January temperature on mean wing length of Red-cockaded Woodpeckers (temperature data from U.S.D.A. 1941). The slope of the regression line differs very significantly from zero ($P < .0001$). The regression analysis was done using temperatures in degrees Fahrenheit; using this scale the equation for the line drawn is $Y = 121.32 - .7X$.

generally, does not tend to accumulate much fat. Records of weight, however, are scarce; all immediately available to us, for birds not clearly subadult, are: a mean of 43.7 g for nine specimens from Florida given by Ligon (1968:207), a mean of 49.9 g for eight birds from Kentucky (Mengel 1965:308), and a mean of 49.0 g for 14 birds banded by Jackson in east-central Mississippi (Noxubee National Wildlife Refuge). If from our data we take the mean wing length of central Florida birds as 117.5 mm (Gainesville area) and that of Kentucky birds as 122.9 mm, the predicted weight of the latter, assuming proportionality,

TABLE 2. Culmen, tail, and wing length variation in the Red-cockaded Woodpecker.

Locality* letter	Sample Size Male	Sample Size Female	Culmen Male Mean SE	Culmen Female Mean SE	Tail Male and Female Mean SE	Wing Male and Female Mean SE
A	7	3	22.9 ± .40	21.7 ± .33	74.5 ± .99	120.5 ± .89
B	7	4	22.4 ± .30	21.5 ± .65	73.6 ± .59	119.4 ± .41
C	5	2	22.4 ± .24	21.5 ± .50	76.3 ± .12	119.7 ± .57
D	12	12	22.3 ± .19	22.0 ± .25	73.6 ± .50	119.4 ± .35
E	4	0	22.5 ± .10	— —	75.0 ± .23	119.3 ± .18
F	4	4	23.0 ± .41	21.7 ± .88	76.4 ± .16	120.0 ± .12
G	2	0	23.5 ± .50	— —	76.0 ± .10	123.0 ± .20
H	2	4	23.0 ± .00	22.8 ± .63	79.8 ± .65	123.8 ± .75
I	2	0	23.0 ± .00	— —	77.0 ± .10	120.5 ± .50
J	5	3	21.8 ± .49	21.3 ± .67	76.8 ± .13	119.3 ± .73
K	5	5	22.8 ± .37	22.0 ± .45	77.9 ± .80	120.4 ± .64
L	11	12	22.0 ± .19	21.6 ± .29	72.8 ± .70	118.1 ± .52
M	21	13	22.4 ± .23	20.6 ± .24	73.9 ± .56	117.5 ± .35
N	30	13	22.3 ± .16	21.6 ± .29	73.9 ± .45	118.5 ± .33
O	9	7	22.8 ± .46	22.4 ± .20	75.4 ± .93	117.6 ± .67
P	22	13	22.5 ± .26	21.5 ± .29	74.3 ± .49	117.5 ± .40
Q	8	2	21.9 ± .30	20.5 ± .50	75.3 ± .50	117.7 ± .67
R	17	9	22.8 ± .24	21.6 ± .41	71.9 ± .62	115.7 ± .53
S	22	8	23.0 ± .25	22.8 ± .16	74.0 ± .75	114.8 ± .52
T	32	18	22.7 ± .14	22.2 ± .32	74.6 ± .36	116.1 ± .30
U	5	3	23.6 ± .40	22.3 ± .67	71.6 ± .61	114.0 ± .53
V	14	14	22.4 ± .20	22.0 ± .33	72.0 ± .52	114.8 ± .52
W	12	8	22.3 ± .33	21.8 ± .37	72.0 ± .69	114.8 ± .57
X	8	7	22.8 ± .31	23.0 ± .38	74.3 ± .64	114.5 ± .46

* Localities are those included in Table 1.

is 50.0 g ($117.5^3/122.9^3 = 43.7/X$, X = 50.0 g), a very accurate fit indeed to the recorded weight of 49.9 g. Note that, for Kentucky birds, in the coldest part of the range, a linear increase of 4.4 percent in wing dimensions predicts a cubic (weight) increase of 13.5 percent over Florida birds.

Using the same statistical approach, we would predict the mean wing length of Red-cockaded Woodpeckers from east-central Mississippi to be 122.0 mm. Jackson's wing length measurements (on live birds using a metric rule with a stop at the end) averaged 121.9 mm. The geometric analysis done on the computer by SYMAP predicted a mean wing length of about 119.5 (Fig. 1) for this population. The distribution of sample localities indicates that this prediction was based on interpolation between data from eastern Alabama and western Arkansas. Two conclusions can be drawn from this comparison of new data with the predictions of SYMAP: (1) larger birds extend farther south in Mississippi than indicated in Figure 1; and, (2) caution must be exercised in interpreting contours between widely spaced sample localities.

The geographic variation in size based on wing length is almost perfectly clinal and shows that larger birds tend to occur farther south in the elevated region of the Appalachian plateaus, and also farther south in the westerly portions of the range (where over-all climate for any temperature level is somewhat drier). This pattern repeats one that is frequent among birds of the area concerned and that has been demonstrated and expressed in the same way for a number of species by James (1970). This author gave a superior review of the possible relationships of these phenomena to Bergmann's rule (which in essence states that within a species the average size of individuals in cooler or drier regions will tend to be greater than that of those in warmer or more humid regions). Indications are that physiological responses to climate, especially, but not solely temperature variables, are indeed expressed in size. It is not surprising, therefore, that the most significant regression on climatic factors found in the present study is that of wing length on mean January temperatures (dry bulb).

Finally, since bill length, as noted, does not vary geographically (albeit there is some sexual and random interpopulation variation), it follows that larger northern birds have on the average relatively shorter bills than smaller southern birds. This may be seen from informal examination of our data, wherein the bill length of 185 birds from south Florida averages 22.55 mm against exactly 22.55 for 33 specimens from the Cumberland and Ozark uplands in the northernmost part of the range. In other words, bill length varies allometrically with geography, which may be seen as apparent confirmation of Allen's ecogeographic rule (namely that within a species the populations of cooler regions will tend to have relatively smaller appendages).

SYSTEMATIC CONSIDERATIONS

Various authors (e.g., Jackson 1970; for an excellent summary see James 1970) have pointed out difficulties created by the use of Linnaean trinomial names (i.e., recognition of subspecies) to express the geographic variation of clinally varying, continental populations. We concur that the difficulties are significant and the results distinctly suboptimal. Nevertheless, in the continued absence of a widely acceptable and convenient alternative, the system is still in general use to indicate geographical variability (e.g., American Ornithologists' Union Check-List, 1957), and it does convey some information.

Todd (1946:313) has already questioned the validity of the southern subspecies *Picoides borealis hylonomus* Wetmore. The total size variation of the Red-cockaded Woodpecker (±114–123 mm wing length), however, is comparable to that length resulting in subspecific separation of numerous species (e.g., Blue Jay, *Cyanocitta cristata*; Hairy Woodpecker, *Picoides villosus*; Downy Woodpecker, *P. pubescens*). In all of these cases only widely separated populations differ sufficiently to qualify for subspecific recognition by the comparatively rigorous standards urged by some authors (e.g., Amadon 1949, Rand and Traylor 1950), for instance, that one standard deviation above the mean of the smaller should fail to overlap one standard deviation below that of the larger (84 percent of one population separable from 84 percent of the other). This condition is here met only if one compares birds from the Cumberland and Ozark plateaus with samples from peninsular Florida. Consideration of James' (1970) Figures 2, 6, and 9 shows that approximately the same applies to the other species just mentioned.

In any case, if two subspecies of *P. borealis* are to be recognized, then the line between them should not be drawn through peninsular Florida but logically should conform with the isophene of 118.5 mm wing length (Fig. 1), including peninsular Florida (but not the Florida "panhandle") and ranging north along the Atlantic Coastal Plain (but not into the interior, i.e., the Piedmont Plateau) through South Carolina, in short, midway between the extremes of the cline.

This brings into consideration the type locality and the nomenclature. *Picus borealis* Vieillot (1807) is based on a figure and textual description of the species (no type specimen is extant), said to occur "dans le nord des Etats-Unis" (translated by the A.O.U. Check-List Committee 1957:329 to "=Southern States"). As first reviser, Wetmore (1941) restricted the type locality to Mt. Pleasant (near Charleston), South Carolina. Adjusting the subspecific boundaries as we suggest, therefore, would render *hylonomus* Wetmore a synonym of *borealis* (Vieillot) and leave the northern subspecies without a name, a circumstance neither desirable nor anticipated by the first reviser.

A sensible way out of the dilemma violates no hard rule of nomenclature. Since Vieillot's movements in the United States are unknown in any detail (Allen 1951:552), Wetmore's (1941) undefended restriction was entirely arbitrary. Given recognition of two subspecies, in the interest of stability we therefore propose that his restriction be set aside and that the type locality of *Picus borealis* Vieillot be restricted to coastal Virginia near Norfolk, well to the north of the range of *hylonomus* by any interpretation. It is quite possible that Vieillot obtained one or more specimens from that far north on the Coastal Plain, which would make more comprehensible "dans le nord des Etats-Unis."

In conclusion, increasing fragmentation of this species by the loss of intermediate populations to habitat destruction may eventually produce the artifactual situation where nearest neighboring populations do differ significantly from one another and in a manner more appropriate to subspecific recognition. To maintain the integrity of the species, however, management plans for the Red-cockaded Woodpecker should include preservation of the species in all possible parts of its range rather than in selected "showcase" populations (Jackson 1976).

SUMMARY

The Red-cockaded Woodpecker varies clinally, with longer-winged and longer-tailed birds occurring away from the coasts and farther north than shorter-winged and shorter-tailed birds, in apparent confirmation of Bergmann's ecogeographic rule. Variation in culmen length shows no geographic pattern per se but culmens are relatively shorter in the interior and in the north. There appears to be no sexual dimorphism in wing or tail length but males on the average have a slightly longer culmen than do females. There is a significant negative regression of both wing and tail length with mean January and mean July temperature, stronger in the first case. Geographic variation in the species, like that of other birds in the same region, is not well represented by description of subspecies, although two have been recognized in the present case. In case of continued recognition, the boundary of the southern one should be extended north along the Atlantic Coastal Plain through South Carolina, including all of Florida except the "panhandle."

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