

The Population Phenetics and Behavioral Ecology of  
the Florida Scrub Lizard (Sceloporus woodi)

By

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THE POPULATION PHENETICS AND BEHAVIORAL ECOLOGY OF  
THE FLORIDA SCRUB LIZARD (SCELOPORUS WOODI)

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Sceloporus woodi does not occupy all available sand-pine scrub habitat in Florida but is found only on the Lake Wales and northern Bartow Ridges, in the Ocala National Forest region, along the central and southern Atlantic Coast, and on the southwestern Gulf Coast. The poor dispersal is related to habitat restriction. Canonical analysis clustered S. woodi populations according to phenetic affinity more effectively than did principal components analysis. The clusters correspond to the geographic regions above except that Lake Wales Ridge woodi are differentiated into northern and southern entities. Differentiation of populations within the geographic regions is inversely related to the opportunity for gene flow. Phenetic and paleogeographic considerations suggest an origin of S. woodi in the Pliocene on the Lake Wales Ridge from a southwestern progenitor and dispersal northward in the early Pleistocene; dispersal occurred in the late Pleistocene from the Ocala National Forest region to the Atlantic Coast and from the Lake Wales Ridge to the Gulf Coast.

Sceloporus woodi and S. u. undulatus have different foraging tactics for exploitation of similar food resources. These differences are necessitated by differences in physiognomy between the sand-pine scrub association inhabited by S. woodi and the long-leaf-pine/turkey-oak association inhabited by S. undulatus. On three ecotones between these plant associations, S. woodi and S. undulatus hybridize in a very narrow zone. Habitat selection by the two species minimizes the width of the zone. No ethological reproductive isolating mechanisms were detected, and their failure to be evolved is ascribed to the minimal overlap of the species' distributions.

Among twenty S. woodi populations, levels of fluctuating asymmetry in six characters were not correlated. Hybrid zone populations showed levels of asymmetry intermediate between those for non-hybridizing populations of the two species. These results do not support a relationship between genetic coadaptation and asymmetry level.

## INTRODUCTION

Biologists have long recognized that certain organisms are especially apt subjects for particular kinds of biological investigations. Drosophila, Neurospora, and Zea in genetics, sea urchins and amphibians in embryology, and Darwin's finches and horses in evolution are well-known examples. Although to suggest placing the lizard Sceloporus woodi in that select company would border on sacrilege, it does lend itself to studies of problems that are important in ecology and evolution.

The scattered habitat of the lizard, together with the possibility for dating the origin of particular areas of it, allows us to evaluate the dispersal abilities of an extremely habitat-limited terrestrial vertebrate. The physical isolation of many populations makes possible the measurement of evolutionary divergence of such populations that have occupied very similar environments for estimable time periods. The influence of gene flow on differentiation of populations may be gauged by comparing divergence among isolated populations with divergence among populations genetically connected.

The presence of a congener, S. undulatus, in a habitat that frequently borders that of S. woodi presents opportunities for the study of the relation between habitat structure and foraging behavior,

of competition, and of the evolution of reproductive isolating mechanisms. Finally, the existence of populations under presumably different selection regimes allows an evaluation of the reality of the population asymmetry property and of its correlation with genetic coadaptation.

## CHAPTER I

### DISTRIBUTION AND POPULATION PHENETICS OF SCELOPORUS WOODI

#### Introduction

The genus Sceloporus, which forms a conspicuous element of the western North American vertebrate fauna, contains only one species not found west of the Mississippi River: the Florida endemic, Sceloporus woodi. Since its description by Stejneger (1918), little has been published on the species. Barbour (1919), Jones (1927), and Lee and Funderburg (1970) dealt with aspects of the geographic distribution; Carr (1940) reported on the natural history; aspects of the physiological ecology were investigated by Bogert and Cowles (1947) and Hutchison and Larimer (1960), and reproduction was studied by Funderburg and Lee (1970).

Sceloporus woodi is, except in special circumstances, restricted to a single plant association, the sand-pine scrub or Pinus clausa-Quercus spp. Association (Laessle, 1942). The sand-pine scrub is a two-layered fire subclimax in which Pinus clausa, often closely spaced, is the sole overstory species. The understory is a dense thicket of largely sclerophyllous shrubs dominated by Quercus chapmanii, Q. myrtifolia, Q. virginiana maritima, and Serenoa repens. Herbaceous plants are rare and the ground surface consists of bare sand, leaf litter, and lichens.

Scrub communities exist as scattered stands, large and small, surrounded by other plant communities (see Davis, 1967, for mapping of the larger scrubs); yet they are remarkable for floristic and physiognomic uniformity from place to place. The disjunct nature of the habitat of S. woodi offers interesting problems of geographic distribution and variation. This study has sought to define the distribution of S. woodi precisely by determining in which scrub localities it is present. Phenetic variation within and among several populations is examined with reference to affinities among populations and to the relation of these affinities to certain environmental factors and to gene flow.

#### Methods

Approximately one hundred scrub communities were searched for S. woodi; these are mapped in Figure 1 and their locations are listed in Table 1. They probably constitute a substantial majority of those extant in Florida and certainly include all the large ones. During weather suitable for lizard activity, each locality was visited at least twice if no lizards were seen, and some as many as four times. Additionally, in view of the close relationship of S. woodi to S. undulatus, the distribution of the latter species in the peninsula was investigated.

Twenty populations were selected for phenetic analysis (Figure 1). The sample for each population consisted of a minimum of twenty adults (body length  $\geq 40$  mm). Nineteen characters were examined for each individual (Table 2). Unless otherwise specified, the characters were scored according to Smith (1939; 1946). Criteria for choosing the

Figure 1. Distribution of sand-pine scrub and Sceloporus woodi in Florida. Stippling indicates large continuous areas of scrub. Enclosed numbers = scrubs containing woodi; circles = woodi populations examined phenetically; squares = other woodi populations. Unenclosed numbers = scrubs apparently lacking woodi.

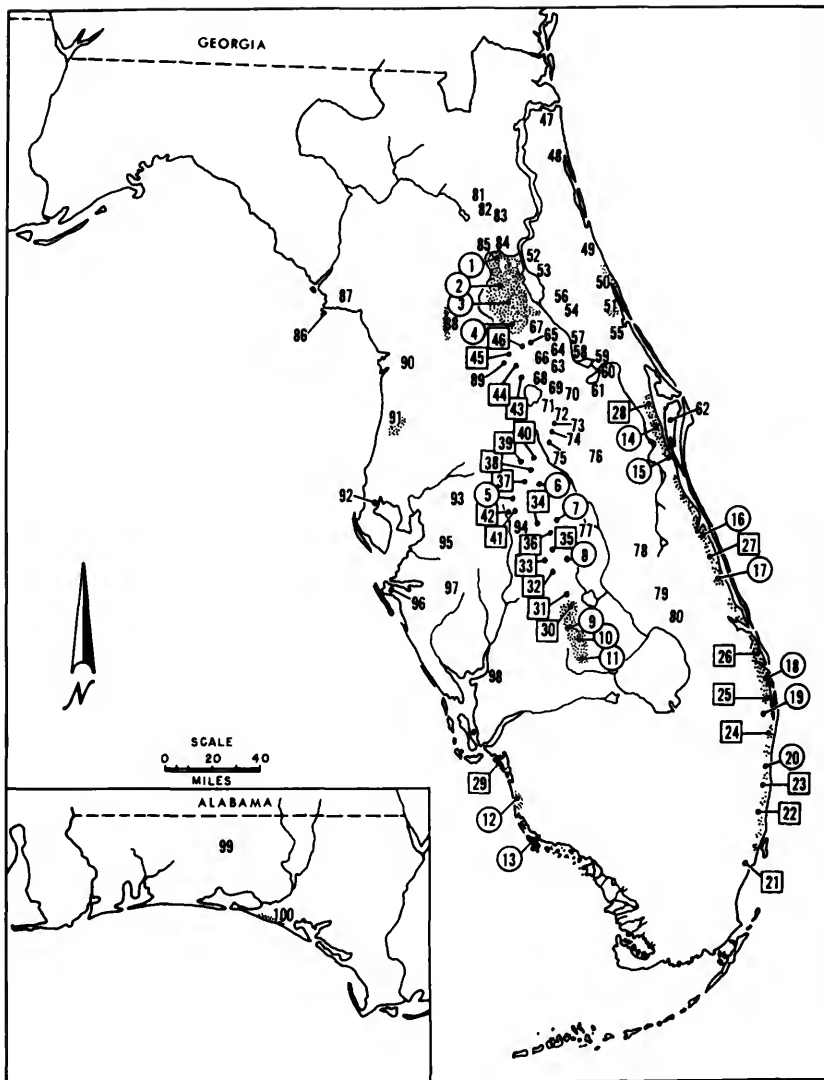




TABLE 1. Locations of Scrubs

1. intersection of Forest Service Roads 77 and 88, Ocala National Forest, Marion Co. Section 32, T. 11 S., R 25 E. elev 85
2. on State Road (SR) 314 3.5 mi. NE Eaton Creek, Ocala National Forest, Marion Co. Section 7, R. 14 S., R. 25 E. elev. 80
3. near Central Tower, Ocala National Forest, Marion Co. Section 14, T. 15 S., R. 25 E. elev. 150
4. intersection of Forest Service Roads 73 and 88, Ocala National Forest, Marion Co. Section 36, T. 16 S., R. 25 E. elev. 100
5. Blue Lake, 4 mi. NW Winter Haven, Polk Co. Section 13, T. 28 S., R. 25 E. elev. 150
6. on SR 580 6.5 mi. E Haines City, Polk Co. Sections 19 and 20, T. 27 S., R. 28 E. elev. 80
7. Flaming Arrow Boy Scout Camp, Heperides, Polk Co. Section 7, T. 30 S., R. 29 E. elev. 115
8. on SR 64 8.7 mi. NE Avon Park, Polk Co. Section 35, T. 32 S., R. 29 E. elev. 95
9. Placid Lakes Subdivision, 3 mi. SW town of Lake Placid, Highlands Co. Section 22, T. 37 S., R. 29 E. elev. 130
10. Red Hill, Archbold Biological Station, Highlands Co. Section 8, T. 38 S., R. 30 E. elev. 210
11. on U. S. 27 6 mi. S Bair's Den, Highlands Co. Section 4, T. 39 S., R. 30 E. elev. 190
12. Naples, Collier Co. elev. 10
13. near Tommy Barfield School, Marco Island, Collier Co. elev. 55
14. on SR 528 2.5 mi. NW Cocoa, Brevard Co. Sections 18 and 19, T. 24 S., R. 36 E. elev. 50
15. 0.3 mi. S Pineda, Brevard Co. Section 12, T. 26 S., R. 36 E. elev. 30
16. 1 mi. N Sebastian, Indian River Co. Section 31, T. 30 S., R. 39 E. elev. 35
17. 4 mi. N. Ft. Pierce, St. Lucie Co. Section 17, T. 34 S., R. 40 E. elev. 45

TABLE 1. Continued

18. 2 mi. S Jupiter, Palm Beach Co. Section 8, T. 41 S., R. 43 E. elev. 15
19. several mi. W West Palm Beach, Palm Beach Co.
20. S. W. 4th Avenue, Boca Raton, Palm Beach Co. Section 30, T. 47 S., R. 43 E. elev. 30
21. Miami, Dade Co.
22. 1 mi. N. Hallandale, Broward Co.
23. Pompano Beach, Broward Co.
24. Lake Worth, Palm Beach Co.
25. Juno Beach, Palm Beach Co.
26. Johnathan Dickinson State Park, Martin Co.
27. Vero Beach, Indian River Co.
28. Ti-Co Airport, 12 mi. N. Cocoa, Brevard Co. elev. 35
29. north end of Estero Island, Lee Co.
30. 6.5 mi. NNW town of Lake Placid, Highlands Co.
31. on U. S. 27 1 mi. SW DeSoto City, Highlands Co. Section 16, T. 35 S., R. 29 E. elev. 95
32. South Florida Jr. College, 1.6 mi. SW Avon Park, Highlands Co. Section 34, T. 33 S., R. 28 E. elev. 140
33. on U. S. 27 7 mi. N Avon Park, Polk Co. Section 30, T. 32 S., T. 28 E. elev. 100
34. on U. S. 27 4 mi. S SR 60, Polk Co. Section 35, T. 30 S., R. 27 E. elev. 140
35. on U. S. Alt-27 2.5 mi. S Frostproof, Polk Co.
36. at Audubon Center, Babson Park, Polk Co.
37. Haines City, Polk Co.
38. Davenport, Polk Co.
39. 22.8 mi. S Minneola, Polk Co.

TABLE 1. Continued

40. on SR 545 1.5 mi. N SR 532, Osceola Co. Section 35, T. 25 S., R. 27 E. elev. 100
41. Lake Thomas-Lake Sears, 3 mi. SW Winter Haven, Polk Co.
42. Eagle Lake, 5 mi. SW Winter Haven, Polk Co.
43. near intersection of SR 561 and SR 448, Lake Co.
44. Tavares, Lake Co.
45. on SR 44 2 mi. W Grand Island, Lake Co. Section 1, T. 19 S., R. 25 E. elev. 70
46. 5 mi. N Eustis, Lake Co.
47. 2 mi. S. Mayport, Duval Co. Section 38, T. 1 S., R. 29 E. elev. 10
48. on SR 210 1.5 mi. E U. S. 1, St. Johns Co. Section 1, T. 5 S., R. 28 E. elev. 60
49. on SR 100 3 mi. W Flagler Beach, Flagler Co. Section 39, T. 12 S., R. 31 E. elev. 35
50. on SR 40 0.7 mi. W Ormond Beach, Volusia Co. Section 21, T. 14 S., R. 32 E.
51. near Mainland High School, Daytona Beach, Volusia Co. Section 39, T. 15 S., R. 32 E. elev. 55
52. Lake Como, Putnam Co.
53. 1 mi. S Crescent City, Putnam Co.
54. 0.7 mi. N DeLeon Springs, Volusia Co.
55. on SR 44 7 mi. W New Smyrna Beach, Volusia Co.
56. 2 mi. S Barberville, Volusia Co.
57. 1 mi. S Orange City, Volusia Co. Section 22, T. 18 S., R. 30 E. elev. 75
58. DeBary, Volusia Co. Section 3, T. 19 S., R. 30 E. elev. 80
59. Osteen, Volusia Co. Section 12, T. 19 S., R. 30 E. elev. 40
60. on SR 46 2.5 mi. NW Geneva, Seminole Co. Section 8, T. 20 S., R. 32 E. elev. 25

TABLE 1. Continued

61. Oviedo, Seminole Co. Section 14, T. 21 S., R. 31 E. elev. 75
62. Merritt Island-Cape Kennedy Air Force Base, Brevard Co.
63. on SR 46 10 mi. W Sanford, Lake Co.
64. on SR 44 2.5 mi. NE Cassia, Lake Co.
65. on Dist. 5-7878 0.6 mi. S SR 450 near Umatilla, Lake Co. Section 8, T. 18 S., R. 27 E. elev. 155
66. intersection of SR 44A and Dist. 4-6585 about 7 mi. E Eustis, Lake Co. Section 36, T. 18 S., R. 27 E. elev. 135
67. intersection SR 445 and Alexander Springs Creek, Lake Co.
68. on U. S. 441 2 mi. SE Zellwood, Orange Co. Section 35, T. 20 S., R. 27 E. elev. 140
69. Forest City, Orange Co. Section 18, T. 21 S., R. 29 E. elev. 120
70. Altamonte Springs, Seminole Co. Section 24, T. 20 S., R. 29 E. elev. 95
71. 1.7 mi. E Ocoee, Orange Co. Section 17, T. 22 S., R. 28 E. elev. 160
72. Orlovista, Orange Co. Section 25, T. 22 S., R. 28 E. elev. 130
73. intersection Skylane Drive and Turkey Lake Road about 4 mi. SW Orlovista, Orange Co. Section 14, T. 23 S., R. 28 E. elev. 175
74. on Vineland-Apopka Road 0.2 mi. S Dr. Phillips, Orange Co. Section 34, T. 23 S., R. 28 E. elev. 125
75. intersection I-4 and SR 535 about 9 mi. NW Kissimee, Orange Co. Section 27, T. 24 S., R. 28 E. elev. 115
76. 0.5 mi. E Ashton, Osceola Co. Section 8, T. 26 S., R. 31 E. elev. 75
77. Indian Lake Estates, Osceola Co. Section 3, T. 31 S., R. 30 E. elev. 100
78. on U. S. 441 1.5 mi. N Yeehaw Junction, Osceola Co. Section 10, T. 32 S., R. 34 E. elev. 75
79. on SR 68 3 mi. E U. S. 441, Okeechobee Co. Section 7, T. 35 S., R. 36 E. elev. 60

TABLE 1. Continued

80. on SR 70 10 mi. E Okeechobee at St. Lucie-Okeechobee Co. line  
Section 31, T. 36 S., R. 37 E. elev. 55
81. Deer Lake, Goldhead State Park, Putnam Co. Section 36, T. 7 S.,  
R. 23 E. elev. 200
82. 2 mi. N Grandin, Putnam Co. Section 32, T. 8 S., R. 24 E. elev. 150
83. Florahome, Putnam Co.
84. on SR 310 3 mi W U. S. 19, Putnam Co.
85. on SR 315 1.4 mi. N Orange Creek, Putnam Co.
86. Way Key, Cedar Keys, Levy Co. Section 30, T. 15 S., R. 13 E.  
elev. 25
87. on SR 24 7 mi. E Cedar Keys, Levy Co. Section 2, T. 15 S., R. 13 E.  
elev. 20
88. on I-75 4 mi. N SR 484, Marion Co. Section 23, T. 16 S., R. 21 E.  
elev. 95
89. on U. S. 441 6 mi. E Leesburg, Lake Co. Section 22, T. 19 S.,  
R. 25 E. elev. 80
- 90 on SR 490 5 mi. E Lecanto, Citrus Co. Section 6, T. 19 S., R. 19 E.  
elev. 140
91. Weeki Wachee, Hernando Co. Section 1, T. 23 S., R. 17 E. elev. 50
92. on SR 580 0.5 mi. E U. S. 19, Pinellas Co. Section 30, T. 28 S.,  
R. 16 E. elev. 85
93. airport, Plant City, Hillsborough Co. Section 36, T. 28 S.-  
R. 21 E. elev. 150
94. Surveyors Lake, 8 mi. SE Bartow, Polk Co. Section 27, T. 30 S.,  
R. 26 E.
95. 2.5 mi. NE Balm, Hillsborough Co. Section 18, T. 31 S., R. 21 E.  
elev. 120
96. near DeSoto National Monument, Manatee Co. Section 19, T. 34 S.,  
R. 17 E. elev. 20
97. on SR 64 8 mi. W Manatee-Hardee Co. line, Manatee Co. Section 3,  
T. 35 S., R. 21 E. elev. 100

TABLE 1. Continued

98. on SR 764 1.3 mi. E U. S. 17 near Cleveland, Charlotte Co.
99. Mossy Head, Walton Co. Section 23, T. 3 N., R. 21 W. elev. 250
100. 1 mi. NW Sunnyside, Bay Co. Section 4, T. 3 N., R. 17 W.  
elev. 30
-

TABLE 2. Description of Characters Examined\*

1. Dorsal scales
2. Scales around midbody
3. Femoral pores (sum of both sides)
4. Subdigital lamellae of fifth hind toe (sum of both sides)
5. Circumorbitals (sum of both sides)
  
6. Supraoculars in lateral rows (sum of both sides)
7. Supraoculars in right medial row
8. Parietals and frontoparietals
9. Frontals
10. Prefrontals and frontonasals
  
11. Right foreleg: length from bent wrist to elbow
12. Right thigh: length from midline to knee
13. Right shank: length from knee to ankle
14. Right hind foot: length from heel to base of second toe
15. Hind fourth toe: length from base excluding claw (sum of both sides)
  
16. Length of longest auricular lobule (sum of both sides)
17. Interparietal length
18. Interparietal width
19. Head: length from snout to posterior edge of interparietal

\*1-10 counts; remainder linear measurements; 11-15 and 19 by dial calipers to nearest 0.1 mm; 16-18 by ocular micrometer.

characters included (1) expression in a quantitative form to allow analysis by multivariate techniques, (2) sampling a wide portion of the phenotype, and (3) inclusion of both characters whose differences from one population to another were likely to be explicable in terms of ecology, and others of more obscure adaptive function. Since the majority of the characters were sexually dimorphic and the sex ratio in every sample was not one, separate analyses were done for males and females.

The first ten characters, being counts, could be compared directly between populations, but the metric characters needed prior treatment. In organisms with continuous growth, consideration of metric characters is hindered by sample differences in mean body size that arise from collection at different times and the consequent differences in mean age between the samples. Though ratios are sometimes employed to deal with this problem (Metter, 1967), they suffer from the same difficulty -- unequal representation of age classes -- since the ratio of a structure to body length will differ for different body lengths unless the bivariate trend line passes through the origin; further, the distribution of ratios is frequently not normal. Consequently, the difficulty is best overcome by adjustment to a common body size (Steel and Torrie, 1960). Soule (1967a), because his clustering procedure worked with means, adjusted sample means. In the present study, the clustering procedures required input of individual values and adjustment of these was accordingly necessary. Analyses of covariance were carried out for each metric character regressed linearly on body length for raw and log-log transformed data (Dixon, 1968; BMD 01R), and as a second degree polynomial for raw data (Dixon, 1968; BMD 05R). Adjustment of values for each character was made by the regression method



which minimized the deviation about the regression line; this method was linear regression of raw data for all characters except 11, 12, and 13 of the males, for which regression on body length was most effective when the polynomial was used. Comparison of regression coefficients among the samples often revealed differences. Most of these were felt to be illusory, however, and to be due to some samples comprising a relatively narrow range of body sizes. Thus, following the recommendation of Sokal (1965), adjustment of all samples to the overall mean body size was made by the within-groups regression.

Several methods of clustering samples according to phenetic affinity are available. The usual numerical taxonomic method, clustering from a matrix of interpopulation correlation coefficients (Sokal and Sneath, 1963), was not chosen because it ignores the variance-covariance structure of the data; this is likely to be important when the samples are very similar phenetically. Soule (1970) felt this approach did not very successfully cluster his intraspecific samples.

Employment of multivariate statistics in phenetic studies is becoming standard (Metter and Pauken, 1969; Ingram and Tanner, 1971; Atchley, 1971). Certain multivariate techniques cluster samples by providing optimal representation in three dimensions of samples actually in  $n(>3)$ -dimensional space. The data may be considered from a single universe and subjected to a principal components analysis (Seal, 1964) which creates, from the original variable axes, new orthogonal axes corresponding to the major trends of variation in the data. The samples are then plotted on the most important of these principal components (Schnell, 1970; Johnston and Selander, 1971). Principal components for the data of this study were extracted using the program BMD 03M (Dixon, 1968).

Seal (1964), however, recommends canonical analysis as the method most appropriate for describing the affinities among several multivariate samples. Canonical analysis constructs new orthogonal axes, termed canonical variates, on which the among-sample variance-covariance matrix  $A$  is maximized with respect to the within-sample variance-covariance matrix  $W$ . Each canonical variate ( $Y_i$ ) is the sum of the products of the original variables ( $X_j$ ) and canonical coefficients ( $V_j$ );  $Y_i = V_{i1}X_1 + V_{i2}X_2 + \dots + V_{ip}X_p$ . The sets of coefficients are the eigenvectors associated with the solutions (eigenvalues) of the equation  $|W^{-1}A - \lambda I| = 0$  (Cooley and Lohnes, 1962). Each eigenvalue and its corresponding canonical variate represent an identifiable fraction of the total variation. Canonical analysis of the data was done with program BMD 07M (Dixon, 1968).

Sample means or individuals are plotted on those canonical variates which account for the greater fractions of total variation. The relative importance of each original variable to a particular canonical variate is shown by standardization of the canonical coefficients through multiplication by the standard deviations of the corresponding original variables (Rees, 1969). The standardized coefficients of each original variable are plotted on the canonical axes and summed to a resultant vector which visually indicates the influence of the original variable on that combination of canonical variates. A plot on the three most important canonical variates accounts for only part of the total variation; serious distortions present in the plot may be revealed by linking each sample to its nearest neighbor in character hyperspace. These linkages are generalized distances ( $D^2$ ). The generalized distance between two samples was obtained by multiplying each

coefficient from the discriminant function for the samples by the difference between the sample means for the corresponding character, and then summing the products.

Since the generalized distance is the most complete estimate of phenetic, the presumably genetic, affinity, it is interesting to compare average  $D^2$ 's for sets of populations. Four sets were defined geographically: populations 1, 2, 3, and 4 (Ocala National Forest); populations 5, 6, 7, and 8 (Bartow and Northern Lake Wales Ridges); populations 9, 10, and 11 (Southern Lake Wales Ridge); and populations 14, 15, 16, 17, 18, 19, and 20 (Atlantic Coast). Within each set the average distance between population mean vectors was calculated as the arithmetic mean of all such distances.

### Results

As shown in Figure 1, Sceloporus woodi has been found only in scrubs of four regions: the Ocala National Forest (1-4) and certain localities immediately to the south (43-46); the Lake Wales Ridge (6-11 and 30-40) and, to the west, the northern portion of the Bartow Ridge (5, 41, and 42); the southwest Gulf Coast in Collier and Lee Counties (12, 13, and 29); and the Atlantic Coast from the vicinity of Titusville south to Miami (14-28). It is conspicuously absent from scrubs in and near Orange County northeast, east, and southeast of Lake Apopka (68-75); from the Atlantic Coast north of Titusville; and from scrubs north and west of the Oklawaha River (81-91). Sceloporus undulatus occupies sandhill vegetation [Pinus australis-Quercus laevis Association (Laessle, 1942)] and drier hammocks in northern and

central Florida except for seven islands of sandhill vegetation completely surrounded by scrub in the Ocala National Forest.

Thirteen of the characters examined proved to be sexually dimorphic (Table 3). Of the dimorphic scale characters, males tend to have more femoral pores but fewer dorsal scales, prefrontals and frontonasals, parietals and frontoparietals, scales around midbody, and lateral supraoculars than females. This may be a reflection of the supposed role of femoral pores in intraspecific communication and of the more slender body form of the males. Males have longer forelegs, shanks, thighs, hind feet, heads, auricular lobules, and interparietal scales. The longer limbs of males are probably connected with their greater tendency to territorial activity.

Character means and standard deviations for the twenty populations are presented in Tables 4-7. Tables 8 and 9 show the correlations between characters. It is clearly desirable that intercharacter correlations be low so that informational redundancy is avoided, and such is generally the case for the characters used; the highly correlated limb length characters are an exception.

For the males the first three principal components accounted for 45, 10, and 6 percent, respectively, of the total variation, or 61 percent in combination. The first three principal components for the females contained 63 percent of the total variation, or 45, 11, and 7 percent individually. When the population means were plotted on the first three principal components, occurrence was found between phenetic affinity and geographic proximity, but less distinctly than on the canonical variates to be described below.

TABLE 3. Mean Values of Sexually Dimorphic Characters

<u>Character*</u>	<u>Male Mean</u>	<u>Female Mean</u>	<u>Probability</u>
Dorsal scales	40.58	41.05	<0.1
Scales around midbody	41.89	42.01	<0.1
Femoral pores	34.74	33.76	<0.001
Lateral supraoculars	26.98	27.77	<0.1
Parietals-frontoparietals	4.78	5.02	<0.01
Prefrontals-frontonasals	5.91	6.22	<0.02
Right foreleg length	7.86	7.73	<0.01
Right thigh length	13.89	13.55	<0.001
Right hind foot length	7.09	7.04	<0.02
Auricular lobule length	1.67	1.61	<0.001
Interparietal length	2.78	2.67	<0.001
Head length	9.98	9.74	<0.001

\*Adjusted to 47.65 mm snout-vent length

TABLE 4. Population Means for

<u>Character</u>	<u>Populations**</u>						
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>
	(10)	(10)	(10)	(10)	(10)	(13)	(10)
1. Dorsal scales	40.2	40.5	40.4	39.6	41.4	43.2	42.9
2. Scales around midbody	41.7	41.8	42.2	42.0	42.2	42.5	43.2
3. Femoral pores	31.6	31.8	32.1	32.3	33.8	33.3	34.2
4. Subdigital lamellae	26.7	26.8	27.1	27.9	26.6	27.3	27.4
5. Circumorbitals	22.4	23.8	21.8	22.2	21.0	23.2	21.9
6. Lateral supraoculars	31.3	28.9	26.3	29.1	25.7	28.8	29.6
7. Right medial supraoculars	5.5	5.6	5.5	5.5	5.5	5.3	5.4
8. Parietals-frontoparietals	4.7	4.9	4.8	4.8	4.5	4.5	5.2
9. Frontals	2.5	3.1	3.2	3.0	2.2	3.1	3.0
10. Prefrontals-frontonasals	7.0	6.2	5.8	5.8	5.3	5.5	5.8
11. Right foreleg	7.9	8.0	8.0	7.8	7.6	7.7	7.8
12. Right thigh	13.9	14.0	13.7	14.0	13.8	13.5	13.4
13. Right shank	12.5	12.6	12.5	12.7	12.3	12.5	12.5
14. Right hind foot	6.9	7.1	7.1	7.1	6.5	7.0	6.8
15. Hind fourth toe	22.8	23.4	23.2	22.9	21.1	22.1	21.8
16. Auricular lobule	1.9	1.9	1.9	2.0	2.0	2.0	2.0
17. Interparietal length	3.1	3.0	3.0	3.0	3.1	3.1	3.1
18. Interparietal width	3.0	2.9	2.9	3.0	3.2	3.0	3.0
19. Head length	9.9	9.9	9.7	10.0	9.8	9.8	10.0

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\*Means of values adjusted to 47.65 mm snout-vent length

Male Sceloporus woodi\*

Populations**												
8	9	10	11	12	13	14	15	16	17	18	19	20
(10)	(9)	(11)	(10)	(6)	(10)	(10)	(9)	(14)	(11)	(12)	(13)	(9)
40.3	41.9	42.2	42.0	41.8	38.7	39.1	39.4	41.4	39.7	37.8	40.0	38.9
39.9	44.0	42.4	44.0	40.8	39.7	41.5	41.8	41.8	42.4	40.5	42.2	40.8
34.5	37.9	37.9	38.1	34.3	36.4	36.2	35.3	36.5	35.9	33.6	34.5	34.3
29.5	27.4	28.2	28.2	27.7	28.6	28.1	29.2	28.7	26.9	27.0	27.8	27.7
20.2	20.7	21.7	21.6	23.7	21.5	21.6	21.7	22.1	23.7	23.5	21.5	20.4
24.0	27.1	27.2	25.5	26.5	23.2	26.3	25.2	26.4	26.1	26.1	29.5	25.2
5.8	5.3	5.5	5.6	5.8	5.2	5.1	5.2	5.4	5.4	5.1	5.5	5.2
4.1	4.8	5.1	5.1	5.2	4.3	4.5	4.4	4.9	4.7	4.9	5.1	5.0
3.1	2.4	2.2	2.2	2.7	3.0	2.3	1.9	2.4	2.4	2.3	2.9	2.6
5.3	5.8	7.2	6.0	7.0	6.2	5.1	5.3	5.5	6.0	6.0	6.4	5.2
8.1	7.8	7.8	7.9	8.0	8.0	7.8	7.8	7.9	7.8	7.8	7.9	7.8
13.9	13.8	14.1	14.0	13.8	14.1	13.9	13.8	14.0	14.2	14.2	13.8	13.8
13.1	12.6	12.8	12.7	13.3	12.9	12.4	12.3	12.3	12.6	12.4	12.4	12.5
7.5	7.2	7.0	7.0	7.4	7.3	7.2	7.2	7.1	7.2	7.1	7.1	7.0
25.4	24.0	23.7	23.4	24.4	24.3	23.3	22.9	23.3	23.8	23.2	23.3	22.0
2.0	1.7	1.8	1.9	1.9	1.8	1.8	2.0	1.8	1.7	1.8	1.6	1.8
3.1	3.0	3.1	3.0	2.9	2.9	3.2	3.4	3.0	3.2	3.2	3.0	3.1
2.9	2.8	3.0	3.2	2.8	2.9	3.0	2.9	3.0	3.0	3.0	2.8	3.0
10.0	10.1	10.2	10.1	10.1	9.9	10.0	10.3	9.8	10.1	10.3	9.9	9.8

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 \*\*Sample sizes in parentheses

TABLE 5. Population Means for

<u>Character</u>	<u>Populations**</u>						
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>
	(10)	(10)	(10)	(10)	(10)	(7)	(10)
1. Dorsal scales	40.9	41.1	41.2	40.6	42.1	44.4	43.2
2. Scales around midbody	42.4	42.1	43.8	41.4	41.4	43.0	42.6
3. Femoral pores	32.2	32.3	31.1	32.3	30.7	32.0	32.8
4. Subdigital lamellae	27.0	26.6	28.2	26.5	26.1	27.8	27.3
5. Circumorbitals	23.9	22.9	23.1	23.6	19.7	23.3	21.9
6. Lateral supraoculars	29.8	29.4	30.2	30.4	23.9	28.6	25.9
7. Right medial supraoculars	5.4	5.6	5.6	5.7	5.4	5.6	5.5
8. Parietals-frontoparietals	5.0	5.1	5.2	5.1	4.6	4.7	5.1
9. Frontals	2.7	3.0	3.5	3.3	2.1	3.1	2.9
10. Prefrontals-frontonasals	7.0	6.1	6.1	6.5	5.6	5.7	6.1
11. Right foreleg	7.8	8.2	8.2	8.2	7.8	7.8	8.1
12. Right thigh	14.0	14.2	14.1	14.3	14.1	13.7	13.9
13. Right shank	12.6	12.9	13.0	12.7	12.3	12.2	12.6
14. Right hind foot	7.1	7.3	7.2	7.3	6.7	6.9	7.0
15. Hind fourth toe	23.2	23.8	23.2	23.4	21.5	22.3	22.7
16. Auricular lobule	1.8	1.9	2.0	2.0	2.1	1.8	2.0
17. Interparietal length	3.0	2.8	3.0	2.9	3.1	3.0	3.0
18. Interparietal width	3.0	3.0	2.9	3.1	3.1	2.9	2.8
19. Head length	9.9	9.7	9.9	9.8	10.0	9.8	9.9

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 \*Means of values adjusted to 50.52 mm snout-vent length



Female Sceloporus woodi\*

Populations**												
8	9	10	11	12	13	14	15	16	17	18	19	20
(10)	(11)	(11)	(10)	(14)	(10)	(10)	(11)	(14)	(9)	(8)	(13)	(11)
41.6	42.3	42.4	41.8	42.2	38.2	39.6	40.6	41.3	39.2	39.9	40.5	38.3
40.2	44.5	43.7	44.2	40.6	39.0	41.7	42.0	40.8	41.7	41.8	42.8	41.1
34.7	35.8	36.2	36.8	35.3	33.6	35.8	33.5	34.6	34.4	33.6	33.5	32.4
30.2	27.4	28.2	27.3	28.6	28.2	29.2	29.3	28.2	27.8	28.6	27.5	27.4
21.6	22.0	21.7	21.2	23.2	17.7	23.1	22.2	22.0	22.9	25.2	23.2	20.5
28.4	27.9	28.4	27.5	29.6	21.1	26.6	26.3	26.0	24.8	29.8	33.0	26.8
5.7	5.5	5.7	5.8	5.6	5.1	5.2	5.1	5.3	5.7	5.1	5.7	5.4
4.6	4.7	5.4	5.4	5.8	4.5	4.9	4.0	4.7	5.0	5.8	5.3	5.4
2.6	2.6	2.4	2.5	2.7	2.5	2.5	2.0	2.7	2.8	2.8	3.2	2.3
6.1	6.3	6.4	6.1	7.8	5.9	5.5	5.5	6.1	6.4	5.5	6.7	5.8
8.0	8.1	8.5	8.2	8.2	8.4	8.1	8.0	8.1	8.1	8.1	8.3	8.1
14.0	14.2	14.9	14.2	14.2	14.5	14.2	14.5	14.5	14.4	14.5	14.5	14.2
12.9	13.0	13.4	13.0	13.3	13.3	12.9	12.7	12.7	12.6	12.6	12.8	12.8
7.5	7.4	7.5	7.2	7.5	7.5	7.3	7.2	7.3	7.4	7.3	7.1	7.2
24.8	25.0	24.4	23.9	24.6	24.5	23.8	23.3	24.0	23.9	23.6	23.4	22.5
1.9	1.9	1.9	1.9	1.9	1.8	1.9	1.9	2.0	1.9	1.7	1.6	1.8
3.2	3.0	3.2	3.1	3.0	3.0	3.2	3.3	2.9	3.2	3.1	2.9	3.1
2.9	2.9	3.1	3.1	3.1	2.9	3.0	3.2	3.1	3.0	3.0	3.0	3.0
10.4	10.3	10.5	10.3	10.4	10.3	10.2	10.5	10.0	10.1	10.4	10.2	10.0

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\*\*Sample sizes in parentheses

TABLE 6. Standard Deviations

Character	Populations*						
	1 (10)	2 (10)	3 (10)	4 (10)	5 (10)	6 (13)	7 (10)
1. Dorsal scales	1.87	2.01	1.35	1.96	2.17	1.96	2.23
2. Scales around midbody	1.57	2.15	2.30	2.00	1.55	1.85	1.75
3. Femoral pores	1.50	3.26	2.18	2.06	2.53	2.90	2.20
4. Subdigital lamellae	2.06	1.32	2.28	1.97	0.84	1.49	2.27
5. Circumorbitals	3.60	2.74	4.02	2.39	3.86	3.36	3.04
6. Lateral supraoculars	6.25	4.79	5.60	7.96	5.85	5.32	5.34
7. Right medial supraoculars	0.53	0.52	0.53	0.53	0.53	0.48	0.52
8. Parietals-frontoparietals	1.06	0.99	0.92	0.79	1.27	0.78	1.03
9. Frontals	0.53	0.88	0.79	0.94	0.42	0.95	0.94
10. Prefrontals-frontonasals	1.05	0.63	1.14	1.23	0.48	0.88	1.03
11. Right foreleg	0.21	0.23	0.16	0.17	0.41	0.20	0.19
12. Right thigh	0.29	0.36	0.26	0.25	0.53	0.47	0.35
13. Right shank	0.41	0.36	0.28	0.33	0.35	0.32	0.22
14. Right hind foot	1.70	1.26	3.06	1.48	2.75	2.08	1.64
15. Hind fourth toe	0.81	0.62	0.85	0.57	0.95	0.63	0.83
16. Auricular lobule	0.20	0.14	0.22	0.16	0.14	0.19	0.24
17. Interparietal length	0.19	0.20	0.18	0.13	0.20	0.18	0.15
18. Interparietal width	0.15	0.24	0.13	0.15	0.22	0.19	0.18
19. Head length	0.17	0.33	0.25	0.25	0.25	0.23	0.14

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\*Sample sizes in parentheses

for Male Sceloporus woodi

Populations*												
<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>	<u>12</u>	<u>13</u>	<u>14</u>	<u>15</u>	<u>16</u>	<u>17</u>	<u>18</u>	<u>19</u>	<u>20</u>
(10)	(9)	(11)	(10)	(6)	(10)	(10)	(9)	(14)	(11)	(12)	(13)	(9)
1.77	1.90	2.04	1.82	1.17	1.25	1.29	1.81	1.78	1.42	1.47	1.35	1.36
1.45	1.32	1.86	1.70	1.47	1.34	1.43	1.56	1.93	1.81	1.09	1.82	1.39
2.99	3.14	3.19	4.23	2.42	1.50	2.48	2.24	2.14	2.02	2.02	1.81	1.00
1.72	1.24	2.09	1.69	1.50	1.17	1.97	1.86	1.68	1.97	1.91	1.99	1.80
1.62	3.20	2.37	4.09	2.66	3.17	1.26	2.29	2.58	1.85	3.90	2.44	2.24
4.27	4.65	4.00	5.48	3.67	3.68	5.76	5.21	3.86	3.56	5.20	5.58	6.12
0.42	0.50	0.52	0.52	0.75	0.42	0.32	0.67	0.50	0.50	0.29	0.52	0.44
0.99	0.83	1.14	0.88	0.98	0.48	0.71	0.73	1.07	0.79	0.79	0.95	0.87
0.99	0.53	0.60	0.42	0.52	0.67	0.48	0.33	0.76	0.67	0.87	0.86	0.73
0.48	0.67	1.17	0.94	0.63	0.92	0.32	0.71	0.85	0.63	0.95	1.04	0.44
0.16	0.17	0.14	0.12	0.36	0.32	0.16	0.19	0.21	0.19	0.24	0.28	0.25
0.45	0.24	0.32	0.32	0.43	0.52	0.45	0.48	0.45	0.50	0.39	0.39	0.32
0.46	0.26	0.34	0.32	0.59	0.45	0.36	0.30	0.30	0.37	0.36	0.26	0.30
1.97	1.90	2.25	1.37	2.43	3.27	1.89	1.39	2.73	2.44	2.83	3.04	2.47
0.88	1.06	0.82	0.63	1.02	1.18	0.93	0.84	1.18	0.83	1.26	0.89	0.88
0.21	0.14	0.13	0.19	0.19	0.14	0.17	0.19	0.16	0.14	0.19	0.11	0.15
0.12	0.15	0.24	0.20	0.23	0.20	0.22	0.09	0.18	0.14	0.11	0.10	0.10
0.16	0.13	0.26	0.21	0.40	0.16	0.13	0.14	0.17	0.19	0.28	0.24	0.17
0.16	0.36	0.29	0.25	0.51	0.36	0.33	0.25	0.41	0.30	0.24	0.43	0.25

TABLE 7. Standard Deviations

<u>Character</u>	<u>Populations*</u>						
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>
	(10)	(10)	(10)	(10)	(10)	(7)	(10)
1. Dorsal scales	2.23	1.73	2.78	2.22	1.45	1.72	2.44
2. Scales around midbody	1.71	1.45	1.81	0.97	1.71	2.16	1.84
3. Femoral pores	2.20	4.03	2.51	2.36	2.26	1.41	1.93
4. Subdigital lamellae	1.94	1.58	1.40	1.19	1.37	2.34	1.25
5. Circumorbitals	2.60	3.35	4.31	3.31	2.75	3.86	2.73
6. Lateral supraoculars	5.12	8.18	6.89	5.30	3.41	5.19	5.11
7. Right medial supraoculars	0.52	0.52	0.52	0.48	0.52	0.53	0.53
8. Parietals-frontoparietals	1.05	0.99	1.32	1.20	0.84	0.95	1.37
9. Frontals	0.67	0.82	1.27	0.48	0.32	1.07	0.88
10. Prefrontals-frontonasals	1.33	1.20	0.74	1.08	0.84	0.76	1.29
11. Right foreleg	0.20	0.20	0.23	0.25	0.38	0.16	0.14
12. Right thigh	0.44	0.52	0.42	0.30	0.52	0.50	0.41
13. Right shank	0.25	0.29	0.39	0.30	0.35	0.21	0.35
14. Right hind foot	1.33	1.37	2.42	3.58	2.27	2.29	2.07
15. Hind fourth toe	0.94	1.10	0.99	0.70	0.55	0.69	0.78
16. Auricular lobule	0.21	0.18	0.23	0.20	0.17	0.30	0.25
17. Interparietal length	0.19	0.20	0.15	0.13	0.09	0.08	0.13
18. Interparietal width	0.08	0.14	0.16	0.14	0.06	0.13	0.14
19. Head length	0.28	0.32	0.26	0.30	0.22	0.38	0.19

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 \*Sample sizes in parentheses

for Female Sceloporus woodi

Populations*												
8	9	10	11	12	13	14	15	16	17	18	19	20
(10)	(11)	(11)	(10)	(14)	(10)	(10)	(11)	(14)	(9)	(8)	(13)	(11)
2.17	1.90	2.42	1.23	2.52	0.92	1.17	1.91	1.68	1.72	2.03	1.61	1.49
1.14	1.37	2.00	2.10	1.01	1.56	1.34	2.14	1.53	1.94	1.58	2.58	1.38
2.94	3.63	2.56	2.74	2.23	3.02	2.35	2.66	1.83	3.20	1.30	2.57	2.38
1.55	0.93	2.09	0.94	1.60	1.87	2.20	1.42	1.85	2.44	1.68	2.07	1.37
3.81	2.53	2.00	3.58	2.49	2.63	2.33	3.74	1.75	2.26	2.96	2.03	3.17
4.43	4.83	4.27	5.28	8.39	2.33	2.68	5.66	4.42	2.82	5.12	6.49	4.66
0.48	0.52	0.47	0.42	0.50	0.32	0.42	0.54	0.61	0.50	0.35	0.48	0.50
0.84	0.90	1.04	1.35	1.19	0.71	0.99	0.44	0.91	0.87	1.16	0.94	0.81
0.97	0.81	0.50	0.85	0.61	0.53	0.85	0.00	0.61	0.83	0.89	0.90	0.46
0.57	1.10	0.93	0.99	0.95	1.10	0.97	0.93	1.09	0.73	0.53	1.18	1.08
0.19	0.26	0.27	0.17	0.16	0.31	0.22	0.29	0.41	0.17	0.13	0.30	0.15
0.70	0.23	0.48	0.53	0.47	0.49	0.57	0.25	0.44	0.36	0.30	0.42	0.37
0.32	0.36	0.32	0.43	0.35	0.28	0.42	0.28	0.45	0.32	0.38	0.25	0.27
3.29	2.29	2.14	2.95	1.39	3.13	2.26	1.86	2.95	1.79	1.19	3.25	3.04
1.08	1.08	0.75	1.17	0.91	0.79	1.13	0.96	1.20	0.92	0.75	0.70	0.41
0.21	0.17	0.20	0.16	0.11	0.20	0.19	0.15	0.21	0.11	0.14	0.19	0.24
0.16	0.12	0.20	0.20	0.21	0.07	0.18	0.14	0.14	0.10	0.10	0.22	0.22
0.19	0.25	0.15	0.18	0.25	0.13	0.14	0.12	0.24	0.19	0.22	0.28	0.24
0.30	0.17	0.46	0.38	0.28	0.46	0.56	0.35	0.40	0.22	0.34	0.47	0.34

TABLE 8. Character Correlation

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>
1	1.000								
2	0.613	1.000							
3	0.322	0.358	1.000						
4	0.349	0.320	0.527	1.000					
5	0.258	0.330	0.289	0.371	1.000				
6	0.258	0.335	0.116	0.227	0.544	1.000			
7	0.337	0.353	0.291	0.496	0.423	0.381	1.000		
8	0.221	0.294	0.236	0.321	0.331	0.344	0.340	1.000	
9	0.180	0.053	-0.012	0.191	0.266	0.203	0.224	0.181	1.000
10	0.233	0.305	0.139	0.263	0.347	0.304	0.384	0.321	0.079
11	0.319	0.373	0.467	0.708	0.409	0.309	0.596	0.353	0.277
12	0.233	0.382	0.505	0.692	0.406	0.290	0.575	0.335	0.176
13	0.360	0.382	0.481	0.708	0.419	0.318	0.607	0.307	0.253
14	0.250	0.315	0.482	0.725	0.369	0.231	0.551	0.272	0.220
15	0.210	0.296	0.530	0.712	0.343	0.176	0.546	0.244	0.194
16	0.262	0.203	0.149	0.331	0.202	0.098	0.306	0.071	0.158
17	-0.347	-0.276	-0.276	-0.410	-0.250	-0.184	-0.266	-0.306	-0.362
18	-0.222	-0.254	-0.262	-0.407	-0.245	-0.137	-0.268	-0.198	-0.177
19	-0.392	-0.441	-0.476	-0.721	-0.450	-0.345	-0.589	-0.328	-0.239

Matrix for Male Sceloporus woodi

<u>10</u>	<u>11</u>	<u>12</u>	<u>13</u>	<u>14</u>	<u>15</u>	<u>16</u>	<u>17</u>	<u>18</u>	<u>19</u>
1.000									
0.362	1.000								
0.389	0.894	1.000							
0.390	0.933	0.895	1.000						
0.352	0.881	0.855	0.882	1.000					
0.373	0.827	0.816	0.838	0.913	1.000				
0.066	0.479	0.434	0.520	0.404	0.307	1.000			
-0.312	-0.396	-0.341	-0.361	-0.357	-0.387	-0.047	1.000		
-0.168	-0.420	-0.398	-0.425	-0.444	-0.451	-0.213	0.376	1.000	
-0.389	-0.898	-0.892	-0.883	-0.842	-0.770	-0.494	0.426	0.426	1.000

TABLE 9. Character Correlation

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>
1	1.000								
2	0.488	1.000							
3	0.348	0.447	1.000						
4	-0.240	-0.442	-0.376	1.000					
5	0.309	0.430	0.374	-0.363	1.000				
6	0.316	0.408	0.257	-0.288	0.575	1.000			
7	0.322	0.380	0.397	-0.573	0.446	0.440	1.000		
8	0.164	0.244	0.277	-0.275	0.367	0.454	0.341	1.000	
9	0.199	0.244	0.081	-0.216	0.273	0.349	0.266	0.247	1.000
10	0.238	0.229	0.290	-0.334	0.407	0.422	0.373	0.376	0.110
11	0.174	0.408	0.524	-0.803	0.359	0.284	0.528	0.282	0.202
12	0.169	0.422	0.507	-0.806	0.390	0.272	0.512	0.277	0.161
13	0.224	0.436	0.562	-0.798	0.388	0.292	0.524	0.315	0.162
14	0.186	0.370	0.592	-0.725	0.357	0.291	0.509	0.303	0.163
15	0.202	0.368	0.612	-0.667	0.362	0.259	0.484	0.275	0.146
16	0.169	0.202	0.164	-0.450	0.070	0.065	0.145	-0.017	0.053
17	-0.262	-0.239	-0.207	0.440	-0.238	-0.211	-0.290	-0.288	-0.353
18	-0.147	-0.278	-0.170	0.432	-0.255	-0.098	-0.215	-0.158	-0.245
19	-0.287	-0.481	-0.473	0.913	-0.428	-0.321	-0.584	-0.321	-0.247



Matrix for Female Sceloporus woodi

<u>10</u>	<u>11</u>	<u>12</u>	<u>13</u>	<u>14</u>	<u>15</u>	<u>16</u>	<u>17</u>	<u>18</u>	<u>19</u>
1.000									
0.307	1.000								
0.301	0.874	1.000							
0.364	0.927	0.889	1.000						
0.298	0.871	0.830	0.896	1.000					
0.334	0.831	0.800	0.868	0.909	1.000				
0.080	0.443	0.449	0.437	0.416	0.393	1.000			
-0.285	-0.409	-0.310	-0.376	-0.406	-0.401	-0.099	1.000		
-0.167	-0.411	-0.405	-0.423	-0.410	-0.394	-0.312	0.356	1.000	
-0.363	-0.845	-0.852	-0.847	-0.797	-0.758	-0.450	0.499	0.501	1.000

Tables 10 and 11 give the coefficients of the first six canonical variates and the proportion of the total variance associated with each variate. The percentage of total variance accounted for by the first three canonical variates is very close to that for the three largest principal components. For each sex three-dimensional plots of population means were made on the first three (Figure 2 and Figure 3) and second three canonical variates. The trends on the first three canonical variates are similar to those on the principal component axes but the clusters are tighter.

Inspection of Figure 2 indicates four clusters surrounded by several outliers. The tightest cluster is formed of populations 1, 2, 3, and 4 of the Ocala National Forest. Populations 14, 15, 16, 17, 18, 19, and 20 from the Atlantic Coast compose a looser cluster near the Ocala group. Another cluster comprises populations 9, 10, and 11 from the southern end of the Lake Wales Ridge. Populations 6 and 7 form a cluster from the northern portion of the Lake Wales Ridge and are closest to population 5 from the Bartow Ridge. Finally, populations 12 and 13 from the Gulf Coast and 8 from the Lake Wales Ridge are well separated from other populations. Linkage of each population to that other with the smallest generalized distance between them reveals no serious distortion by the canonical plot of the relationships in character hyperspace. Further, examination of Table 12 indicates general agreement between the plot and second, third, and fourth nearest neighbors in hyperspace.

The clustering pattern of the females (Figure 3) is essentially similar. The main difference is the merging of the Ocala National Forest populations (1, 2, 3, and 4) with part of the Atlantic Coast

TABLE 10. Coefficients of the First

<u>Character</u>	<u>Canonical Variate</u>			
	<u>1</u>		<u>2</u>	
	<u>Raw</u>	<u>Std.</u>	<u>Raw</u>	<u>Std.</u>
1	1.56	0.27	-2.35	-0.41
2	1.49	0.25	1.02	0.17
3	-1.02	-0.26	0.98	0.24
4	0.31	0.06	0.96	0.17
5	-0.04	-0.01	0.79	0.23
6	0.13	0.07	0.01	0.01
7	0.10	0.05	-0.70	-0.35
8	0.12	0.11	0.02	0.02
9	-0.07	-0.05	-0.34	-0.25
10	-0.39	-0.34	-0.06	-0.05
11	-8.85	-0.20	6.28	0.14
12	7.01	0.28	13.00	0.52
13	-3.33	-0.12	-20.86	-0.72
14	-1.13	-0.26	0.88	0.20
15	-5.76	-0.52	-3.49	-0.32
16	1.81	0.31	-2.23	-0.38
17	0.12	0.02	1.52	0.26
18	1.65	0.33	-0.05	-0.01
19	-5.93	-0.18	8.36	0.25
% of canonical variation		24%		20%

## Six Canonical Variates for Males

Canonical Variate							
3		4		5		6	
<u>Raw</u>	<u>Std.</u>	<u>Raw</u>	<u>Std.</u>	<u>Raw</u>	<u>Std.</u>	<u>Raw</u>	<u>Std.</u>
-2.78	-0.48	-0.04	-0.01	2.56	0.44	-2.10	-0.36
-0.40	-0.06	0.09	0.02	-2.80	-0.48	-1.82	-0.31
-2.27	-0.56	1.37	0.34	-1.02	-0.25	0.35	0.09
0.98	0.18	2.09	0.37	0.65	0.12	0.28	0.05
1.02	0.30	-0.36	-0.10	1.54	0.45	0.48	0.14
0.03	0.02	-0.47	-0.24	-0.03	-0.02	-0.93	-0.48
-0.15	-0.08	0.21	0.10	-0.34	-0.17	0.43	0.22
-0.10	-0.09	-0.04	-0.04	-0.02	-0.02	0.03	0.03
0.46	0.34	0.01	0.01	-0.36	-0.26	-0.28	-0.21
-0.27	-0.24	-0.76	-0.66	0.30	0.26	0.09	0.08
9.85	0.22	-15.21	-0.34	-16.28	-0.37	-4.42	-0.10
-3.58	-0.14	-3.80	-0.15	4.49	0.18	7.86	0.32
-6.18	-0.21	8.21	0.28	1.32	0.04	12.95	0.45
1.75	0.40	1.61	0.37	0.58	0.13	-1.36	-0.31
-2.80	-0.25	-1.94	-0.18	1.38	0.12	-2.53	-0.23
0.55	0.10	0.66	0.11	2.28	0.39	0.71	0.12
1.76	0.30	0.67	0.11	2.16	0.37	-2.37	-0.40
-1.40	-0.28	0.58	0.12	0.21	0.04	1.64	0.33
-12.36	-0.37	-5.76	-0.17	15.21	0.46	-7.82	-0.23
16%		9%		8%		6%	

TABLE 11. Coefficients of the First

<u>Character</u>	<u>Canonical Variate</u>			
	<u>1</u>		<u>2</u>	
	<u>Raw</u>	<u>Std.</u>	<u>Raw</u>	<u>Std.</u>
1	-0.52	-0.10	1.43	0.28
2	-1.81	-0.31	2.38	0.41
3	1.50	0.39	-0.71	-0.18
4	1.06	0.18	-2.07	-0.35
5	-0.74	-0.22	-0.92	-0.27
6	-0.09	-0.05	-0.41	-0.22
7	0.20	0.10	1.17	0.58
8	-0.05	-0.05	0.13	0.13
9	0.21	0.16	0.27	0.20
10	0.45	0.45	0.30	0.30
11	-8.78	-0.22	14.39	0.36
12	-7.59	-0.34	-4.74	-0.21
13	13.73	0.46	14.84	0.50
14	1.55	0.38	-1.22	-0.30
15	4.22	0.38	2.15	0.20
16	-0.15	-0.03	1.51	0.29
17	1.26	0.21	-1.25	-0.20
18	-0.45	-0.08	-0.13	-0.02
19	7.36	0.26	-9.28	-0.33
% of canonical variation		26%		18%

## Six Canonical Variates for Females

Canonical Variate							
3		4		5		6	
Raw	Std.	Raw	Std.	Raw	Std.	Raw	Std.
2.57	0.50	2.78	0.54	0.14	0.03	1.87	0.36
1.79	0.31	-3.79	-0.65	2.53	0.43	-0.66	-0.11
0.24	0.06	-0.96	-0.25	-1.13	-0.29	0.80	0.21
0.45	0.08	1.04	0.18	0.51	0.09	-1.66	-0.28
-0.79	-0.23	0.81	0.24	2.08	0.61	0.68	0.20
-0.20	-0.11	-0.41	-0.22	0.21	0.11	-0.25	-0.13
0.25	0.12	0.09	0.04	-0.22	-0.11	-0.20	-0.10
0.10	0.10	-0.16	-0.16	-0.14	-0.14	-0.07	-0.07
-0.41	-0.31	0.24	0.18	0.39	0.30	-0.14	-0.10
-0.22	-0.22	0.15	0.15	-0.05	-0.05	0.26	0.26
-5.24	-0.13	-14.89	-0.37	1.99	0.05	0.05	0.00
-6.88	-0.31	-8.83	-0.40	-5.01	-0.22	12.51	0.56
2.70	0.09	4.82	0.16	-10.28	-0.35	-20.12	-0.68
-1.17	-0.29	0.91	0.22	1.68	0.42	-0.29	-0.07
1.35	0.12	-0.01	-0.00	3.27	0.30	4.19	0.38
0.66	0.13	2.00	0.39	-0.87	-0.17	1.13	0.22
3.06	0.50	0.60	0.10	2.13	0.35	-1.95	-0.32
-0.85	-0.16	-0.08	-0.01	-0.16	-0.03	1.89	0.35
10.25	0.36	-9.73	-0.34	-3.68	-0.13	8.25	0.29
	12%		10%		8%		6%

Figure 2. Projection of population means for males on the three canonical variates;  $K_3$  vertical. Nearest neighbors by generalized distance ( $D^2$ ) are linked.

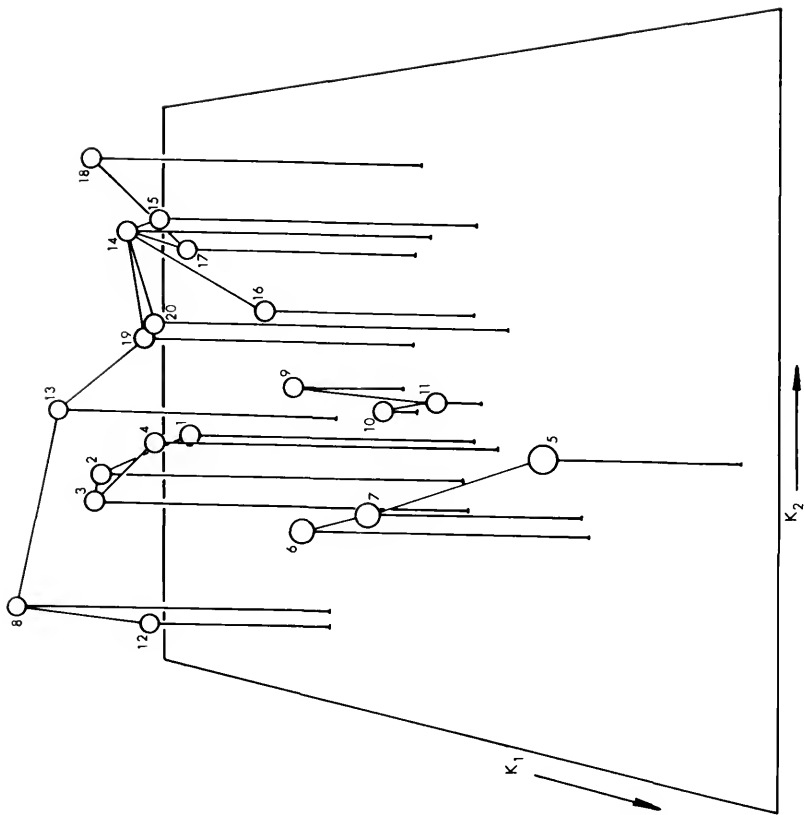




Figure 3. Projection of population means for females on the first three canonical variates;  $K_3$  vertical. Nearest neighbors by generalized distance ( $D^2$ ) are linked.

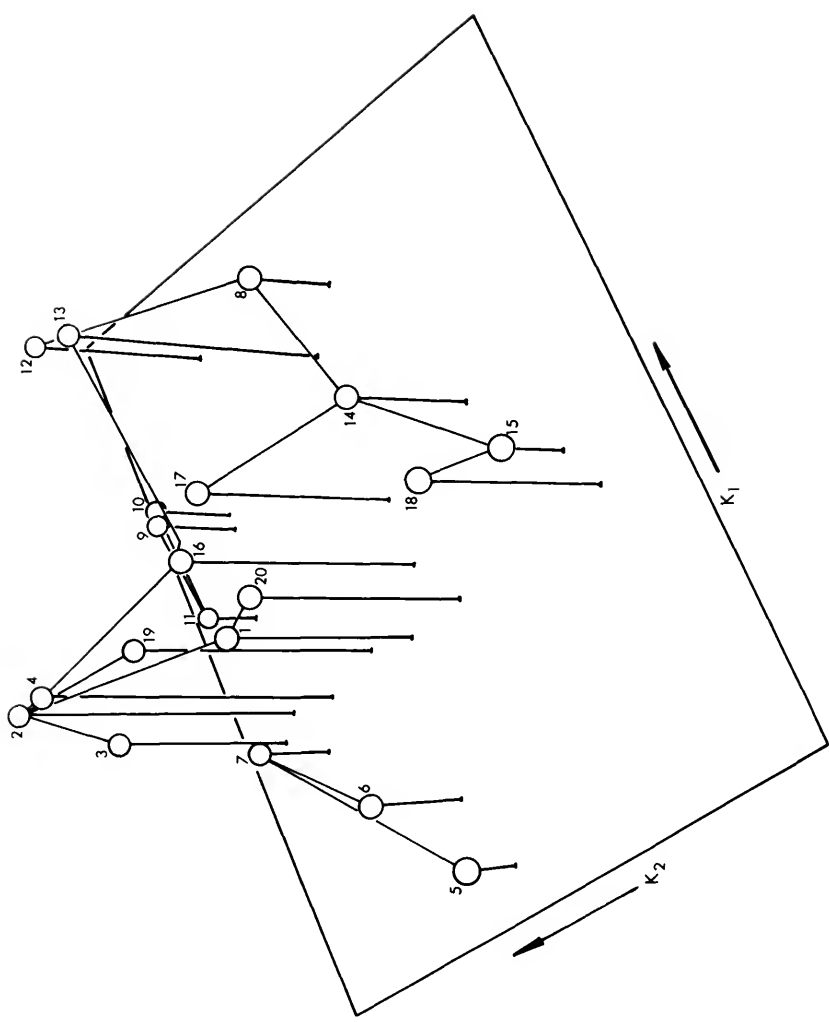


TABLE 12. Generalized Distances ( $D^2$ ) Between

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>
1	0.0									
2	4.24	0.0								
3	6.82	2.24	0.0							
4	6.46	4.38	4.30	0.0						
5	17.85	20.26	18.21	13.22	0.0					
6	11.18	8.28	8.12	7.77	11.54	0.0				
7	9.73	10.38	9.00	7.31	9.94	3.42	0.0			
8	22.82	15.83	14.52	16.02	39.62	21.53	24.02	0.0		
9	16.74	15.17	14.58	13.89	26.55	17.83	12.96	19.48	0.0	
10	13.30	17.80	21.49	17.36	23.32	20.21	14.57	24.32	8.57	0.0
11	16.31	15.96	15.50	13.59	15.03	16.70	11.17	25.72	7.56	7.12
12	20.72	15.99	20.73	20.04	41.33	23.34	22.54	13.31	19.75	16.26
13	15.33	11.59	12.16	12.15	33.50	22.52	21.98	11.18	13.63	15.30
14	14.86	11.85	12.12	8.90	22.63	14.92	15.36	20.70	9.86	17.62
15	16.39	17.34	18.37	11.44	22.57	15.83	15.86	25.14	17.70	19.99
16	12.03	9.38	10.45	9.18	15.72	10.79	11.42	21.30	8.90	11.29
17	12.61	9.44	12.55	10.77	22.90	16.19	16.76	22.74	8.90	11.67
18	12.18	11.96	17.05	11.90	26.79	21.13	21.27	30.09	18.53	18.06
19	7.90	8.04	8.25	8.38	25.57	16.98	12.74	20.77	7.54	13.33
20	13.90	11.28	9.12	6.84	15.01	12.74	11.23	24.51	17.41	22.96

Sceloporus woodi Populations (Males)

<u>11</u>	<u>12</u>	<u>13</u>	<u>14</u>	<u>15</u>	<u>16</u>	<u>17</u>	<u>18</u>	<u>19</u>	<u>20</u>
0.0									
23.13	0.0								
17.29	14.24	0.0							
14.08	28.30	10.63	0.0						
19.54	33.17	19.63	5.37	0.0					
7.67	24.74	12.00	4.65	10.63	0.0				
11.01	23.47	12.21	4.56	11.13	6.22	0.0			
21.17	29.71	14.98	6.14	8.30	10.30	5.02	0.0		
14.35	22.54	9.60	7.45	15.16	7.80	8.51	10.58	0.0	
15.94	28.94	12.72	5.66	11.27	8.46	12.28	12.32	9.49	0.0

TABLE 13. Generalized Distances ( $D^2$ ) Between

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>
1	0.0									
2	6.08	0.0								
3	10.29	6.41	0.0							
4	6.28	2.74	8.03	0.0						
5	15.64	20.53	22.06	19.10	0.0					
6	9.07	12.97	13.08	15.17	11.75	0.0				
7	9.12	9.30	7.24	11.07	10.09	5.88	0.0			
8	18.22	23.73	25.33	24.06	38.20	25.58	20.80	0.0		
9	11.53	12.37	15.98	16.90	29.55	20.99	14.03	15.26	0.0	
10	18.21	15.46	14.82	17.38	28.28	26.94	15.16	20.18	9.00	0.0
11	13.91	12.65	13.79	15.99	20.41	20.93	10.41	22.09	5.75	5.71
12	16.95	18.18	22.56	17.71	39.77	31.97	21.05	10.62	15.38	12.64
13	18.34	16.85	24.72	19.42	34.86	32.78	23.05	14.52	16.92	17.14
14	9.83	16.02	16.68	16.04	25.52	19.27	15.62	10.56	14.20	15.16
15	11.88	22.01	21.59	20.18	18.30	17.75	18.82	16.71	18.89	17.51
16	7.20	7.37	16.29	5.64	16.73	14.61	12.35	17.29	14.34	15.89
17	7.14	10.49	13.30	7.15	23.37	19.68	14.20	15.46	12.34	12.39
18	12.63	20.31	23.87	18.71	26.02	19.51	23.43	24.90	23.71	23.43
19	9.19	8.90	12.97	10.96	22.61	16.25	15.12	26.84	13.89	13.66
20	8.08	10.68	13.14	12.01	16.28	17.72	13.79	23.06	19.68	17.54

Sceloporus woodi Populations (Females)

<u>11</u>	<u>12</u>	<u>13</u>	<u>14</u>	<u>15</u>	<u>16</u>	<u>17</u>	<u>18</u>	<u>19</u>	<u>20</u>
0.0									
18.04	0.0								
19.21	13.74	0.0							
13.65	16.70	13.30	0.0						
18.66	24.07	21.30	6.02	0.0					
14.80	15.86	12.30	10.72	12.15	0.0				
12.04	14.33	14.11	6.68	11.07	6.76	0.0			
23.98	29.20	24.32	8.47	7.83	12.90	11.36	0.0		
11.66	23.36	17.04	15.33	17.24	10.82	11.77	12.94	0.0	
14.10	22.66	12.56	8.09	12.67	11.83	10.35	13.34	10.28	0.0

group (16, 17, 19, and 20) and the partial separation of these from the remaining Atlantic Coast populations (14, 15, and 18). The Southern Lake Wales Ridge populations (9, 10, and 11) still form a unit. Population 6 is farther from its neighboring population 7 and closer to population 5. Populations 8, 12, and 13 are again outliers. Certain discrepancies between the canonical plot and nearest neighbor by  $D^2$  are obvious. Several populations form pairs, 5 and 6, 9 and 10, 16 and 17, on the canonical plot without being nearest neighbors in hyperspace. Examination of distance rankings (Table 13) usually shows these pairs to be second or third nearest neighbors, so it can be stated that this canonical plot does not seriously distort the configuration in hyperspace.

When the populations were plotted on a combination of the fourth, fifth, and sixth canonical variates, formless scatters of points were obtained that displayed only traces of the correspondence between phenetic and geographic affinities of the previous canonical plots. Some of the discrepancies between proximity on the first three canonical axes and generalized distance were resolved, but many more were generated. The canonical variates after the third apparently represent the residue of phenetic variation not related to geographic proximity, i.e., the independent evolutionary tack of each population. Thus geographic proximity, whether because of gene flow or similar ecological conditions, is associated with about half the phenetic variation observed. A multivariate analysis of variance showed the phenetic differences among geographic regions to be statistically significant.

Figures 4 and 5 show the influence each character would have on the first two canonical variates if it varied alone. Comparison of this information with the projections of the population means on the canonical axes (Figure 2 and Figure 3) exposes the major trends of variation. Among the males, populations with low  $K_1$  and  $K_2$  values have longer shanks and fourth toes and to a lesser degree longer foreleg and hind feet. High values on  $K_2$  are associated with longer thighs. Populations with large  $K_1$  but small  $K_2$  values are characterized by a larger number of dorsal scales and longer auricular lobules. Low values on  $K_3$  correlate particularly with larger numbers of femoral pores.

Character vectors among the females are similar in general direction but not in magnitude; the limb measurements do not so greatly dominate the canonical variates. Populations with large values on  $K_1$  tend to possess longer shanks, hind feet, and fourth toes, while large values on  $K_2$  are particularly associated with a larger number of right medial supraoculars. Small  $K_2$  values tend to characterize populations possessing more fifth toe lamellae and longer heads, and small values on  $K_3$  are correlated with a high dorsal scale count.

The average regional generalized distances separating populations are given in Table 14 for four regions. The same trend is evident in both sexes. The Ocala National Forest populations are most similar, but little more so than populations from the Southern Lake Wales Ridge. The Northern Lake Wales-Bartow Ridge populations are most distinct, and the Atlantic Coast populations show an intermediate degree of separation from each other.

Color variation in life is not extensive in S. woodi, but some trends are noticeable. The Marco Island population (13) differs most



Figure 4. For each character the vector shows the direction and magnitude of its influence on the first two canonical variates of the males. See Table 2 for character code.

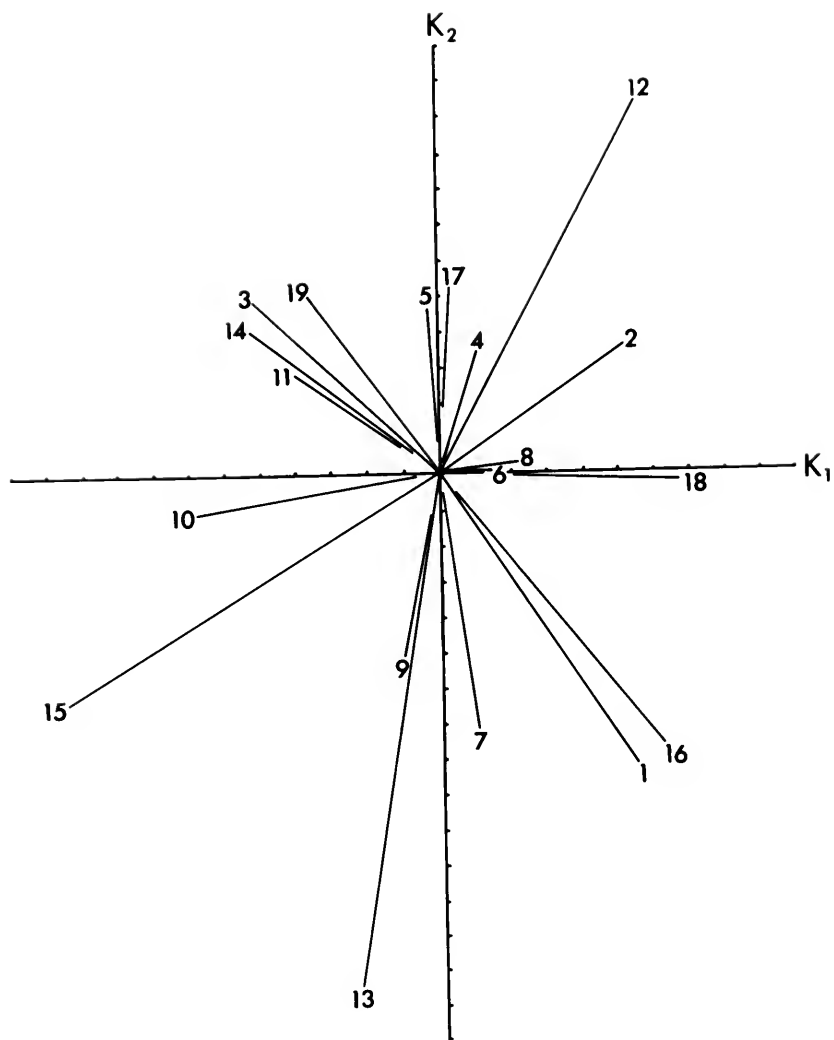


Figure 5. For each character the vector shows the direction and magnitude of its influence on the first two canonical variates of the females. See Table 2 for character code.

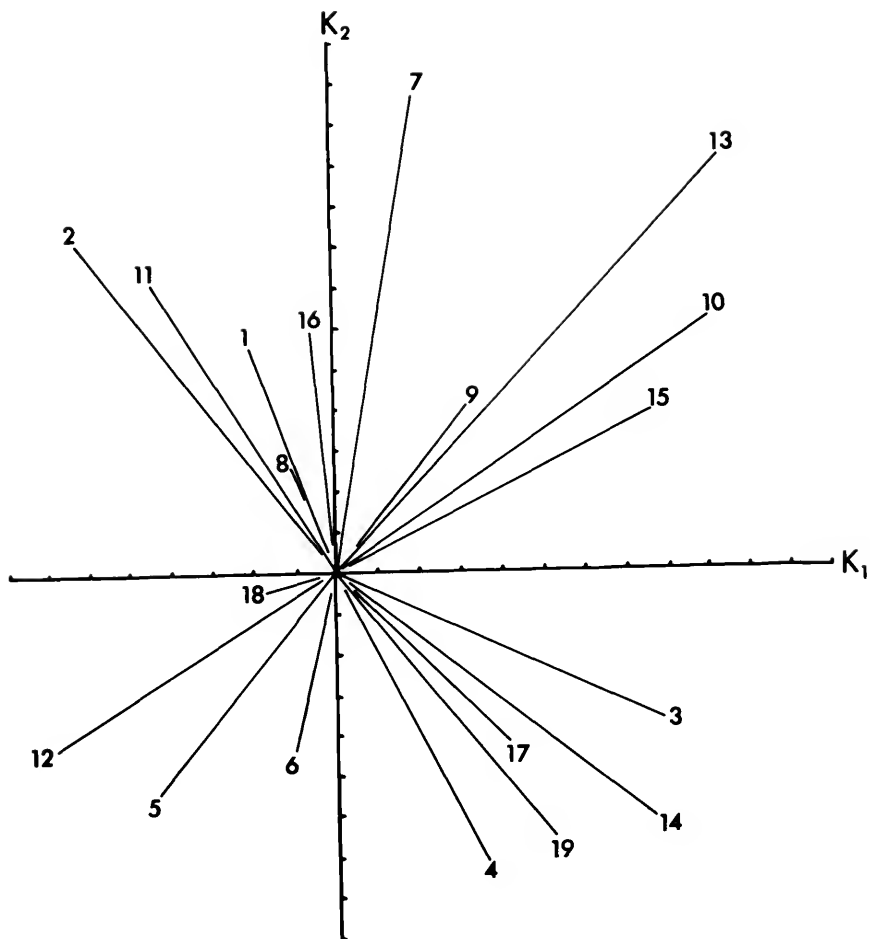


TABLE 14. Mean Regional Generalized Distances Between Populations

	Ocala National Forest (1,2,3,4)	Southern Lake Wales Ridge (9,10,11)	Atlantic Coast (14,15,16,17, 18,19,20)	Northern Lake Wales and Bartow Ridges (5,6,7,8)
Males	4.74	7.75	8.63	18.35
Females	6.64	6.82	10.89	18.72

strongly by being notably pallid and by a tendency for the males to retain the dorsal markings usually limited to juveniles and females. Since the Marco Island scrub lacks the normally dense Pinus clausa overstory and has instead only widely spaced Caribbean pine (Pinus caribaea), the light coloration may be an adaptation to higher ambient illumination and thus an example of the phenomena described by Gloger's rule (H. W. Campbell, pers. com.). Generally, specimens from the Southern Lake Wales Ridge lack the reddish cast seen in woodi to the north and east and are grayer. The dorso-lateral dark stripe of males is least well-defined on the Lake Wales Ridge, more prominent in the Ocala National Forest, and very conspicuously dark and straight-edged on the Atlantic Coast.

### Discussion

#### Phenetic Affinities

For mean character states of the characters considered, a pattern of geographic variation exists among S. woodi populations. Northern and Southern Lake Wales Ridge populations form distinct assemblages with affinities between the northern populations and the Bartow Ridge woodi. Populations from the Ocala National Forest represent another phenetic unit with close affinities to the Atlantic Coast populations and more distant ones to woodi from the Northern Lake Wales Ridge. The two Gulf Coast populations show similarities but are not particularly close.

### Adaptive Interpretation of Variation

The adaptive meaning of variation in most of the characters is cryptic and probably comprehensible only through extensive ecological and genetic knowledge of each population. However, two of the stronger variational patterns are interpretable, at least qualitatively. Elongation of the limbs is generally considered a cursorial adaptation in terrestrial lizards (Kramer, 1951; Snyder, 1962). Examination of a character correlation matrix based on woodi population means shows that mean lengths of the shank, hindfoot, fourth toe, and, to a lesser degree, thigh and foreleg tend to vary as a unit; this suggests that running ability of these ground-dwelling lizards is more important in some populations. Generally, a correspondence exists between a tendency to longer legs and my own subjective impression of the openness of the habitat. Whether this characteristic of a locality is consistent over long periods is unknown. The understory at localities 5, 6, 7, and 20 is dense and continuous and oak leaves carpet the ground, whereas localities 8, 9, 11, 12, and 13 have oaks and other shrubs scattered as clumps among considerable expanses of bare sand. Other localities are intermediate. Since the typical escape behavior of S. woodi is rapid flight into a tangle of shrubs, cursorial ability would reasonably be at a premium where cover is minimal. Additionally, the Florida Scrub Jay (Aphelocoma c. coerulescens), probably a major predator of S. woodi, occurs most abundantly in open scrub (Westcott, 1970).

Although many lizards exhibit geographic variation in dorsal scale number, the adaptive nature of the variation is not understood. Hellmich (1951) and Soule (1966) associated increase in dorsal scale

number and the concomitant decrease in scale size in Liolaemus and Uta, respectively, with climates subjectively assessed as progressively cooler, but actual climatological data were not available for the regions concerned. Existence of such data for Florida allows statistical evaluation of any association between dorsal scale number and environmental temperature in S. woodi.

The January, August, and annual temperature regimes for each woodi population were estimated by averaging the corresponding mean temperatures over the ten-year period 1961-1970 at the nearest weather station (Climatological Data, ESSA). Table 15 gives these overall means and indicates the assignment of weather stations for the lizard populations. Since the Ocala National Forest was represented by a single weather station, an overall mean dorsal scale number was used for populations 1, 2, 3, and 4; for the same reason, populations 9, 10, and 11 were lumped. In each sex, significant negative product-moment correlations were obtained between mean dorsal scale number and both mean annual temperature (males:  $r = -.467$ ,  $p = .038$ ; females:  $r = -.549$ ,  $p = .012$ ) and mean January temperature (males:  $r = -.435$ ,  $p = .052$ ; females:  $r = -.543$ ,  $p = .017$ ). The correlations with mean August temperature were negative but not significant (males:  $r = -.264$ ,  $p = .174$ ; females:  $r = -.226$ ,  $p = .212$ ). Hellmich (1951) and Soule (1966) hypothesized that variation in dorsal scales is based on thermoregulatory adaptation and specifically that, other things being equal, a lizard with smaller scales retains heat more effectively. In the absence of heat-flux data, that interpretation seems reasonable for the present case. Variation in mean August temperature in peninsular Florida is very small and accounts for only



TABLE 15. Assignment of Temperature Data to S. woodi Populations

<u>Population</u>	<u>Weather Station</u>	Temperature ( $^{\circ}$ F)		<u>Annual <math>\bar{x}</math></u>
		<u>January <math>\bar{x}</math></u>	<u>August <math>\bar{x}</math></u>	
1,2,3,4	Ocala	57.6	82.0	71.1
5	Winter Haven	60.4	81.5	72.0
6	Lake Alfred	59.0	81.6	71.1
7	Mountain Lake	60.3	81.5	71.7
8	Avon Park	62.0	82.9	73.3
9,10,11	Lake Placid	61.2	81.9	72.4
12	Naples	64.4	82.1	73.6
13	Everglades	64.3	82.2	74.1
14	Titusville	59.6	81.7	71.5
15	Melbourne	60.7	80.9	71.8
16	Vero Beach	61.7	81.2	71.9
17	Ft. Pierce	62.1	81.1	72.2
18	Stuart	63.9	82.1	73.4
19	West Palm Beach	65.1	82.3	74.2
20	Pompano Beach	67.1	82.7	75.2

a small percentage of the variation in mean dorsal scale number; however, mean January temperatures are associated with approximately 25 percent of mean dorsal scale variation and range from those forcing S. woodi into frequent quiescence in north and central Florida to those of coastal south Florida, which are high enough for sustained activity. Thus more numerous, smaller dorsal scales may function in extending the temporal range of woodi in localities marginally suited to winter activity. Obviously, the majority of dorsal scale variation remains unaccounted for.

#### Dispersal History

The location of scrubs has been correlated by Laessle (1958) with such ancient marine features as dunes, beaches, bars, and submerged hilltops. Scrub grows on siliceous sands that were very well sorted by wind or marine currents when sea levels were higher than at present. Under the condition that these fossil marine features can be dated, this correlation allows educated speculation regarding the history and dispersal of Sceloporus in Florida. Unfortunately geologists do not yet agree on the number or ages of the higher sea levels. Basing their interpretations largely on topographic data, Cooke (1945) defined seven marine terraces and MacNeil (1950) four (Table 16), but both considered all the terraces formed during Pleistocene interglacials. Employing physiographic and stratigraphic data, Alt and Brooks (1965) recognized five ancient shorelines; they believed the oldest to be Miocene and suggested that Pleistocene sea levels were never higher than 70-80 feet above present. More recently both Alt (1967) and

TABLE 16. Estimated Ages

<u>Terrace Elevation (in feet)</u>	<u>Sea</u>	<u>Authority</u>	
		<u>Cooke (1945)</u>	<u>MacNeil (1950)</u>
270		Aftonian	
200-250		Yarmouthian	
170		Yarmouthian	
140-150	Okefenokee		Yarmouthian
90-100	Wicomico	Sangamon	Sangamon
70-80		Sangamon	
45		Sangamon	
25-30	Pamlico	Mid-Wisconsin	Mid-Wisconsin
16-18	Princess Ann		
5-10	Silver Bluff		Post-Wisconsin

## of Florida Marine Terraces

<u>Authority</u>			
<u>Alt and Brooks (1965)</u>	<u>Alt (1967)</u>	<u>Brooks (1968)</u>	<u>Brooks (pers. comm., 1971)</u>
Late Miocene	Late Miocene	Late Miocene	Late Miocene
		Late Pliocene	Late Pliocene
Pliocene	Pliocene	Aftonian	Aftonian
Late Pliocene		Yarmouthian	Yarmouthian
Early Pleistocene	Aftonian	Yarmouthian	Yarmouthian
Pleistocene	Yarmouthian	Sangamon	Yarmouthian
		Mid-Wisconsin	Sangamon
	Sangamon		Sangamon

Brooks (1968; pers. comm., 1971) have separately modified their earlier scheme; the important difference between the modifications is the age of the 90-100 terrace. Alt dates it as Pliocene, while Brooks believes it marks the first interglacial period, the Aftonian. Of course, later interglacials would be correlated with higher sea levels by Brooks than by Alt. Because the interpretations of Alt and Brooks are grounded on more extensive evidence than those of Cooke and MacNeil, they will be followed below, specifically in the form of Brooks (pers. comm., 1971).

There is no doubt on morphological grounds that S. woodi is a member of the undulatus group of Smith (1938) and, as will be shown later, woodi hybridizes sparingly with undulatus where their distributions meet now. However, a distributional peculiarity suggests that woodi might not have been derived directly from S. undulatus undulatus in Florida; this is the absence of undulatus in the seven islands of sandhill vegetation that are surrounded by scrub in the Ocala National Forest. The north-south oriented ridge that runs through the northern portion of the Ocala National Forest is mostly covered by scrub, but Hughes, Salt Springs, Kerr, and Riverside Islands are extensive stands of sandhill vegetation largely above 90 feet and with some elevations near 150 feet. The three eastern sandhill islands, Pats, Syracuse, and Norwalk, are between 90 and 50 feet in elevation. Laessle (1958) suggested the scrub bordering the western edges of Salt Springs, Kerr, and Riverside Islands grows on sand sorted by marine currents when sea levels were 150 and 90 feet above present and that these sandhill islands and their lower neighbors to the east were completely surrounded by scrub after extensive dunes formed on the shore of the sea 25 feet above present (near the present

west shore of Lake George) and migrated westward. Brooks (pers. comm., 1971), however, believes these paleodunes, presently vegetated by scrub, developed as aeolian deposits under more xeric soil conditions when the water table was lower because of lowered glacial sea levels; he considers them Kansan, Illinoian, and Wisconsin in age.

Lack of undulatus in the eastern sandhill islands is not conclusive since Laessle (1958) believes dunes could have covered them, killing the vegetation, and then moved on, so that sandhill vegetation may not have been continuously present in these islands. However, the western four islands were presumably never overblown and probably have been vegetated by open forests since the earliest Pliocene, when the sea which covered the area during the Miocene retreated. The western sandhill islands were not definitely connected with the mainland until the Nebraskan glaciation, but they would have joined it during proposed low sea levels during the Pliocene (Webb and Tessman, 1967). Certainly during all the glacial periods and during the late Yarmouthian interglacial these islands would have joined the emergent peninsula and would doubtless have been colonized by undulatus if it were present in Florida then. During the Yarmouthian, following Laessle, or perhaps earlier, following Brooks, the sandhill islands were surrounded by scrub-covered dunes, which have prevented entrance by undulatus both by offering unsuitable habitat and by harboring woodi from which undulatus is not reproductively isolated. The only fossil undulatus from Florida is of uncertain age but is no older than Sangamon (Brattstrom, 1953; Auffenberg, 1956).

In coloration, proportions, and in ground-dwelling tendencies, woodi is nearer the southwestern members of the undulatus group than

to S. u. undulatus. Consequently, and in view of the possible late arrival of S. u. undulatus in Florida, woodi may have been derived from a form close to S. virgatus or S. u. consobrinus that invaded Florida from the southwestern United States or northern Mexico. Considerable biogeographic and paleontological evidence indicates biotic exchange between this region and Florida from Oligocene through Pleistocene (Neill, 1957; Auffenberg and Milstead, 1965). Pitelka (1951) suggested that the Florida Scrub Jay (Aphelocoma c. coerulescens), the other vertebrate most closely associated with scrub, reached Florida from the southwest in the Pliocene during a maximum expansion of sclerophyll woodland. The progenitor of woodi probably entered the peninsula at the same time.

Laessle (1958) linked no scrub to the 200-250-foot terrace, but that on the slopes of Red Hill at the Archbold Biological Station may be on sands sorted during the Miocene (H. K. Brooks, pers. comm., 1971). Recession of the Late Pliocene 140-160-foot sea left considerable expanses of well-sorted sand along the Southern Lake Wales Ridge and smaller deposits in the northern portion of the Ridge and in the present Orange County area (scrubs 71-74). Development of the scrub as a plant community probably took place on the Lake Wales Ridge in the Pliocene; endemism among scrub plants is highest there today (John D. Beckner, pers. comm., 1971). Presumably woodi arose there at the same time in response to the ecological opportunity offered by the scrub to a ground-dwelling sit-and-wait feeder.

The enigmatic present distribution of woodi, with central and peripheral habitats colonized but suitable areas in between unoccupied, could conceivably have arisen in two ways. The distribution of scrub

could have formerly been much more extensive allowing expansion of the lizard's range followed by extinction in many relict scrubs. Though it is known that more xeric climates have existed in Florida, there is no evidence for assuming that most scrubs were parts of a single continuous unit. Further, the hypothetical extinctions would have occurred non-randomly. An alternative and much more probable hypothesis for generating the present distribution requires dispersal by woodi to some scattered scrubs through other vegetation types. This dispersal has been impeded by the lizard's habitat requirement of ground largely free of herbaceous vegetation. S. woodi is never found in hammocks or low flatwoods and in this study has been seen in only a few locations with sandhill or scrubby flatwoods vegetation (Laessle, 1942). These were exceptional in having very sparse wiregrass (Aristida; Sporobolus) growth and were closely adjacent to scrub. Besides scrub, the only extant vegetation in which woodi could have maintained populations even temporarily would have been sandhills or scrubby flatwoods so sterile, dry, or subject to frequent ground fires that little wiregrass existed.

Due to the short distances separating scrubs on the Lake Wales Ridge, woodi spread to most of them, including some that developed on sands of the 90-foot Wicomico sea. Slight morphological differences developed between Southern Lake Wales Ridge populations and those toward the northern end of the Ridge, while more isolated populations diverged uniquely. By an unknown route, woodi reached several small scrubs (43, 44; Figure 1) between Lake Dora and Lakes Harris and Eustis and probably from there colonized the extensive scrub of the present Ocala National Forest. This large population became slightly differentiated from those of the Lake Wales Ridge.



The lack of woodi in a scrub is not proof the lizard has not been there. Extinction of small populations is a possibility because stands of Pinus clausa, which has largely serotinous cones (Laessle, 1968), must burn by crown fires each several decades to be maintained. Nevertheless, in view of the existence of numerous scrubs without woodi and of its presence in some very small scrubs, poor dispersal, stemming from habitat restriction, must in many cases be responsible for absence of the species. The absence of woodi in certain scrubs is particularly astonishing because of their great age, large size, or proximity to woodi populations. Scrubs 71, 72, 73, and 90 were submerged hilltops in the Okefenokee Sea and so have been exposed for over 2 million years. Scrubs 64, 88, and 91 seemingly afford substantial targets, since each is several square miles in area. Though less than 5 miles from two woodi populations (44 and 45), scrub 89 is separated from them by cypress sloughs. It lacks the lizard. Only a narrow strip of sandhills and Alexander Springs Creek with its half-mile-wide hammock prevent the colonization of scrub 67. And scrub 65 is less than two miles, through sandhills, from the route (now followed by SR-19) by which woodi probably reached the Ocala National Forest scrub.

Derivation of the Atlantic Coast populations from Ocala National Forest woodi is suggested by their phenetic similarities. Given the lizard's apparent ineptitude at overland dispersal, and the want of any intervening relict populations, dispersal may have been by rafting. When the Pamlico Sea stood at full height, the eastern edge of the Ocala National Forest scrub was very near sea level and across a lagoon that occupied the present St. Johns River valley a chain of barrier

islands consisting mainly of dunes, undoubtedly covered with scrub, began some 50 miles to the southeast and extended south for about 125 miles (MacNeil, 1950). If individuals from the Ocala National Forest population had been set adrift, south-flowing currents (Laessle, 1958) would have carried them through a lagoon bordered on the east by over 100 miles of suitable habitat. During those interglacials when the sea did not cover the Atlantic scrubs, the Ocala National Forest scrub was the only woodi-inhabitated scrub at seaside. Once a beachhead was made, the present range on the Atlantic Coast would have been readily achieved because of the almost continuous distribution of scrub there. Dispersal north of Titusville has apparently been prevented by low flatwoods.

Spread of woodi to the Gulf Coast is less understandable. It must have been post-Silver Bluff, for the colonized scrubs are merely 10 feet above sea level. The present flatwoods between these scrubs and the scrub at the south tip of the Lake Wales Ridge frequently approach the physiognomy of scrubby flatwoods; survival of woodi in these may have been possible during more xeric times. Inasmuch as Marco Island is a Wisconsin dune (H. K. Brooks, pers. comm., 1971), the woodi there are very recently derived from those near Naples. The reason for their rapid divergence is not apparent, but may relate to the Marco scrub being floristically atypical, lacking Pinus clausa and containing a number of Antillean plant species.

### Comparison with Other Species

Patterns of distribution and differentiation of several other animals confined to the Florida xeric plant associations have been described and may be compared with those of the present study. First, if presence of woodi on the coasts is regarded as fortuitous, dispersal overland to available xeric habitats has been poor by woodi and Neoseps reynoldsi (Telford, 1959; 1962) but good by the scarabaeid genus Mycotrupes (Hubbell, 1954), the lycosid species-pair Geolycosa patellonigra-G. xera (McCrone, 1963), Stilosoma extenuatum (Highton, 1956), Eumeces egregius (Mount, 1965), Tantilla relicta (Telford, 1966), and Rhineura floridana (Zug, 1968) since these forms occur between the central highlands and the coasts. A geographic range identical to that of woodi in the central highlands implies that Neoseps finds poorly drained plant communities as great a barrier as does woodi, but why other fossorial reptiles do not is unknown. Though the direction of causality is unclear, effective dispersal may be related to a second observation: that only woodi and Neoseps show no evidence of fragmentation into Lake Wales Ridge and north Florida populations during the higher (>100 feet) stands of sea level. Possibly they never reached north Florida because of poor dispersal ability or perhaps some of the other species mentioned invaded the regions centered on Orange and Hernando Counties more readily from north Florida than from the Lake Wales Ridge.

Quantitative techniques for comparing the degree of intraspecific differentiation between species scrutinized for different characters are yet to be developed, and qualitative assessments are very subjective. Nevertheless, though most investigators of variation in the xeric

Florida species cited above have not been reluctant to apply formal nomenclature to infraspecific taxa, it appears that such taxa are fairly well-defined in their organisms. This is not the case for S. woodi. A powerful multivariate technique and adequate sample sizes have permitted detection of differentiation, but differences among the means (Tables 4 and 5) are generally minuscule and most populations show nearly the whole range of variation in each character. Even on the canonical axes, individuals are not clustered closely about their population mean but overlap greatly with individuals of other populations. The weak development of morphological differences, even under conditions of isolation, is probably a consequence of both the uniformity of scrub and the restriction of woodi to it. The extensive radiation of insular Uta populations, isolated in the Gulf of California for periods equivalent to those of woodi populations, occurred on islands differing considerably in ecological conditions (Soule, 1966). Secondly, isolated populations of species with broader habitat tolerance would be more likely to diverge by making dissimilar adaptive compromises with geographic regions that differ in proportional representation of habitats. Differentiation in Rhineura may have resulted from such an effect (Zug, 1968). The only other Florida reptile examined and found to lack strong geographic variation is Rhadinaea flavilata (Myers, 1967), which is limited to a single habitat, pine flatwoods.

#### Gene Flow and Differentiation

Ehrlich and Raven (1969) began what surely will be a fruitful polemic by suggesting that gene flow, unlike stabilizing selection, is usually unimportant in preventing divergence among populations.

One line of their evidence was the small degree of divergence in many organisms between colonies that have lacked gene flow for great periods. However, these observations are without controls that would allow divergence among populations connected by gene flow to be compared with that among isolated populations. Further, degree of divergence as assessed subjectively by systematists with varying taxonomic philosophies seems unnecessarily qualitative given the availability of multivariate methods which measure distances in character space. Metter and Pauken (1969) showed that differentiation, expressed as  $D^2$ , generally corresponds with paleoecological changes that have restricted gene flow in Ascapus truei.

Although it is clear from the small absolute differences between isolated woodi populations that strong stabilizing selection must be operative, the degree of divergence among the populations of several regions (Table 14) is noteworthy since it can be correlated with the likelihood of gene flow. Populations 1-4 are parts of one continuous population extending throughout the scrub of the Ocala National Forest; no physical or ecological barriers separate these populations, which average 10 miles apart. Populations 9-11 were similarly connected prior to the interposition of citrus groves in recent decades. Their average physical separation is 7 miles. Gene flow among populations in both these sets is restricted only by distance. Kerster (1964) estimated neighborhood area in Sceloporus olivaceus to be approximately 425 m in diameter. Populations 14-20 are from a linear series of scrubs partly separated by ecological and physical barriers presently, but probably more nearly continuous during the Wisconsin glaciation. They average 27 miles apart. Populations 5-8 are from scrubs completely isolated by sandhills and flatwoods and about 15 miles apart.

Inferentially, the four regions can be ranked by amount of gene flow between the populations examined: Ocala National Forest and Southern Lake Wales Ridge, high; Atlantic Coast, moderate; Northern Lake Wales Ridge, extremely low. The ordination is the inverse of that for differentiation of the populations and implies that gene flow retards differentiation.

Two objections to that implication can be raised. First, although the regions seem equal in the degree of similarity of their scrubs, there are no data to prove the range of selection regimes does not differ between the regions. Second, the regions vary in the time that has been available for differentiation. Populations 5-8 are probably Kansan in age (1.2 million years) though 5 could be Nebraskan (1.5 million years). Populations 1-4 and 14-20 probably date from the Yarmouthian (0.5 million years) with the latter set somewhat the younger. Thus, populations 5-8, having had more than twice as long to diverge, might be expected to be less similar. On the other hand, populations 14-20, in spite of being younger than populations 1-4, are more widely separated phenetically. And populations 9-11, being Pliocene in age, are older than populations 5-8; nevertheless, they are more alike. Finally, it is the populations most isolated from genetic exchange with other populations (5, 12, and 13) that are the most phenetically distinct; however, here the founder effect cannot be discounted as a cause. Obviously data from a single species do not substantiate the conservative effect of gene flow; numerous other studies are needed and material for them might be most readily found among reptiles of montane western North America.

## CHAPTER II

### THE PHENETICS AND ECOLOGY OF AN EXTRAORDINARILY NARROW HYBRID ZONE

#### Introduction

Hybrid zones between races and semi-species hold considerable interest for evolutionary biology. They may be examined from the point of view of the selection pressures that adapt each population to its geographic range (Dice and Blossom, 1937; Blair, 1943). More importantly though, the width and age of the hybrid zone and the mechanisms which restrict gene flow across it are of particular relevance to understanding the origin and evolution of ethological isolating mechanisms.

In this chapter three very narrow hybrid zones between the iguanid lizards Sceloporus woodi and S. u. undulatus are considered. Sceloporus woodi is normally restricted to the sand-pine scrub association of the Florida peninsula. S. u. undulatus inhabits dry, open forests in the southeastern United States; in Florida it is most abundant in the longleaf-pine/turkey-oak association (hereafter termed sandhill vegetation). Laessle (1942) defined these associations, and the striking differences in physiognomy between them have been detailed (Laessle, 1958; 1968). The overstory of sand-pine scrub consists of

only Pinus clausa, normally in even-aged populations. The understory is a dense thicket of sclerophyllous shrubs and is dominated by oaks which range in height from one-half to two meters. The ground surface is a mosaic of bare sand and thin, but well-compacted, leaf litter over which herbaceous growth is extremely sparse. Pinus australis was the dominant tree in primeval sandhill vegetation, and Quercus laevis was both less common and lower in height. However, logging and fire control have favored Quercus, and it is presently the more abundant tree in most stands of sandhill vegetation. In contrast to sand-pine scrub, shrubs are relatively few and scattered while herbaceous ground cover is well-developed. The herbaceous layer, composed mainly of wiregrasses (Aristida; Sporobolus) but with many species of forbs, combines with fallen pine needles and oak leaves and forms a loose cushion that varies in depth depending on the recency of ground fire. Both associations occur on well-drained soils and often are adjacent. The transition between them usually takes place over a distance of only a few meters; in some places, one can place a foot in both associations simultaneously.

The three hybrid zones studied are along ecotones in the Ocala National Forest. The Lake Eaton ecotone is near the intersection of FS-79A and FS-96, about .5 mile south of Lake Eaton (Section 26, T. 14 S., R. 24 E.). The Forts Bear Hole ecotone is south of FS-95 about 1.5 miles southwest of Forts Bear Hole (Sections 17 and 18, T. 16 S., R. 25 E.). The Alexander Springs ecotone parallels SR-445 .3 mile to its west and about 2.0 miles southwest of Alexander Springs.



### Methods

The identification of an individual as belonging to one of two groups is a problem best solved by the use of a linear discriminant function. The function is generated using data taken from individuals which have been classified into groups a priori. It is then used to classify unknown individuals. In order to distinguish unambiguously between individuals of the two species that were from populations unexposed to hybridization, a linear discriminant function based on ten characters was computed using the BMD 04M program (Dixon, 1968). For each sex of S. undulatus, twenty-five specimens from Alachua and Marion Counties, Florida, comprised the parental sample. The parental sample for each sex of S. woodi was twenty-five specimens from the central portion of the scrub of the Ocala National Forest. The discriminant function allows a value,  $Z$ , to be obtained for each individual by summing the products of each measurement and the corresponding discriminant coefficient. If the discriminant function is effective, there is no overlap in the distributions of  $Z$  values of the two species. Calculation of  $Z$  values for individuals from the ecotones permits evaluation of their morphological affinities.

Table 17 lists the characters included in the discriminant function. All were counts except for the last, which is the sum of values for five qualitatively scored characters; these characters were the degree of contact between the first canthal and the lorilabials on either side, the degree of reduction to one row of scales between the subocular and the supralabials, and the size of the auricular lobules. Possible values for each character ranged from 0-2, with the low values assigned to the condition typical in undulatus and the high values to

TABLE 17. Description of Characters in the Discriminant Function

1. Femoral pores: sum of both sides
2. Subdigital lamellae of hind fifth toe: sum of both sides
3. Circumorbitals: sum of both sides
4. Lateral supraoculars: sum of both sides
5. Subdigital lamellae of right hind fourth toe
6. Supradigital lamellae of right front fourth toe
7. Infratarsals on right foot between base of second toe and base of fifth toe
8. Infratibials on right leg between base of fifth toe and knee
9. Mid-dorsal scales between interparietal and hind margin of thigh
10. Qualitative head scalation: value from 0-10

that in woodi. Several metric characters were examined but could not be used in the discriminant function, since adjustment for differences in body size would require a priori a choice between the regressions of the two species. Additionally, the color pattern of each specimen was scored subjectively on a five-point scale in regard to its approach to a pattern typical of one of the species. A pattern typical of woodi was scored as 5 and one like that of undulatus was scored as 1.

In order to identify the factors that minimize gene flow across the ecotone, several behavioral and ecological characteristics of each species were studied. For each species, male choice tests (Ferguson, 1969) were made during the middle of the breeding season in a non-hybridizing population and in a population adjacent to a hybrid zone. These populations were near Gainesville, Florida, and near the Alexander Springs ecotone, respectively, for undulatus. They were located west of FS-88, about 1.5 miles south of FS-75, in the Ocala National Forest (Section 32, T. 12 S., R. 25 E.) and near the Lake Eaton ecotone, respectively, for woodi. An adult male encountered in the field was simultaneously offered an adult female of each species. Each female was tethered at the end of a thin pole nine feet long. The females were of equal size and were positioned so that they were equally exposed to the view of the male. Any test in which movement by a female caused the male to court her was discarded. A test was completed when the male courted (and frequently attempted mating with) one of the females. The male was then collected so that he would not be retested.

Direct female choice tests are not feasible in lizards because of agonistic interactions between males and variations in female receptivity. Experiments by Hunsaker (1962) indicate that female

Sceloporus, when given a choice of compartments in a cage, choose most frequently that in which there is a conspecific male. In nature, such a tendency would function to reduce interspecific matings. To test such a possibility, females were placed in cages divided into three 15-inch square compartments; a male woodi was tethered in one end compartment and a male undulatus in the other. Each compartment was lighted by a 60-watt bulb positioned so that the temperature of the cage floor below it was 30° C. Every half hour the compartment occupied by the female was noted. Finally, interspecific agonistic behavior between males was investigated by placing a male of one species, tethered to the end of a pole, near a male of the other in the field.

The tendency of each species to remain restricted to the usual plant community, even in the absence of the other species across the ecotone, was investigated by observation at appropriate localities. More than fifty sand-pine scrub localities that lacked woodi were searched for undulatus. The seven islands of sandhill vegetation in the Ocala National Forest unoccupied by undulatus were examined for woodi. In one of these (Riverside Island; Sections 32 and 29, T. 12 S., R. 25 E.) the amount of bare ground and the density of grass blades were measured by line intercept; from each central point two-meter lines were run in the four cardinal directions. Three sets of twenty-five points were obtained. The points of one set were chosen by use of a random number table in an area where woodi had never been observed. The points of the second set were taken in an area where large expanses of open sand had been created by logging operations; each point was determined as the position of an undisturbed individual

of woodi when first seen by the investigator. Locations of points of the last set were chosen by the random number table in the same area where the second set had been taken.

Foraging behavior was investigated by direct observation of undisturbed individuals in the field; forty hours' observation was logged for each species in addition to many hours of more casual field observation. Since Sceloporus normally sits and waits for prey movement instead of actively foraging, the time spent by an individual on perches of varying heights above the ground and the orientation of the individual's head were recorded together with information on actual prey capture. Stomach contents of seventy adults of each species collected between May and August were examined; each species sample had an equal sex ratio.

## Results

### Phenetics on the Ecotones

Character means for the two species and the discriminant coefficients for each character are given in Table 18. The discriminant functions distinguish the non-hybridizing populations without misclassification of any individuals (Figure 6 and Figure 7). Of the twenty-seven male Sceloporus collected near the Alexander Springs ecotone, eight had Z values within the range observed for undulatus and ten had values within the range for woodi. The Z values of the remaining nine individuals fell between the ranges of the allopatric undulatus and woodi samples. These individuals are interpreted as hybrids. Thirty-eight females from the Alexander Springs ecotone

TABLE 18. Results of the Discriminant Analysis

Character	Male	Male	Discriminant Coefficient	Female	Female	Discriminant Coefficient
	woodi Mean	undulatus Mean		woodi Mean	undulatus Mean	
1. Femoral pores	52.20	29.68	0.00318	31.64	28.04	-0.00601
2. Fifth toe lamellae	27.28	28.24	-0.07294	26.92	28.04	-0.05759
3. Circumorbitals	23.56	19.76	-0.00118	23.44	20.84	-0.00658
4. Lateral supraoculars	28.56	22.12	0.00862	27.92	23.40	0.01240
5. Fourth toe lamellae	24.96	21.52	0.05662	25.12	21.24	0.03252
6. Supradigital lamellae	15.08	13.20	0.03471	14.84	12.88	0.03298
7. Infratarsals	13.28	10.76	0.04350	13.28	10.76	0.06019
8. Infratibials	17.32	14.24	0.06902	17.68	14.00	0.03811
9. Mid-dorsal scales	41.16	34.60	0.01608	41.32	36.04	0.00857
10. Head scales	6.32	0.96	0.05376	6.72	0.28	0.06004

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Species	Male	Mean	Standard	Female	Mean	Standard
	Sample Size	Male Z	Deviation Male Z	Sample Size	Female Z	Deviation Female Z
<u>woodi</u>	25	3.0421	0.1545	25	1.9888	0.1635
<u>undulatus</u>	25	1.9372	0.1490	25	0.9924	0.1218

Figure 6. Distribution of Z values for males of two non-hybridizing populations (below) and three hybrid zone populations (above). Means are marked by arrows; asterisks mark means that differ significantly from those of the non-hybridizing populations.

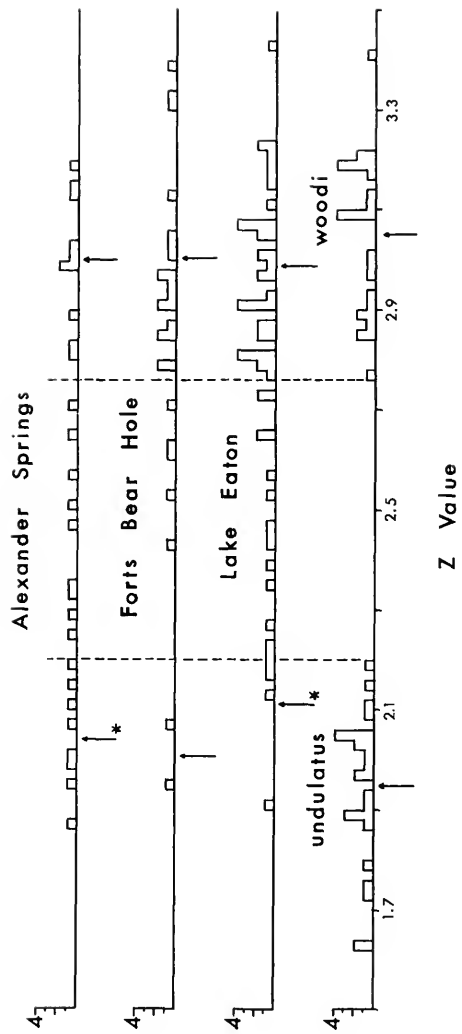
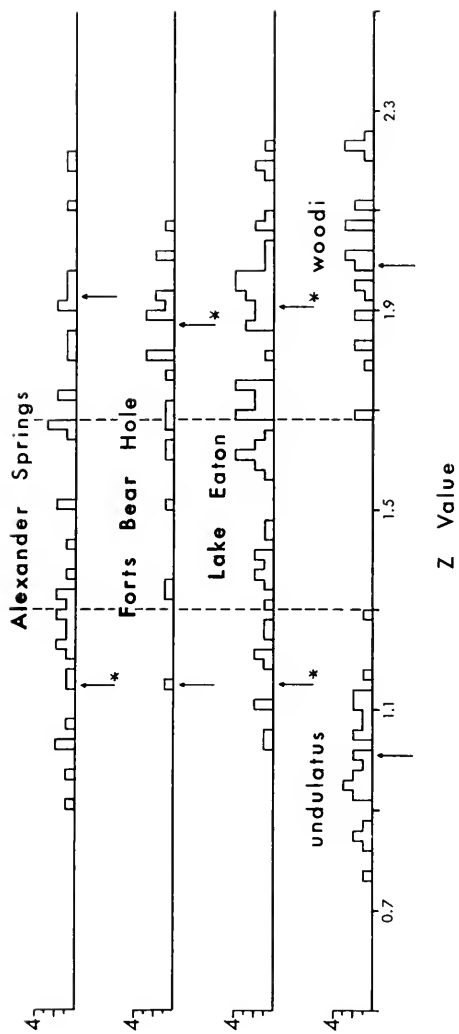




Figure 7. Distribution of Z values for females of two non-hybridizing populations (below) and three hybrid zone populations (above). Means are marked by arrows; asterisks mark means that differ significantly from those of non-hybridizing populations.



were examined. The discriminant function classified fourteen as undulatus and thirteen as woodi; eleven were intermediate. Figure 8 maps the location of each specimen from the Alexander Springs ecotone and approximately indicates its position on the phenetic continuum. All the undulatus were restricted to the sandhill side of the ecotone and most were found in the area between SR-445 and FS-38 that was minimally disturbed by logging. The woodi were collected in the main body of the scrub, in the small scrub patches within the sandhills, and in the parts of the sandhills that have been severely modified by logging. Most of the hybrids occurred in these disturbed areas, but some were found outside them in the sandhills.

Twenty-five males and twenty-two females were collected near the Forts Bear Hole ecotone. Two males and a single female were classified as undulatus. Eighteen males and fifteen females were classified as woodi. Five males and six females were intermediate. The phenetic position and location of each specimen is shown in Figure 9. The woodi were in scrub and in disturbed portions of the sandhills, particularly along sand roads; inexplicably, large areas of undisturbed sandhills were without undulatus, although those collected were in such an area. The hybrids occurred primarily near sand roads through the sandhills.

Fifty-three males were available from the Lake Eaton ecotone. Four had Z values within the undulatus range and thirty-five had Z values within the range for woodi. Fourteen individuals with intermediate Z values are judged to be hybrids. Of the sixty-nine females collected near the Lake Eaton ecotone, nine were classified as undulatus,

Figure 8. Map of the Alexander Springs ecotone. Sand-pine scrub indicated by stippling; sandhill vegetation indicated by unshaded areas. Dark circles represent *S. woodi* individuals. Open circles represent *S. undulatus* individuals. Partially dark circles represent hybrids of varying degrees.

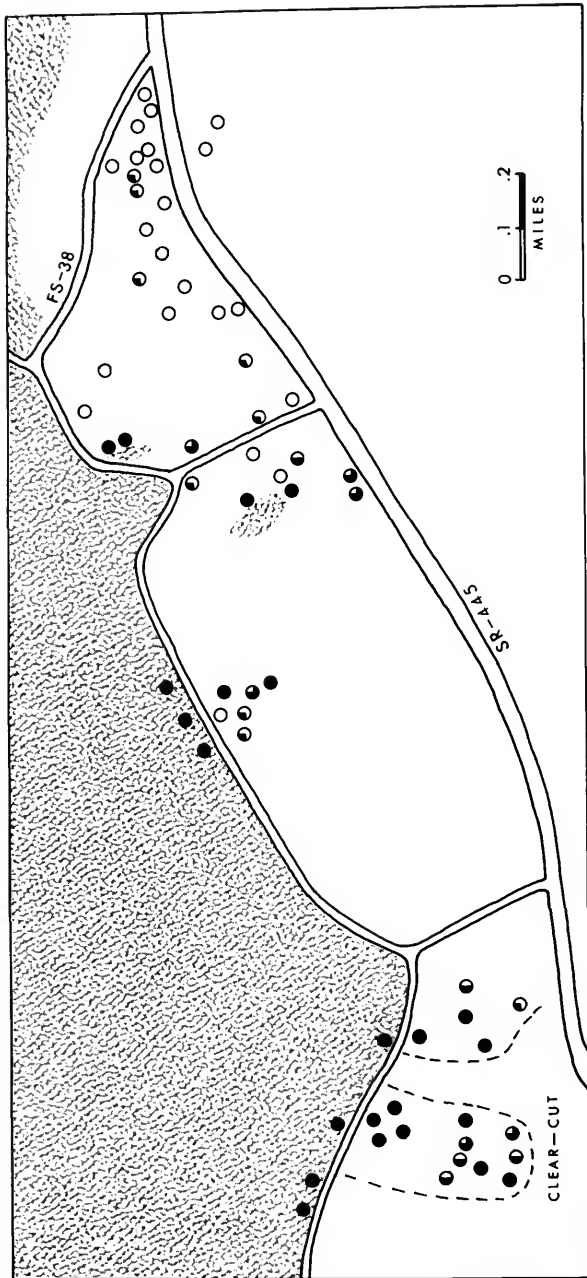
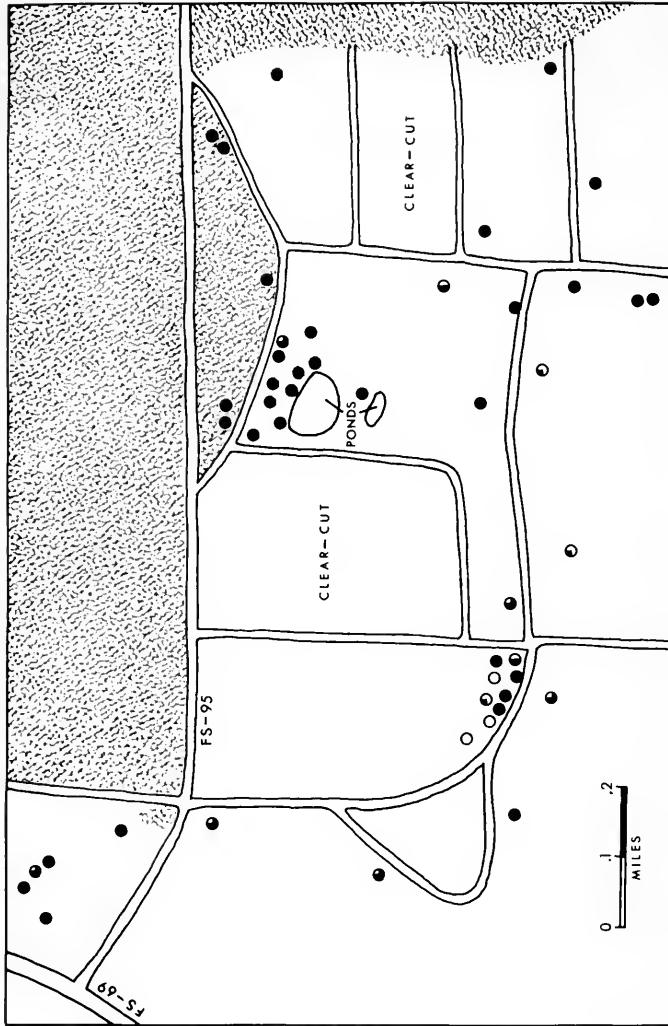


Figure 9. Map of the Forts Bear Hole ecotone. Sand-pine scrub indicated by stippling; sandhill vegetation indicated by unshaded areas. Dark circles represent S. woodi individuals. Open circles represent S. undulatus individuals. Partially dark circles represent hybrids of varying degrees.



forty-one as woodi, and nineteen as hybrids. Figure 10 shows that most of the woodi were located in the scrub or near sand roads adjacent to it, but that woodi was also present in the sandhill vegetation in a band that extended perpendicularly from the ecotone across FS-96 to FS-79A. The band contained considerable bare sand within it. The undulatus were only collected in the sandhill vegetation; they were concentrated in an area with heavy wiregrass growth parallel to FS-79A. Almost all the hybrids were located in the sandhill vegetation.

When the mean Z value of the non-hybridizing woodi was compared with such values calculated for individuals from each ecotone which were classified as woodi, the mean Z values of the ecotonal woodi were in every case shifted in the direction of undulatus (Figures 6 and 7). Those of the females from the Forts Bear Hole and the Lake Eaton ecotones were significantly shifted ( $p < .05$ ; one-tailed test). The equivalent comparison for undulatus reveals a shift of all mean ecotonal Z values toward those of woodi. Here, however, only the means from the Forts Bear Hole ecotone were not significantly different from the mean of the non-hybridizing population, and this exception is probably the result of the small sample sizes.

#### Interspecific Behavior

The results of the male choice tests are presented in Table 19. Both away from and near the ecotones, males showed no tendency to distinguish between females of the two species. Ferguson (1969) showed in similar tests that free-living Uta males in Colorado discriminate against Texas female Uta in favor of Colorado female Uta; he suggested



Figure 10. Map of the Lake Eaton ecotone. Sand-pine scrub indicated by stippling; sandhill vegetation indicated by unshaded areas. Dark circles represent *S. woodi* individuals. Open circles represent *S. undulatus* individuals. Partially dark circles represent hybrids of varying degrees.

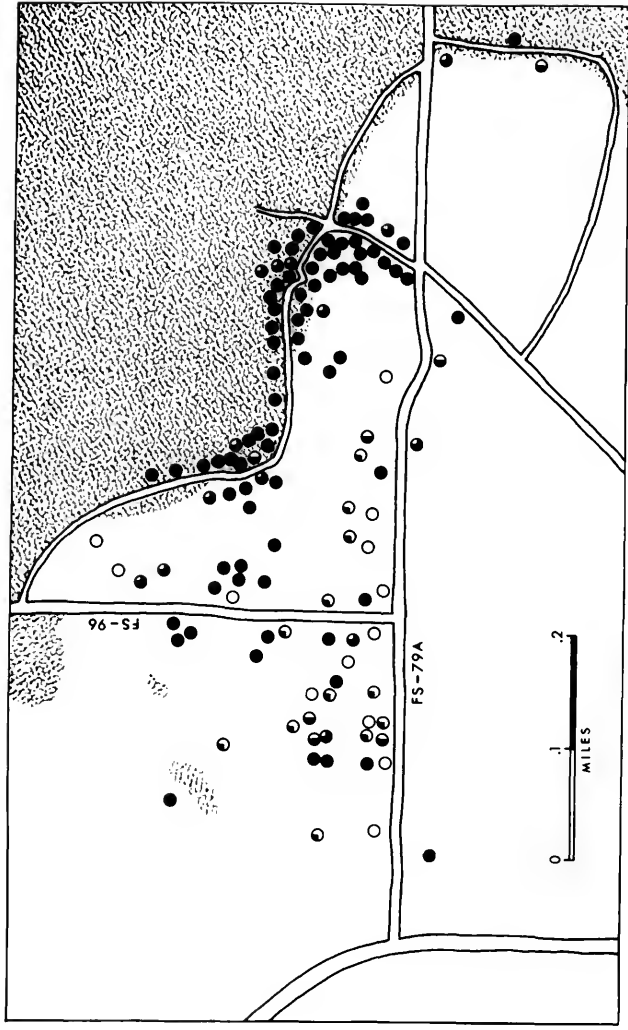


TABLE 19. Results of Male Choice Tests

<u>Males Tested</u>	<u>Female Courted*</u>	
	<u>woodi</u>	<u>undulatus</u>
Lake Eaton ecotone <u>woodi</u>	7	6
Alexander Springs ecotone <u>undulatus</u>	6	7
non-hybridizing <u>woodi</u>	7	7
non-hybridizing <u>undulatus</u>	7	8

\*p > .95 in all cases that males do not discriminate

this happens because the Texas Uta resembles Sceloporus graciosus, which is sympatric with the Colorado Uta.

Results of the female association tests are more ambiguous (Table 20). Female woodi and female undulatus from non-hybridizing populations both tended to associate more frequently with a male woodi than with a male undulatus or with neither. Female woodi from ecotonal populations were more often with a male than expected by chance, but did not discriminate between the species. The female undulatus from ecotonal populations were unassociated with a male more often than expected, but they tended to be in the compartment with the male undulatus more frequently than in that of the male woodi. Although undulatus females from the ecotonal populations tend to discriminate in favor of conspecific males more than undulatus females from non-hybridizing populations, woodi females show the opposite trend. Consequently, the data are perhaps best interpreted as failing to clearly show character displacement of association behavior on the ecotones.

When males of either species were presented to males of the other species in the field, territorial defense behavior was elicited; this included head bobbing, lateral compression, lateral presentation, and biting.

#### Habitat Selection

Sceloporus undulatus was found in only two of the fifty-three scrub communities that lack woodi, and both these localities are atypical. One is a scrub one mile northwest of Sunnyside, Bay County, portions of which contain very large and widely separated sand-pine and have a

TABLE 20. Results of Female Association Tests

<u>Females Tested</u>	<u>Compartment Chosen</u>			probability
	<u>woodi</u>	no lizard	<u>undulatus</u>	
ecotonal <u>woodi</u>	59	41	56	n.s.
ecotonal <u>undulatus</u>	34	74	56	p < .005
non-hybridizing <u>woodi</u>	54	37	34	.05 < p < .1
non-hybridizing <u>undulatus</u>	26	13	13	p < .05

relatively sparse shrub layer. Several undulatus were found in these portions, but they were not abundant. Part of the second scrub, at Dr. Phillips in Orange County, had been modified for development by almost complete mechanical clearing of the shrub layer (by discing) such that scattered sand-pine stood above a layer of ruderal herbs. In this part of the scrub, undulatus was common even though it was absent from the undisturbed areas of the scrub.

The sandhill islands of the Ocala National Forest, which lack undulatus, have woodi populations only in areas where logging has created patches of bare sand. Portions of these islands that have dense wire-grass growth are without woodi. Table 21 presents the data on grass leaf density and percentage of open ground (without a loose cushion of leaf litter) in areas that differ in regard to occupancy by woodi. Both parameters are significantly different ( $p < .01$ ) between the area occupied by woodi and the area without it. Additionally, the parameters differ significantly ( $p < .01$ ) between the set of measurements taken where an individual lizard was actually observed and the set chosen randomly in the same area. Thus, woodi is not randomly distributed in this sandhill locality, but apparently selects home ranges low in grass cover and high in open ground.

#### Food and Foraging Behavior

Table 22 shows the distribution of prey taxa in the stomach contents of undulatus and woodi. By weight, the woodi contained more ant and orthopteran food and less spider and larval lepidopteran food. Otherwise the diets are very similar and consist mainly of those arthropods that fly little or not at all and are commonly seen on the ground surface.

TABLE 21. Characteristics of the Ground Surface in Three Tracts of Sandhill Vegetation

<u>Tract</u>	<u>Mean Number of Grass Blades Intercepted per Two Meter Transect</u>	<u>Mean Percent of Open Ground Intercepted per Two Meter Transect</u>
with <u>woodi</u> ; points chosen as location of individuals	14.8 (10.9)*	85.0 (16.6)
with <u>woodi</u> ; points chosen randomly	36.1 (20.2)	36.6 (25.0)
without <u>woodi</u> ; points chosen randomly	74.6 (27.7)	0 (0)

\*Standard deviation in parentheses

TABLE 22. Percentage of Total Individuals (I) and Total Weight (W) by Prey Taxa

<u>Taxon</u>	<u>undulatus</u> (n=70)		<u>woodi</u> (n=70)	
	<u>I</u>	<u>W</u>	<u>I</u>	<u>W</u>
Formicidae	75.2	25.9	68.0	34.2
Coleoptera: adults	8.1	28.9	14.4	25.0
Orthoptera	2.8	16.4	7.6	25.4
Araneae	1.6	5.9	4.8	3.7
Lepidoptera: larvae	3.5	13.1	0.6	1.0
Coleoptera: larvae	1.7	1.7	1.2	2.7
Diptera	0.6	3.2	0.4	2.8
Hymenoptera (except ants)	0.6	1.6	1.6	2.2
Homoptera-Hemiptera	0.6	1.1	1.2	1.7
Odonata	0.1	1.2	0.2	1.3
Isoptera	4.5	1.0		
Mollusca	0.7	trace		



The distribution of prey individuals and prey volume over prey length is depicted in Figure 11. The distributions of prey individuals for the two species are almost identical. In terms of prey volume, they differ in that the undulatus contained somewhat higher proportions of large prey items. This may reflect the greater ability of undulatus to handle larger prey because of its slightly greater body size. Consideration of both prey taxa and prey particle size, however, shows the two species to be utilizing very similar food resources.

The percent of total observation time spent by the two species in the various foraging attitudes is given in Table 23. Both sexes of woodi spend nearly all foraging time in watching the ground surface, either on the ground or from low perches on logs or tree trunks. Individuals of undulatus perched head down on tree trunks above six feet were observed both moving their heads to watch insects on the ground and descending rapidly to the ground to feed. Hence, summation of the time in head down positions six feet or less above the ground provides a reasonable minimum estimate of the proportion of foraging time that undulatus spends watching the ground surface. This amounts to about 70 percent; however, in contrast to woodi, most of this time is spent hanging head down on tree trunks several feet above the ground.

#### Discussion

The restriction of the two species to separate plant associations, which results in ranges that are contiguously allopatric, is understandable when foraging behavior is considered with regard to the structural characteristics of the vegetation. It has been shown that both species take prey items of essentially the same taxa and size and

Figure 11. Distribution of prey individuals and prey volume over prey length for S. undulatus and S. woodi.

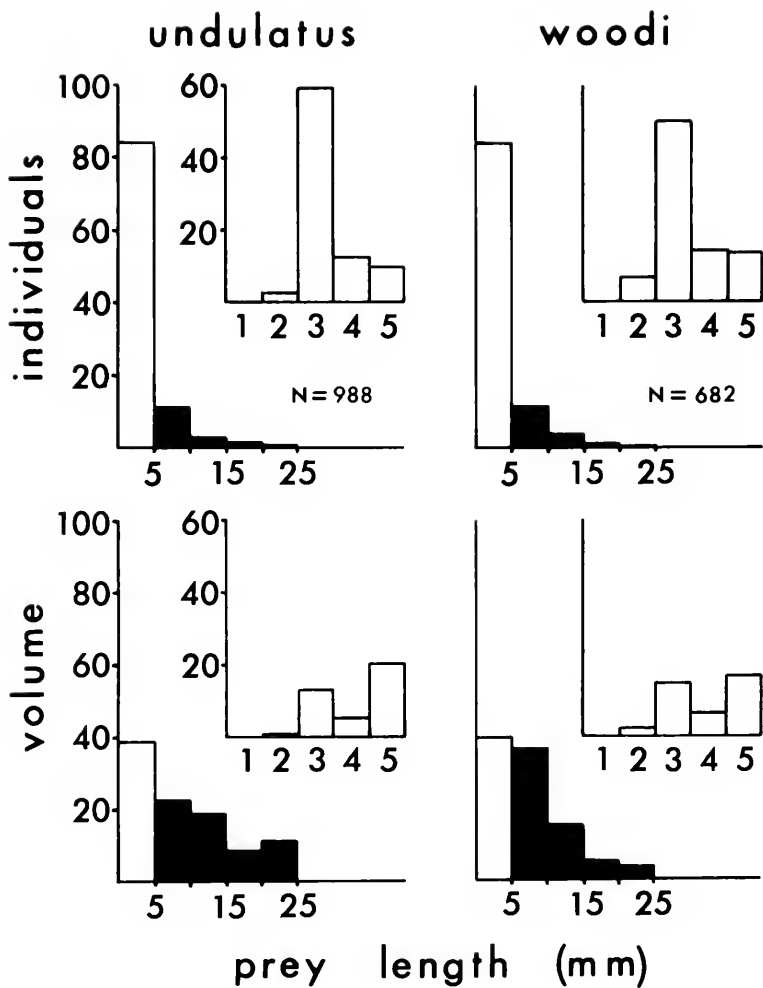


TABLE 23. Percentage of Foraging Time in Various Positions\*

<u>Group</u>	<u>0-6"</u>	<u>6'-1'</u>	<u>Height Above Ground</u>				<u>7-10'</u>	<u>&gt;10'</u>
			<u>2'</u>	<u>3'</u>	<u>4'</u>	<u>5'</u>		
<u>male undulatus</u>	12.0	5.4	$\frac{0.9}{10.7}$	$\frac{11.5}{10.5}$	$\frac{5.4}{8.9}$	$\frac{2.9}{12.9}$	$\frac{2.4}{5.6}$	$\frac{6.9}{4.0}$
<u>female undulatus</u>	27.4	9.1	$\frac{2.4}{13.2}$	$\frac{1.5}{15.4}$	$\frac{1.8}{7.9}$	—	$\frac{7.9}{1.8}$	$\frac{6.4}{5.2}$
<u>male woodi</u>	82.3	7.2	$\frac{1.2}{3.2}$	$\frac{3.5}{2.4}$	—	—	—	—
<u>female woodi</u>	90.4	2.6	$\frac{4.4}{2.6}$	—	—	—	—	—

\*For heights above one foot, number above the line gives percent of time in head up position and number below the line gives percent of time in head down position

that prey-seeking activity of both species is primarily directed to the forest floor. But exploitation of the same food resource has required different foraging tactics because of the structural differences between the two plant associations; the importance of vegetation structure to lizard ecology is well recognized (Schoener, 1968; Pianka, 1969; Sexton and Heatwole, 1968).

Watching for prey on the ground from elevated stations on tree trunks is not feasible in the scrub because the dense shrub layer prevents an unobstructed view of the ground. Therefore, prey on the forest floor must be sought from the ground or from very low stations. Furthermore, no herbaceous layer obstructs the visibility or the movement of a terrestrial lizard in the scrub. Exactly the opposite conditions obtain in sandhill vegetation. The herbaceous layer and leaf litter reduce visibility from low stations and inhibit free movement on the ground by the two species. But observation of the ground from stations on tree trunks is not blocked by shrubs, and presumably a greater area of forest floor can be watched from these elevated stations than from low ones. Significantly, undulatus seems to be absent from sandhill vegetation in Highlands County. This may be due to the unusual abundance of oak shrubs in the understory there, noted by Harper (1927).

The most conspicuous morphological differences between undulatus and woodi relate to the difference in foraging tactics. The lighter body form and longer legs and hind toes of woodi are cursorial adaptations appropriate to a ground-dwelling form. The tan color of woodi is cryptic against the forest floor of the scrub, while undulatus is well matched to oak trunks by its mottled gray coloration. It is worth

mentioning that although sixty-four of two hundred and forty-four individuals from the ecotones had hybrid Z values and many of the others probably had genes introgressed from the other species, only forty-two were classified as hybrid by subjective evaluation of their color pattern. Because cryptic coloration is presumably subject to strong selection pressures, its canalization may have been deepened in ecotonal populations compared with other characters of less extreme importance to the individual.

Contiguous allopatry is normally taken as strongly indicative of competition between species (Miller, 1967). The numerous large areas of scrub and sandhill vegetation that are without the typical Sceloporus species and yet are unoccupied by the other species suggest that the allopatric ranges result from specialization to the structural aspects of the vegetation that makes each species only marginally suited to the plant association of the other. Competition would be likely to occur only in sandhill vegetation with a sufficiently scant herbaceous layer to permit the existence of woodi there.

If the Z value of an individual is an accurate reflection of the genetic contributions to it by both species, then two observations indicate that the hybrids are fertile. First, if hybrids were all  $F_1$  individuals, a cluster of hybrids would be expected on the Z axis midway between the means for the two species. This is not the case for any of the hybrid zones (Figure 6 and Figure 7). Hybrids are scattered completely across the continuum between the species, and, if anything, mid-point hybrids are less common than those closer to the parental species. Second, unless hybrids were backcrossing to the parental species, there would be no reason for the shift in the mean Z value of each ecotonal parental population toward that of the other species.

Given hybrid fertility and backcrossing, reasons for the extraordinary narrowness of the hybrid zone require consideration. It is clear that the tendency for each species to avoid the vegetation typically inhabited by the other species, when it is unmodified by man, would minimize interspecific matings. If there were a tendency for females to choose a home range within that of a conspecific male, then interspecific territoriality between males would also reduce the frequency of interspecific matings. Yet in spite of the factors minimizing the production of hybrids, the hybrid zone would be expected to have broadened unless natural selection were acting against hybrids. For each sex, an attempt to show such selection was made by regressing body lengths on the absolute deviation of Z values from the mid-hybrid Z value. A significant positive regression would imply selection against hybrids. Neither regression was significantly different than zero. The inability to show selection may be due to the small proportion of mid-point hybrids available in the sample, or it may be that hybrids are at no great disadvantage along the ecotone, but that genes of each species are eliminated as they flow off the ecotone into the habitat of the other.

Since lack of reproductive success of some kind by the hybrids must be assumed to account for the narrowness of the hybrid zone, the evolution of ethological reproductive isolating mechanisms to prevent interspecific mating might have been expected. The extent of the hybridization argues against the presence of such mechanisms, as does the failure of males on the ecotones to distinguish between the species, since the males would either learn individually or be genetically programmed to discriminate if they were normally rejected by

non-conspecific females. It could be argued that, since most of the hybridization occurred along roads or in logged portions of the sandhill vegetation, the hybridization, and hence selection against it, is a very recent phenomenon. However, primeval ground fires that maintained the fire sub-climax sandhill vegetation must have regularly opened it to peripheral invasion by woodi. The scrub of the Ocala National Forest grows on Pleistocene paleodunes. If, following Laessle (1958), they are considered the result of higher sea levels, they would be approximately 400,000 years old. Even if a late arrival by undulatus in Florida is assumed, the two species would have been parapatric along the ecotones for at least 100,000 years.

Current evolutionary theory holds that strongly divergent evolution of two forms during allopatry results in at least partial reproductive isolation and that when sympatry is achieved natural selection perfects premating reproductive isolating mechanisms. Although Smith (1969) has argued that most speciation is parapatric speciation "because only in contiguity is there a survival value placed on reproductive isolating mechanisms," the persistence of many narrow hybrid zones (Mayr, 1963; Thaeler, 1968) suggests that natural selection can strengthen premating reproductive isolating mechanisms only in populations that are extensively sympatric. Significant increases in ethological reproductive isolating mechanisms have been produced in captive Drosophila by artificial selection in thirty generations or less (Koopman, 1950; Knight, Robertson, and Waddington, 1956; Kessler, 1966). Since the amount of hybridization between undulatus and woodi that took place in the past is not known, it is not possible to state that there has been no improvement of ethological



isolating mechanisms, but in three replicates after many thousand generations interspecific mating has not been eliminated. Bigelow (1965) has pointed out that the evolution of barriers to interspecific matings would be retarded on narrow hybrid zones by the influx of genes from the allopatric portions of the species populations, where there is not a strong selective advantage in discriminating against mates of the other species. Continuance of interspecific mating between undulatus and woodi probably results from the very sharp boundary between the two plant associations; this sharpness allows such a small portion of each species population to be sympatric with the other that gene flow to the ecotone swamps any tendency toward development of ethological reproductive isolating mechanisms.

West of the Great Basin, Sceloporus occidentalis and S. graciosus are similar to undulatus and woodi, respectively, in foraging habits and in requirements of vegetation structure (Marcellini and Mackey, 1970). However, the vegetations required by occidentalis and graciosus are intermingled in much more patchy fashion than are scrub and sand-hill vegetation. That hybridization between occidentalis and graciosus is unknown is surely a consequence of ethological reproductive isolating mechanisms that were able to develop because of extensive sympatry of the two species.

## CHAPTER III

### A SEARCH FOR THE POPULATION ASYMMETRY PROPERTY

#### Introduction

Measurable differences normally exist between the right and left sides for any bilateral character. This asymmetry may be of several kinds (Van Valen, 1962). If the mean of one side is significantly greater than that of the other, the asymmetry is directional. If there is usually a difference between the two sides but either side is equally likely to show the greater value, the condition is termed antisymmetry. The most common kind of asymmetry, however, is fluctuating asymmetry, which obtains when the signed differences between the right and left sides are distributed normally about a mean of zero. Although contrary opinions exist (Mason, Ehrlich, and Emmel, 1967), the level of fluctuating asymmetry has been considered a measure of buffering capacity in development, since any differences between paired structures that are non-consistent are thought to result from developmental accidents (Thoday, 1958).

Soule (1967b) introduced the idea that the levels of fluctuating asymmetry may be concordant for many characters of a population; thus, some populations would tend to be highly asymmetrical

for several characters, while others would show less fluctuating asymmetry in the same characters. This concordance of asymmetries in a population was called the population asymmetry property, and evidence for its existence was found in lizards (Soule, 1967b) and butterflies (Soule and Baker, 1968). Soule attempted to relate asymmetry levels to the genetic environments in which the populations function. In particular, any factors that destroy coadapted gene complexes were hypothesized to increase asymmetry. In the present study, the population asymmetry property was sought in several populations of Sceloporus.

#### Methods

The populations considered were the twenty woodi populations examined for geographic variation (Figure 1), the woodi populations from the three hybrid zones, the undulatus that composed the non-hybridizing sample for generation of the discriminant function, the undulatus populations from the three hybrid zones, and the hybrids from the three hybrid zones. The sexes were not analyzed separately because, although three of the characters considered were sexually dimorphic, absolute differences in these characters were small. Femoral pores, subdigital lamellae of the fifth toe, circumorbitals, lateral supraoculars, fourth toe length, and auricular lobule length were the characters examined. The mean ( $\bar{d}$ ) of the absolute values of the differences between the sides of a paired structure is the estimate of population asymmetry for that character.

The distribution of signed values (right minus left) for each character of each population was tested for normality by the

Kolmogorov-Smirnov test. Plots of the significantly non-normal distributions revealed that skewness accounted for departures from normality except in one sample that was bimodal. This single indication of antisymmetry is probably an artifact of sampling. A check for directional asymmetry was made by t-tests for differences between means of the two sides. Five of two-hundred and sixteen tests were significant at the .01 level. Any tendency toward directional asymmetry must be corrected for before the mean of the absolute differences between the sides will represent fluctuating asymmetry. This correction was made in these five cases by subtracting the mean of the signed differences from every value for the side with the larger mean.

### Results

The population asymmetry estimates for each character are shown in Table 24. Also shown for the twenty woodi populations is the overall rank ( $R_j$ ) of each population in relative asymmetry level;  $R_j$  is the sum of the rankings, in terms of asymmetry, of a population over all six characters. The Kendall coefficient of concordance,  $W$ , was calculated on the character asymmetry ranks of the twenty woodi populations. A significant  $W$  would indicate that populations highly asymmetric for one character are likely to show high asymmetry in others. Since  $W$  was found to be non-significant ( $W = .096$ ;  $p > .90$ ), there is no evidence in woodi for a population asymmetry property.

Soule (1967b) predicted high asymmetry levels on hybrid zones and in populations under strong directional selection; these predictions were examined with the specimens discussed in Chapter II. A weighted

TABLE 24. Asymmetry Values ( $\bar{d}$ ) of Six Characters in Sceloporus Populations\*

Population	Character						R <sub>j</sub>
	Femoral Pores	Toe Lamellae	Circum-orbitals	Supra-oculars	Toe Length	Auricular Lobule	
<u>woodi</u>							
1	.60	.35	1.25	1.05	.68	.65	79.5
2	.65	.30	1.25	1.15	1.35	.20	70.0
3	.70	.25	1.25	1.05	.70	.30	64.0
4	.80	.30	.70	.85	.55	.30	41.5
5	.55	.32	.85	1.30	.30	.45	56.0
6	.96	.10	1.00	.95	.55	.50	71.0
7	.90	.25	.80	.85	.35	.45	49.0
8	.90	.25	.90	1.10	1.05	.25	70.0
9	.65	.15	.90	1.45	.85	.40	64.5
10	.86	.36	1.09	.95	.50	.41	72.0
11	.75	.35	1.00	.90	.55	.25	53.0
12	.75	.15	.80	1.25	.45	.45	56.0
13	.90	.40	.70	.95	.58	.40	63.0
14	.80	.45	.85	.95	.45	.40	61.5
15	.65	.58	1.00	1.10	.20	.35	62.0
16	.78	.43	.93	1.00	1.36	.50	89.0
17	.45	.40	.75	1.10	.70	.45	64.5
18	.80	.35	.70	.95	.30	.60	56.0
19	.77	.45	.86	.95	.54	.41	65.5
20	.65	.25	.80	1.10	.45	.45	51.5

L. Eaton <u>woodi</u> (76)	.66	.22	.82	.95	.62	.32
F. B. H. <u>woodi</u> (33)	.67	.24	.78	1.09	.68	.46
Alex. Sprs. <u>woodi</u> (23)	.64	.30	1.17	1.15	.42	.32
discriminant <u>undulatus</u> (50)	.70	.18	.78	.92	.48	.40
Dr. Phillips <u>undulatus</u> (26)	.62	.23	.73	.96	.88	.55
L. Eaton <u>undulatus</u> (13)	.85	.23	1.00	1.31	.22	.54
F. B. H. <u>undulatus</u> (3)	.67	.33	2.00	1.00	.67	.31
Alex. Sprs. <u>undulatus</u> (22)	.76	.18	1.04	.96	.69	.31
L. Eaton hybrids (34)	.79	.18	1.00	.97	.44	.48
F. B. H. hybrids (10)	.40	.22	.80	.80	.33	.57
Alex. Sprs. hybrids (20)	.58	.35	.70	1.55	.20	.33

\*Sample sizes in parentheses

average asymmetry for the three woodi populations from the hybrid zones was calculated and compared with an overall average asymmetry based on the twenty non-hybridizing woodi populations (Table 25). The ecotonal woodi were less asymmetric in every character; this trend is significant ( $p < .05$ ) by the Wilcoxon signed ranks test. When average asymmetry of the hybrid zone undulatus was compared with that of the non-hybridizing undulatus (parental sample of undulatus used for construction of the discriminant function), the hybrid zone undulatus tended to be more asymmetric, but the trend barely missed significance by the Wilcoxon signed ranks test. Finally, average asymmetries based on individuals from the hybrid zones that were classified as hybrids were compared with asymmetries obtained by averaging the mean asymmetries of woodi with those of undulatus. Three characters of the hybrids are more asymmetric than this average, and three are less asymmetric.

Z values calculated for the undulatus from the Dr. Phillips scrub showed a slight, but statistically significant, shift in the direction of woodi on the discriminant axis. This fact, coupled with the abundance of undulatus in this scrub, might suggest that this population is under directional selection for adaptations to scrub vegetation. If such is the case, it has not resulted in notably high asymmetry in the population. Four characters are more asymmetric than the undulatus average, but two are not (Table 25).

TABLE 25. Average Asymmetry Values ( $\bar{d}$ ) of Hybridizing and Non-hybridizing Sceloporus Populations\*

<u>Population</u>	Character					
	<u>Femoral Pores</u>	<u>Toe Lamellae</u>	<u>Circum-orbitals</u>	<u>Supra-oculars</u>	<u>Toe Length</u>	<u>Auricular Lobule</u>
non-hybridizing <u>woodi</u> (416)	.74	.32	.92	1.05	.62	.41
hybridizing <u>woodi</u> (132)	.66	.24	.87	1.02	.59	.36
non-hybridizing <u>undulatus</u> (50)	.70	.18	.78	.92	.48	.40
hybridizing <u>undulatus</u> (38)	.78	.21	1.10	1.08	.54	.40
Dr. Phillips <u>undulatus</u> (26)	.62	.23	.73	.96	.88	.55
<u>woodi-undulatus</u> average	.72	.25	.85	.98	.55	.40
<u>woodi-undulatus</u> hybrids (64)	.66	.24	.88	1.12	.35	.45

\*Sample sizes in parentheses



### Discussion

Developing a model that he himself called "somewhat contrived," Soule (1967b) sought to explain observed differences in asymmetry among insular Uta populations in the Gulf of California as the result of presumably different levels of coadaptation of gene complexes. The relative levels of coadaptation were deduced from assumptions about gene flow to the population, the selection regime of the population, and the time that had been available for evolution of coadaptation. A stabilizing selection regime, minimal influx of foreign genes into the population, and longer periods of evolution in situ all should result in greater genetic coadaptation and lower asymmetry. In this context, that woodi populations do not differ markedly in asymmetry is perhaps expected, since selection pressures in all the populations are probably in the main stabilizing. The minimal geographic variation and superficial uniformity of the habitat support this statement. As discussed in Chapter I, opportunities for gene flow and evolutionary time in situ do differ among the populations, yet no trends in asymmetry levels are observed by comparing the differing populations. That the Ocala National Forest would have both the least asymmetric and the second most asymmetric populations hardly supports the relation between asymmetry and the genetic parameters of populations. Even more damaging, however, is the failure of hybrid zone populations to be consistently more asymmetric, since disruption of coadapted gene complexes must occur where populations are exposed to introgression of another species' genes into their presumably coadapted gene pools. The woodi on the hybrid zones have lower than usual asymmetry, the undulatus there are more

asymmetric than usual, and the average asymmetry of non-hybridizing woodi populations is greater in every character than that of non-hybridizing undulatus. These facts, and the fact that the asymmetry levels of the hybrids are near those which represent an average between the two species, suggest that species differences in asymmetry may average out in hybridizing populations.

Although the concept of populational differences in asymmetry level and their correlation with genetic characteristics of the population is of such great inherent interest to developmental biology, genetics, and evolution, that much more energy should be spent in investigating its reality, the results presented here do not lend credence to that reality.

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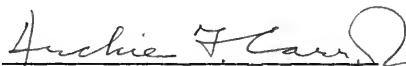
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
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