

AN ABSTRACT OF THE THESIS OF

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Title: A DIETARY AND MORPHOMETRIC ANALYSIS OF SCELOPORINE (IGUANIDAE)

LIZARD POPULATIONS

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Abstract approved: _____

Dr. Robert M. Storm

Analyses of sympatric and allopatric populations of Sceloporus
occidentalis and S. graciosus from central Oregon indicate a high degree
of similarity in diet. Relative abundance, the equivalent number of
equally common taxa (E), and the probability of similarity (SIMI) were
used in the analyses. Shifts in diet between populations of S.
occidentalis can be attributed to subtle differences in available prey
rather than interspecific competition for food with its sympatric
congener. Both the diets and available prey exhibited temporal
variation at all collection sites.

The allopatric and sympatric S. occidentalis populations had
significantly different body sizes. Absence of significant differences
in ratios of metric variables between the populations indicated no
difference in overall body shapes. The shift in body size should be
attributed to factors other than interspecific dietary competition
between the sympatric congeners.

Examination of 19 morphological characters in populations of S.
occidentalis from Santa Barbara County, California, and three counties

from Oregon (Deschutes, Harney, and Jackson) revealed significant degrees of concordance in the morphometric analysis. The results initially suggest that the central population (Santa Barbara) was less variable than the peripheral populations--contrary to a generally accepted observation. The high levels of variation in the peripheral populations were most likely derived from the lumping of small isolated populations within each county.

The four populations of S. occidentalis could be separated by the variation of metric characters using canonical correlation analysis. The Santa Barbara populations separated from the Oregon populations according to limb characteristics while each Oregon population separated along a gradient associated with skull characteristics.

A Dietary and Morphometric Analysis of Sceloporine
(Iguanidae) Lizard Populations

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TABLE OF CONTENTS

| | Page |
|--|------|
| I. INTRODUCTION | 1 |
| II. DIETARY ANALYSIS OF SYMPATRIC POPULATIONS OF <u>SCELOPORUS OCCIDENTALIS</u> AND <u>S. GRACIOSUS</u> | 3 |
| Methods | 5 |
| Results | 18 |
| Discussion | 35 |
| Summary | 41 |
| III. MORPHOLOGICAL VARIATION IN <u>SCELOPORUS OCCIDENTALIS</u> | 42 |
| Methods | 43 |
| Results | 49 |
| Discussion | 52 |
| Summary | 59 |
| IV. CONCLUSION | 60 |
| BIBLIOGRAPHY | 61 |

LIST OF FIGURES

| Figure | | Page |
|--------|--|------|
| 1 | Map of Deschutes County, OR, showing the locations of the three study sites: <u>occidentalis</u> , <u>sympatric</u> , and <u>graciosus</u> . | 7 |
| 2 | Summary of precipitation and temperature data for 1974-76 from Bend, OR. | 10 |
| 3 | Monthly diets for sympatric and allopatric populations of <u>S. occidentalis</u> and <u>S. graciosus</u> . | 28 |
| 4 | Monthly samples of available prey for the <u>graciosus</u> , <u>sympatric</u> , and <u>occidentalis</u> sites. | 29 |
| 5 | Monthly dietary diversity values for sympatric and allopatric populations of <u>S. occidentalis</u> and <u>S. graciosus</u> expressed as the equivalent number of equally common taxa. | 30 |
| 6 | Monthly available prey diversity values for the <u>sympatric</u> , <u>graciosus</u> , and <u>occidentalis</u> sites expressed as the equivalent number of equally common taxa. | 32 |
| 7 | Phenogram of 20 blocks of dietary data based upon the probability of similarity analysis. | 33 |
| 8 | Phenogram of 18 blocks of available prey data based upon the probability of similarity analysis. | 34 |
| 9 | Four collection areas for <u>S. occidentalis</u> : Jackson, Deschutes, Harney, and Santa Barbara. | 44 |
| 10 | Scatter diagram of the centroids for the four populations projected upon the axes of the first two canonical variates. | 53 |
| 11 | The influence each character would have upon the first two canonical variates if the character varied alone. | 54 |

LIST OF TABLES

| Table | | Page |
|-------|---|------|
| 1 | Plant associations for the three study sites. | 9 |
| 2 | Morphological characters used in the analyses. | 17 |
| 3 | Total diet for sympatric and allopatric populations of <u>S. occidentalis</u> and <u>S. graciosus</u> | 19 |
| 4 | Available prey from the sympatric, graciosus, and occidentalis study sites for 1975 and 1976. | 22 |
| 5 | Diversity values for diet and available prey. | 27 |
| 6 | Comparison of morphological characters of <u>S. occidentalis</u> from the sympatric and allopatric populations. | 36 |
| 7 | Comparison of morphological characters of <u>S. graciosus</u> from sympatric and allopatric populations. | 37 |
| 8 | Coefficients of variation for meristic characters and the relative variance for the metric character ratios. | 50 |
| 9 | Calculated values for S, Kendall's coefficient of concordance (W), and corresponding X^2 . | 51 |
| 10 | Results of asymmetry analysis. | 55 |

A Dietary and Morphometric Analysis of Sceloporine (Iguanidae) Lizard Populations

I. INTRODUCTION

A large amount of theory is associated with the many tenets of population biology (e.g., competition theory, predator prey interactions, resource utilization); however, one also finds that the supporting empirical data have lagged behind the theories and models. Peters (1976) argued that many of these tenets are not theoretical because they are essentially tautological, and testable predictions cannot be made from them. He points out, however, that tautological arguments can be utilized as means for ordering and elucidating the relationships between sets of empirical data. Fretwell (1977) noted that ". . . if ecological theory is to be useful, real-world descriptive biologists will have to use their expertise to gather data to test the theories of the model builders."

The intent of this dissertation is to consider several questions relevant to saurian populations. The questions were generated from observations of "real-world" situations in light of ecological theory. The scope of the questions is of the type associated with population biology theory, and answering the questions has resulted in two separate reports. Consequently this dissertation is divided into two portions.

Initially I ask what effect sympatry might have upon the diet selection of two closely related lizard species. The question is posed without the a priori assumption that competition for food is the driving force behind utilization of available resources. The second study

considers whether levels of morphological variation in a wide ranging lizard species exhibit patterns relative to the geographical location of specific populations. That is, are centrally located populations more or less variable than peripheral populations?

II. DIETARY ANALYSIS OF SYMPATRIC POPULATIONS OF SCELOPORUS OCCIDENTALIS AND S. GRACIOSUS

Documentation of the dietary patterns of organisms is a standard part of most natural history studies. However, the large amounts of empirical dietary data that were gathered were done so by methods not amenable to testing theory--that is, with an absence of experimental conditions and controls. Because the role of diet selection as an adaptive strategy has recently become the object of much discussion by theoretical ecologists (for reviews see Schoener, 1971; Ellis et al, 1976), there is now an apparent need for empirical dietary data appropriate for testing the theoretical postulates. Much of what is known about reptilian dietary preferences is based upon descriptive data of gut contents that were derived from the lumping of unrelated field and museum collections (e.g. Johnson, 1965; Burkholder and Tanner, 1974; Clark, 1973; Tanner and Hopkin, 1972). Some authors have in turn used such data to develop diet selection models for lizards (e.g., Huey and Pianka, 1974; Huey et al, 1974; Parker and Pianka, 1975; Pianka, 1975; Pianka and Parker, 1975).

However, such studies fail to consider temporal variability in diet selection and the effect of available prey upon diet selection. There are few saurian studies where temporal variation in diet and/or availability of prey were examined. Simon (1975) found that territorial size for Sceloporus jarrovi was inversely correlated with natural food abundance, and the abundance of food was in turn subject to temporal variation. Rose (1976a, 1976b) considered variation in diet composition

through time in sympatric populations of Sceloporus occidentalis and S. graciosus in California.

When similar species overlap spatially as in studies comparable to Rose's (1976a, 1976b), they frequently display differences from one another in one or more morphological features. Brown and Wilson (1956) described this phenomenon as character displacement. Since the introduction of this term, others have continued to argue that competition is the driving force behind such morphological shifts (see Cody, 1973). More recently, Huey and Pianka (1974) suggested that while character displacement is intuitively appealing as an explanation for apparent morphological shifts, definitive examples of shifts occurring in response to competition for food are uncommon.

With the intention of addressing the theory alluded to by some of the studies presented above, I have asked the question whether two closely related congeneric lizard species alter their dietary patterns when sympatric. Would the status of sympatry also evoke any shifts in morphological characters? If there are discernable differences in the dietary patterns, might they simply reflect the variations in abundance and quality of available prey rather than some interspecific behavioral modification, such as competition? Also, if morphological shifts are evident, is it an a priori necessity to use competition for food as the explanation for the shift?

To answer these questions I used the iguanid lizards Sceloporus occidentalis and S. graciosus. Lizards of the wide-ranging genus Sceloporus are capable of occupying extremely diverse habitats in

virtually any terrestrial location from below sea level to over 3000 m (Smith, 1939). The two species used in this study range from Baja California to Washington and from the Pacific Coast to the extreme eastern boundary of the Great Basin (Stebbins, 1966). The lizards are thought to be closely related (Larsen and Tanner, 1975), and because their preferred habitats often overlap, sympatric populations can be found. In this study I compared two allopatric populations (one for each species) with two sympatric populations. Because habitat differences can result in greater intraspecific variation in life history patterns than interspecific variation (Tinkle and Ballinger, 1972), I restricted the study to locations within the same plant community.

Methods

The Lizards:

S. occidentalis has been the subject of three extensive demographic and natural history studies (Fitch, 1940; Davis, 1967; Tanner and Hopkin, 1972), but there are no published data on populations from central Oregon. There are also several demographic and ecological studies of S. graciosus (Stebbins, 1944, 1948; Stebbins and Robinson, 1946; Tinkle, 1973; Burkholder and Tanner, 1974). The minimum snout-vent length for adult S. occidentalis is 58 mm, thus making it larger than its congener, S. graciosus, which has a minimum adult snout-vent length of 48 mm. The preferred habitat of S. occidentalis is either arboreal or rocky, depending upon the specific plant community present (Marcellini and

Mackey, 1970; Davis and Verbeek, 1972; Fuentes, 1976). S. graciosus is more terrestrial than S. occidentalis, even in areas of sympatry (Marcellini and Mackey, 1970), and is most abundant in low shrub habitats where there is little ground cover (Stebbins, 1966).

The annual periods of activity for both species fluctuate from year to year, depending upon the mildness or severity, i.e., temperature, of the preceding winter. S. occidentalis emerges at cooler temperatures than S. graciosus and therefore may be sporadically active earlier in the year. In this study (1974-1976), S. occidentalis was active as early as April and as late as October while S. graciosus was first seen in May and last seen in September.

Both S. occidentalis and S. graciosus are sedentary feeders utilizing a sit-and-wait predation strategy (Parker and Pianka, 1975). They are also opportunistic carnivores with the bulk of their diets composed of arthropods (Johnson, 1965; Tanner and Hopkin, 1972; Clark, 1973; Burkholder and Tanner, 1974). When sympatric their diets tend to be very similar (Rose, 1976a, 1976b).

Study Sites:

Having located a site where the two species were sympatric (Figure 1), a search was made for allopatric populations close enough to minimize variability due to distance or elevation. All sites were in Deschutes County, Oregon, and were identified as "occidentalis," "sympatric," and "graciosus" (Figure 1).

The occidentalis site was on the east side of Cline Butte (T15S, R12E, Sections 22,27), elevation 944 m. The sympatric site was north

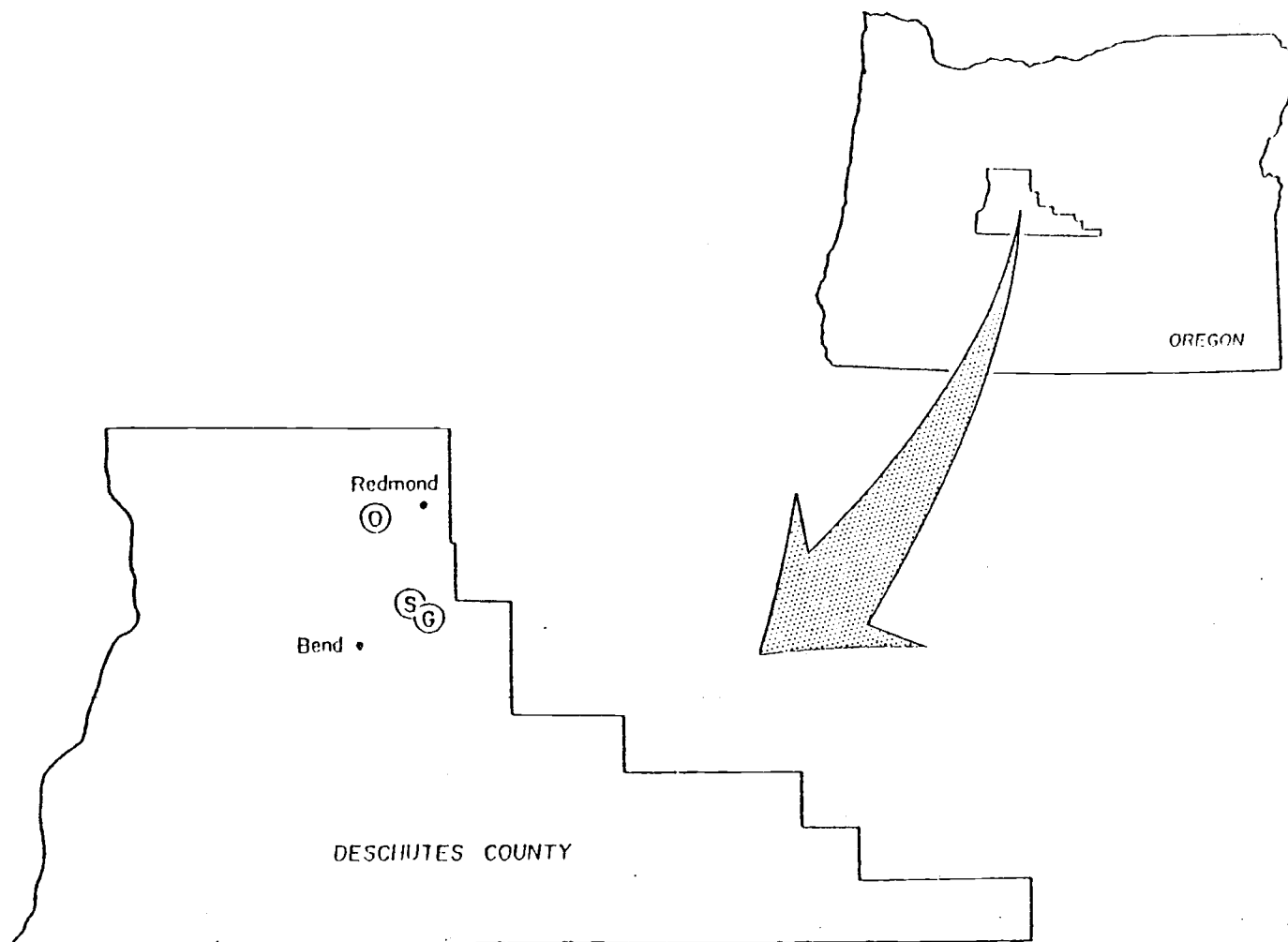


Figure 1. Map of Deschutes County, OR showing the locations of the three study sites: *occidentalis* (O), *sympatric* (S), and *graciosus* (G).

of the Bend Airport (17S, R13E, Sections 5,8), elevation 1025 m. The *graciosus* site was also north of the Bend Airport but it was east of the sympatric site (T17S, R13E, Section 9), elevation 1021 m. The *graciosus* site was 17 km southeast of the *occidentalis* site.

The *occidentalis* site was located along a north-south ridge of basalt approximately 2 m high and 225 m long and comprised 0.95 ha. *S. occidentalis* was found among the rocks. The sympatric site was also oriented along a ridge of basalt and included 2.91 ha. Both *S. occidentalis* and *S. graciosus* were found on and near the rocks. The *graciosus* site contrasted with the other sites in that there were no major rock outcrops. The area utilized in the collections encompassed 3.40 ha. All three sites were in *Juniperus occidentalis* transition zones approaching shrub steppe habitats (Franklin and Dyrness, 1973) (see Table 1).

The summers at the study sites were mildly hot and dry with few overcast days between May and October. Occasional cool fronts may have briefly restricted lizard activity or even delayed the spring emergence. Temperature and precipitation data for 1974-76 are summarized in Figure 2. July and August were the warmest months of the year with the average daily maximum temperatures ranging from 23-28.3 C. The data were recorded for Bend, Oregon, which is 19.8 and 10.6 km south of the *occidentalis* and *graciosus* sites respectively.

Sampling Scheme:

Sample sizes were limited by the constraints imposed when one works with a finite population, i.e., large sample sizes would severely

Table 1. Plant associations for the three study sites.

| <u>Plant Types</u> | <u>Study Sites</u> | | |
|----------------------|--|---|---|
| | <u>Sympatric</u> | <u>Graciously</u> | <u>Occidentalis</u> |
| Dominant Association | <u>Juniperus occidentalis/</u> <u>Artemesia tridentata</u> | <u>J. occidentalis/</u> <u>A. tridentata</u> | <u>J. occidentalis/</u> <u>A. tridentata</u> |
| Additional Shrubs | <u>Chrysothamnus viscidiflorus</u> <u>Leptodactylon pungens</u> | <u>C. viscidiflorus</u> <u>L. pungens</u> | <u>C. nauseosus</u> <u>L. pungens</u> <u>Purshia tridentata</u> |
| Grasses | <u>Agropyron spicatum</u> <u>Sitanion hystrix</u> | <u>A. spicatum</u> <u>S. hystrix</u> | <u>A. spicatum</u> <u>S. hystrix</u> |

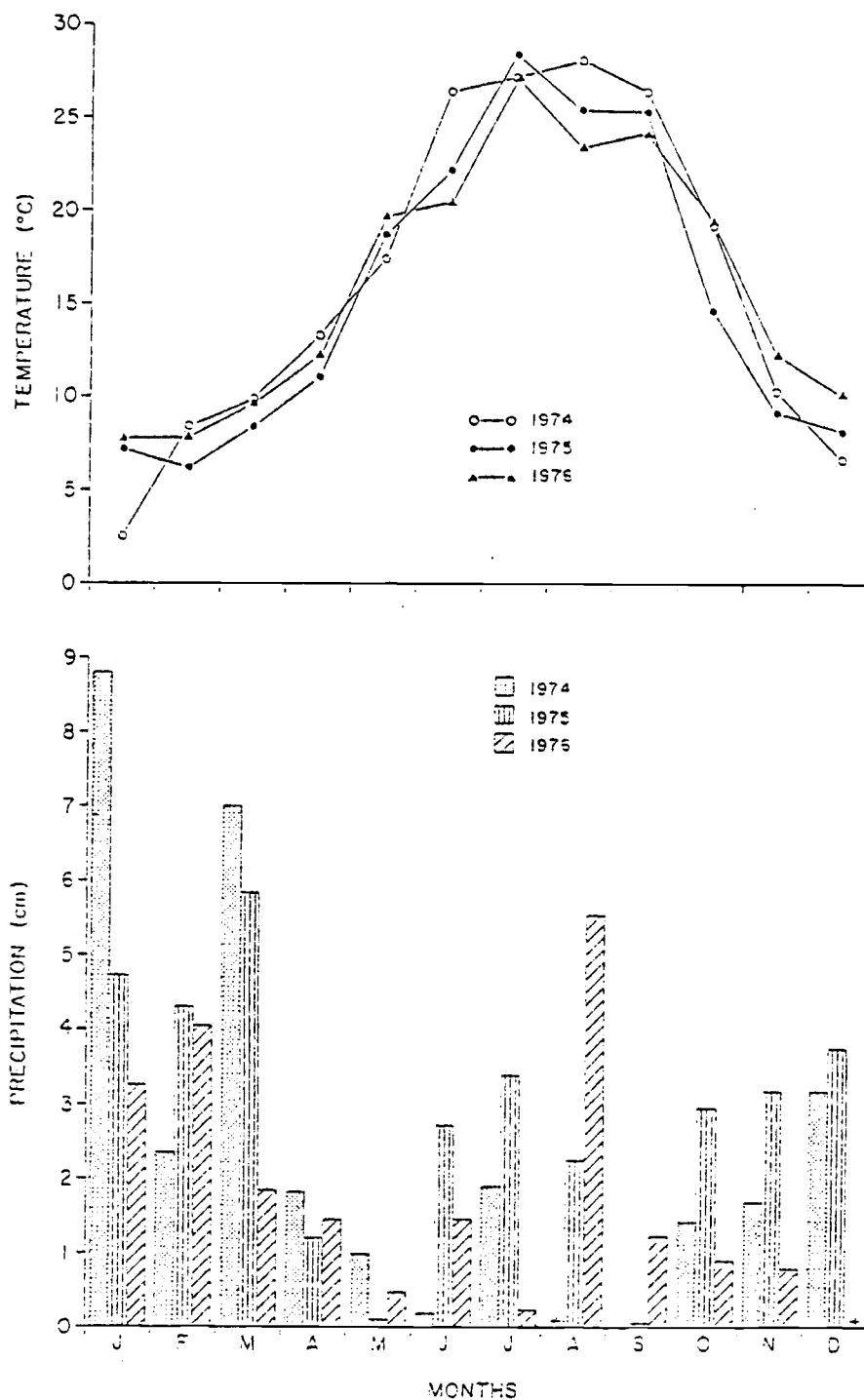


Figure 2. Summary of precipitation and temperature data for 1974-76 from Bend, OR. Based upon meteorological data from the U.S. Department of Commerce (1974-76).

deplete the population before the study was completed. Collections were made during April, May, June, August, September, and October, 1975. Five specimens of each species from each study site were collected with .22 caliber dust shot. Adult lizards were used to expedite capture time and to remove biases associated with age class differences. Specimens were fixed in AFA after an initial series of measurements were recorded: age class, weight, sex, and snout-vent length. After 24 h specimens were transferred to and maintained in 70% alcohol. Digestive tracts were removed and the frequency of prey was recorded. Borror and DeLong (1960) were used to identify prey to the ordinal and familial taxa. Parasites of the lizards were removed and preserved in alcohol for subsequent identification.

The contents of five digestive tracts were treated as one sample. The adequacy of the sample size was determined by plotting the cumulative frequency of new taxa against the number of samples (a "species-area curve"). Only three of 20 samples had plots that had not "leveled off," indicating possible inadequate sample sizes for those samples. However, in all three cases the increase in taxa was due to the addition of one new taxon in the final sample. The additional taxa were of the less common forms and as such would have little influence upon the overall results of the study because the indices used weight the more common taxa. Therefore, the sample sizes may still be considered satisfactory for this study.

Huey and Pianka (1974) indicated that determination of prey items at ordinal and familial levels, without any determination of prey size,

is sufficient for the demonstration of dietary patterns in lizards. However, this generalization is severely compromised by their assumption that prey selection is independent of prey size. Unless independence is demonstrated, then prey size must be considered as a possible major component of prey selection. Adult S. occidentalis (Davis, 1967; Rose, 1976a) and adult S. graciosus (Derickson, 1976) have been reported to select prey essentially independent of size. Because adult lizards were used in my study, the results were not compromised by the use of only a taxonomic characterization of prey rather than a morphological characterization (e.g., prey size).

Sampling of available prey required a method that would assess the prey potentially available to the lizards concurrently with the period of the lizards' collection. Because S. occidentalis and S. graciosus utilize a sit-and-wait predation strategy it was only necessary to sample animals that crawl and/or land near known lizard habitats. Analyses of available prey must recognize that not all available prey are actually potential prey--that is, there may be size constraints imposed upon the predator by the prey or there may be a degree of unpalatability associated with the prey. However, S. occidentalis and S. graciosus from Oregon are capable of ingesting virtually all arthropods with which they might come in contact (Storm, personal communication). Differential palatability of prey was assumed to have a negligible effect on diet selection because S. occidentalis and S. graciosus seem to exhibit a lack of discrimination relative to the prey that are capable of being caught (White, personal observation).

A procedure outlined by Lewis and Taylor (1967) was modified by using pitfall and water traps. Each pitfall trap was a 473 ml jar (8 x 8.5 cm) sunk into the ground half filled with alcohol, and covered by an elevated wire screen with a mesh size of 1.2 x 1.2 cm. Water traps were white enamel pans (5 x 19 x 34 cm) half filled with water.

Detergent was added to the water to sink the specimens.

Three sampling points were selected along a transect running through each study site. At each sampling point five pitfall and two water traps were randomly distributed and left open for approximately 24 h. Lizards were collected during the diurnal portion of this period. Data from all the traps at each site were lumped and treated as one sample. Examination of species area curves for the samples indicated that 15 pitfall traps and six water traps per site were adequate for the analyses. Three additional sampling periods for each site from 1976 were included for comparison with the 1975 samples.

Data Analysis:

1. Relative Abundance: Abundance was defined as the proportion of a total sample comprised by a particular taxonomic group. Relative abundance measurements are useful for qualitatively comparing the relationships between taxonomic groups within and between samples. The ordinal taxonomic level was used in this analysis with the exception of such morphologically distinct groups as formicid hymenopterans or lepidopteran larvae.
2. Diversity: Simpson's diversity index, λ , is a population parameter that characterizes the distribution of the proportions of taxa. Because

diversity measures usually employ a notation that grades their values according to the propensity to include or exclude the rarer taxa in enumeration (Hill, 1973), Simpson's index was selected because it gives greater weight to the more common taxa (Peet, 1974). The estimator of λ is Sd^2

$$Sd^2 = \sum_{i=1}^S P_i^2 = \sum_{i=1}^S \frac{n_i^2}{N^2} = \frac{\sum_{i=1}^S n_i^2}{N^2}$$

where

$P_i = n_i/N$ = proportion of total individuals in the i^{th} species

n_i = number of individuals of the i^{th} species in sample

N = total number of individuals in sample

S = number of taxonomic groups in sample

However, the reciprocal value of λ was suggested as a better measure of diversity because of certain desirable mathematical qualities (MacArthur, 1972) and its intuitive appeal. The reciprocal of Sd^2 is E , the equivalent number of equally common taxa, and is defined as

$$E = \frac{1}{Sd^2} = \frac{1}{\sum_{i=1}^S P_i^2}$$

The intuitive appeal stems from the fact that this parameter generates values relative to the number of taxa in a sample rather than arbitrary values ranging from zero to one.

3. Similarity: Similarity indices emphasize how similar samples are whereas diversity indices describe how different the samples are. In

addition, a scaled similarity index such as SIMI provides a simultaneous comparison of all samples relative to the partitioning of data, i.e., spatial, temporal, or taxonomic. $SIMI_{1,2}$, the similarity between samples 1 and 2, is given by

$$SIMI_{1,2} = \frac{\sum_{i=1}^S P_{1i} P_{2i}}{Sd_1 Sd_2}$$

where

P_{1i} = proportion of i^{th} species in the 1st collection

P_{2i} = proportion of i^{th} species in the 2nd collection

and the Sd values are the square root of Sd^2 as defined previously.

This index has limits of 0 and 1 and is analogous to a correlation coefficient. It gives the probability that two individuals drawn from each sample will belong to the same species, relative to the square root of the probability of randomly drawing them from each population alone (Stander, 1970; Pianka, 1973, 1975).

Clustering of the collections based upon their relative SIMI values was done with Spearmann's sums of variables with paired groups (Sokal and Sneath, 1963; Sneath and Sokal, 1973). This is an agglomerative type centroid method as applied to a correlation matrix and is therefore compatible with a SIMI matrix. The procedure sequentially reduces the correlation (or SIMI) matrix by first selecting the matrix's largest correlation coefficient r_{AB} . The correlation coefficients for variables A and B are then "averaged" to form a new variable (A + B) and a new correlation matrix is computed from all possible combinations with the new $r_{(A+B)}$. The new correlation coefficient between the new variable

(A + B) and any variable (Q) in the matrix is defined as

$$r_{(A+B),Q} = \frac{r_{AQ} + r_{BQ}}{\sqrt{2 + 2r_{AB}}}$$

where

r_{AQ} = correlation between variables A and Q

r_{BQ} = correlation between variables B and Q

The procedure is repeated until the matrix is collapsed to only one element.

Morphology:

Univariate parametric statistics were used to determine whether any direct morphological differences existed between the populations. Because of the high degree of intercorrelatedness among the metric variables (Table 2), ratios were used for the comparisons between populations. The ratios were expressed as a function of snout-vent length (SVL)

$$\text{ratio variable} = R = \frac{\bar{x}}{\text{SVL}}$$

where

\bar{x} = mean of the metric variable x

Because hidden variables often exist in ratio measurements, compensation must be made by the calculation of a new variance estimate for each ratio variable

$$s^2 = R^2(1 - f)[(cv_x^2 + cv_y^2 - 2 \cdot r \cdot cv_x \cdot cv_y)/n]$$

where

Table 2. Morphological characters used in the analyses. Metric characters are expressed in mm and measured with dial calipers.

| <u>Character</u> | <u>Description</u> |
|--|--|
| 1. Snout-vent length (SVL) | Distance from snout to anterior edge of venter |
| 2. Axilla-groin (AG) | Distance from axillary region to groin |
| 3. Snout-occipital length (SNO) | Distance from snout to posterior edge of interparietal scale |
| 4. Jaw length (JL) | Distance from anterior midpoint of lower jaw to bulge of angular bone on lower jaw |
| 5. Jaw width (JW) | Distance between angular bones |
| 6. Foreleg (FL) | Distance from bent wrist to elbow of right leg |
| 7. Thigh (TH) | Distance from midline to knee of right leg |
| 8. Shank (SH) | Distance from knee to ankle of right leg |
| 9. Foot (FT) | Distance from heel to base of second toe of right foot |
| 10. Toe (TOE) | Distance from base to tip of fourth toe of right foot |
| 11. Dorsal scales (DO) | Total number of dorsal scales |
| 12. Mid-body scales (MB) | Total number of scales around the mid body. |
| 13. Parietal-frontoparietal (PFP) | Total number of parietal scales plus frontoparietal scales |
| 14. Frontals (FR) | Total number of frontal scales |
| 15. Prefrontals-frontonasals (PFN) | Total number of prefrontal plus frontonasal scales |
| 16. Circumorbitals (CI) | Total number of circumorbital scales from left and right sides |
| 17. Femoral Pores (FP) | Total number of femoral pores from left and right sides |
| 18. Subdigital lamellae (SD) | Total number of subdigital lamellae on fifth toes of left and right feet |
| 19. Scales between femoral pores (SFP) | Total number of scales between femoral pores |

s^2 = variance estimate

R^2 = ratio estimate

f = sampling fraction of total population

CV_x = coefficient of variation for x in ratio estimate

CV_y = coefficient of variation for y in ratio estimate

r = product moment correlation coefficient of x and y

n = sample size

" f " was considered to be zero because of large population sizes (Hansen et al, 1953). The standard error is simply the square root of the new sample variance (Rice, personal communication).

Results

The diets of S. occidentalis and S. graciosus are dominated by ants (Formicidae) (Table 3). Approximately 70-80% of the two species' diets were limited to the taxa Formicidae, Coleoptera, Orthoptera, and Diptera (Table 3). The same taxa also comprised approximately 80% of the available prey at the three sites (Table 4). Differences in consumption of Formicidae can be used to separate the S. occidentalis populations from one another as well as from S. graciosus. There were significant differences between the two S. occidentalis populations ($\chi^2 = 17.46$, $P < 0.001$), but not between the two S. graciosus populations ($\chi^2 = 0.02$). The sympatric S. occidentalis consumed a greater proportion of Formicidae than the allopatric S. occidentalis, placing them between the S. graciosus populations and the allopatric S. occidentalis in formicid consumption.

Table 3. Total diet for sympatric and allopatric populations of S. occidentalis and S. graciosus, based upon 60 specimens of S. occidentalis and 40 specimens of S. graciosus. Number of individuals are presented with proportions of total diet in parentheses.

| <u>Prey</u> | <u>S. occidentalis</u> | | <u>S. graciosus</u> | |
|---------------|-----------------------------|----------------------------|----------------------------|-----------------------------|
| | <u>Allopatric</u> N = 30 | <u>Sympatric</u> N = 30 | <u>Sympatric</u> N = 20 | <u>Allopatric</u> N = 20 |
| Hymenoptera | | | | |
| Formicidae | 89 (.355) | 203 (.523) | 154 (.672) | 208 (.667) |
| Sphecidae | 5 (.020) | 12 (.031) | 3 (.013) | 0 |
| Braconidae | 6 (.024) | 8 (.021) | 0 | 2 (.006) |
| Vespidae | 1 (.004) | 1 (.003) | 0 | 0 |
| <i>Total</i> | <u>101 (.402)</u> | <u>224 (.577)</u> | <u>157 (.686)</u> | <u>210 (.673)</u> |
| Coleoptera | | | | |
| Carabidae | 1 (.004) | 14 (.036) | 3 (.013) | 0 |
| Scarabaeidae | 10 (.040) | 1 (.003) | 0 | 1 (.003) |
| Tenebrionidae | 1 (.004) | 6 (.015) | 0 | 1 (.003) |
| Curculionidae | 2 (.008) | 3 (.008) | 4 (.017) | 5 (.016) |
| Staphylinidae | 2 (.008) | 1 (.003) | 0 | 1 (.003) |
| Larvae | 2 (.008) | 3 (.008) | 0 | 0 |
| Unknown | 25 (.100) | 20 (.052) | 6 (.026) | 3 (.010) |
| <i>Total</i> | <u>43 (.171)</u> | <u>48 (.124)</u> | <u>13 (.057)</u> | <u>11 (.035)</u> |
| Orthoptera | | | | |
| Locustidae | 40 (.159) | 29 (.075) | 12 (.052) | 5 (.016) |
| Gryllidae | 1 (.004) | 5 (.013) | 0 | 0 |
| <i>Total</i> | <u>41 (.163)</u> | <u>34 (.088)</u> | <u>12 (.052)</u> | <u>5 (.016)</u> |

Table 3 (Continued)

| <u>Prey</u> | <u>S. occidentalis</u> | | <u>S. graciosus</u> | |
|--------------------|------------------------|------------------|---------------------|-------------------|
| | <u>Allopatric</u> | <u>Sympatric</u> | <u>Sympatric</u> | <u>Allopatric</u> |
| Diptera | | | | |
| "Fly-like" | 11 (.044) | 15 (.039) | 8 (.035) | 7 (.022) |
| Tipulidae | 2 (.008) | 2 (.005) | 2 (.009) | 0 |
| "Gnat-like" | 1 (.004) | 1 (.003) | 0 | 2 (.006) |
| Asilidae | 0 | 1 (.003) | 0 | 0 |
| Unknown | 0 | 2 (.005) | 2 (.009) | 1 (.003) |
| <i>Total</i> | <u>14 (.056)</u> | <u>21 (.054)</u> | <u>12 (.052)</u> | <u>10 (.032)</u> |
| Lepidoptera | | | | |
| Heterocerca (moth) | 0 | 1 (.003) | 0 | 0 |
| Larvae | 5 (.020) | 6 (.015) | 1 (.004) | 13 (.042) |
| Unknown | 0 | 19 (.049) | 0 | 0 |
| <i>Total</i> | <u>5 (.020)</u> | <u>26 (.067)</u> | <u>1 (.004)</u> | <u>13 (.042)</u> |
| Hemiptera | | | | |
| Pentatomidae | 4 (.016) | 2 (.005) | 2 (.009) | 0 |
| Reduviidae | 0 | 4 (.010) | 0 | 0 |
| Scutelleridae | 1 (.004) | 1 (.003) | 0 | 1 (.003) |
| Anthocoridae | 0 | 1 (.003) | 0 | 0 |
| Unknown | 0 | 0 | 0 | 1 (.003) |
| <i>Total</i> | <u>5 (.020)</u> | <u>8 (.021)</u> | <u>2 (.009)</u> | <u>2 (.006)</u> |
| Homoptera | | | | |
| Cercopidae | 5 (.020) | 1 (.003) | 0 | 0 |
| Cicadellidae | 1 (.004) | 2 (.005) | 0 | 6 (.019) |
| Aphidae | 0 | 0 | 1 (.004) | 0 |
| <i>Total</i> | <u>6 (.024)</u> | <u>3 (.008)</u> | <u>1 (.004)</u> | <u>6 (.019)</u> |

Table 3 (Concluded)

| <u>Prey</u> | <u>S. occidentalis</u> | | <u>S. graciosus</u> | |
|----------------------|------------------------|------------------|---------------------|-------------------|
| | <u>Allopatric</u> | <u>Sympatric</u> | <u>Sympatric</u> | <u>Allopatric</u> |
| Neuroptera | | | | |
| Myrmelionidae | 1 (.004) | 1 (.003) | 0 | 0 |
| Raphidiidae | 1 (.004) | 3 (.008) | 0 | 0 |
| <i>Total</i> | <u>2 (.008)</u> | <u>4 (.010)</u> | <u>0</u> | <u>0</u> |
| Insect Eggs | 27 (.108) | 12 (.031) | 28 (.122) | 47 (.151) |
| Unknown Insects | 4 (.016) | 2 (.005) | 0 | 2 (.006) |
| Arachnida | | | | |
| Araneida | 2 (.008) | 5 (.013) | 2 (.009) | 4 (.013) |
| Acari | 0 | 0 | 0 | 2 (.006) |
| <i>Total</i> | <u>2 (.008)</u> | <u>5 (.013)</u> | <u>2 (.009)</u> | <u>6 (.019)</u> |
| Reptilia | | | | |
| Sceloporus graciosus | 0 | 1 (.003) | 1 (.004) | 0 |
| Eumeces skiltonianus | 1 (.004) | 0 | 0 | 0 |
| <i>Total</i> | <u>1 (.004)</u> | <u>1 (.003)</u> | <u>1 (.004)</u> | <u>0</u> |
| Grand Total | <u>251</u> | <u>388</u> | <u>229</u> | <u>312</u> |

Table 4. Available prey from the sympatric, graciosus, and occidentalis study sites for 1975 and 1976. Raw counts are presented with proportions of the total sample in parentheses.

| Prey | Sympatric | | Graciosus | | Occidentalis | |
|----------------|---------------|---------------|---------------|---------------|---------------|---------------|
| | 1975 N = 6 | 1976 N = 3 | 1975 N = 6 | 1976 N = 3 | 1975 N = 6 | 1976 N = 3 |
| Diptera | | | | | | |
| Gnat-Like | 258 (.124) | 19 (.047) | 194 (.093) | 34 (.068) | 186 (.072) | 36 (.048) |
| Fly-like | 595 (.287) | 172 (.429) | 495 (.237) | 144 (.286) | 337 (.130) | 180 (.240) |
| Culpidae | 27 (.013) | 0 | 17 (.008) | 0 | 8 (.003) | 0 |
| Unknown | 0 | 0 | 1 () | 0 | 0 | 1 (.001) |
| Tipulidae | 3 (.001) | 1 (.002) | 0 | 0 | 1 () | 0 |
| Asilidae | 0 | 3 (.007) | 1 () | 1 (.002) | 0 | 0 |
| Total | 883 (.426) | 195 (.486) | 708 (.340) | 179 (.356) | 531 (.205) | 217 (.289) |
| Hymenoptera | | | | | | |
| Formicidae | 663 (.320) | 128 (.319) | 931 (.447) | 230 (.457) | 1626 (.629) | 444 (.591) |
| Sphecidae | 5 (.002) | 10 (.025) | 2 (.001) | 21 (.042) | 5 (.002) | 1 (.001) |
| Vespidae | 123 (.059) | 4 (.010) | 106 (.051) | 6 (.012) | 75 (.029) | 4 (.005) |
| Braconidae | 22 (.011) | 0 | 25 (.012) | 0 | 1 () | 2 (.003) |
| Andrenidae | 0 | 0 | 1 () | 0 | 0 | 0 |
| Tenthredinidae | 1 () | 0 | 1 () | 0 | 0 | 0 |
| Total | 814 (.392) | 142 (.354) | 1065 (.511) | 257 (.511) | 1707 (.660) | 451 (.601) |
| Coleoptera | | | | | | |
| Tenebrionidae | 8 (.004) | 0 | 4 (.002) | 0 | 5 (.002) | 1 (.001) |
| Chrysomelidae | 1 () | 0 | 0 | 0 | 0 | 0 |
| Staphylinidae | 14 (.007) | 0 | 4 (.002) | 3 (.006) | 9 (.003) | 4 (.005) |
| Larvae | 1 () | 0 | 1 () | 0 | 1 () | 1 (.001) |
| Unknown | 3 (.001) | 0 | 1 () | 0 | 0 | 0 |
| Carabidae | 1 () | 0 | 7 (.003) | 0 | 2 (.001) | 0 |
| Scarabaeidae | 7 (.003) | 4 (.010) | 16 (.008) | 2 (.004) | 7 (.003) | 4 (.005) |
| Pselaphidae | 0 | 0 | 0 | 1 (.002) | 1 () | 0 |
| Melandryidae | 0 | 0 | 0 | 0 | 1 () | 4 (.005) |

Table 4 (Continued)

| Prey | Sympatric | | Graciosus | | Occidentalis | |
|---------------|-------------------|------------------|-------------------|------------------|-------------------|------------------|
| | 1975 | 1976 | 1975 | 1976 | 1975 | 1976 |
| Scolytidae | 1 () | 0 | 0 | 0 | 0 | 0 |
| Curculionidae | 0 | 0 | 0 | 0 | 2 (.001) | 0 |
| Histeridae | 0 | 0 | 1 () | 0 | 0 | 0 |
| Silphidae | 0 | 0 | 0 | 0 | 1 () | 0 |
| <i>Total</i> | <u>36 (.017)</u> | <u>4 (.010)</u> | <u>34 (.016)</u> | <u>6 (.012)</u> | <u>29 (.011)</u> | <u>14 (.019)</u> |
| Orthoptera | | | | | | |
| Locustidae | 18 (.009) | 9 (.022) | 2 (.001) | 3 (.006) | 25 (.010) | 4 (.005) |
| Gryllidae | 7 (.003) | 1 (.002) | 1 () | 2 (.004) | 3 (.001) | 0 |
| <i>Total</i> | <u>25 (.012)</u> | <u>10 (.025)</u> | <u>3 (.001)</u> | <u>5 (.010)</u> | <u>28 (.011)</u> | <u>4 (.005)</u> |
| Homoptera | | | | | | |
| Cicadellidae | 207 (.100) | 27 (.067) | 126 (.060) | 25 (.050) | 164 (.063) | 38 (.051) |
| Aphididae | 1 () | 0 | 2 (.001) | 0 | 1 () | 0 |
| Fulgoridae | 1 () | 0 | 0 | 0 | 1 () | 0 |
| Membracidae | 0 | 0 | 0 | 0 | 1 () | 0 |
| Unknown | 0 | 0 | 0 | 0 | 1 () | 0 |
| Chermidae | 0 | 0 | 1 () | 0 | 0 | 0 |
| Nymph | 0 | 1 (.002) | 0 | 1 (.002) | 0 | 0 |
| <i>Total</i> | <u>209 (.101)</u> | <u>28 (.070)</u> | <u>129 (.062)</u> | <u>26 (.052)</u> | <u>168 (.065)</u> | <u>38 (.051)</u> |
| Lepidoptera | | | | | | |
| Heterocera | 20 (.010) | 3 (.007) | 35 (.017) | 2 (.004) | 44 (.017) | 0 |
| Rhapalocera | 14 (.007) | 3 (.007) | 7 (.003) | 2 (.004) | 27 (.010) | 9 (.012) |
| Larvae | 22 (.011) | 0 | 13 (.006) | 0 | 9 (.003) | 0 |
| <i>Total</i> | <u>56 (.027)</u> | <u>6 (.015)</u> | <u>55 (.026)</u> | <u>4 (.008)</u> | <u>80 (.031)</u> | <u>9 (.012)</u> |
| Hemiptera | | | | | | |
| Nabidae | 0 | 0 | 0 | 0 | 1 () | 1 (.001) |
| Pentatomidae | 0 | 0 | 1 () | 0 | 0 | 0 |

Table 4 (Continued)

| <u>Prey</u> | <u>Sympatric</u> | | <u>Graciosus</u> | | <u>Occidentalis</u> | |
|-----------------|------------------|-----------------|------------------|------------------|---------------------|-----------------|
| | <u>1975</u> | <u>1976</u> | <u>1975</u> | <u>1976</u> | <u>1975</u> | <u>1976</u> |
| Scutelleridae | 1 () | 0 | 0 | 0 | 1 () | 0 |
| Aradidae | 0 | 0 | 0 | 0 | 1 () | 0 |
| Miridae | 0 | 1 (.002) | 0 | 0 | 0 | 0 |
| <i>Total</i> | <u>1 ()</u> | <u>1 (.002)</u> | <u>1 ()</u> | <u>0</u> | <u>3 (.001)</u> | <u>1 (.001)</u> |
| Thysanura | | | | | | |
| Machilidae | 6 (.003) | 1 (.002) | 1 () | 1 (.002) | 6 (.002) | 5 (.007) |
| Isoptera | | | | | | |
| Kalotermitidae | 0 | 0 | 1 () | 0 | 0 | 0 |
| Neuroptera | | | | | | |
| Myrmeleonidae | 3 (.001) | 1 (.002) | 0 | 0 | 2 (.001) | 0 |
| Chrysopidae | 1 () | 2 (.005) | 0 | 1 (.002) | 3 (.001) | 2 (.003) |
| Raphidiidae | 3 (.001) | 2 (.005) | 2 (.001) | 3 (.006) | 5 (.002) | 1 (.001) |
| <i>Total</i> | <u>7 (.003)</u> | <u>5 (.012)</u> | <u>2 (.001)</u> | <u>4 (.008)</u> | <u>7 (.003)</u> | <u>3 (.004)</u> |
| Strepsiptera | 0 | 0 | 0 | 0 | 1 () | 0 |
| Ephemoptera | 0 | 0 | 0 | 0 | 1 () | 0 |
| Unknown Insects | 0 | 0 | 1 () | 0 | 0 | 0 |
| Arachnida | | | | | | |
| Araneida | 26 (.013) | 6 (.015) | 33 (.016) | 10 (.020) | 16 (.006) | 7 (.009) |
| Acari | 11 (.005) | 1 (.002) | 51 (.024) | 9 (.018) | 8 (.003) | 1 (.001) |
| Scorpion | 0 | 0 | 0 | 1 (.002) | 0 | 0 |
| <i>Total</i> | <u>38 (.013)</u> | <u>8 (.020)</u> | <u>85 (.041)</u> | <u>21 (.042)</u> | <u>25 (.010)</u> | <u>9 (.012)</u> |

Table 4 (Concluded)

| <u>Prey</u> | <u>Sympatric</u> | | <u>Graciosus</u> | | <u>Occidentalis</u> | |
|---------------------|------------------|-------------|------------------|-------------|---------------------|-------------|
| | <u>1975</u> | <u>1976</u> | <u>1975</u> | <u>1976</u> | <u>1975</u> | <u>1976</u> |
| Reptilia | | | | | | |
| <u>Sceloporus</u> | | | | | | |
| <u>occidentalis</u> | 0 | 1 (.002) | 0 | 0 | 1 () | 0 |
| Grand Total | <u>2075</u> | <u>401</u> | <u>2085</u> | <u>503</u> | <u>2587</u> | <u>751</u> |

Low diversity values of E, the equivalent number of equally common taxa, for the diets of both S. graciosus populations are indicative of the limited nature of the S. graciosus diet (Table 5). The calculated value of E for the sympatric S. occidentalis population was intermediate between S. graciosus and the allopatric S. occidentalis. A shift in diet as indicated by the differences in diversity values for the two populations of S. occidentalis should not necessarily be construed as a response to the presence of S. graciosus because the diversity of available prey at the sympatric site was also intermediate between the graciosus site and the occidentalis site (Table 5). That is, where there was a high diversity of available prey, there was a correspondingly high prey diversity in the diet of S. occidentalis. S. graciosus did not follow the same general pattern with respect to the diversity of available prey and diet because of the dominating influence of the formicids in the diet.

However, examination of temporal variation in the dietary and available prey data (Figures 3, 4) provides additional information regarding the behavior of the two species. Dietary diversity (Figure 5) for both populations of S. graciosus and the sympatric S. occidentalis are initially high and then drop through June, whereupon the diversity returns to a higher level. Sympatric S. graciosus and S. occidentalis diversity values are nearly parallel while the allopatric S. graciosus is slightly higher. In contrast, the diversity of diet for allopatric S. occidentalis essentially remained high. The diversities of available prey at the sympatric and graciosus sites were more similar to one

Table 5. Diversity values for diet and available prey. Diversity is expressed as the equivalent number of equally common taxa (E).

DIET:

| <u>Population</u> | <u>S. occidentalis</u> | <u>S. graciosus</u> |
|-------------------|------------------------|---------------------|
| Sympatric | 2.624 | 2.030 |
| Allopatric | 5.094 | 2.098 |
| Both populations | 3.726 | 2.065 |

AVAILABLE PREY:

| <u>Site</u> | <u>1975</u> | <u>1976</u> |
|--------------------|-------------|-------------|
| Sympatric | 3.106 | 2.896 |
| Graciosus | 2.948 | 2.922 |
| Occidentalis | 3.371 | 2.293 |
| All sites combined | 3.354 | 2.942 |

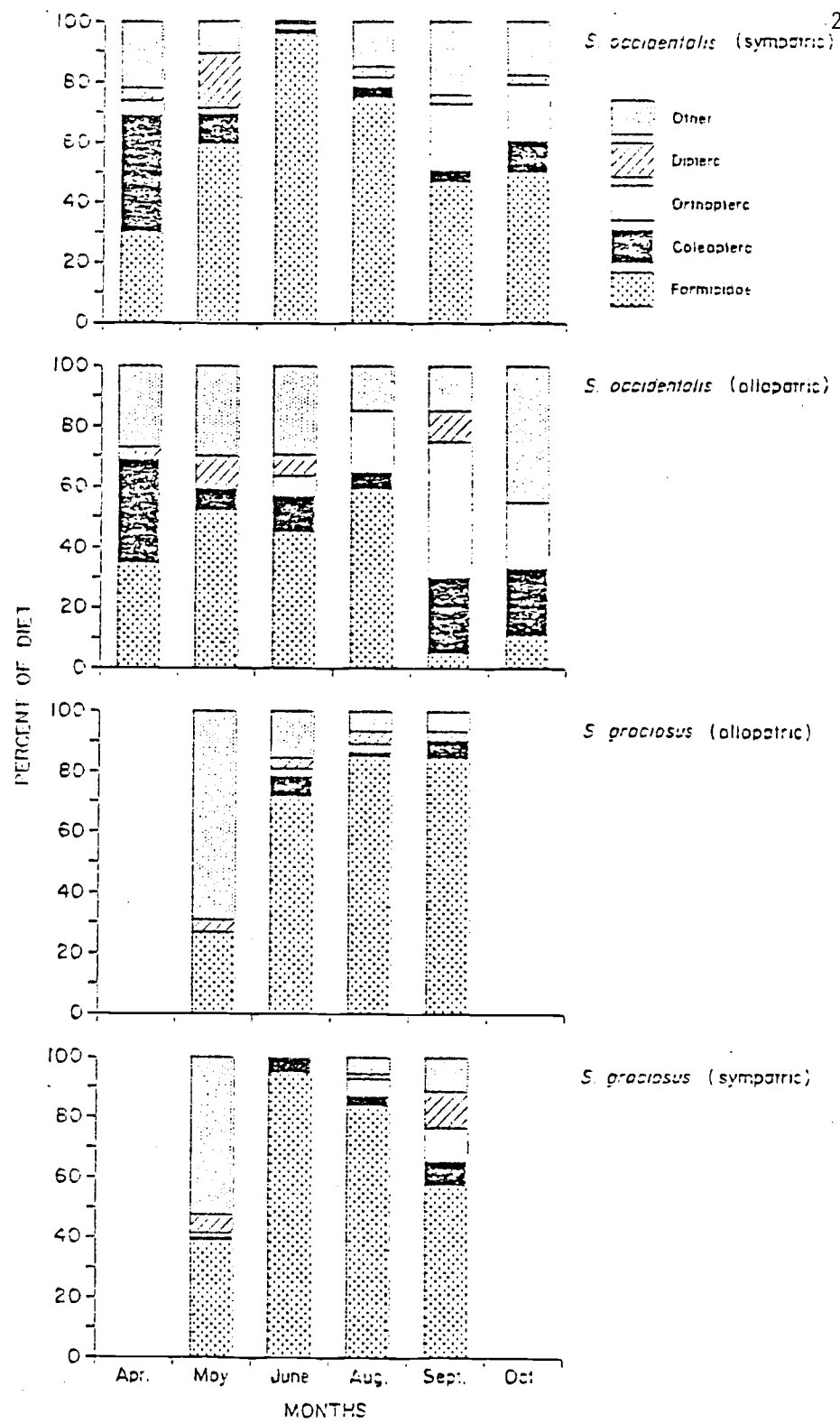


Figure 3. Monthly diets for sympatric and allopatric populations of *S. occidentalis* and *S. graciosus*. Data are presented as proportions of total number of prey items.

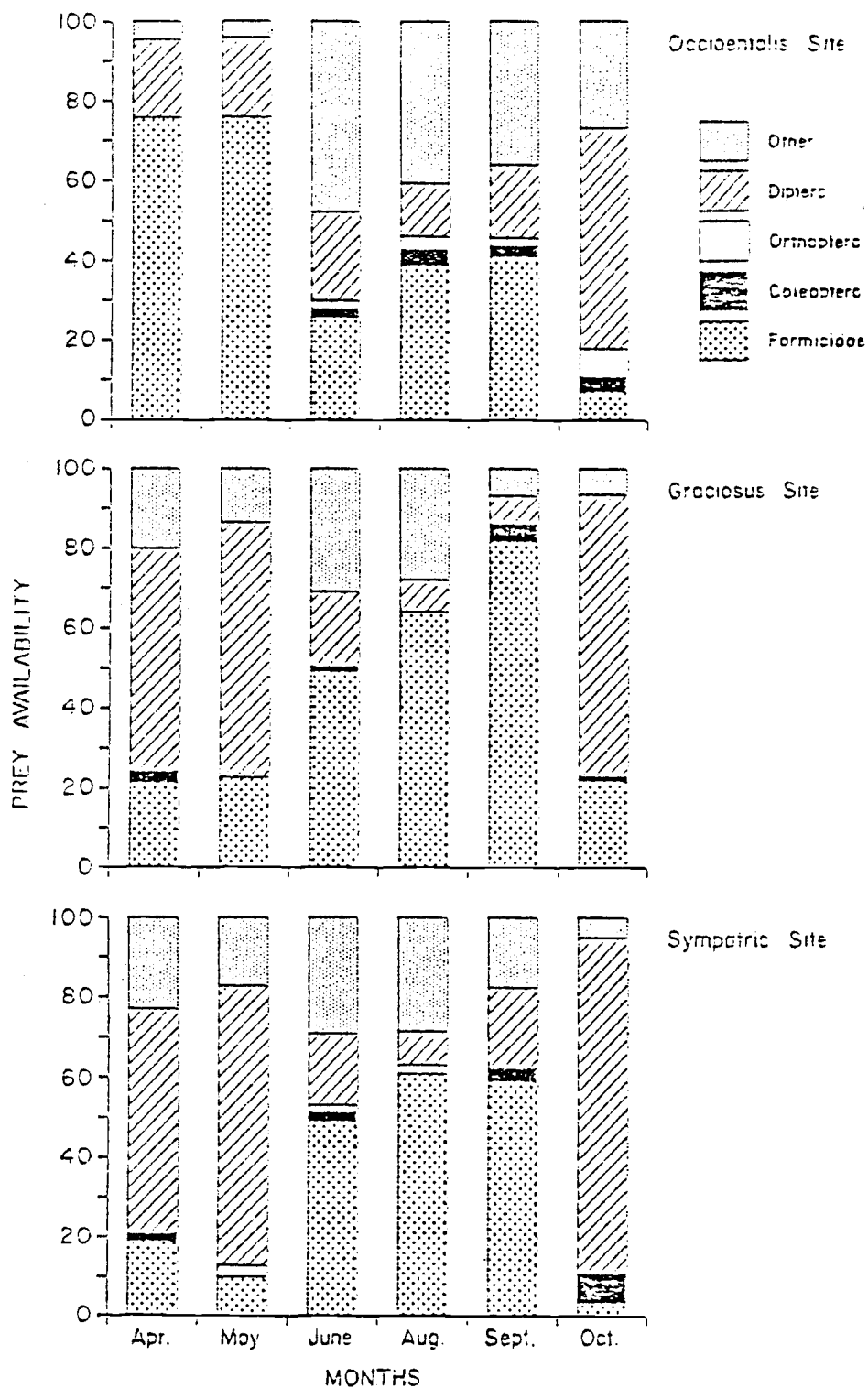


Figure 4. Monthly samples of available prey for the graciosus, sympatric, and occidentalis sites. Data are presented as proportions of total number of prey items.

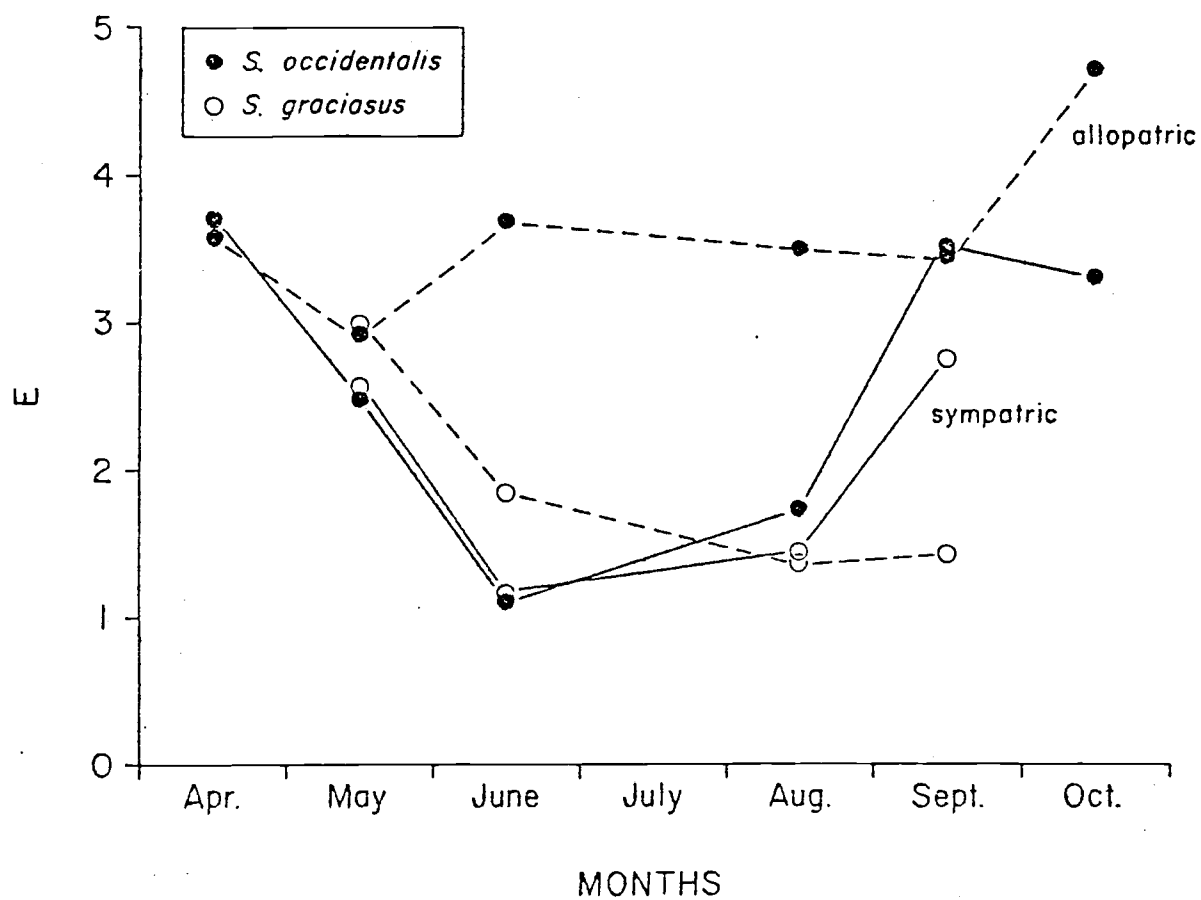


Figure 5. Monthly dietary diversity values for sympatric and allopatric populations of *S. occidentalis* and *S. graciosus* expressed as the equivalent number of equally common taxa (E).

another than that at the occidentalis site (Figure 6). Except for the April and May samples, the occidentalis site had a consistently more diverse fauna of available prey than the other sites. Lizards at the occidentalis site also had a more diverse diet. Low diversity values for May and June at the occidentalis site were due to a disproportionately large number of Formicidae in the samples (Figure 4), which were a result of random placement of pit traps near several ant colonies during those months. Presumably, if the colonies had been missed E would have remained large for the occidentalis site.

Although the emphasis has been upon the differences between populations, the SIMI analysis strongly suggests that the diets of both lizard species are actually very similar, as are the available prey from the three sites. As an example, the annual diets of S. occidentalis and S. graciosus have a SIMI value of 0.967, or a probability of 0.967 that their diets were identical. Available prey from the three sites had a SIMI of 0.952.

There was also seasonal variation in dietary similarity. During the summer months the similarity for all lizard populations was greater than 0.950 (Figure 7, Blocks 7-14). Outlying blocks of lower similarity were confined to spring and fall samples. Except for the June occidentalis sample (Block 9), the available prey also exhibited a pattern of high similarity among the summer samples with lower similarity among spring and fall samples (Figure 8, Blocks 6-15). Block 9 "fell out" because of a lower Formicidae frequency (Figure 6). Despite the apparent similarity in seasonal patterns between diet and available prey, there

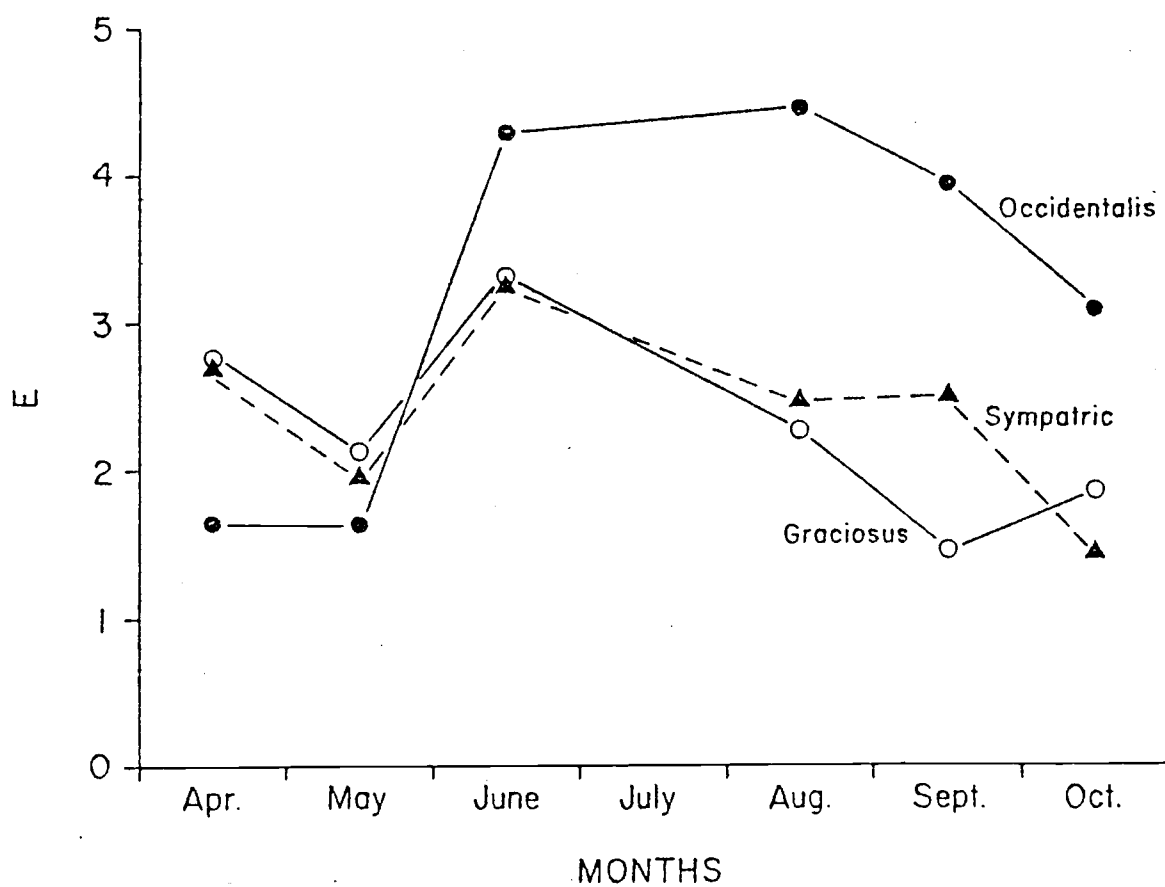


Figure 6. Monthly available prey diversity values for the sympatric, graciosus, and occidentalis sites expressed as the equivalent number of equally common taxa (E).

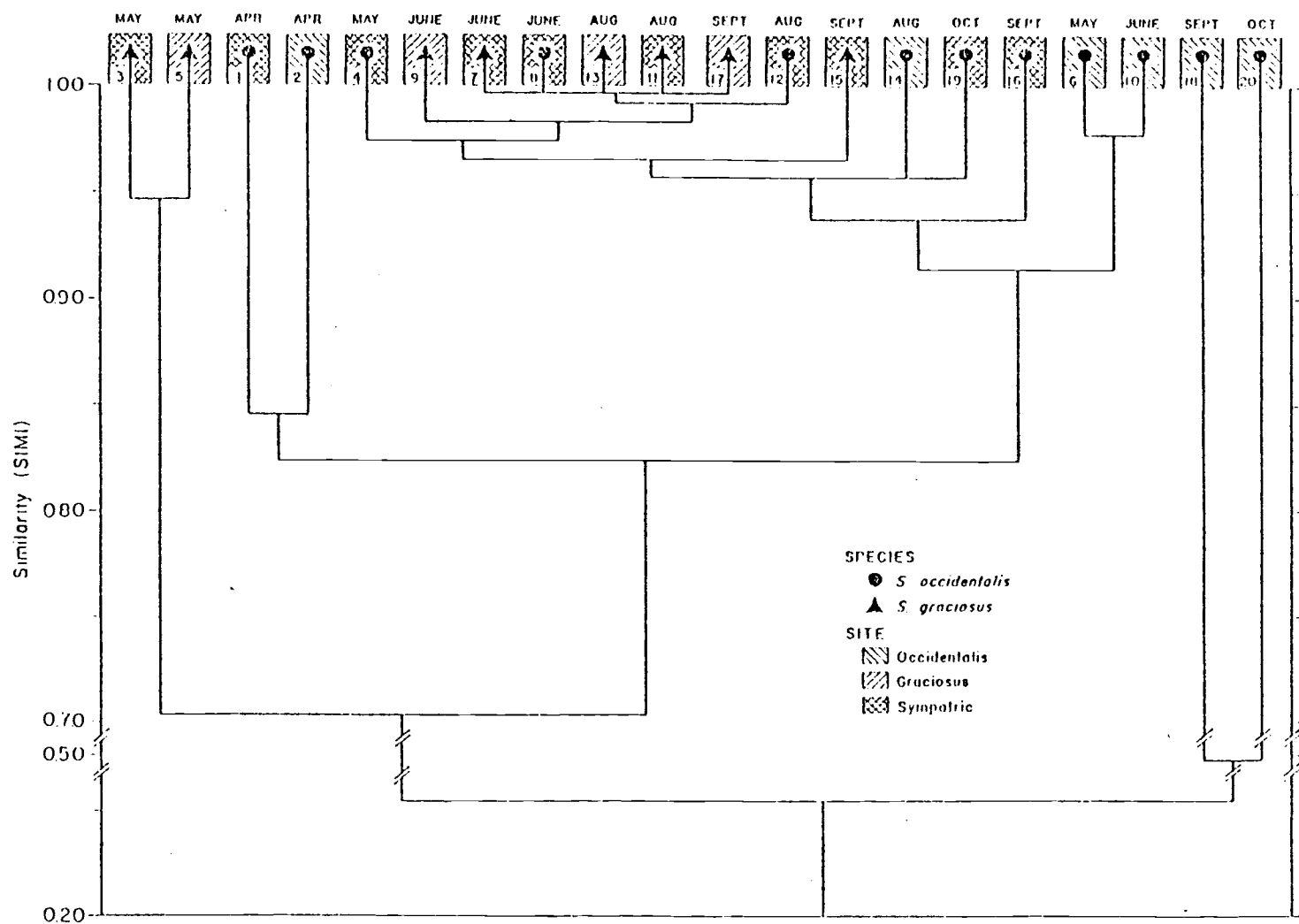


Figure 7. Phenogram of 20 blocks (samples) of dietary data based upon the probability of similarity analysis (SIMI).

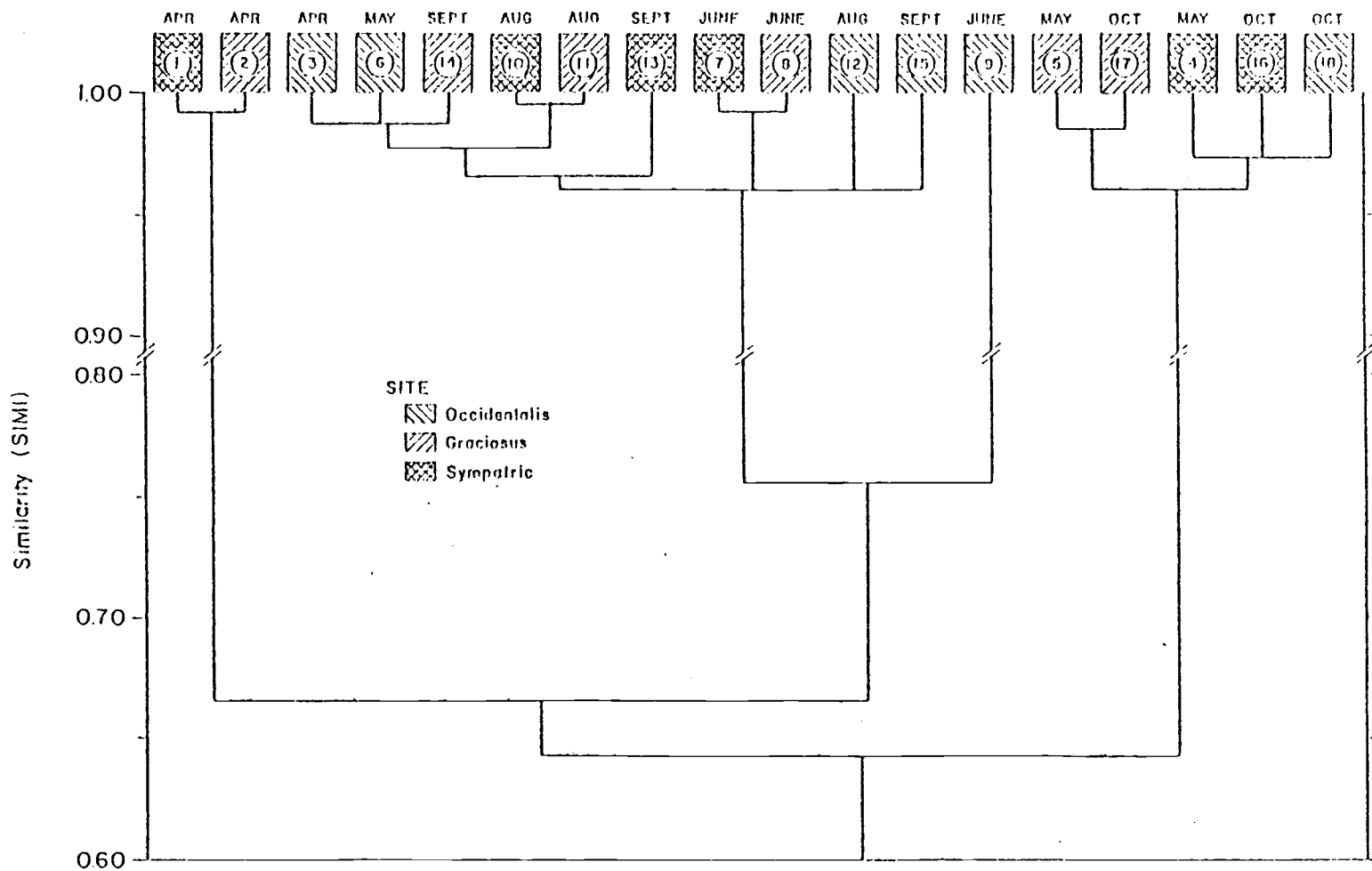


Figure 8. Phenogram of 18 blocks (samples) of available prey data based upon the probability of similarity analysis (SIMI).

were no significant correlations between the two data sets. The variation of the outliers was such as to prevent correlation of the entire data sets.

The morphological data suggest the presence of an apparent shift in body size by S. occidentalis, but not by S. graciosus when populations are sympatric. There were highly significant differences ($P < 0.001$) between the two S. occidentalis populations for snout-vent length (SVL), dorsal scales, mid-body scales, femoral pores, and subdigital lamellae (Table 6). Although the sympatric S. occidentalis had a larger mean SVL, the absence of significant differences between character ratios indicates that there was no difference in relative body shape between the two populations. There were no significant differences between the S. graciosus populations for any morphological character (Table 7).

Discussion

Investigation of dietary patterns within lizard communities has constructive uses. Diet has been suggested as the mechanism by which North American lizard populations can be separated (Pianka, 1975). Competition for food between closely related species may also lead to shifts in diet selection and/or morphology (Mayr, 1970). However, when such shifts are found, care must be taken not to reject immediately explanations that stand apart from dietary competition. Comparisons of feeding strategies between populations must be made with respect to the known available prey. Also, one cannot assume, as Rose (1976a) did, that "different" habitats will contain different available prey. If the

Table 6. Comparison of morphological characters of *S. occidentalis* from the sympatric (N = 30) and allopatric (N = 27) populations. Means are presented with the standard errors in parentheses. See Table 2 for descriptions of the characters.

| <u>Character</u> | <u>Sympatric</u> | <u>Allopatric</u> | <u>Significance</u> |
|-------------------------|------------------|-------------------|---------------------|
| SVL | 69.27 (1.15) | 61.96 (1.15) | *** |
| Axilla-Groin/SVL | 0.49 (0.53) | 0.48 (0.56) | NS |
| SNO/SVL | 0.20 (0.14) | 0.20 (0.17) | NS |
| Jaw Length/SVL | 0.16 (0.26) | 0.17 (0.28) | NS |
| Jaw Width/SVL | 0.20 (0.17) | 0.21 (0.20) | NS |
| Foreleg/SVL | 0.13 (0.03) | 0.13 (0.04) | NS |
| Thigh/SVL | 0.24 (0.14) | 0.25 (0.41) | NS |
| Shank/SVL | 0.17 (0.17) | 0.17 (0.20) | NS |
| Foot/SVL | 0.11 (0.17) | 0.11 (0.17) | NS |
| Toe/SVL | 0.17 (0.28) | 0.17 (0.26) | NS |
| Dorsal Scales | 42.27 (0.35) | 39.15 (0.36) | *** |
| Midbody Scales | 49.37 (0.45) | 46.74 (0.49) | *** |
| Parietal-Fronto Par. | 5.07 (0.18) | 4.89 (0.17) | NS |
| Frontal Scales | 1.70 (0.09) | 1.52 (0.13) | NS |
| Prefrontal Scales | 5.70 (0.12) | 5.63 (0.14) | NS |
| Scales Between Fem. Pr. | 9.93 (0.25) | 7.37 (0.23) | *** |
| Circumorbitals | 20.10 (0.33) | 19.56 (0.27) | NS |
| Femoral Pores | 33.37 (0.31) | 30.59 (0.54) | *** |
| Subdigital Lamellae | 31.40 (0.23) | 28.07 (0.38) | *** |

*** $P < 0.001$

Table 7. Comparison of morphological characters of S. graciosus from sympatric (N = 17) and allopatric (N = 16) populations. Means are presented with the standard errors in parentheses. See Table 2 for descriptions of the characters.

| <u>Character</u> | <u>Sympatric</u> | <u>Allopatric</u> | <u>Significance</u> |
|-----------------------|------------------|-------------------|---------------------|
| SVL | 46.51 (0.92) | 46.16 (1.14) | NS |
| Axilla-Groin/SVL | 0.49 (0.60) | 0.48 (0.58) | NS |
| SN0/SVL | 0.21 (0.32) | 0.21 (0.25) | NS |
| Jaw Length/SVL | 0.17 (0.33) | 0.16 (0.33) | NS |
| Jaw Width/SVL | 0.20 (0.25) | 0.19 (0.20) | NS |
| Foreleg/SVL | 0.13 (0.29) | 0.13 (0.34) | NS |
| Thigh/SVL | 0.25 (0.44) | 0.23 (0.67) | NS |
| Shank/SVL | 0.17 (0.24) | 0.16 (0.26) | NS |
| Foot/SVL | 0.11 (0.04) | 0.10 (0.19) | NS |
| Toe/SVL | 0.16 (0.32) | 0.16 (0.37) | NS |
| Dorsal Scales | 52.18 (0.35) | 52.88 (0.39) | NS |
| Midbody Scales | 53.12 (0.44) | 53.63 (0.45) | NS |
| Scales Betw. Fem. Pr. | 12.65 (0.37) | 11.75 (0.36) | NS |
| Circumorbitals | 20.12 (0.38) | 19.38 (0.47) | NS |
| Femoral Pores | 28.24 (0.47) | 28.13 (0.56) | NS |
| Subdigital Lamellae | 27.18 (0.64) | 27.13 (0.35) | NS |

available prey are not known, then any comparative statement about the degree of selectivity exhibited by an organism would be compromised, since the relative differences in diet selection may be attributable merely to the relative differences in prey available to each population.

The abundance of insects, the lizard's primary food source, varies directly with primary production (Brown, 1973). The primary production is in turn regulated largely by the amount of annual precipitation (Rosenzweig, 1968; Brown, 1975). Because annual precipitation is highly unpredictable in shrub-steppe regions (Wiens, 1974), one should expect to find annual variations in dietary patterns among lizard populations.

With respect to the sympatric and allopatric populations of S. occidentalis, observed shifts in diet were apparently associated with differences in the availability of prey rather than with competition with sympatric S. graciosus. Dominance of the diet by the taxa Formicidae, Coleoptera, Orthoptera, and Diptera is not novel and has been reported for S. occidentalis and S. graciosus in California (Rose, 1976b). Formicidae were also reported as the major prey item of S. graciosus from the Great Basin (Burkholder and Tanner, 1974). These three authors speculated that because greater variation was found between monthly samples within one year than between samples taken in the same calendar month in successive years, temporal variation in prey availability must have influenced diet selection--something they failed to measure. The present study does in fact show that there was temporal variation in the diversity of both diet and available prey. Burkholder and Tanner (1974) also reported annual variations in diet for S. graciosus.

The significant differences in frequency of Formicidae in the diet between the S. occidentalis populations might suggest that a shift in diet selection has occurred. Dietary shifts among isolated sympatric lizard populations are not uncommon and have been reported for other Iguanidae (Pianka and Parker, 1975). However, the patterns of diversity for diet and available prey were similar in that the high diversity levels for the occidentalis site were analogous to the high dietary diversity levels for the allopatric S. occidentalis. The observation suggests that any "shifts" in diet were a response to differences in available prey between sites.

High similarity values establish that when the samples of diet and available prey are considered in toto, there is a high degree of overlap. That is, despite the fact that the occidentalis site and its constituent lizards can be separated from the other sites based upon diversity values, a sample from most any site, with respect to either available prey or diet, has a high probability of being identical to one of the other samples. High levels of dietary overlap were reported for sympatric populations of S. occidentalis and S. graciosus (71%) and two disjunct populations of S. occidentalis (88%) (Rose, 1976b). Overlap values calculated by Rose were lower than those presented here. However, I believe that the differences merely reflect the conservative nature of the index used by Rose---that is, recording the minimum percent occurrence of species in different prey taxa (from Holmes and Pitelka, 1968).

An interesting aspect of Rose's data (1976a) was that the largest overlap values were for the two S. occidentalis populations, whereas the

two S. graciosus populations in the present study had the greatest amount of overlap. One explanation is that the sympatric site, with its rocky outcrops, can be considered to represent the limit of penetrance of S. occidentalis into the shrub-steppe. Because the lizards are restricted to these "rock islands" the populations of S. occidentalis may be more sensitive to variations in available prey than those populations located in preferred habitats such as chaparral. In contrast, the S. graciosus populations are actually in a preferred habitat situation in central Oregon, and therefore, perhaps are less sensitive to subtle shifts in available prey. I suggest that the reverse case occurred in Rose's study because her study sites were characterized, at least in part, by chaparral. It is unfortunate that she did not have data from an allopatric S. graciosus population for a complete comparison.

Although a significant difference in body size was found, care should be taken before invoking the explanation that morphological shifts in the sympatric population resulted from interspecific competition for available resources. One cannot presume that observed morphological differences must result from competition alone (Wiens, 1977), as other factors such as the unpredictability of the environment (Maiorana, 1976) or the average annual precipitation levels (Case, 1976) have been correlated with shifts in body sizes. Tinkle and Ballinger (1972) also reported that populations of Sceloporus undulatus from diverse habitats exhibit significant differences in both life history strategies and morphological characters. I have also found significant differences in morphological characters between several disjunct populations of S. occidentalis (White, unpublished data).

Because the diets for all populations of lizards were so similar, I do not believe that competition for food can be invoked as the causative agent for the larger morphs found in the sympatric S. occidentalis population. The absence of a shift in body shape was also reported by Rose (1976a) with reference to relative jaw sizes for S. occidentalis. She suggested that the correlation between head size and differential prey utilization, suggested by Schoener (1968, 1970), was not evident for S. occidentalis. Just as territorial behavioral shifts are known to occur in areas of sympatry for lizards (Ferguson, 1973), a morphological shift in body size might result from pressure to increase species identity recognition (Rose, 1976a). A larger size would increase the effectiveness of such behavioral cues as gular patch patterns, which are known components of sceloporine territorial display (Brattstrom, 1974).

Summary

The findings of the study suggest that differences in diet between populations of S. occidentalis are related more to variations in the availability of prey than to interspecific competitive interactions. Because the overall diets of all lizard populations were extremely similar, observed differences in the body size of S. occidentalis between the sympatric and allopatric populations are most likely the result of factors other than dietary competition.

III. MORPHOLOGICAL VARIATION IN SCELOPORUS OCCIDENTALIS

Investigations of morphological variation often attempt to establish causal relationships between environmental factors and morphological characters. Consideration of patterns of variation exhibited by natural populations should enhance the comprehension of the overall biology of an organism. This study examines two types of morphological variation, geographical variation and fluctuating asymmetry.

Geographical variation has long been of interest to naturalists (for examples see Mayr, 1970; Gould and Johnston, 1972), but as Gould and Johnston noted, there have been very few investigations of differences in the amount of morphological variation characterizing different populations. There are several notable studies of variation in insular reptile populations (Soulé, 1972; Soulé and Yang, 1974; Clover, 1975), but few for mainland reptile populations. Another aspect of geographical variation is the apparent difference between central and peripheral populations (Mayr, 1970). There is a general observation that central populations tend to be more variable than peripheral populations. The factors contributing to this observation are summarized by Soulé (1973).

Fluctuating asymmetry in populations is the condition of minor departures from perfect bilateral symmetry that seem to have no specific adaptive function, but are nearly universal in some natural populations. Fluctuating asymmetry is distinguished from other forms of asymmetry when the signed differences between the left and right sides are distributed normally around a mean of zero (Van Valen, 1962). As differences between

paired structures that are not consistent might reflect developmental accidents (Thoday, 1958), fluctuating asymmetry has been used to measure buffering capacity within development. Others (Valentine et al, 1973) suggested that fluctuating asymmetry be used as a statistical indicator of environmental stress. Soulé (1967) proposed that the levels of fluctuating asymmetry might be concordant for several characters within a population. Therefore, a given population might exhibit high levels of fluctuating asymmetry for several characters while another population might exhibit low levels of fluctuating asymmetry. He called this concordance of asymmetries the population asymmetry parameter (PAP). A PAP could serve as an index of a species' response to environmental gradients.

In this study I used the wide ranging (Stebbins, 1966) iguanid lizard, Sceloporus occidentalis, to consider several questions regarding morphological variation. Can any patterns in the levels of variation between distinct populations of S. occidentalis be discerned? Do these patterns, if they exist, support the hypothesis that peripheral populations exhibit less variation than central populations? Finally, does a population asymmetry parameter exist in S. occidentalis?

Methods

Study Sites:

I used samples from four study areas in this analysis (Figure 9). The Santa Barbara County site was of interest because of its southcentral position in the range of S. occidentalis. The three Oregon sites

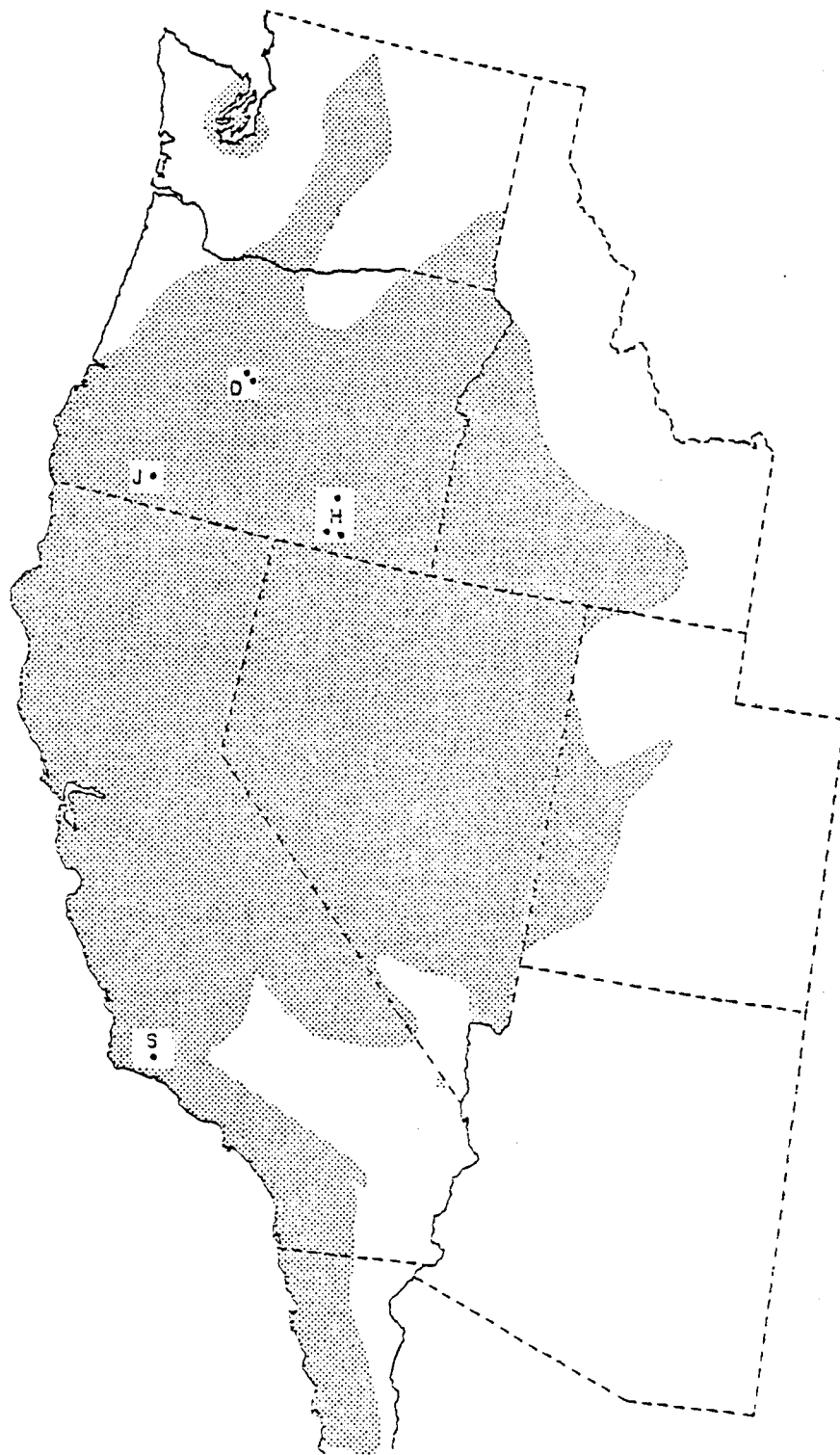


Figure 9. Four collection areas for *S. occidentalis*: Jackson (J), Deschutes (D), Harney (H), and Santa Barbara (S).

contained populations peripheral to the distributional range and they also represented a variety of habitat types. The majority of specimens were collected from the four localities. Additional Oregon specimens were provided by the Museum of Natural History, Department of Zoology, Oregon State University. The sites are described as follows:

1. Santa Barbara County, California. The habitats typical for collections were either chaparral, foothill woodland, or valley grassland (Munz, 1966). A complete description of the collection sites was presented by White (1972).

2. Jackson County, Oregon. Collections were made along the edges of the Rogue River Valley near Sam's Valley (T35S, R2W, Sections 24, 34). The habitat ranged from sclerophyllous shrubs to a mixed conifer-evergreen zone (Franklin and Dyrness, 1973).

3. Harney County, Oregon. Collections were made in three general areas of this Great Basin county, primarily in rocky areas where S. occidentalis was readily found. The locations were dominated by shrub steppe and steppe plant communities (Franklin and Dyrness, 1973).

4. Deschutes County, Oregon. The majority of specimens were the same as those used for the dietary study. The two specific sites were north of Bend (T15S, R12E, Sections 22,27; T17S, R13E, Sections 8,9), in a Juniperus occidentalis transition zone approaching a shrub steppe condition (Franklin and Dyrness, 1973).

Characters:

Twenty-five morphological characters were scored in the preliminary observations. The criteria for final selection were the ease of

quantification, the ease of scoring, and the use of the characters by other authors (Jackson, 1973a; Larsen and Tanner, 1974). The first criterion eliminated the use of any characters dealing with continuous variation in color or pattern (Clover, 1975). The final 19 characters used in the analyses and the manner in which they were scored are listed in Table 2. The first 10 characters were metric and the remaining characters were meristic. Three of the meristic characters were bilaterally symmetrical and were scored separately with respect to their two sides. These three characters were used for the measurement of a populations asymmetry parameter. In the remaining analyses the symmetrical characters were summed and included in a 19 x n data matrix for each sample. When the variables were plotted against the inverse of the cumulative standard normal distribution the plots were linear, which would be necessary for normality. I therefore used parametric statistics for a portion of the data reduction.

Coefficients of Variation:

I used the coefficient of variation (CV) to characterize the variability of the meristic counts. Kerfoot (1969) suggested use of the CV with scale counts because of its reliability, as the measure is independent of the mean. However, Simpson et al (1960) cautioned against the overuse of the CV, and Lande(1977) noted biases imposed by mathematical constraints that may restrict the use of CV in comparisons. The use of the CV for the comparison of traits of equal dimensionality within species, as I have done, was justified because the means were independent of the CV's (Lande, 1977). With a sample mean of \bar{x} and a

standard deviation of s , the CV of a sample is defined by the expression (Sokal and Rohlf, 1973):

$$CV = \frac{s}{\bar{x}}$$

Several authors (Hansen et al, 1953; Clover, 1975) recommended the use of an alternative measure, the relative variance (RV), when characterizing ratios or variables functionally related to size. I scaled the intercorrelated metric measures against the snout-vent length (SVL) to create a ratio estimate:

$$\text{ratio estimate (R)} = \frac{\bar{x}}{\bar{y}}$$

where \bar{y} is the mean SVL and \bar{x} is the mean value for a specific variable.

The relative variance is then defined by the expression:

$$RV = (1 - f) \left[(CV_x^2 + CV_y^2 - 2 \cdot r \cdot CV_x \cdot CV_y) / n \right]$$

where

f = sampling fraction of total population

CV_x = coefficient of variation for x in ratio estimate

CV_y = coefficient of variation for y in ratio estimate

r = product moment correlation coefficient of x and y

n = sample size

" f " was considered to be zero because of large population sizes.

Kendall's Coefficient of Concordance:

Kendall's coefficient of concordance (W) was the appropriate statistic for determination of distinguishable patterns of variation in the samples (Siegal, 1956). The samples were ranked with respect to their

CV's and RV's. With k sets of rankings and N entities or sites, W is defined as:

$$W = \frac{S}{\frac{1}{12} k^2 (N^3 - N)}$$

where S is equal to the sum of squares of the observed deviations from the mean ranking, \bar{R}_j :

$$S = (R_j - \bar{R}_j)^2$$

W has special applications in providing a standard method of ordering the samples according to a consensus when there is no objective order to the samples.

The significance of any observed value of W may be tested by using the following formula which approximates a X^2 distribution with $N - 1$ degrees of freedom (Siegal, 1956):

$$X^2 = k(N - 1)W$$

Asymmetry:

Three bilaterally symmetrical meristic characters, the numbers of circumorbitals, subdigital lamellae, and femoral pores were utilized for measurement of asymmetry. The estimate of population asymmetry was the mean, \bar{d} , of the absolute values of the differences between the sides of a paired structure. Each \bar{d} was divided by the character mean for that population in order to eliminate scaling effects (Soulé, 1967). Such division allowed for the direct comparison between characters by expressing asymmetry as the mean percentage of unpaired units (scutes or millimeters) per individual (Jackson, 1973b).

Kendall's coefficient of concordance, W , was the appropriate test for a population asymmetry parameter or a property that can be estimated by a random sample of uncorrelated character asymmetries. If such a parameter existed there would be a significant degree of concordance.

Canonical Correlation:

Canonical correlation was used to examine the relationship between the four populations because it provided an overall measure of the relationship while removing the intercorrelations. I will not present a detailed account of the computational procedures but I recommend Harris (1975) for an introduction to the subject, and Cooley and Lohnes (1971) for examples of multivariate applications and computer programs. I used the BMD07M program (Dixon, 1968) for the analysis.

Results

The peripheral populations (Jackson, Deschutes, and Harney) of S. occidentalis had higher levels of morphological variation than the central population (Santa Barbara). Based upon the rankings of CV's and RV's (Table 8), there was a highly significant amount of concordance ($W = 0.614$) for the metric characters (Table 9) but not for the meristic characters ($W = 0.126$). When metric and meristic characters were ranked together a significant amount of concordance still was obtained ($W = 0.223$).

Canonical correlation tends to emphasize the factors of variation associated with shape and appearance rather than the more common sources of variation such as size and age (Clover, 1975). This is due to the

Table 8. Coefficients of variation for meristic characters (11-19) and the relative variances for the metric character ratios (2-10). The sum of rankings is $= \Sigma R_j$.

| <u>Population</u> | <u>Characters</u> | | | | | | | | | ΣR_j |
|-------------------|-------------------|-------|-------|-------|-------|-------|-------|-------|-------|--------------------|
| <u>CV's</u> | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | |
| Deschutes | 6.28 | 5.92 | 18.00 | 36.10 | 15.00 | 20.58 | 8.03 | 8.63 | 7.97 | 28 |
| Harney | 5.06 | 5.31 | 17.40 | 19.71 | 20.60 | 11.20 | 10.14 | 7.16 | 5.82 | 18 |
| Jackson | 3.06 | 4.24 | 22.98 | 28.00 | 19.65 | 13.72 | 11.68 | 7.45 | 5.20 | 22 |
| Santa Barbara | 3.97 | 4.07 | 20.68 | 23.85 | 19.16 | 17.50 | 11.11 | 7.77 | 6.06 | <u>22</u> |
| | | | | | | | | | | $\bar{R}_j = 22.5$ |
| <u>RV's</u> | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| Deschutes | 0.613 | 0.499 | 1.321 | 0.605 | 1.580 | 0.966 | 0.606 | 1.174 | 1.177 | 28 |
| Harney | 1.033 | 0.221 | 0.567 | 0.325 | 1.367 | 0.350 | 0.777 | 0.954 | 1.314 | 24 |
| Jackson | 0.960 | 0.368 | 1.488 | 0.718 | 1.159 | 0.550 | 1.192 | 0.995 | 1.022 | 29 |
| Santa Barbara | 0.132 | 0.068 | 0.200 | 0.100 | 0.563 | 0.200 | 0.285 | 0.425 | 0.402 | <u>9</u> |
| | | | | | | | | | | $\bar{R}_j = 22.5$ |

Table 9. Calculated values for S (see Text for description), Kendall's coefficient of concordance (W), and corresponding X^2 .

| <u>Characters</u> | <u>S</u> | <u>W</u> | <u>X^2</u> |
|-----------------------------------|----------|----------|-------------------------|
| Meristic | 51 | .126 | 3.40 |
| Metric | 257 | .614 | 16.58*** |
| Combined (Meristic and Metric) | 362 | .223 | 12.07** |
| Asymmetry Analysis | 27 | .600 | 3.60 |

** P < 0.01

*** P < 0.001

standardization of the covariance matrix of means by the pooled within-group covariance matrix and subsequent elimination of inter-character correlations. The first two canonical variables of the analysis, those associated with shape, account for nearly 88% of the variability and the third variate accounts for the remaining 12%.

The four populations separate from one another (Figure 10) primarily on the basis of variation in metric characters (Figure 11). The Santa Barbara group clustered with respect to the shank, toe and foot--all rear leg characteristics. The Oregon samples separated along an axis associated with head shape: snout-occipital length and jaw length. The variation associated with meristic characters seems to be negligible with the exception of frontal scales, which are associated, to a degree, with head shape.

Because of no significance in the concordance of asymmetries (Table 9), the asymmetry analysis (Table 10) suggests that there is no measurable population asymmetry parameter for S. occidentalis.

Discussion

Although there are significant degrees of concordance in morphological variation among populations, the fact that peripheral populations have higher levels of variability than central populations requires a reexamination of the original hypothesis, which suggested that peripheral populations should be less variable than central populations.

One possibility is that because Sceloporus has recently experienced a high rate of speciation (Larsen and Tanner, 1975) there might be high

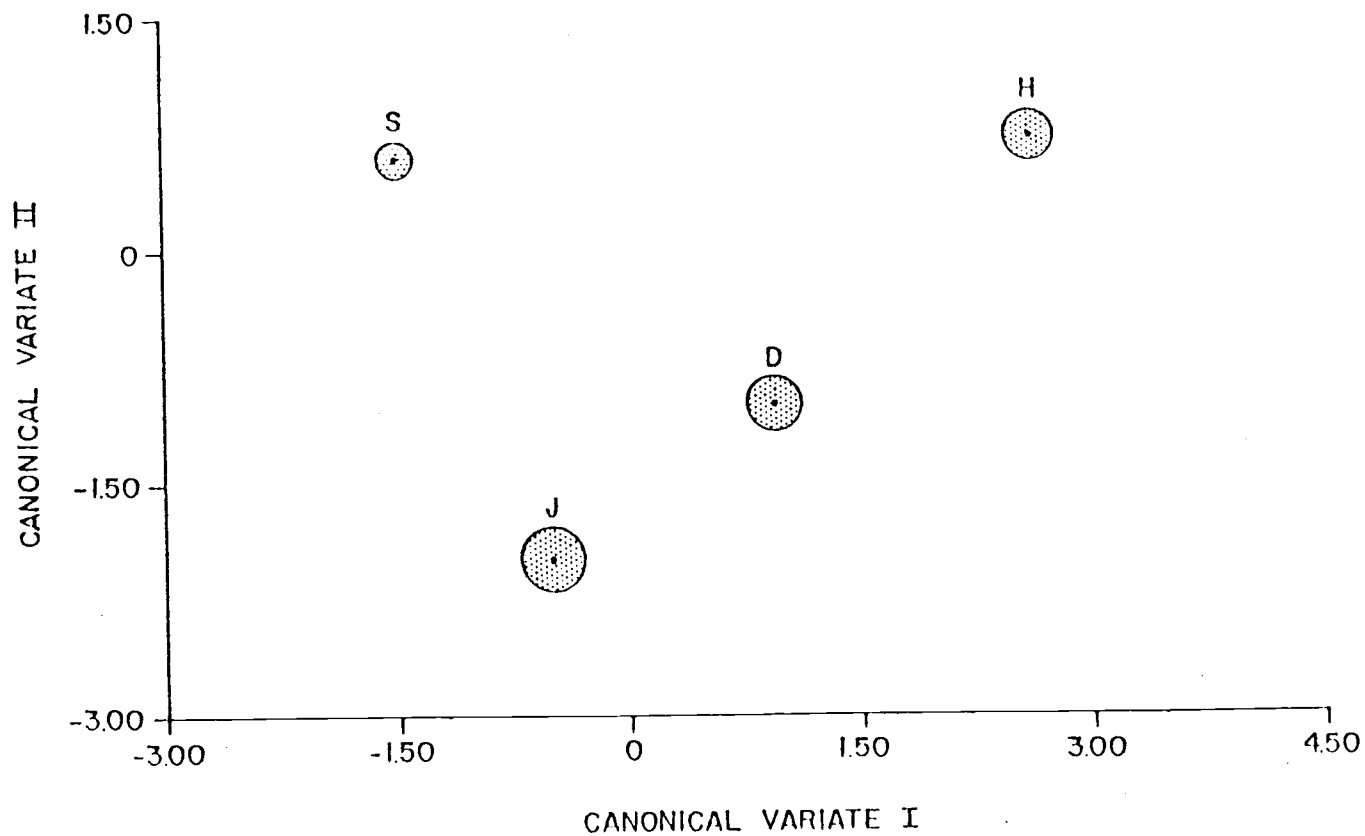


Figure 10. Scatter diagram of the centroids for the four populations projected upon the axes of the first two canonical variates. The respective circle around each centroid represents the 95% confidence limits for that mean (Seal, 1964). Populations are Santa Barbara (S), Jackson (J), Deschutes (D), and Harney (H).

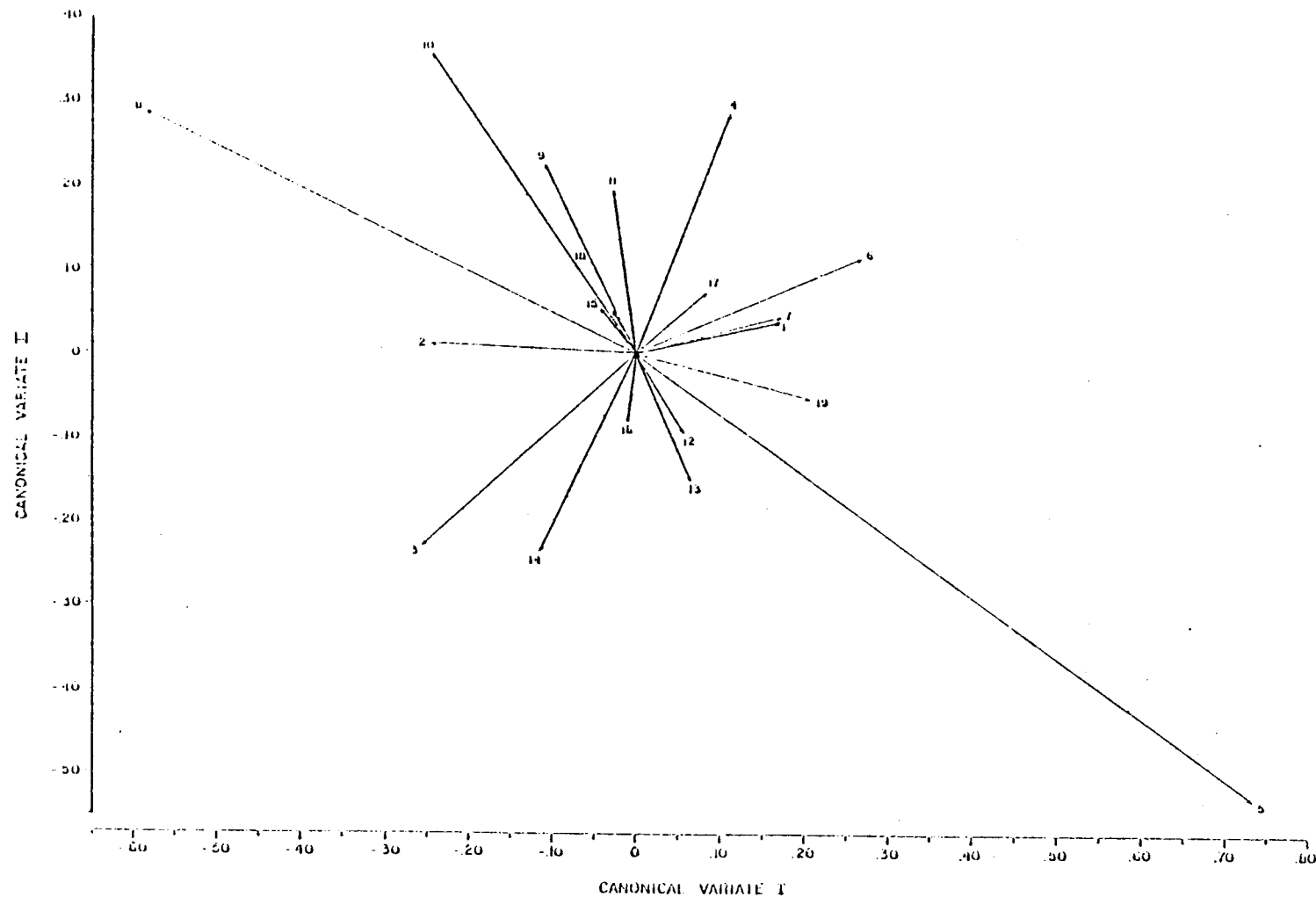


Figure 11. The influence each character would have upon the first two canonical variates if the character varied alone. For each character the vector shows the direction and magnitude of its influence on the variates, e.g., the shank (#8) exerts a nearly equal influence upon both variates (Jackson, 1973a). See Table 2 for descriptions of the characters.

Table 10. Results of asymmetry analysis. Values in the columns are the mean percentages of unpaired scutes per individual. The sum of rankings is ΣR_j .

| <u>Population</u> | <u>Circumorbitals</u> | <u>Subdigital Lamellae</u> | <u>Femoral Pores</u> | <u>ΣR_j</u> |
|-------------------|-----------------------|----------------------------|----------------------|--------------------------------|
| Deschutes | .0459 | .0175 | .0176 | 10 |
| Harney | .0424 | .0190 | .0218 | 10 |
| Jackson | .0452 | .0164 | .0090 | 6 |
| Santa Barbara | .0414 | .0151 | .0142 | 4 |
| | | | | $\overline{R_j} = 7.5$ |

levels of variation in those peripheral areas subject to speciation and geographical expansion (Kluge and Kerfoot, 1973). However, according to Savage (1960) the populations that I defined as peripheral are actually relict populations from a previously greater geographical range; therefore, they should be less variable.

A second possibility is based upon the fact that the various collection sites in Santa Barbara County were disjunct, but the habitat between sites was suitable for lizards. In other words there was a potential continuum in the lizards' distribution. The Oregon collection sites were isolated from one another by unsuitable habitats and the sites could effectively be described as "islands." Grant (1971) predicted that in regions of uniform conditions selection favors little morphological variation, and with spatially patchy conditions (as in Oregon) the reverse should be true.

A third possibility is that increased variation resulted from the lumping of actually separate, isolated samples in the peripheral populations. Mayr (1970) suggested that a species may be more variable peripherally because of the formation of population isolates that each has reduced variability resulting from inbreeding and restricted gene flow. There would be low intrapopulation variability, but the variability of the combined samples would be high. I reexamined a portion of the data by partitioning the two Deschutes sites from one another. The levels of variation are low within sites and there is a strong correlation between sites (Kendall's τ , $P < 0.0001$); but there is an increase in variation levels that followed the lumping of data

as was done in the original analysis. Therefore the third explanation is the most probable.

I reported previously (White, 1975) that color polymorphism with respect to gular patch patterns is extremely common in Santa Barbara County. In contrast there is no variation in patch patterns for Oregon lizards, which are monomorphic for a single patch color (single patch as opposed to multiple patches). This observation lends support to the hypothesis of higher levels of variability for central populations. Species recognition pressure may have influenced selection for little variation in gular patch types in peripheral populations. Iguanid lizards display their enlarged gular or dewlap regions during territorial displays (Carpenter, 1967; Brattstrom, 1974), and Webster and Burns (1973) demonstrated that the color of the dewlap was important for species recognition in Anolis. Crews and Williams (1977) found that for one species, A. carolinensis, the size of the dewlap and not the color was important in the displays. However, the significance of the gular patch pattern in sceloporine lizards has not been demonstrated and therefore cannot be discounted as a significant component in species recognition.

Separation of the populations with the canonical correlation analysis was based almost entirely upon the variation of metric characters rather than the meristic ones. The Santa Barbara group separated out according to limb characteristics. In his study of Sceloporus woodi, Jackson (1973a) was able to separate populations based upon the same limb features. As elongation of limbs is generally

considered to be a cursorial adaption in terrestrial lizards (Kramer, 1951; Snyder, 1962), Jackson speculated that populations with increased limb length were associated with habitats lacking ground cover because those lizards could escape to the sparse cover more readily. My data are insufficient to accept or reject his hypothesis. S. occidentalis is more arboreal in chaparral habitats (Marcellini and Mackey, 1970) as in Santa Barbara County than in Oregon, and I have often seen specimens rapidly running from the ground to a refuge point in the trees. Increased limb length could enhance this rapid escape.

The Oregon populations separated along a gradient associated with skull characters. The relationship between trophic dynamics and skull characters is often reported (for examples see Schoener, 1971), but because empirical dietary data are unavailable, to attribute the separation of the Oregon populations to differential resource utilization would be pure speculation. Variation of frontal scutes, the most variable of the meristic characters, does concur with the observation by Brown (1976) that scute polymorphism among iguanids is generally infrequent or conservative, with the exception of head scutes.

I have been unable to find a population asymmetry parameter for the populations investigated. Other authors found a PAP for lizards (Soulé, 1967) and for butterflies (Soulé and Baker, 1968), but in a comprehensive search, Jackson (1973b) was unable to find a PAP using six morphological characters of the iguanid S. woodi. I must concur with Jackson's concluding remark that "... although the concept of population differences in asymmetry level and their correlation with

genetic characteristics of the population is of such inherent interest to developmental biology, genetics and evolution that much more energy should be spent in investigating that reality, the results presented here do not lend credence to that reality."

Summary

Examination of 19 morphological characters of four populations of S. occidentalis revealed significant levels of concordance between the populations with respect to their variability. However, the central population was less variable than the peripheral populations. These results could be an artifact of the analyses which resulted from the lumping of small isolated populations in the peripheral populations. Separation between central and peripheral populations was based upon metric characteristics. There is no population asymmetry parameter for S. occidentalis.

IV. CONCLUSION

A series of population biology questions relative to saurian populations were examined in the two studies presented in this dissertation. The empirical data that were gathered did not necessarily fit the current models or theories of population biology.

Sceloporus occidentalis exhibited a shift in diet selection, but the response was associated with the variation in available prey rather than competitive interactions with its sympatric congener, S. graciosus. Differences in body sizes of the two populations of S. occidentalis were also attributable to factors other than dietary competition. Future data for dietary studies similar to the one presented here should be garnered from long term studies thus allowing for more accurate appraisals of the effect of temporal variation on natural communities.

Examination of four populations of S. occidentalis revealed that in contrast to a generally accepted observation, central populations were less variable than peripheral populations. There was also no population asymmetry parameter to report for S. occidentalis.

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