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Phenetic relationships in insular populations of *Lacerta sicula* and *L. melisellensis* correspond to geologic ages of the islands in two regions of the Adriatic Sea. Populations of *L. melisellensis* on older islands are more similar to populations of *L. sicula* than are *L. melisellensis* from younger islands, and examination of characters reflecting trophic structures of these lizards suggests that convergent evolution has progressed further in the populations on older islands.

A rough correspondence between phenetic similarities of populations and island sizes was investigated by means of multiple regression analyses in which geographic features of islands were used as independent variables and means of selected morphologic characters were dependent variables. Island area, length and distance to the mainland were the most important variables "explaining" interpopulation variations in measures of trophic structures, dorsal scale

counts, and numbers of femoral pores in *L. melisellensis*. Lizards from small isolated islands generally have larger bodies, relatively wider snouts and heads, relatively longer heads, more dorsal scales, and more femoral pores than *L. melisellensis* from larger islands near the mainland. Larger lizards with relatively larger head dimensions on small islands are believed to be the results of adaptations to situations of reduced interspecific interactions and restricted distributions of food resources. Dorsal scale count variations may be related to climatic heterogeneity, but the evidence is inconclusive. Likewise, variations in the number of femoral pores may be related to variations in a balance between conflicting selective pressures for avoiding predation and facilitating intraspecific communication, but basic information on the functional significance of these characters is lacking.

Measures of relative variation for ten meristic characters in *L. melisellensis* showed no significant pattern of variation, but levels of intrapopulation variation in ratios of head measurements to snout-vent lengths were generally lower in populations on small islands and higher in large island populations. Island area, length, the distance to potential sources of colonists and elevation were shown to be important variables in "explaining" geographic variations in levels of intrapopulation variability of trophic characters. Low levels of relative variation for trophic characters in populations from small isolated islands are generally associated with relatively high levels of sexual dimorphism in head width, suggesting that strong directional selection resulting from intraspecific competition for food has depleted genetic variation affecting these characters. Evidence from gene frequency data and body size distributions on small islands shows that genetic drift and founder effects complicate selectionist interpretations of these trends.

The similarity of the trends identified in insular populations of *Lacerta* to trends identified in other insular populations of lizards suggests a generalized response of lizards to isolation.

Morphological Variations in Populations of Lacerta from Islands in the Adriatic Sea

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MORPHOLOGICAL VARIATIONS IN POPULATIONS OF LACERTA FROM ISLANDS IN THE ADRIATIC SEA

I. INTRODUCTION

The role of natural selection as the major force in evolutionary processes has been widely accepted since publication of the theory in 1859 by Darwin. Yet at intervals the importance of other evolutionary mechanisms such as mutation, gene flow and random drift has been emphasized (Wright, 1935; Kimura, 1968; King and Jukes, 1969), sometimes excessively (Wright (1955); and Wills (1973)).

On islands the influence of different evolutionary mechanisms on populations of terrestrial organisms may differ in degree from their influence on mainland populations. Gene flow is undoubtedly reduced among insular populations, and the founder principle (Mayr, 1963) may be of considerable importance in determining the range of possible responses of a population to forces of natural selection. In conjunction with genetic drift, the founder effect may lead to different responses of related populations to very similar environmental conditions.

In recent years several workers have begun to investigate various aspects of insular populations in an effort to ascertain what roles different island features play in determining the direction and extent of evolutionary modifications of the organisms inhabiting them. Much of the work has concentrated on the factors governing the numbers of species which occur on islands (MacArthur and Wilson, 1963, 1967; Preston, 1962a, 1962b) and the characteristics of colonization (Simberloff, 1969; Simberloff and Wilson, 1969a, 1969b). Others have been concerned with the effects of insularity on the behavioral, morphologic and genetic systems of populations (e.g., Van Valen, 1965; Crowell, 1962; Keast, 1970; Soulé, 1972; Morse, 1971; Ayala, et al., 1972). This paper is concerned with morphological variation in insular populations of lizards.

Phenotypic variation has been categorized as deriving from genetic, environmental, historical, and stochastic sources (Milkman, 1970). In general, variation at two levels of organization are important to population biologists. Intrapopulation variation concerns differences among individuals within a population. Inter-individual differences, to the extent that they are heritable, provide the substrate for natural selection as well as other mechanisms for changing gene frequencies. The adjustment of local populations to their environment by natural selection leads to interpopulation variation. Differences among populations are usually apparent when mean values or variances for measurements of morphological characters are compared. Both levels of variation are important in understanding evolutionary trends in local populations.

Island populations of terrestrial vertebrates are particularly useful in the search for generalizations concerning phenotypic variation for several reasons. First, since island populations are more buffered against gene flow than most mainland populations, the results of most evolutionary processes should be more apparent in insular populations. Second, islands of various sizes, shapes, positions, and appearance present a considerable range of ecological heterogeneity. Patterns of morphological variation associated with variations in ecological heterogeneity provide strong inference for potential selective factors. Third, for terrestrial vertebrates the spatial boundaries of island populations are clearly delimited, and difficulties arising from interpopulational dispersal or interchange are reduced. These features of insular systems make them useful in determining the relationships between environmental and morphological attributes of populations.

My objectives in this study were to examine the phenotypic variation exhibited in 32 insular populations of lacertid lizards, to summarize the patterns of variation and covariation of the characteristics of these lizards, and to examine these patterns with respect to possible associations with environmental and biographical factors.

II. THE LIZARDS AND THE ISLANDS

The Lizards

The coastal region of Yugoslavia is inhabited by four species of lizards belonging to the genus Lacerta. Two species, Lacerta sicula and L. melisellensis, are broadly distributed along the coastal strip of the Adriatic and the adjacent islands. A third species, L. oxycephala, has a limited distribution in this area, occurring in the southern portion of the Adriatic coastal region. A large-bodied species of the genus, L. trilineata, is found only on the mainland, and is relatively rare. I have confined my study here to L. melisellensis and L. sicula.

Lacerta melisellensis is considered by Radovanović (1959) to be an endemic species to the coastal regions of Yugoslavia. It is a highly polytypic species; Mertens and Wermuth (1960) list 18 subspecies, of which only one occurs on the mainland, the remainder being insular forms. The geographical range of the species extends from northern Slovenia to Albania and includes many of the islands of the Adriatic. Within this range the lizards are found in shrubs, fig trees, grassy areas, and in or around stone walls. Near areas inhabited by humans they are found in olive and grape orchards. Populations and individuals differ from one another considerably in color and pattern, and these differences have been used extensively in taxonomic descriptions of the numerous subspecies (Radovanović, 1959).

Lacerta sicula is similar to *L. melisellensis* morphologically, ecologically, and taxonomically. In addition to being found in habitats similar to those in which *L. melisellensis* is found, *L. sicula* occurs in grassy pasture areas and on and around buildings in urban areas. Color and pattern variation is extreme, and has been used extensively in taxonomic descriptions. Like *L. melisellensis*, this species is highly polytypic; Mertens and Wermuth (1960) listed 39 subspecies, and several additional subspecies have since been recognized (e.g., Brelih, 1961; Lanza, et al., 1971; Lanza and Capolongo, 1972). Most of the subspecific designations involve isolated insular populations. The range of *L. sicula* is centered in Italy, and it extends from the islands in the Spanish Mediterranean, down the Balkan peninsula to the coastal edge of Turkey and the islands of the Sea of Marmara.

The distributions of these two species in the Yugoslav coastal region have generated much interest among evolutionary biologists and biogeographers. *L. sicula* is found along the northern coast of mainland Yugoslavia from the Istrien peninsula south to the city of Split. From Split to Dubrovnik exists a "sicula-frei Zone" (Radovanović, 1959). The occurrence of *L. sicula* on some of the south-central Adriatic islands offshore from this region suggests colonization from Italy, either overwater or by some land connection, to explain its distribution on these islands and the southern portion of the Balkan peninsula (Gorman, *et al.*, MS). On the mainland outside of the "*sicula*-frei Zone" the two species are apparently spatially separated. Radovanović (1965: 535) stated that *L. sicula* is restricted to a very small strip along the sea coast and does not extend inland in Yugoslavia. In contrast, the endemic species in this region, *Lacerta melisellensis*, has a significantly wider distribution. On larger islands where both species occur, *L. sicula* is restricted to the periphery of the islands, while *L. melisellensis* occupies the center portions. Both species are abundant on small islands, but they are never naturally sympatric. The insular distributions of the two species are totally reticulate and are believed the results of competitive exclusion processes (Radovanović, 1960, 1965; Mayr, 1963). Field "experiments" (Radovanović, 1965) gave some support to the hypothesis that *L. sicula* is a relatively recent invader of the Adriatic islands and is displacing *L. melisellensis* on small islands. The evidence is incomplete, however, and at least one "reversal" has occurred (Nevo, et al., 1972).

The Islands

The coast of Yugoslavia is dotted with over 1,000 islands of diverse size and habitat complexity ranging from rocky shoals protruding from the Adriatic to land masses hundreds of square kilometers in area. Knowledge of the geologic history of the Adriatic basin is incomplete, but it is generally agreed that the islands of at least the northern portion of the basin are of recent origin (Radovanović, 1959). With one possible exception (Palagruza) the islands considered in this study are classed as continental. Most are within the 100 meter contour line; many are small islands geographically close to a large island or to a group of islands.

Two major regions of the Yugoslav island world are considered in this study. The southern islands (Figure 1; populations 1-11, 17, 26, 28, and 29) are fairly widely separated and ecologically diverse. Some of the islands in this region might best be considered as groups within which the members are geologically closely related, as evidenced by the shallow waters among them and the rocky substrate (Nevo, personal communication). One group consists of Vis, with several satellite islands, including Greben (11) and Bisevo (9). Lastovo (7, 26) is associated with a number of satellite islands including Tajan (17), Pod Mrcaru (8), Pod Kopiste (2), and Kopiste (14). A third group consists of Svetac (6), Brusnik (5), Kamik (28), and perhaps Jabuka (10).

The islands of the northern region are more homogeneous in appearance than those of the southern region. The largest islands in this region are only one-tenth the area of the largest island in the southern group. These islands are part of one geologically related group, the Kornati group of islands, with the exception, perhaps of

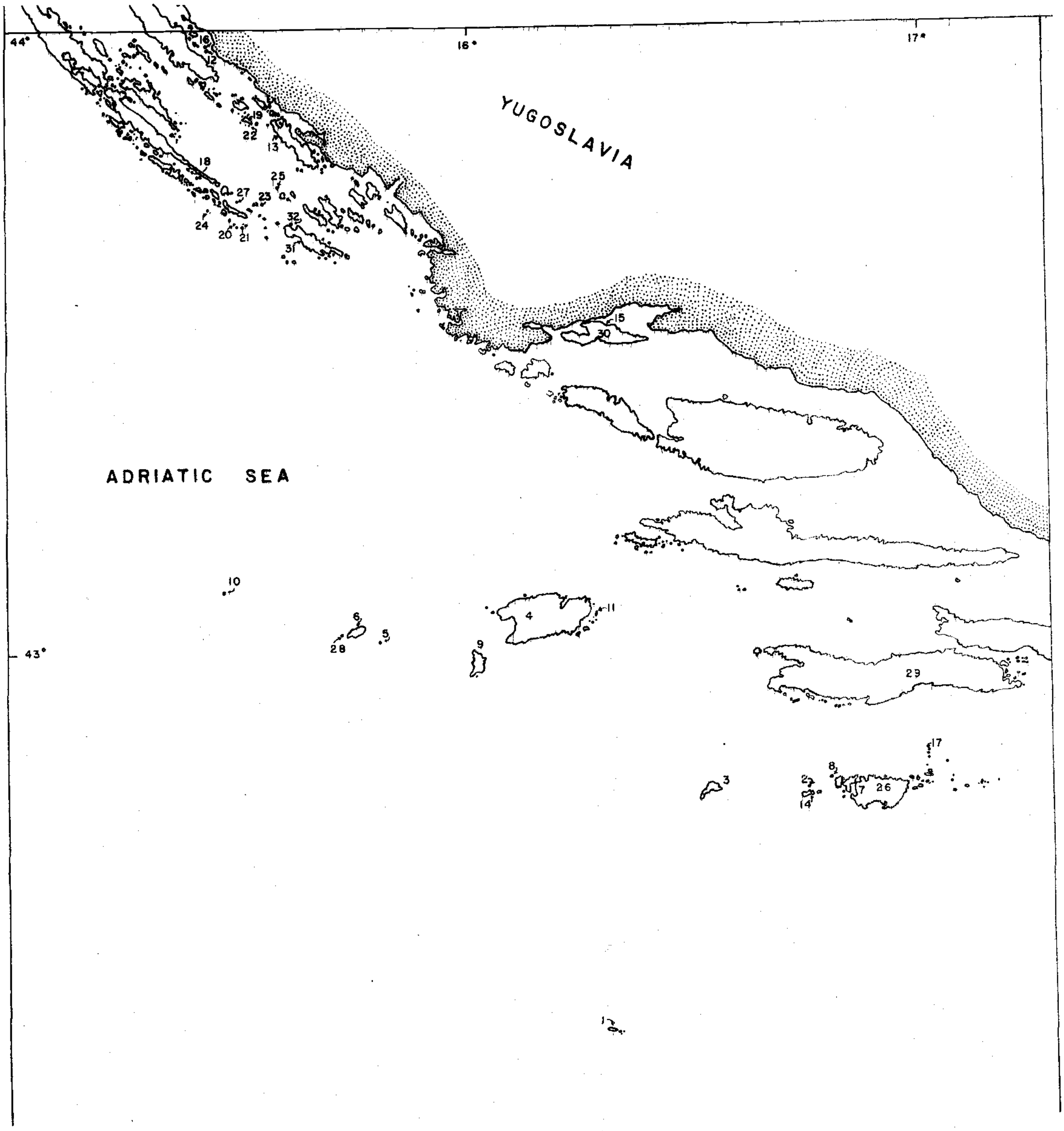

Figure 1. Map of the coastal region of Yugoslavia. The numbers on or near islands correspond to the localities listed in Table 1.

Planac (16) and Sveta Katarina (12). These islands are generally of low ecological diversity, having little vegetation other than a few shrubs and grasses. The numerous small islands in this region exhibit a tight pattern of geographic dispersion. The mean distance between islands from which I have samples of lizards and the nearest land mass of equal or larger size is 0.94 Km in the northern region and 10.33 Km in the southern region.

Many of the larger islands in both regions are inhabited by humans. The smaller islands may be seasonally occupied by domestic livestock (Radovanović, 1960). Information concerning the probability of predators existing on individual islands and some information regarding the physical appearances of the islands and the dominant vegetation is found in Table 2.

Table 1. Localities and sample sizes of the populations investigated in this study. The islands sampled are identified by the numbers 1 - 32 in Figure 1 and the text. LS = *L. sicula*, LM = *L. melisellensis*.

	Island	Species	Males	Females	Total
1	Palagruza	LS	12	4	16
2	Pod Kopiste	LS	18	12	30
3	Susac	LS	26	7	33
4	Vis	LM	8	8	16
5	Brusnik	LM	20	6	26
6	Svetac	LM	17	12	29
7	Lastovo (Pasador)	LM	12	11	23
8	Pod Mrcaru	LM	15	19	34
9	Bisevo	LM	14	13	27
10	Jabuka	LM	8	10	18
11	Greben	LM	15	19	34
12	Sveta Katarina	LS	11	6	17
13	Murter	LS	13	8	21
14	Kopiste	LS	21	18	39
15	Ciovo Town	LS	4	4	8
16	Planac	LM	14	5	19
17	Tajan	LM	12	12	24
18	Krpeljina	LM	12	3	15
19	Mrvenjak	LM	26	10	36
20	Vodeni Puh	LM	20	26	46
21	Veli Puh	LM	12	6	18
22	Vrtlic	LM	14	12	26
23	Mrtovenjak	LM	38	25	63
24	Purara	LM	26	26	52
25	Cavlin	LM	29	30	59
26	Lastovo (Zaklopatika)	LM	19	8	27
27	Babina Guzica	LM	26	20	46
28	Kamik	LM	22	14	36
29	Korcula	LM	14	0	14
30	Ciovo	LM	7	6	13
31	Zirje	LM	10	5	15
32	Mikavica	LM	12	5	17

Table 2. Biotic features of the islands listed in Table 1.

	Island	Grasses, Forbs[1]	Shrubs[2]	Trees[3]	Competitors[4]	Predators[5]
1	Palagruza	x	x	-	-	b
2	Pod Kopiste[6]	x	x	-	-	-
3	Susac	x	x	x	-	-
4	Vis	x	x	x	LO	s, b
5	Brusnik			No information		
6	Svetac			No information		
7	Lastovo (Pasador)	x	x	x	LO, H	(s, b)
8	Pod Mrcaru[6]	x	x	-	LO	-
9	Bisevo	x	x	x	-	s, b
10	Jabuka			No information		
11	Greben	x	x		LO	
12	Sveta Katarina	x	x	x	-	(b)
13	Murter	x	x	x	LO	(b)
14	Kopiste	x	x	x	LO	(b)
15	Ciovo Town	x	x	x	LM	(s)
16	Planac	x	x	-	-	-
17	Tajan	x	-	-	LO	-
18	Krpeljina	x	x	-	-	-
19	Murvenjak	x	x	-	-	-
20	Vodeni Puh	x	-	-	-	-
21	Veli Puh	x	-	-	-	-
22	Vrtlic	x	x	-	-	-
23	Mrtovenjak	x	-	-	-	-
24	Purara	x	x	-	-	-
25	Cavlin	x	x	-	-	-
26	Lastovo (Zaklopatica)	x	x	x	LO	(s, b)
27	Babina Guzica	x	-	-	-	-
28	Kamik			No information		
29	Korcula	x	x	x	LO, H	l, s, b
30	Ciovo	x	x	x	-	(s, b)
31	Zirje	x	x	-		
32	Mikavica	x	-	-	-	-

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[1] Includes *Silene inflata*, *Lotus* sp., *Portulaca oleracea*, several Chenopodiaceae, *Cynodon dactlyon*, *Crithmum maritimum*, *Asparagus* sp.

[2] Includes *Pistacea lentiscus*, *Juniperus excelsa*, *Helicrysum italicum*, and fig trees.

[3] Includes olive trees, pine trees and cypress.

[4] LO = *Lacerta oxycephala*, H = *Hemidactylus turcicus*; LM = *L. melisellensis*, LS = *L. sicula*.

[5] Potential predators include: snakes (s)--*Coluber najadum*, *Malpolon monspessulanus*; lizards (l)--*L. trileniata*, *Ophisaurus apodus*; birds (b)--*Corvus* sp.

[6] See Nevo, et al., 1972 for a more complete description.

III. METHODS

Localities

The populations considered in the following analyses were sampled within the framework of a larger research effort than reported here. The primary thrust of the collecting effort was to obtain sufficient samples of lizards to permit electrophoretic analysis of genetic variation within and among populations. The results of that work will be reported elsewhere (see Gorman, et al., MS; Gorman, 1972 for preliminary results). Of the 38 localities from which lizards were collected, 32 island populations (Table 1) were suitable for the present analyses.

The islands visited were chosen on the basis of prior knowledge of the occurrence of either species, the position and size of the islands, economic cost of visiting an island, and projected time requirements of sampling. The first of these criteria helped maximize collection time efficiency, while the second and fourth led to the inclusion of many small islands because of their abundance and the high densities of lizards on such islands.

Specimens

Most individuals were caught by hand or with nooses, but a few were collected with rubber bands or blow guns. Since the major objective of the collecting effort was to obtain reasonably large samples of living lizards for electrophoretic analyses, several biases may be apparent in the samples. Larger (older) lizards were explicitly sought in order to facilitate tissue preparation. Thus, the samples do not represent the true age structures of the populations. In addition, the emphasis on large individuals increased the probability of obtaining biased sex ratios, since considerable sexual dimorphism in size exists in both species.

The animals were kept alive in polyethylene containers for up to 4 weeks. Shortly after capture, they were toe clipped to identify each individual by locality. Individual weights, sex, snout-vent lengths, and tail lengths were recorded from the live lizards shortly after capture. Upon arrival at San Diego, California, the specimens were frozen and kept at -86 C until preparation for electrophoresis.

The lizards were again sexed and snout-vent measurements were taken prior to removal of the skin and head after a brief thawing. The skins were then spread on glass slides and the heads wrapped with each skin in at least 2 layers of aluminum foil. Following examination and character scoring, each skin and head was rewrapped and kept frozen in order to preserve color for later analysis.

Characters

Thirty-five characters of individuals were examined in preliminary work. The criteria for character selection included the ease of quantification, consideration of more than one organ system, ease of scoring, and occurrence of the character in all samples. The first criterion eliminated characters dealing with continuous variation in color or pattern. The second was met by consideration of scales and morphometric features. The third requirement excluded characters requiring extensive preparations or microtechniques. Lizards from Korcula (29) were not used in most analyses because several meristic characters were destroyed while skins were being removed. Twenty-nine characters were found to be in accord with the above criteria. Fourteen of these characters were scored on the right and left sides of the animals and are normally bilaterally symmetrical structures. Aspects of asymmetry in these characters will be reported elsewhere, and I have used only the totals of both sides as characters in this paper. In addition to the remaining fifteen characters, five ratios of morphometric characters were calculated for each sample. The nature of these characters, the methods of observation, and where applicable the manner in which each was scored are indicated in Table 3. Except where noted, I have restricted my analyses to adult male lizards in order to eliminate the possible confounding effects of sexual dimorphism and unequal numbers of individuals from each sex.

Table 3. Descriptions of the characters and the methods of scoring them. The numbers are used to identify characters in the text and tables. All metric characters were recorded in millimeters.

Number	Character
1	Head width (HW). Micrometer eyepiece; maximum width of occipital cap.
2	Internal distance (NW). Micrometer eyepiece; minimum distance between medial sides of external nares.
3	Width of occipital scale (OW). Micrometer eyepiece; width at posterior edge.
4	Head length (HL). Helios dial calipers. Distance from tip of snout to posterior edge of the occipital scales at the midline of the head.
5	Total number of lower labials (LL).
6	Total number of chin shields (CS).
7	Total number of upper labials (UL).
8	Total number of circumorbitals (CO).
9	Total number of scale organs (plaques) on the third post-nasals (P3).
10	Total number of scale organs (plaques) on the second post-nasals (P2).
11	Gular scales (G). Number of transverse scales in gular region.
12	Belly scutes (BS). Number in a longitudinal row.
13	Dorsal scales (DS). Number in a row across middle of back, row determined by number of belly scales/2.
14	Total number of femoral pores (FP).
15	Snout-vent length (SV). Millimeter rule held against ventral side.
16	Head width/snout vent length (HW/SV).
17	Internasal distance/Snout-vent length (NW/ SV).
18	Occipital width/Snout-vent length (OW/SV).
19	Head Length/Snout vent length (HL/SV).
20	Head width/Head length (HW/HL).

Statistics and Data Processing

The data obtained from each lizard consist of two kinds of variables. Measurements of the head, occipital scale width and snout-vent length are continuous variables which can theoretically take an infinite number of values depending upon the precision of the measuring instrument. These data are often normally distributed, and preliminary investigations showed this to be the case with the specimens considered here. Since scale counts are discrete variables, medians should best indicate the central tendencies of scale counts for a given population. I have examined histograms of each meristic variable and found that nearly all are unimodal and fairly symmetric. Additionally, plots of these variables against the inverse of the cumulative standard normal distribution are nearly linear, indicating close resemblances to normal distributions. Therefore, the use of parametric statistics for summarizing the $29 \times n_i$ raw data matrices involves only very minor violations of the assumptions of such statistics. The facility of using means and variances for all characters is obvious and I have followed this course.

In some cases it was advantageous to examine ratios of the continuous variables which were highly inter-correlated. Ratios are often distributed peculiarly because of the dependence of their components upon one another. The best estimate of an average ratio for a population is obtained by dividing the sum of the numerators by the sum of the denominators (Hansen, Hurwitz, and Madow, 1953):

$$\text{Ratio estimate} = R = \frac{\sum_{i=1}^{n} Y_i}{\sum_{i=1}^{n} X_i} = \frac{\overline{Y}}{\overline{X}}$$

The "relative variance" (= coefficient of variation squared) of a ratio estimate was calculated by the formula:

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

where CV_x and CV_y are the coefficients of variation of the variables in the denominator and numerator, respectively, r is the product moment correlation coefficient between the two variables, and f is the sampling fraction of the total population. The sampling fraction, f, was considered to be zero, indicating that the populations were assumed to be quite large in comparison to the size of each sample. This assumption may inflate the relative variances of ratios in some of the populations considered here, but any estimates of f would be hazardous.

A number of multivariate statistical and taxonomic methods were employed in several aspects of this study. Descriptions of these methods and their use are found in numerous texts and papers.

Appendix I contains brief descriptions of the methods I have used and cites references to be consulted for more detailed accounts.

IV. PHENETIC RELATIONSHIPS

Although several investigators have been concerned with the systematics of insular populations of Lacerta in the Adriatic (Wettstein, 1949; Kramer and Mertens, 1938; Mertens and Wermuth, 1960; Radovanović, 1959), little attention has been given to the relationships of different populations to each other. Descriptions of insular populations have emphasized differences in designating numerous subspecies. The usefulness of the subspecies concept has been seriously questioned on a number of grounds (Wilson and Brown, 1953). The most important objections are that 1) geographic trends in variation are often obscured, and 2) phenotypically similar populations may occur in widely separated areas. Thus, an emphasis on differences among groups of populations may conceal patterns of similarity indicative of widespread adaptation or genetic cohesiveness. These patterns and the processes governing them are among the essential components of interest to population biologists (Ehrlich and Holm, 1962).

Patterns of similarity among populations may be estimated by examining the dispersion of scores on a single character for each population sample. Overall similarity may be estimated by examining dispersions of scores on a set of characters simultaneously. I agree with the fundamental principle of numerical taxonomists which states that the greater the amount of information (i.e., the more characters) used in describing samples, the better the estimates of similarity (Sneath and Sokal, 1973). Phenetic relationships are based on overall phenotypic similarities of a set of characters of the organisms under consideration. Although no necessary implications of relationships by ancestry are made by phenetic relationships, phylogenetic inferences can be made, given certain assumptions about evolutionary pathways and mechanisms.

Phenetic relationships can provide a basis for phylogenetic speculation by assuming: 1) that genetic relationships among a group of organisms may be estimated by sampling genetic information, and 2) that samples of the information in genotypes can be obtained by sampling phenotypes and accepting errors introduced by interactions of the genetic information and environmental milieu (Ehrlich and Holm, 1962). The magnitude of this error is variable, but numerous studies have shown the existence of a genetic-phenetic correspondence in natural populations (Soulé, et al., 1973), in comparisons of inbred, hybrid, and randomly bred laboratory populations (Bader and Lehman, 1965), and in artificial selection experiments (e.g., Falconer, 1960).

My objectives here were to examine morphological variation in *L. sicula* and *L. melisellensis* in order to determine the overall relationships between the species and among the populations within each species. Obvious patterns of phenetic variation exist and are evaluated with respect to possible evolutionary processes which may be responsible for the observed relationships.

Procedures

Two general approaches to the estimation of phenetic relationships are cluster analysis and ordination. Clustering techniques put populations (or any other operational taxonomic unit) into discrete classes which are related to each other by the degree to which their attributes are similar. Ordination methods represent the populations' positions on a continuum where partial or complete overlap may occur. Ordination techniques might adequately represent phenetic relationships among populations, but if many individuals are employed for each population, the dispersion of points in the continuum may be unintelligible. Clustering methods, on the other hand, may impose unjustified structures on data from populations (Sneath and Sokal, 1973:367-368).

I have used both clustering and ordination techniques to examine phenetic similarities of insular populations of *Lacerta*. The cluster program used a polythetic hierarchical agglomerative algorithm developed by Ward (1963). This method successively considers combining all possible pairs of groups, selecting at each cycle only those two groups which when combined would have the smallest within-group variance (see Appendix I for more detail and references). Two ordination procedures were used. Principal component analysis was used to examine the way in which meristic characters differentiate among the species and populations. This method extracts the principal components of variation in the covariance matrix of sample means for a number of characters. Each component is independent of every other component, and since each is a linear combination of the original characters, the first few may contain most of the information held in all the original characters. Canonical analysis was used to examine the patterns of variation in each species. This technique uses the information obtained for each individual lizard to calculate a pooled within group covariance matrix which is in turn used to standardize a covariance matrix computed from the means of each sample (the between groups covariance matrix). Finally, the mutually independent components of this matrix are extracted so that the samples are maximally separated along each. Principal component analysis orders the means along independent continua entirely on the basis of interpopulation variation in the characters while canonical analysis orders the populations along independent axes on the basis of individual variation within each population. Both methods are described in detail in Appendix I.

Results

Cluster Analysis

Two cluster analyses were performed using slightly different suites of characters. The first clustering was based on the Euclidean distances (D) between all pairs of samples in character space. The D values were computed from the standardized means of five morphometric characters (1-4, 15) and ten meristic characters (5-14). The second clustering was based on 5 ratios and the ten meristic characters used in the first clustering. Ratios were used to reduce inflation of D values by size-related morphometric characters. The means and standard errors for each character in each sample are in Appendix II.

Four major groups are apparent in the phenogram derived from the first clustering (Fig. 2, A-D). The A group contains all the *L. sicula* samples while the B, C and D groups include all the *L. melisellensis* populations. Within the A group (*L. sicula*) two subclusters indicate that the populations from islands close to the mainland (12, 13, 15) are quite similar. These populations are also the northernmost insular populations of *L. sicula* examined in this study. In the close, northern subcluster of A, the smallest island (12), which is also the island furthest from the mainland (1 km), has the most dissimilar population of the three populations composing the subgroup.

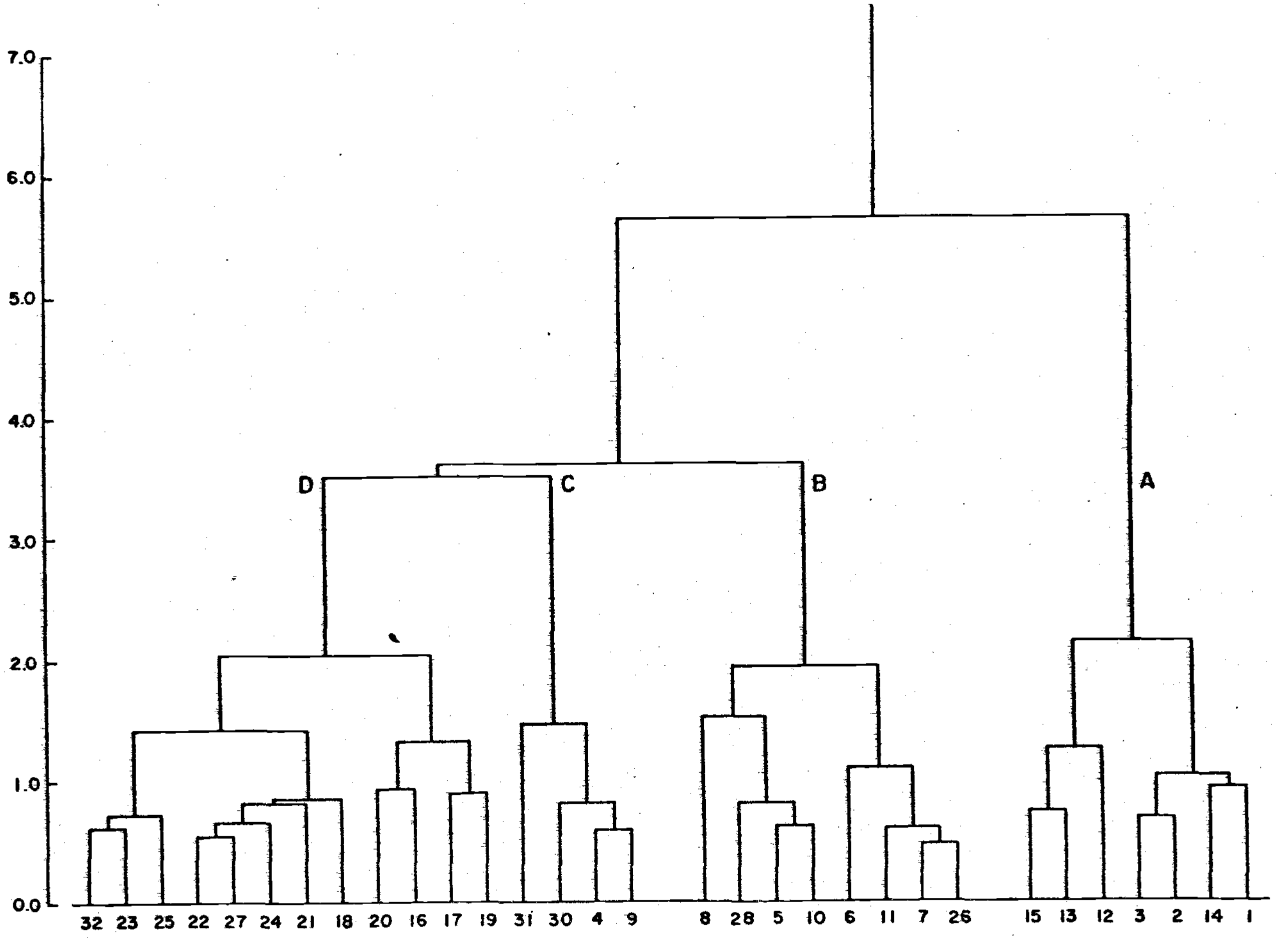

Figure 2. Phenogram of 31 populations of Lacerta based on cluster analysis of D values derived from 15 sample means.

The other subgroup of A (L. sicula) consists of populations from islands more distant from the mainland and located in the southern region of the study area (1, 2, 3, 14). Here the distant island of Palagruza (1) and the similarly sized island of Kopiste (14) have populations which are phenetically more similar to each other than to the remaining populations (2, 3). Populations from Kopiste (14) and Pod Kopiste (2) don't show such close relationships in spite of their geographical proximity. The populations from Susac (3) and Pod Kopiste (2) exhibit a close phenetic relationship even though they are found on islands of different sizes and which are relatively distantly separated.

Cluster B contains populations of L. melisellensis from islands lying south of 43°10' latitude (hereafter referred to as "southern islands"). Within the B cluster two subdivisions are apparent. One subcluster contains four populations from the small isolated islands of the southern region (5, 8, 10, 28), while the other subcluster contains some of the populations from the larger southern islands (6, 7, 26) and one satellite island (11). The latter subcluster indicates that two samples from the same island (Lastovo - 7, 26) are phenetically very similar, and the lizards from the island Greben (11) a satellite of Vis (4 in cluster C) show a similarity to the samples from the larger island. The former subcluster of B (small southern islands) indicates that the lizards from Pod Mrcaru (8) are the least similar of the group. Pod Mrcaru is the least isolated of this group of islands, and the remaining members of the subcluster (5, 10, 28) are from islands which might be considered satellites of Svetac (6).

The populations from the larger islands in the study area are found in cluster C. Two of these populations are from the northern islands of Ciovo (30) and Zirje (31), and the remaining two populations are from the large southern islands of Vis (4) and Bisevo (9).

The last major cluster, D, contains populations from small islands in the northern region, with the exception of Tajan (17). Three major subdivisions can be distinguished within D (small northern islands). Three similar populations (23, 25, 32) are from islands located on the mainland side of the Kornati island group. Two of these populations (23, 25) are among the larger of the islands which might be classified as small (see Table 8) while the other island (32) is a satellite island on the mainland side of Zirje (31), a large northern island. The second subdivision of cluster D (small northern islands) consists of five populations which are all from tiny islands; four of these populations are from islands in the Kornati island group (27, 24, 21, 18), while the fifth is a tiny satellite island (22) of Mrvenjak (19). The remaining subdivision of D consists of populations from islands which have no apparent relationships. One of these populations is from the southern island of Tajan (17), another is from a medium-sized island (19), while the other two are from small islands, one of which (16) is near the mainland and the other on the seaward side of the Kornati (20).

The phenogram derived from the second cluster analysis (Fig. 3) shows several differences from the first. The large island group (C of Fig. 2) has disappeared leaving a *L. sicula* cluster (A), a southern *L. melisellensis* cluster (B) and a northern *L. melisellensis* cluster (C) (Fig. 3). Cluster A remains similar to the *L. sicula* cluster of the first analysis, except that the two most isolated islands (by virtue of their size and position) have similar populations (1, 2), and the two larger island populations (3, 14) exhibit similarity in the phenetics of their lizards.

Cluster B (Southern *L. melisellensis*) shows two distinct subdivisions. One contains populations from the small isolated islands (5, 10, 28) near Svetac (6), while the other contains populations from larger islands (6, 7, 26, 9, 4) and one satellite island (11). Within this subcluster populations from Vis (4) and Bisevo (9) are quite similar; these two islands are both large and geographically close. Greben (11) is a satellite island of Vis (4) and clusters with Vis and Bisevo (9). The two samples from Lastovo (7, 26) form a group with the sample from Svetac, both large but relatively distantly separated islands.

Within the northern island cluster of *L. melisellensis* (C) three major subdivisions are apparent. One consists of the populations from the small islands lying near the southern end of the Kornati

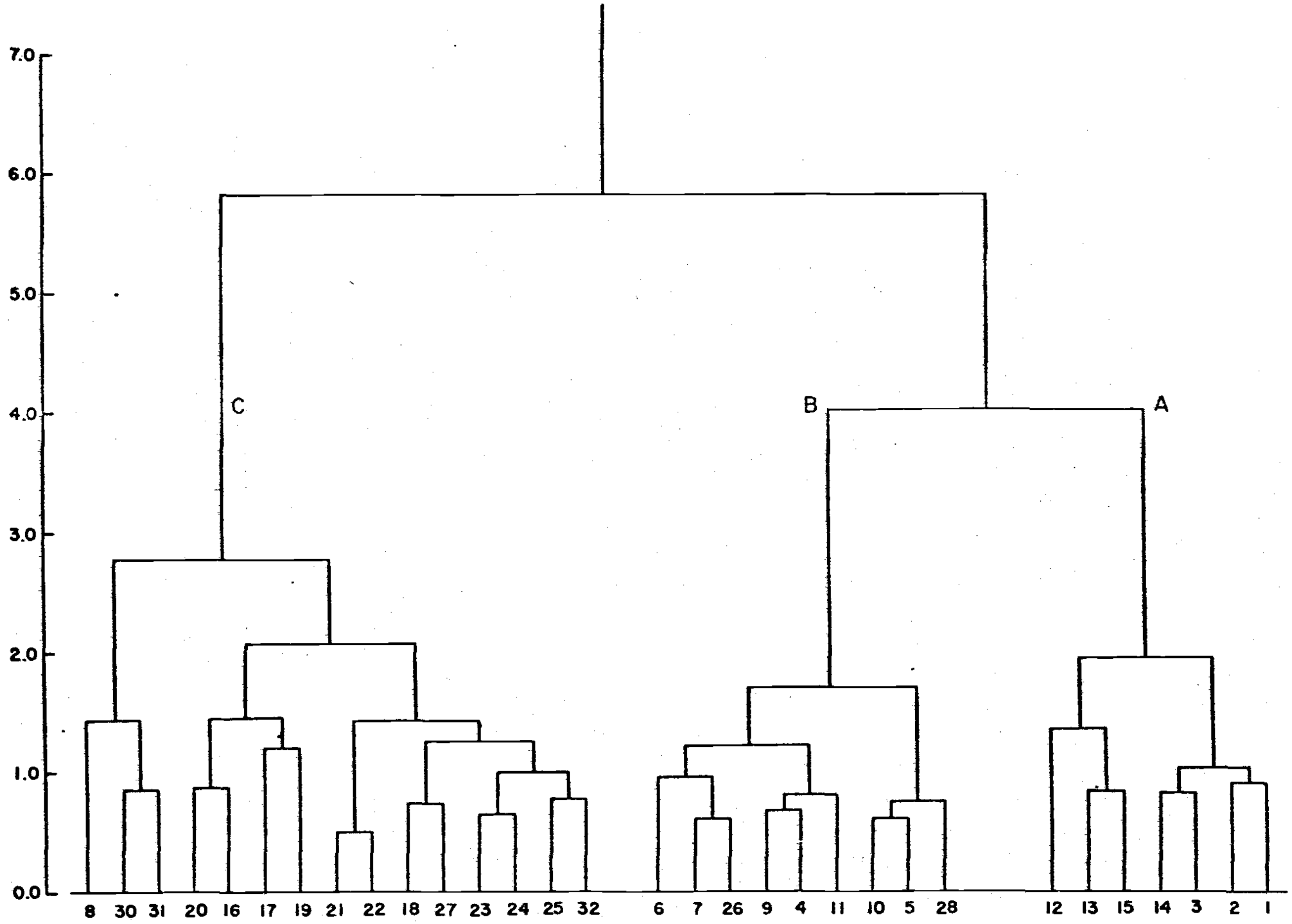

Figure 3. Phenogram of 31 populations of <u>Lacerta</u> based on cluster analysis of D values derived from 10 sample means and 5 mean ratios.

island group (21, 18, 27, 23, 24, 25) in addition to two satellite islands (22, 32). The two large islands in the northern group (30, 31) have similar populations, and they combined with a population from the southern region (8). The remaining subdivision in the northern cluster consists of the four islands with no apparent relationship (20, 16, 17, 19).

Ordination

A principal component analysis was performed on the matrix of means for eight meristic characters (5-8, 11-14; Table 3). The first three components of the covariance matrix computed from these means account for 70.5% of the total variation (Table 4). The ordering of the populations on these components (Fig. 4) shows a close correspondence to the results of the cluster analyses. The first component separates the populations of *L. melisellensis* from southern islands from northern *L. melisellensis* populations. Examination of the coefficients of the first eigenvector (Table 4) shows that the northern populations of *L. melisellensis* (and two southern populations of this species, Tajan (17) and Pod Mrcaru (8)) differ from the southern populations of both species by having more belly scutes and gular scales, and fewer dorsal scales, femoral pores, lower labials and chin shields per individual. The second component distinguishes among the two species, *L. sicula* having more circumorbitals, dorsal

Table 4. Eigen vectors and eigenvalues of the principal component analysis of the means of eight meristic characters.

Character	Eigenvector							
	I	II	III	IV	V	VI	VII	VIII
5	0.42	0.35	0.12	-0.21	0.35	-0.42	0.59	-0.03
6	0.42	-0.04	0.35	-0.02	0.60	0.37	-0.44	-0.02
7	-0.06	0.10	0.74	-0.41	-0.45	-0.00	-0.06	-0.26
8	-0.05	0.61	-0.24	-0.29	-0.09	0.65	0.14	0.15
11	-0.44	0.26	0.21	0.52	0.27	0.14	0.22	-0.53
12	-0.48	-0.06	0.39	0.01	0.26	-0.00	0.18	0.72
13	0.27	-0.51	0.17	0.57	-0.31	-0.19	-0.27	0.32
14	0.38	-0.39	0.18	0.33	-0.27	0.44	0.53	0.09
Eigenvalues	2.64	1.66	1.33	0.631	0.605	0.518	0.349	0.253
Proportion of total variation	.330	.208	.167	.079	.076	.065	.044	.032
Cumulative proportion of total variation	.330	.538	.705	.784	.860	.925	.969	1.00

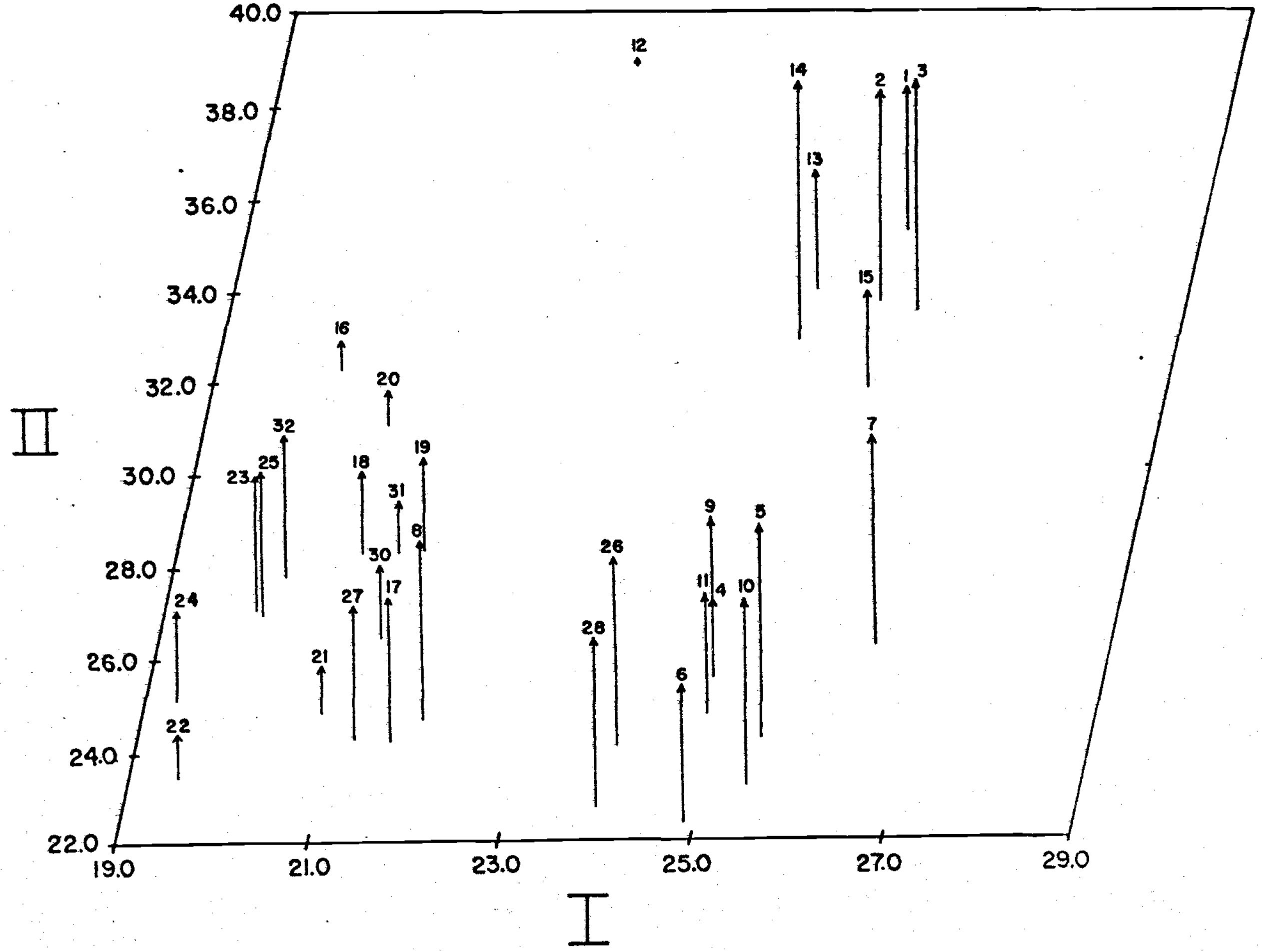

Figure 4. Ordination of 31 population centroids on the first three principal components derived from the means of eight meristic characters.

scales and lower labials, but fewer femoral pores than southern populations of L. melesellensis (see eigenvector II, Table 4). The third component partially separates populations from large islands from those on smaller islands. Those populations on larger islands tend to have fewer chin shields, upper labials, and belly scutes, but more circumorbitals per lizard than lizards on the smaller islands (eigenvector III). There are a number of exceptions to this characterization, however.

To evaluate the intraspecific variations more completely, canonical analyses were performed separately for each species. Although the greatest component of variation in ordinary samples of living organisms is generally size and age, canonical analyses tend to emphasize other factors of variation, such as shape and appearance, due to the standardization of the covariance matrix of means by the pooled with-in-group covariance matrix, and the subsequent elimination of inter-character correlations. Fifteen characters (5 morphometric, 10 meristic--see Tables 6 and 7) scored on a total of 503 individuals in 24 populations of L. melisellensis and 6 populations of L. sicula gave the pooled within-groups covariance and correlation matrices of Tables 5 and 7.

Lacerta melisellensis--The eigenvalues and the associated eigenvectors for the 24 populations of L. melisellensis populations are found in Table 6. Although the first two canonical axes account

Table 5. Pooled within group covariance and correlation matrices for 24 samples of L. melisellensis. The correlation matrix is below the diagonal, the variances are on the diagonal, and the covariance matrix is above the diagonal.

	Character														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	.341	.067	.031	.547	.032	.037	.032	-.110	-.384	-.154	-.010	-.002	.086	.009	2.549
2	.823	.020	.009	.123	.009	.008	.007	-.001	-.086	-.032	.001	-.008	.020	-.005	.559
3	.177	.206	.091	.063	.019	.004	.015	.023	.123	.061	-.019	-.003	.008	.056	.248
4	.926	.868	.207	1.024	.056	.051	.065	-.107	-.566	-.214	-.002	-.020	.070	-.002	4.539
5	.104	.127	.118	.104	.281	.041	.035	.108	.054	-.009	-.011	.018	-.029	.093	.255
6	.141	.126	.033	.112	.171	.202	-.004	-.001	-.100	.141	.016	.049	.034	.085	.337
7	.069	.062	.061	.082	.084	-.011	.623	.078	.083	-.072	.122	.024	.141	.074	.391
8	-.065	-.001	.026	-.037	.070	-.001	.034	8.390	.863	.059	-.109	-.173	1.061	.887	-.817
9	-.171	-.159	.106	-.145	.026	-.058	.027	.077	14.866	2.642	.028	.028	.106	.496	-3.491
10	-.089	-.078	.069	-.071	-.006	.106	-.031	.007	.230	8.848	.079	-.254	.364	.463	-1.763
11	-.014	.009	-.056	-.002	-.018	.031	.135	-.033	.006	.023	1.313	.067	.203	-.188	-.076
12	-.004	-.063	-.010	-.020	.035	.114	.031	-.062	.008	-.089	.061	.916	.165	-.030	.280
13	.067	.065	.012	.031	-.025	.034	.081	.166	.012	.055	.080	.078	4.887	1.091	.452
14	.007	-.016	.081	-.001	.078	.083	.041	.135	.057	.069	-.073	-.014	.418	5.142	.094
15	.887	.811	.167	.911	.098	.152	.101	-.057	-.184	-.120	-.013	.060	.042	.008	24.229

Table 6. Eigenvectors and eigenvalues from canonical analysis of variation in 24 samples of *L. melisellensis*. Values for the first seven canonical axes are shown.

Character	Eigenvector							
	I	II	III	IV	V	VI	VII	VIII--XV
1	2.15	-0.81	-0.79	-0.74	-2.38	-1.06	1.10	
2	-1.07	-9.82	-0.75	-5.27	-3.77	1.33	-4.82	
3	0.75	0.07	-0.64	2.03	-0.57	-0.64	1.03	
4	-1.49	1.43	1.14	0.46	1.09	0.17	-0.36	
5	-0.11	0.15	-0.05	-0.47	0.18	-0.15	0.00	
6	-0.34	0.02	-0.11	-0.04	0.34	0.33	-0.13	
7	-0.01	-0.08	-0.05	-0.26	0.36	-0.04	-0.19	
8	0.16	-0.05	-0.14	0.00	0.14	-0.14	-0.08	
9	0.04	-0.03	0.01	0.04	0.00	0.05	-0.11	
10	0.05	-0.02	0.02	-0.01	0.11	-0.07	0.00	
11	0.25	0.02	0.25	0.12	-0.28	-0.07	-0.03	
12	0.31	-0.01	0.54	0.16	-0.10	-0.08	-0.59	
13	-0.13	0.26	0.01	-0.13	-0.08	-0.27	-0.03	
14	-0.24	-0.13	-0.08	0.22	-0.12	-0.03	-0.13	
15	0.06	-0.06	-0.01	0.13	0.19	-0.03	0.12	
Eigenvalue	4.62	1.95	1.39	1.09	0.75	0.72	.63	
Proportion of total variation	.378	.159	.114	.090	.061	.059	.052	.087
Cumulative proportion of total variation	.378	.537	.651	.741	.803	.861	.913	1.000

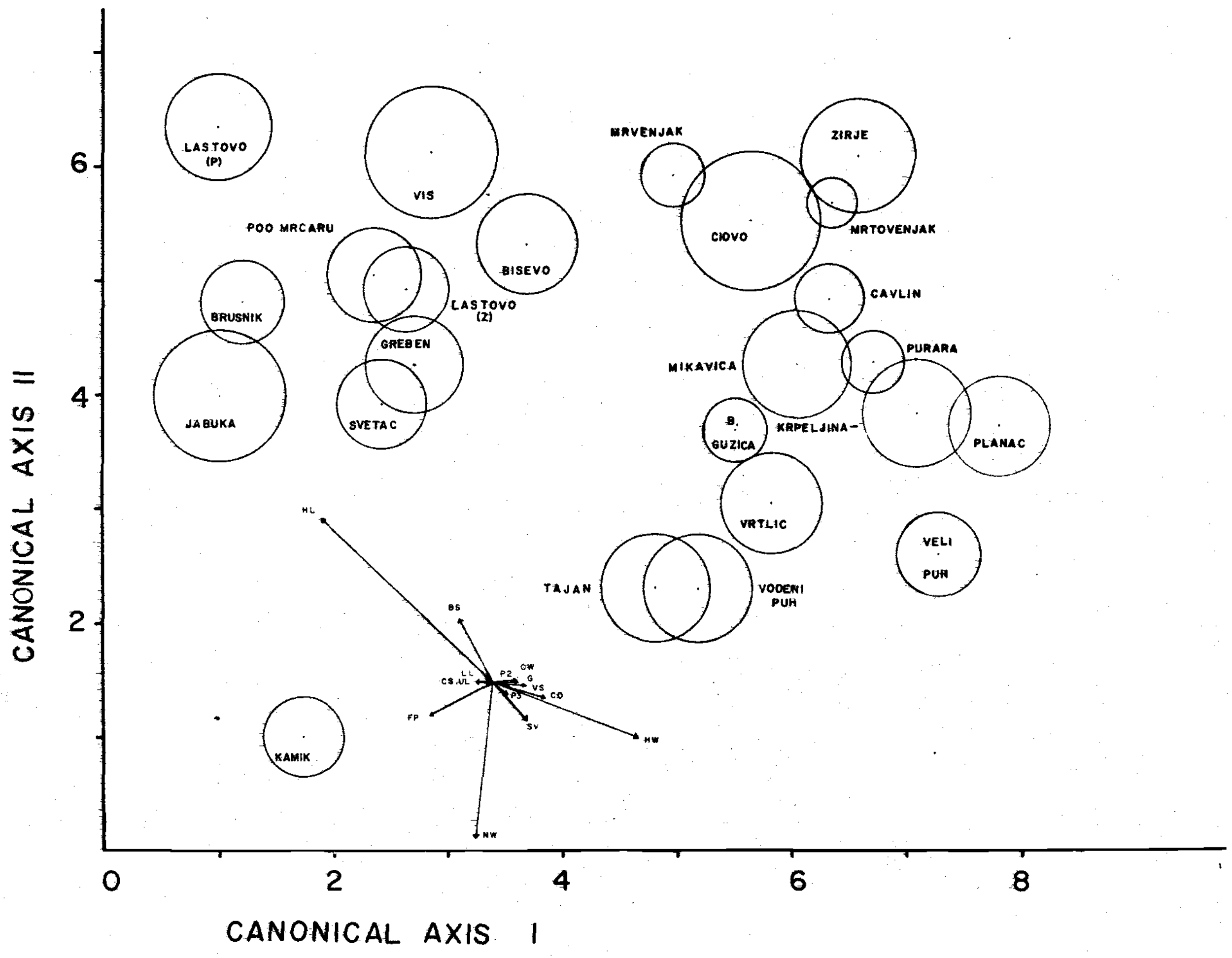

Figure 5. Canonical analysis of 24 populations of L. melisellensis based on 15 characters. The circles include 90% of the individuals in each sample. Each arrow represents one standard deviation for the characters on each axis.

Table 7. Pooled within group covariance and correlation matrices for six samples of *L. sicula*. The correlation matrix is below the diagonal, the variances are on the diagonal, and the covariance matrix is above the diagonal.

	Character														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	.425	.094	.068	.788	.071	.060	.049	-.041	-.030	-.218	.178	-.076	.309	-.172	3.047
2	.829	.030	.020	.191	.023	.017	.009	.070	.039	-.035	.048	-.037	-.033	-.014	.720
3	.325	.358	.103	.155	.001	.008	-.012	-.102	-.025	.003	.071	-.082	-.034	.062	.392
4	.939	.858	.377	1.659	.127	.096	.057	.333	-.082	-.294	.449	-.213	.324	.055	6.135
5	.148	.182	.003	.135	.534	.096	.072	.635	.265	.566	.087	-.166	.808	-.012	.225
6	.160	.174	.046	.130	.229	.328	.018	.271	-.074	.141	-.139	-.035	-.021	-.029	.197
7	.086	.060	-.043	.051	.113	.036	.753	.324	.030	.041	.206	-.034	.827	.048	.021
8	-.014	.090	-.071	.058	.195	.106	.084	19.927	.972	2.247	.107	-.521	4.350	1.995	.173
9	-.015	.073	-.025	-.020	.117	-.041	.011	.070	9.655	4.776	-.247	-.140	1.667	1.534	-.845
10	-.106	-.064	.003	-.072	.245	.078	.015	.159	.486	9.993	-.239	-.669	4.034	.570	-2.352
11	.180	.184	.146	.231	.079	-.160	.157	.016	-.053	-.050	2.284	-.254	-.682	-.175	1.477
12	-.098	-.179	-.217	-.140	-.193	-.051	-.033	-.099	-.038	-.179	-.142	1.394	-.015	-.535	.210
13	.074	-.029	-.016	.039	.172	-.006	.149	.152	.084	.199	-.070	-.002	41.222	1.275	.932
14	-.092	-.028	.068	.015	-.006	-.018	.020	.157	.173	.063	-.041	-.159	.070	8.139	-.838
15	.892	.794	.234	.910	.059	.066	.005	.007	-.052	-.142	.187	.034	.028	-.056	27.418

for only 53.74% of the total variation in these samples, a scatter diagram of the centroids of the populations projected onto these axes shows a biologically meaningful pattern (Fig. 5). The circle around each centroid includes 90% of the individuals in each sample (Seal, 1964). The first canonical axis clearly orders the populations by the geographic regions identified by cluster analyses. Individuals of the southern populations tend to have relatively longer and narrower heads as well as more femoral pores than do individuals in the northern populations. The second canonical axis orders the populations roughly according to the size of the islands from which they came. The populations from larger islands have high scores on this axis, and examination of the second eigenvector indicates that individuals from small islands have relatively wide snouts and short heads, relatively numerous femoral pores and few dorsal scales.

L. sicula--The eigenvalues and eigenvectors derived from the canonical analysis of 6 populations of L. sicula are reported in Table 8. The relationships of these populations with respect to the first two axes are shown in Figure 6. The first axis serves primarily to separate the populations into two distinct groups. The northern islands (12, 13) obtain high scores on this axis (the sample from Ciovo Town (15), was not included because of the small sample size), while the populations of the southern islands got low scores. The second axis serves to distinguish the population from the island of Kopiste (14)

Table 8. Eigenvectors and eigenvalues from canonical analysis of variation in six samples of *L. sicula*. Coefficients for the first four canonical axes are shown. Refer to Table 3 for identification of characters.

Character	Eigenvector				
	I	II	III	IV	V--VI
1	2.04	-2.00	-2.18	-0.33	
2	7.73	3.23	0.01	2.43	
3	-0.57	-0.03	0.73	-0.95	
4	-1.79	0.83	0.21	-0.78	
5	-0.35	0.07	0.43	0.62	
6	-0.20	0.01	-0.11	0.38	
7	-0.33	-0.11	-0.08	0.13	
8	0.09	-0.00	-0.00	-0.11	
9	-0.09	-0.01	0.23	-0.17	
10	0.14	-0.07	-0.11	-0.00	
11	0.04	-0.44	-0.18	-0.13	
12	0.04	-0.21	-0.17	-0.01	
13	-0.02	0.03	-0.00	-0.00	
14	0.01	-0.19	-0.01	0.14	
15	0.04	-0.11	0.29	0.19	
Eigenvalue	4.57	1.11	0.71	0.51	0.26
Proportion of total variation	.639	.155	.099	.071	.036
Cumulative proportion of total variation	.639	.794	.893	.964	1.00

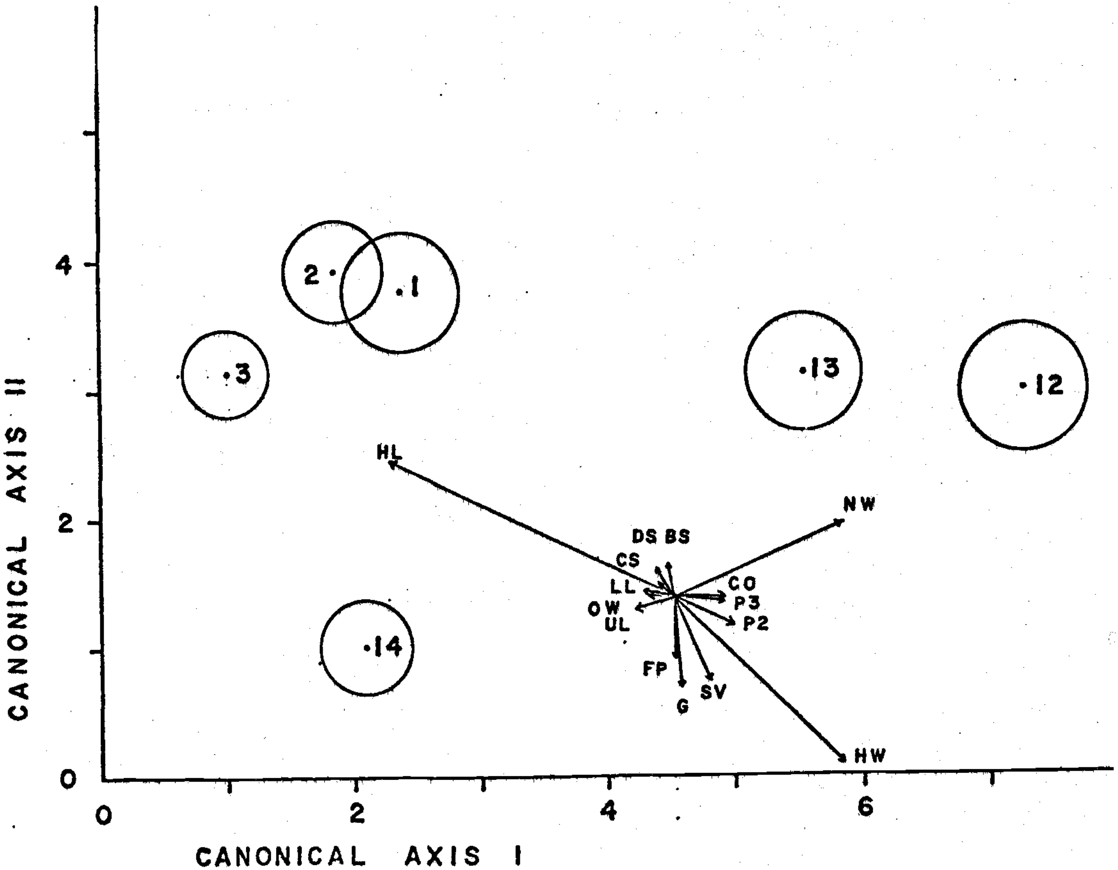

Figure 6. Canonical analysis of six populations of L. sicula based on 15 characters.

from the other five populations. The combination of original characters which best separates the northern and southern populations of this species emphasizes head shape. The lizards of the two northern populations have wider heads and snouts yet relatively shorter heads than the individuals of the southern populations. Corresponding to the above differences in head shape are lower numbers of lower labials, chin shields, and upper labials in the northern populations (eigenvector I). The population from Kopiste (14) is distinct from the remaining populations of _L. sicula_ by virtue of the individuals' having relatively wide heads, yet narrow snouts, and more gular scales and femoral pores.

Synthesis

The relationships indicated by the foregoing analyses suggest at least three important observations relevant to the evolutionary history of these populations. First, distinctive geographical regions appear to be defined by the morphological variations of the lizard populations considered here. Second, although it is clear that considerable differences exist between the two species, _L. sicula_ seems to be phenetically more similar to the southern populations of _L. melisellensis_ than to the northern populations. Third, within each specific and regional group of phenetically similar lizards, there appears to be a rough correspondence between similarity of populations and similarity of island size.

Northern and Southern Populations

The distinctive clustering of populations of both *L. sicula* and *L. melisellensis* into northern and southern groups on the basis of morphological characteristics suggests genetic differentiation between the two areas. *A priori*, at least three overlapping explanations can be offered to account for these patterns.

1. Major differences in the selective regimes experienced by populations in the two regions could lead to intra-regional similarities.

2. Gene flow between populations within each region and/or restriction of gene flow between regions could be cohesive factors leading to overall similarity of the populations within each region.

3. The founders of the populations in the two regions may have come from previously differentiated sources separated in space and/or time. Although all of these possiblities may have played some role in the development of the observed phenetic similarities, I believe the first to have been of less importance, since the range of latitude over which the samples were taken is small, and large differences in climatic and biotic features between the two regions were not apparent. Geological evidence implicates the second and third possibilities as

being more important.

In a series of papers dealing with the importance of geological history of the Adriatic basin, passive dispersal, and competitive exclusion in determining the patchy distributions of L. sicula and L. melisellensis on Adriatic islands, Radovanivić (1952, 1959, 1960, 1965) cited the work of the geographers Suess and Neumayr, Grund, and Milojević. With the exception of Milojević, these authors concluded from geological evidence that the existing Adriatic basin was formed in two steps: First, the southern portion was formed in the mesozoic and extended north from the Mediterranean to a line reaching from Gargano, Italy (the 'spur' on the 'boot' of Italy), through the region of Palagruza (1, Figure 1) to the area of the present-day island group of Vis, Bisevo, and Svetac (4, 9, 6, Figure 1). Then the area north of this line sank only during the course of the last 20 to 30 thousand years, so that the islands in this area were formed as recently as 9,000 years ago. Milojević and apparently some others (Radovanović, 1959) hold the view that the Adriatic basin has persisted continuously since the beginning of the Pliocene and that the sea level fluctuated considerably during the Pleistocene. All workers agree, however, that the northern islands present today have become separated from the mainland since the Pleistocene. Wettstein (1949) and Radovanović (1952) concluded that L. sicula colonized the islands of the southern region by means of a land connection between Italy and islands in the area of Vis (4). Radovanić (1952) proposed that the channel lying between Pod Kopiste (2) and Pod Mrcaru (8) marked the northeastern limit of a previous land connection between Italy and Yugoslavia in the southern region, the islands on the southeast of this hypothetical boundary were already formed by the time L. sicula invaded the area.

The geological evidence suggests that submergence of the northern region, whether due to sinking of the basin or to sea level changes, led to recent formation of the northern islands, while the southern islands were formed by a similar process much earlier. I know of no information concerning the age of the Lacerta populations on these islands, but examination of hydrographic charts of the area shows that the islands in both regions are surrounded by water less than 100 m in depth. It is generally agreed by geologists that the water trapped in ice sheets during the Pleistocene accounted for a drop in sea level of approximately 100 meters (Fairbridge, 1960). These ice sheets began to recede about 17,000 years ago, and the sea reached its present level about 6,000 years ago. This last eustatic rise in sea level may have isolated many of the continental islands considered in this study, and suggests that most of the populations found on these islands were cut off from each other rather than founded by overwater dispersal. Thus, it appears likely that the populations on the southern islands may have existed in insular form longer than the northern populations.

Assuming that the populations of the two regions have been restricted to islands for different lengths of time, it is obvious that gene flow between populations in the southern region has been restricted for a longer time (approximately 15 to 30,000 years), while gene flow among the northern populations remained possible for an additional several thousand years. Also, with the formation of the southern islands, gene flow was restricted between the regions but not within the northern region until a later date. The founders of the populations in the two regions may have come from morphologically differentiated sources from different areas as well. There is little direct evidence of this, but the alternative, namely, that the regions were colonized by samples of lizards from large, panmictic populations at different times is unrealistic in view of the polytypic nature of existing populations of these lizards and the patchy distribution of saurians in general.

Relationships of the Species

The tendency for the samples of *L. melisellensis* from the southern islands to "cluster" with the samples of *L. sicula* in both ordination and clustering procedures (Figures 3 and 4) may be attributed to any number of hypothetical phylogenetic sequences. The extremes of the spectrum of possible sequences are listed below, followed by a discussion of the relative importance of each.

1. Older (southern) populations of one or both species of insular Lacerta may have converged toward an optimal insular body form.
2. The founders of the southern island populations may have been isolated from mainland stocks which had not diverged to the degree that existing mainland forms have.

It is impossible to disprove either of these hypothetical pathways of evolution without some knowledge of phenetic variations of previous forms. Furthermore, since these represent extremes, and elements of each were undoubtedly influential in determining the actual evolutionary pathways of these species, there is little hope of a precise reconstruction of the true course of events. Yet, I argue that convergence, suggested in the first hypothetical sequence, was of more importance than a failure to diverge, implied by the second sequence.

The convergence argument assumes that the northern populations of both species had insufficient time in which to respond to directional selective pressures for island-relevant phenomes to the extent that the southern populations have. The second proposal suggests that the southern populations, because of their longer isolation failed to diverge at the same rate as the mainland populations, from which the northern populations were recently isolated. The general characteristics of islands, such as reduced numbers of predators, prey, competitor species, fewer habitat types, and often new combinations of species, lead to *new* rather than reduced directional selection pressures more probably lending support to the theory of convergence. In addition, the results of canonical analyses (Tables 6 and 8) indicate that the phenetic similarity of *L. sicula* and southern *L. melisellensis* populations is due primarily to similarity of head shape. Since the southern populations of both species differ in roughly the same direction from their northern relatives, convergence with respect to head shape may be of some importance in explaining the phenetic relationships of the two species.

An apparent paradox exists concerning explanations of the north-south regionality and the *L. sicula*--southern *melisellensis* groups. Convergence is held to be largely responsible for the closer relationship of *L. sicula* to southern *L. melisellensis* than to northern *L. melisellensis*. But intra-regional similarity in both species was hypothesized to be largely the result of intra-regional gene flow and derivation from temporally and spatially differentiated source populations rather than due to strong intra-regional selection pressures. The distinction lies in the assumption that islands in general present new selection regimes to lacertids, and that these insular regimes are similar in both the northern and southern islands. Therefore, the response of lizards which have been isolated on islands the longest should be more pronounced, hence the *L. sicula*--southern *L. melisellensis* relationship. The difference between the regions is due to the different durations of insular existence of lizards in the two regions, rather than different selection regimes.

A corollary of the argument above is that where island selective factors are most intense, the lizards should reflect more completely their response to the selective features of island life. This aspect is considered in the next section, where I examine the biogeographical correlates of inter-populational variation.

V. BIOGEOGRAPHICAL CORRELATES OF INTERPOPULATION VARIATION IN LACERTA MELISELLENSIS

Insular organisms often differ morphologically from closely related mainland forms. Among birds, for instance, there is a tendency for some island forms to have drabber plumage, longer tarsi, and longer bills than related mainland populations (Grant, 1965). Morphological differences have been documented between mainland and island populations of lizards (e.g., Soulé, 1966; Kramer, 1951), snakes (Camin and Ehrlich, 1956; Klauber, 1956), many species of mice (e.g., Delaney and Healy, 1964) and a number of other organisms (see review in Carlquist, 1965). Similarly, organisms inhabiting archipelagos or other geographically close islands often exhibit striking differences in body size (e.g., Soulé; 1966), color (Schneider, 1972), shape (Kramer, 1951) and behavior (Gorman, 1968; Carpenter, 1966). Such differences are occasionally imputed to be entirely the result of stochastic processes in evolution such as founder effects and/or genetic drift. For example, Radovanović (1954) compared several insular populations of L. sicula and L. melisellensis with regard to body size, tail length, number of dorsal scales, femoral pores, and dorsal coloration and concluded that interpopulation variations in these characters appeared to have no adaptive significance and were probably of neutral "Selektionswert," having been established through neutral mutations. Hartmann (1953) offered a similar explanation of the variation in degree of melanism of two lacertid species on islands in Balearic group of the Western Mediterranean Sea.

Examination of intraspecific variation for trends which are correlated with extrinsic factors of the environment usually proceeds under the assumption that natural selection orders the variation. If the assumption is valid, associations between morphology and measures of the environment which influence the fitness of morphological variants are expected. Such correlations should be regarded with caution, however, since evolutionary responses to environmental gradients may be confounded with direct physiological and/or developmental responses to the same or different environmental features, in the same or opposite directions. In addition, interrelationships among environmental variables often conceal functional relationships or suggest artificial ones.

Attempts to examine the relationships between morphological features of insular populations and biogeographic features of the islands they inhabit are confounded with correlations between island size and biotic diversity. A number of empirical and theoretical studies have shown that species diversity within diverse taxonomic groups increases linearly with the log of island area (review in MacArthur and Wilson, 1967) and decreases regularly with increasing distance from potential source areas (e.g., Soulé and Sloan, 1966).

Others have shown that the degree of isolation and measures of island complexity are correlated with species diversity of birds (Hamilton, Barth, and Rubinoff, 1964; Hamilton and Rubinoff, 1967). Soulé (1966) demonstrated that the negative correlation between lizard body sizes and island sizes in the Gulf of California was primarily the result of a positive relationship between island area and the number of iguanid competitors by using partial regression techniques. Schoener (1969a) found no correlation between island area and body size in several species of anoline lizards, but did demonstrate a negative relationship between body size and the number of congeneric species on West Indian islands.

In this section I have examined statistical relationships among island features and lizard features in an attempt, with the reservations noted above, to identify patterns of covariation indicative of selective responses of the lizards as reflected in their morphological variations to environmental factors indirectly related to the geographic characteristics of the islands.

Island Features

The environmental agencies governing evolutionary changes in populations are diverse and variable, and include such phenomena as climatic variation, habitat diversity, interspecific and intraspecific interactions, and immigration. These factors are difficult to quantify and to distinguish their relative importance in determining interpopulation variation is a difficult task. Yet, the discrete nature of islands and their unique geographic relationships may permit crude quantitative estimates of the roles of various factors in directing evolution in insular populations through the use of indirect measurements.

Island biogeographic theory (MacArthur and Wilson, 1963, 1967) and empirical evidence (Carlquist, 1965; Preston, 1962a, 1962b; Whitehead and Jones, 1969) indicate that, with possible exceptions for very small islands, species diversity is an increasing function of the log of island area. Theory (MacArthur and Wilson, 1963, 1967) and some experimental evidence (Simberloff, 1969; Simberloff and Wilson, 1969) further show that island sizes affect the temporal stability of insular communities by altering colonization and extinction rates of populations. The rate of immigration of individuals bearing different gene combinations or of individuals of different species depends in part on the size, height, and shape of an island (e.g., Lindroth, 1960). Thus, island sizes, shapes, and heights may be viewed as composite measures of isolation, spatial heterogeneity and temporal heterogeneity.

Indirect measures of climatic heterogeneity include elevation and area. On small islands most of the components of climate are more evenly distributed over the islands' surfaces than on larger islands. Island temperatures are probably modified by surrounding water which neither gains nor loses heat as fast as land areas. Thus, smaller islands should be buffered against extreme temperature variations to a greater degree than larger islands or the mainland. Likewise, small or narrow islands should be subjected to cooling breezes of moist air at their margins, while larger islands have smaller proportions of their surfaces exposed to such breezes. Elevation may establish belts of different humidity and temperature conditions and break the winds in these belts into leeward and windward subhabitats (Udvardy, 1969).

The distance from an island to a neighboring island or to the mainland influences the frequency at which immigrants contact the island (MacArthur and Wilson, 1967). In conjunction with size, distance to possible source areas is a measure of the degree of isolation of an island, and consequently may be a measure of the temporal heterogeneity of community structure and/or the likelihood of gene flow.

The age of an island is an indicator of the duration of isolation of resident populations, particularly on islands which were formed by a gradual rise in sea levels. The depth of channels between an island and an adjacent land mass should be roughly proportional to the age of the island, assuming the sea level rose at a relatively constant rate. Populations on older islands will have had a longer time in which to diverge from ancestral forms than those on younger islands.

Additionally, communities on older islands should more closely approach the equilibrium species distributions hypothesized by MacArthur and Wilson (1967) than younger islands, implying more predictable interspecific interactions for residents of older islands.

Lizard Features

Six morphological characters were chosen for examination of biogeographic patterns of variation on the basis of two criteria. First, characters which demonstrated significant interpopulation variation in canonical analysis were chosen. Among these, those whose functional significance could be surmised were chosen for analysis.

Head length, head width, and internasal width may be considered measures of trophic structures of lizards and possibly responses to prey size distributions (Schoener, 1967, 1968; Hespenhide, 1973). On the basis of energetic requirements, body size may also reflect food size availability (Hespenhide, 1973) as well as social dominance, reproductive rates, thermoregulation and locomotion abilities. If abundances in prey size classes vary among islands of different sizes, interpopulation variation in trophic related characters should be evident.

Variation in dorsal scale sizes has been related to long-term climatic averages in two species of iguanid lizards (Soulé, 1966, Soulé and Kerfoot, 1972). Dorsal scale size and shape were hypothesized to constitue important components in the thermoregulatory and water balance systems in lizards (Soulé and Kerfoot, 1972). If climatic variations on islands are related to island features, and if scale size variations are in some way related to climate, some pattern of biogeographic variation in scale size should emerge.

A sixth character, whose function has not been adequately examined, is the number of femoral pores. These special scales, located on the posterior edge of the hind legs of most lizards, contain openings through which keratin is secreted (Cole, 1966). Although several possible functions have been attributed to femoral secretions, recent evidence (Cole, 1966; Maderson, 1970) suggests a role in olfactory communication (e.g., species recognition, sexual activity, or perhaps boundary marking). If it is assumed that the amount of substance secreted is proportional to the number of femoral pores, patterns of variation in the number of femoral pores may be related to the variations in lizard species diversity or population densities in insular populations.

Procedures

Island Features

Seven measures reflecting spatial and temporal ecological heterogeneity and degree of island isolation were determined for each island from which samples of *L. melisellensis* were obtained. Data were taken from hydrographic charts published by the Hidrografski

Institute Jugoslavenske ratne mornarice--Split. The seven variables included island area, (A), island length (L), linear distance to the mainland (D_1), linear distance to the nearest land mass of size equal to or larger than the island in question (D_2), minimum channel depth between the island and the mainland (C_1), minimum channel depth between the island and the nearest land mass of equal or larger size (C_2), and maximum elevation of the island (E). Island area was estimated from the charts by use of a compensating polar planimeter. Linear distances (D_1, D_2, L) were measured with a ruler, and channel depths were read directly from the maps. Most elevations were taken directly from the charts, but for some small islands, elevations were estimated by eye at the time of my visit.

Characters

The means of five morphological characters (1, 2, 4, 13, 14--Table 3) were used in the statistical analyses, while the mean snout-vent length of the largest third of each sample was used as an estimate of body size. Since the measurement of head size and shape are highly correlated with snout-vent length, the mean scores of the samples of _L. melisellensis_ on the first canonical axis of a canonical variate analysis performed on size related characters (1, 2, 4, 15) were used as an overall measure of head shape.

Statistics

I have used multiple regression analyses not to determine predictive equations for morphological characters, but to roughly estimate the relative importance of different island features in explaining the geographic variation in the morphological features of the lizards. Mean values for the morphological characters were used as dependent variables and the measures of island features (and logarithmic transformations) were used as independent variables in the model

$$Y = a + b_1X_1 + b_2X_2 \ldots b_iX_i$$

where the b_i are the partial regression coefficients and a is a constant. The independent variables, X_i, were added in stepwise fashion; at each step the variable entering was that which had the highest partial correlation coefficient with the dependent variable, Y. When all the independent variables had been entered the procedure was reversed. Since the power of any multiple regression model depends upon the intercorrelations of the variables already in the model and those not yet included (or already dropped), the reverse procedure may not drop the variables in the reverse order of their entering. Some idea of the relative importance and relationships of the independent variables can be obtained by comparing the sequences in which they were added and dropped from the model.

Results

The measurements of the geographic features of each island from which samples of L. melisellensis were collected are found in Table 9. Korcula (29) is not included because dorsal scale counts could not be scored on the lizard skins from this island. The means of the characters used as dependent variables in the regression models are found in Appendix II, and the product moment correlation coefficients between the island variables and the lizard variables are found in Table 10.

Size and Shape of Body and Head

The multiple regression models "explain" 56 to 76 percent of the geographic variation in snout-vent length, head width, nasal width, and head length (Table 11). For each measurement, the stepwise procedure consistently added L', D_1, and A' (or A) in the first few steps. More significantly, these variables were the last to be dropped for three of the four analyses. For these characters, L' entered the models first and was the last dropped in all but one case (snout-vent length), and in that exception, L' was added second, and its untransformed counterpart (L) was dropped last. This consistency may be largely due to the high correlation of each of the head measurements with snout-vent length, as well as with each other. However, much of the interpopulation variation is due not only to differences in

Table 9. Geographical characteristics of the islands from which samples of *Lacerta melisellensis* were obtained. Symbols: A = area (km^2); D_1 = distance (km) to mainland; D_2 = distance to nearest land mass of equal or larger area (km); C_1 = minimum channel depth between island and mainland (m); C_2 = minimum channel depth between island and nearest land mass of equal or larger area (m); L = linear length of island on longest dimension (km); E = highest elevation (m); A', D_1', D_2', C_1', C_2', E' and L' are natural logs of 1+ variable.

Island	Geographic Features													
	A	A'	D_1	D_1'	D_2	D_2'	C_1	C_1'	C_2	C_2'	E	E'	L	L'
4	86.600	4.47	50.6	3.94	16.10	2.84	102	4.64	93	4.54	515	6.25	17.05	2,89
5	.040	.04	55.2	4.03	3.40	1.48	130	4.88	108	4.69	30	3.43	.35	.30
6	3.730	1.55	53.8	4.00	19.40	3.02	130	4.88	91	4.52	316	5.76	3.70	1.55
7	40.380	3.72	29.9	3.43	12.80	2.63	89	4.50	89	4.50	417	6.04	10.88	2.48
8	.013	.01	31.1	3.47	.78	.58	97	4.59	68	4.23	16	2.83	.26	.23
9	6.000	1.95	53.3	4.00	4.20	1.65	120	4.80	101	4.63	239	5.48	4.55	1.71
10	.010	.01	59.8	4.11	22.80	3.17	144	4.98	146	4.99	96	4.58	.25	.22
11	.040	.04	47.7	3.89	1.00	.69	91	4.52	38	3.66	32	3.50	.70	.53
16	.050	.05	.9	.64	.32	.28	11	2.48	11	2.48	20	3.05	.41	.34
17	.013	.01	19.6	3.03	3.42	1.49	70	4.26	72	4.29	15	2.77	.30	.27
18	.018	.02	17.0	2.89	.34	.29	92	4.53	35	3.58	30	3.43	.24	.22
19	.640	.50	4.3	1.67	1.28	.82	42	3.76	35	3.58	64	4.17	1.65	.98
20	.013	.01	18.3	2.96	.90	.64	91	4.52	83	4.43	15	2.77	.19	.17
21	.008	.01	17.2	2.90	.45	.37	89	4.50	30	3.43	15	2.77	.20	.18
22	.004	.004	5.4	1.86	.50	.41	41	3.74	27	3.33	38	3.66	.12	.11
23	.090	.09	13.0	2.64	2.14	1.14	86	4.47	86	4.47	42	3.76	.50	.41
24	.031	.03	19.5	3.02	1.75	1.01	90	4.51	92	4.53	30	3.43	.38	.32
25	.141	.13	8.5	2.25	1.10	.74	76	4.34	44	3.81	32	3.50	.50	.41
26	40.380	3.72	29.9	3.43	12.80	2.63	89	4.50	89	4.50	417	6.04	10.88	2.48
27	.013	.01	15.0	2.77	1.13	.76	91	4.52	82	4.42	20	3.05	.20	.18
28	.010	.01	56.8	4.06	1.18	.78	130	4.88	91	4.52	40	3.71	.20	.18
30	27.600	3.35	.1	.05	.05	.05	43	3.78	43	3.78	209	5.35	15.20	2.79
31	15.600	2.81	11.4	2.52	11.00	2.49	77	4.36	76	4.34	134	4.91	11.80	2.55
32	.006	.01	11.1	2.49	.44	.37	77	4.36	53	3.99	10	2.40	.12	.11

Table 10. Matrix of correlation coefficients between characters and geographical characteristics of islands from which samples of L. melisellensis were obtained for this study. Symbols are explained in Tables 3 and 9.

Island Features	Character 1	2	4	13	14	15
A	-.36	-.35	-.24	.33	.22	-.31
D_1	.20	.30	.36	.37	.82	.25
D_2	-.21	-.16	-.02	.31	.64	-.13
C_1	.28	.32	.37	.31	.68	.30
C_2	.09	.11	.19	.40	.56	.09
E	-.39	-.36	-.21	.40	.47	-.30
L	-.58	-.56	-.49	.34	.14	-.57

Table 11. Multiple regression analyses using independent variables in Table 9 and seven dependent variables (see text). A. Order of entry of entry of variables into regression models and multiple correlation coefficients. The regression model at any step includes a constant (not shown) and the variables included in previous steps. B. Order of exit of independent variables.

	Character													
Step	SV		HW		NW		HL		Canon. I		DS		FP	
	Var.	R^2	Var.	R^2	Var.	R^2	Var.	R^2	Var.	R^2	Var.	R^2	Var.	R^2
A.														
1	$+D_1$	.26	-L'	.39	-L'	.36	-L'	.26	+L'	.28	+A'	.17	$+D_1$	.67
2	-L'	.49	+E	.48	+A'	.50	+E	.51	-E	.48	$+C_2$	.27	$+D_2$	.72
3	+E	.60	$+C'_1$	.51	$+D_1$	.59	$+C'_1$	.54	$-D_1$	.53	-L	.30	$-C_2$	.74
4	+A	.63	+A'	.53	-A	.61	+A'	.55	-A'	.59	-E	.36	$+D'_2$	.74
5	$+C'_1$	.65	$-D'_2$	.54	-E'	.63	$+D_1$	.56	+A	.61	$+D_1$	.42	-A	.75
6	+E'	.67	$+D_1$	.54	$-D'_1$	.64	$-C_1$	.58	$+C_1$	.64	+A	.45	+E	.78
7	$-C_1$	.68	$-C_1$	.55	$-C_2$	.65	$-D'_1$	.59	$-C_1$	.66	$-D'_1$	.48	-E'	.78
8	$+D_1$	.71	$+C'_2$	.55	$+C'_2$	.67	-L	.60	$+D'_1$	.68	+L'	.52	+A'	.79
9	+A'	.71	$-C_2$	.55	$+D'_2$	.69	$+D_2$	.61	+E'	.69	$+C_1$	.55	-L'	.84
10	-L	.73	$-D'_1$	.56	$-C_1$	.69	-E'	.62	$-D_2$	.70	-E'	.57	-D'	.85
11	$+D_2$	.76	-E'	.56	$+D_2$	.69	+A	.62	+L	.70	$+D_2$	.60	$+C'_2$	.86
12	$-C'_2$	.76	-A	.56	-E	.69	$+D'_2$	.62	$+C_2$	.71	$+C'_2$	.63	-L	.88
13	$+C_2$	.76	$-D_2$	.56	-L	.69	$-C_2$	.62	$-C'_2$	.73	$-D'_2$	.65	$+C_1$	.88
14	$+D'_2$	.76	+L	.56	$-C_1$	.69	$+C'_2$	.63	$+D'_2$	.73	$-C'_1$	.65	$-C'_1$	.88

Table 11 (cont.)

Step	Character													
	SV		HW		NW		HL		Canon. I		DS		FP	
	Var.	R^2	Var.	R^2	Var.	R^2	Var.	R^2	Var.	R^2	Var.	R^2	Var.	R^2
B.														
14	$+E'$	.76	$-D'_2$	.56	$-C'_1$	.69	$+D'_2$	.63	$+A$	.73	$-C'_1$	.65	$-C'_1$	.88
13	$+D'_2$	.76	$+L$	.56	$+D'_2$	.60	$-E'$	.62	$-C'_1$	.73	$+C_2$	.64	$-A$	.88
12	$+C_2$	.76	$-D_2$	.56	$-E$	.69	$+C'_1$	.62	$+D'_2$	.73	$+C_1$	.63	$+C_1$	.88
11	$-C'_2$	.76	$+C'_1$	.56	$-L$	.69	$-C_1$	.62	$+E'$	.73	$-E'$	.61	$-E'$	.88
10	$-L'$	.75	$-C_1$	.56	$-C_1$	.68	$+E$	.61	$+C_1$	.72	$-D'_1$	.55	$+D'_2$	.87
9	$+E$	.71	$-A$	.56	$+D_2$	.67	$+A$	.61	$-E$	.67	$+C'_2$	.49	$+C'_2$	.84
8	$+A'$	.70	$-E'$	.56	$-E'$	.66	$+D_2$	.59	$-D_2$	.66	$-D'_2$	.47	$-D'_1$	.82
7	$+D_2$	.69	$+E$	.55	$-D'_1$	.63	$-D'_1$	.57	$+L$	.63	$+D_2$	.45	$-L'$	.81
6	$-C_1$	.67	$-D'_1$	.55	$+C'_2$	.62	$-L$	.56	$+D'_1$	.61	$+L'$	.44	$+E$	.79
5	$+D'_1$	.64	$-C_2$	.53	$-C_2$	.61	$+C'_2$	.54	$-C'_2$	.60	$+A$	.41	$-C_2$	.78
4	$+D_1$	.64	$+C'_2$	.53	$-A$	.59	$-C_2$	.54	$+C_2$	.54	$-L$	.30	$+D_2$	.76
3	$+C'_1$	.54	$+D_1$	.48	$+D_1$	.50	$+A'$	.43	$-A'$	.47	$-E$	.27	$-L$	.70
2	$+A$	.22	$+A'$	.39	$+A'$	.36	$+D_1$	.26	$-D_1$	.28	$+D_1$	.17	$+A'$	.67
1	$-L$		$-L'$		$-L'$		$-L'$		$+L'$		$+A'$		$+D_1$	

absolute size, but also to differences in the sizes of nasal widths, head widths and head lengths relative to snout-vent length and to each other.

To reduce the influence of size related correlations, a canonical variate analysis was performed using the four characters measuring the size and shape of the body and head of these lizards (Table 12). The results indicate that the increase in nasal width relative to snout-vent length is of considerable importance in distinguishing among the populations. The results of a multiple regression analysis using the first canonical variate evaluated at the sample means of the 24 population samples as the dependent variable and the island features of Table 9 as independent variables are shown in Table 11. When all the variables are in the model 73 percent of the geographic variation in the linear combination of the four characters making up the first canonical variate is explained. Three of the island variables (L', A', D_1) enter the model in the first few steps and are the last to be dropped. Together, these variables account for nearly half of the total variation in the dependent variable.

Elevation (E or E') was added to the models early in every case, but when A' was included in the models, the value of partial regression coefficient of E (or E') dropped considerably. Further, E (or E') was dropped early in the reverse stepwise procedure while A' remained. Similarly, C_1, C_2, and D_2 (and their transforms) were

Table 12. Eigenstructure of the covariance matrix derived from four metric characters scored in 24 populations of L. melisellensis. The set of population means evaluated by the linear combination of the first eigenvector were used in a multiple regression analysis (Table 11).

Character	Eigenvector I	II	III	IV
1	1.44	-3.50	-2.08	-1.93
2	-7.52	-8.10	9.22	1.99
4	-0.50	2.90	.31	-1.59
15	-0.04	0.01	-0.18	0.48
Eigenvalue	1.63	1.37	0.65	0.28
Proportion of variation	.415	.349	.165	.071
Cumulative proportion of variation	.415	.764	.929	1.000

generally added late and dropped early in the stepwise procedures, and their partial regression coefficients were never significantly different from zero ($P > .05$).

Elevation and area of islands are highly correlated ($r = .92$), and their behavior in these models is interesting. Both measures are probably measures of spatial heterogeneity, but A', when combined with D_1 and L', may be an indicator of a wider range of relevant sources of spatial heterogeneity than is E in combination with these variables. Alone, however, E may be a better indicator of spatial heterogeneity than A' alone, suggesting that D_1 and/or L' contain information overlapping with that contained in E.

Distance to the mainland (D_1) is only weakly correlated with measures of head and body size (Table 10). Yet D_1 is consistently added early and dropped late in the stepwise procedures (Table 11) suggesting that D_1 reflects sources of variation independent of those reflected by A', L' and E.

Dorsal Scales

Multiple regression analyses using the average number of dorsal scales in a row across the middle of the dorsum as the dependent variable explained 65 percent of the geographic variation in this character when all independent variables were in the model (Table 11). As with body size and head measurements, A', L, D_1 and E were among the first variables entering and the last dropped in the stepwise procedures. The average number of dorsal scales of *L. melisellensis* shows a weak positive association with A' ($r = .41$, $P \simeq .05$) and a statistically significant positive relationship with L' ($r = .44$, $P < .05$). A scatter diagram of dorsal scale number and L' (Figure 7) suggests that the average number of dorsal scales is generally higher in the populations from the southern islands than in the populations

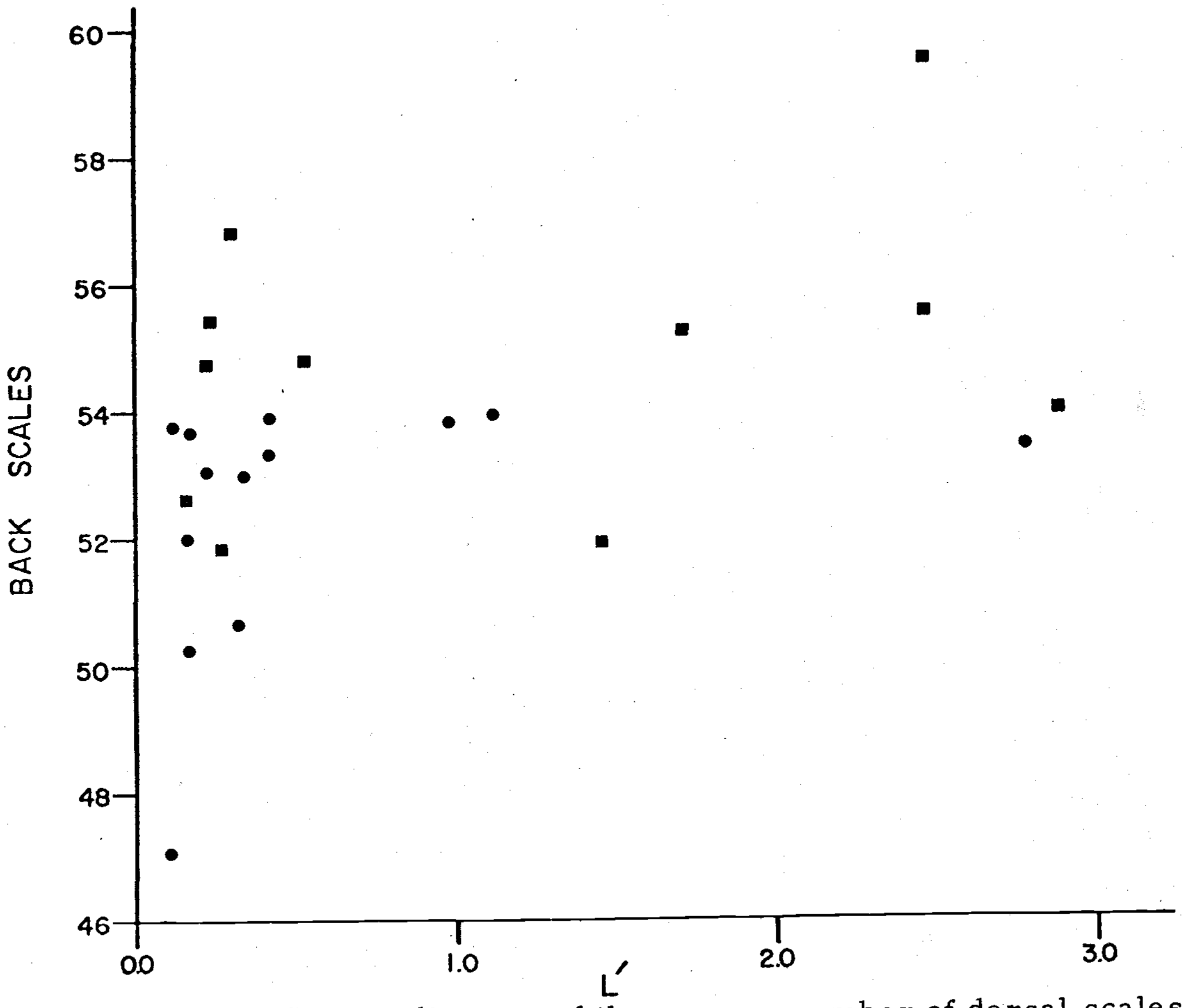

Figure 7. Scatter diagram of the average number of dorsal scales versus the ln (1 + L) for 24 populations of L. melisellensis. Symbols: Squares = southern islands; circles = northern islands.

from the northern islands. This difference is statistically significant ($t = 5.69$, $P < .001$).

Femoral Pores

Correlations and multiple regression models relating the average number of femoral pores of lizard populations to biogeographic features of islands produced some striking results. The variation in the mean number of femoral pores was highly correlated with measures of isolation (D_1, D_2, C_1, and C_2, Table 10). Measures of island size were not significantly correlated with femoral pore number. Multiple regression models were able to account for as much as 88 percent of the geographic variation in this character. One variable (D_1) alone "explains" 67 percent of this variation (Table 11). Examination of the multiple regression analysis indicates that D_1, A' and L considered simultaneously are the most important of the set of predictor variables. When these variables are included in the models, most of the partial regression coefficients for the remaining variables are not significantly different from zero ($p > .05$) while those for D_1, A' and L are.

Discussion

Taken together, the multiple regression analyses implicate A, D_1 and L as the most important features of islands ultimately associated with interpopulation variation in head and body size, dorsal scalation, and femoral pore number. The precise mechanisms by which these geographic features of islands are functionally related to morphological variations would require quantification of a number of ecologically relevant variables believed to be functions of A, D_1 and L. Examination of geographic trends may indicate which ecological parameters would be most likely to provide interpretable results, however.

Head and Body Size

The lengths (L') and areas (A') of the Adriatic islands investigated are naturally highly correlated (r = .94), and both are inversely related to snout-vent lengths of *L. melisellensis* (Table 10). When included together in the regression models, their partial regression coefficients are opposite in sign, and that of L' has a larger value than that of A'. Since A' probably reflects not only island size, but also the degree of isolation and ecological heterogeneity while L' does not reflect the latter except through its relationship to area, L' may be considered the better measure of island size *per se*. Under this assumption, island size (i.e., L') most strongly influences the maximum snout-vent length of *L. melisellensis*. Area (A') has a positive partial regression coefficient when included with L' and may mostly indicate a positive influence of ecological heterogeneity on average snout-vent lengths of these lizards. Thus, on islands of equal length but different area, lizards would be expected to be larger on the islands of larger area. In effect, the larger of equally long islands would have a larger portion of its area suitable for occupancy by *L. melisellensis*.

On islands of equal area but different lengths, a larger proportion of the area of the longer island would be incorporated into shoreline habitat which is generally unsuitable for *L. melisellensis* (Radovanović, 1960; Nevo, et al., 1972). Since the presence or absence of predators and/or competitors on these islands is partly dependent upon island size (Table 2; Radovanovic; 1959, 1960; Kramer, 1951; Nevo, et al., 1972) populations of *L. melisellensis* on small islands may be realizing an "evolutionary tendency" toward increased body sizes through ecological release from predation and interspecific competition. If such a tendency exists in *L. melisellensis*, it should be apparent in comparisons of snout-vent lengths of lizards from islands of different ages. With a longer time span in which to realize the hypothetical tendency, lizards from the southern islands would be expected to have, on the average, longer snout-vent lengths than the northern lizards. Figure 8 appears to support this hypothesis. A *t*-test performed on the snout-vent lengths of lizards from small islands not co-occupied by *L. oxycephala* in the two regions indicates a difference in the means greater than would be expected

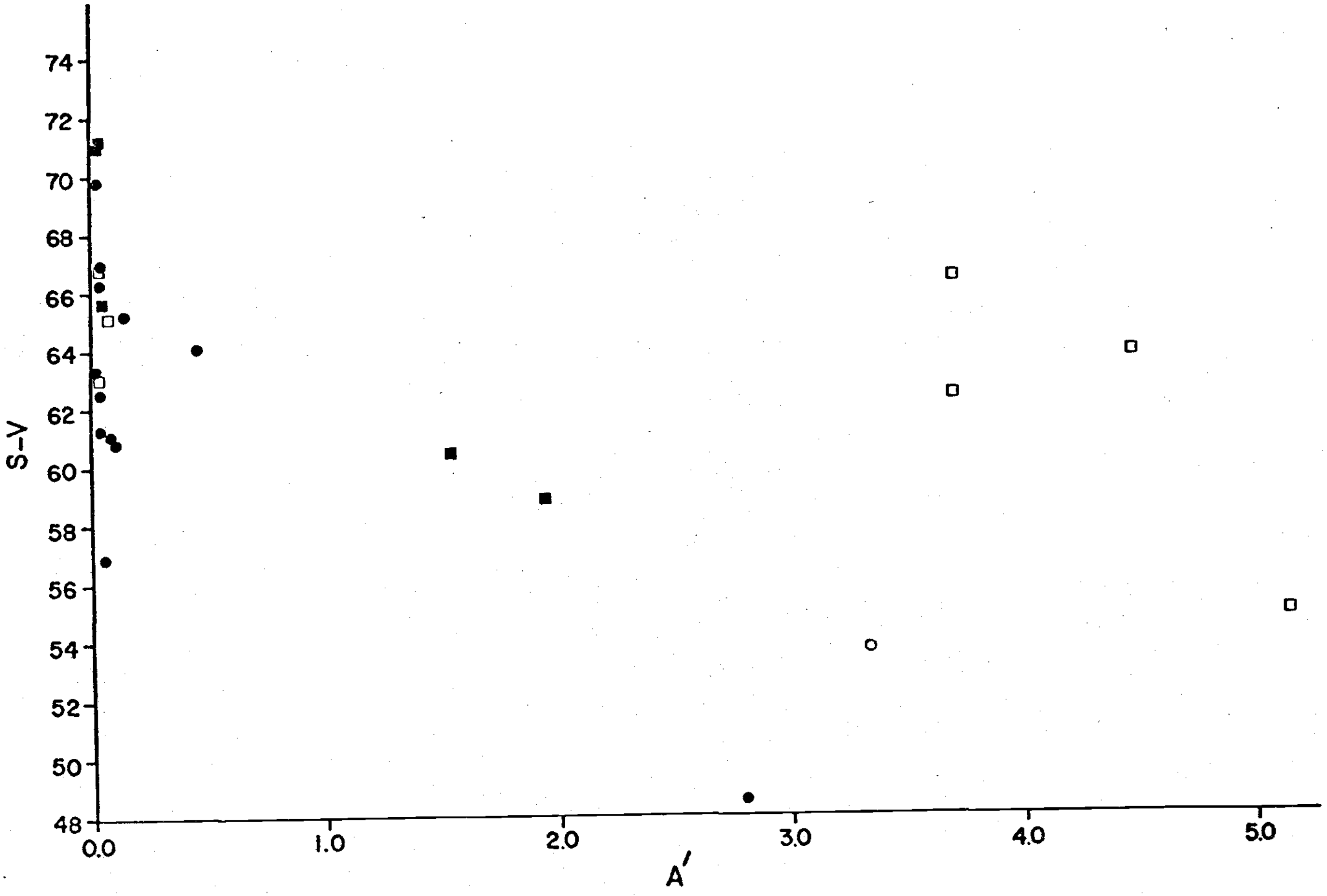

Figure 8. Scatter diagram of average snout-vent lengths of the largest third of the male lizards of each sample of L. melisellensis versus ln (1 + A). Symbols: Squares = southern islands; circles = northern islands; open circles or squares = islands co-occupied by another species of lizard.

due to chance ($t = 6.35$, $P < .001$).

Carlquist (1965) suggested four conditions under which island lizards might evolve different sizes from their mainland relatives; these conditions would not differ qualitatively for comparing size differences in populations from variously sized islands. One involves a conversion to a new diet, whereby larger lizards are able to exploit a wider range of food resources in the absence of interspecific competition. Grant (1965) preferred this hypothesis to explain the adaptive significance of larger bills in several species of birds on the Tres Marias islands of Mexico. A second means of selection for larger lizards on smaller islands might occur through social interactions. If larger lizards are able to secure larger territories (Boag, 1973) and thereby increase their food supply, large lizards would have a selective advantage, at least in periods of food shortages. Third, larger lizards could also be advantaged in aggressive encounters, particularly in the mating season. Finally, in conditions where temporary or seasonal abundances and shortages of food normally occur, large lizards may be better able to store food energy in the form of fat and survive periods of food scarcity.

Although all of these selective mechanisms may operate simultaneously along with changes in population age structures to produce the observed relationships between overall lizard size (snout-vent length) and island length and area, some evidence ranks the first of these as the most important. First, sizes of head measurements relative to snout-vent lengths are a major source of interpopulation variation in L. melisellensis; relatively modest increases in body size are accompanied by relatively large increases in nasal width and head length. If these features of Lacerta morphology are associated with the range of food item sizes taken by individual lizards, as is true in Anolis (Schoener, 1967), the larger absolute and relative sizes of trophic features in L. melisellensis from small islands may represent an adaptation to conditions in which a wider range of food sizes and/or types can be used by individuals. Second, I have observed individual lacertids eating flowers, figs and conspecific lizards on islands whereas stomach contents of mainland Lacerta suggest that such foods are very rarely taken (Eisentraut, 1929, 1949; Radovanović, 1953).

If A' represents a positive association between ecological heterogeneity and lizard size for islands of the same size (L'), the functional relationship may involve selection for larger lizards which can effectively use a wider range of food sizes or kinds. The heterogeneity in foods may be manifest in space or in time.

The role of D_1, a measure of isolation, in predicting lizard head and body sizes in insular L. melisellensis suggests that distant islands are less likely to be inhabited by the same number of predator, competitor and/or food species than are islands near the mainland. Schoener (1969b) argued that optimal predator sizes would be governed by the interaction of the abundances of different food items and the energetic efficiencies of predators of a given size using the foods; when very similar competitors are absent, predators should approach the optimum body size. Following Schoener's reasoning, the positive relationship between size of _L. melisellensis_ and distance to the mainland implies that _available_ prey distributions on distant islands favor larger lizards than do competitor-influenced prey distributions on near islands. However, there is no evidence available to suggest that the distant islands in this study are occupied by fewer competitors than the near islands; just the opposite may be true (Table 2). Given the assumption that an optimal lizard size exists for a given prey distribution, the relationship between D_1 and size of _L. melisellensis_ might be a function of differences in competitor and prey distributions on the mainland and on islands. With fewer competitors on islands, available prey distributions may favor larger size optima in lizards, but near island populations may receive more genetic input from mainland populations where genes for smaller size are more frequent, while distant island populations are more isolated from gene flow and more closely approach the optimum body size for island lizards.

Dorsal Scales

The climate-scale size model (Soulé and Kerfoot, 1972) states that large (or few) scales, by increasing cutaneous surface areas, could facilitate radiative and conductive heat loss in climates where heat loads are chronic. The positive relationship between dorsal scale counts and measures of island size (L', A') are contradictory to the trends observed in *Uta* (Soulé, 1966) and *Sceloporus graciousus* (Soulé and Kerfoot, 1972) which provided the basis for the model.

If, during the summer activity periods of *L. melisellensis*, smaller islands are generally cooler than the mainland or larger islands, the climate-scale size model predicts smaller (more) scales on lizards from small islands and larger (fewer) scales on mainland or large island lizards. However, the number of dorsal scales on *L. melisellensis* from southern islands is higher than the number on northern island lizards. Although the range of latitude of the islands considered in this study is only slightly more than one degree (Figure 1), ocean currents and vertical stratification differ markedly between the northern and southern regions (Stirn, 1969; Franco, 1970). The colder, shallower waters of the northern region could significantly affect the climates of the small islands in the two regions and override small island effects expected under the model.

Alternatively, the northern populations, being recently isolated from the mainland, may reflect primarily the adaptations of mainland

L. melisellensis to continental climates. However, Radovanović (1954) noted that mainland lizards (L. sicula and L. melisellensis) had more dorsal scales than lizards from island populations.

Thus, either (1) the assumptions concerning climates on islands and the mainland are unwarranted, (2) the climate-scale size model is invalid for L. melisellensis, or (3) north-south differences in climate are sufficiently great to have led to adaptive variation in dorsal scale numbers in these lizards. I don't regard argument (3) as being well supported, since it rests on the possibly unwarrented rejection of both (1) and (2). In addition, it is clear that other mechanisms, such as behavioral thermoregulation, variations in skin thickness, or the degree of melanism, could function effectively in adapting lizards to climatic variations by altering heat and water exchange rates. The significance of variations in dorsal scale numbers in lizards is not clear (Horton, 1972), and agreement on the physiological function of reptilian scales is lacking (Licht and Bennett, 1972). The relationships between scalation, melanism, and skin thickness and their patterns of variation with respect to climatic components demands further attention.

Femoral Pores

The strong positive relationship between femoral pore number and distance to the mainland implicates isolation as being an important factor in determining the role of femoral secretions in different ecological conditions. However, a scatter diagram of the average number of femoral pores and D_1 (Figure 9) shows that (1) the southern islands are generally more distantly separated from the mainland than the northern islands, and (2) within each region, a positive relationship between the two variables is still evident. If southern populations of *L. melisellensis* have existed in insular form for a longer time than northern populations, the regionality of variation in femoral pore numbers may represent temporal elements of isolation, while the distance effects represent spatial aspects of isolation.

The question of concern is, from what are southern and distant populations isolated? The most obvious answers are genes from the mainland populations and predators (Table 2; Radovanović, 1959).

A tentative explanation of the observed pattern assumes that femoral pore secretions of *L. melisellensis* function in intra-specific communication and the amount of secretion represents a compromise between maximizing intra-specific communication and minimizing cues for predators which locate prey by olfaction. In the absence of such predators, population densities of *L. melisellensis* are often extremely high (personal observation; Radovanović, 1959) and individual males with many femoral pores may be better able to communicate the boundaries of their territories or their sexual condition while avoiding energetically costly activities, such as display or overt

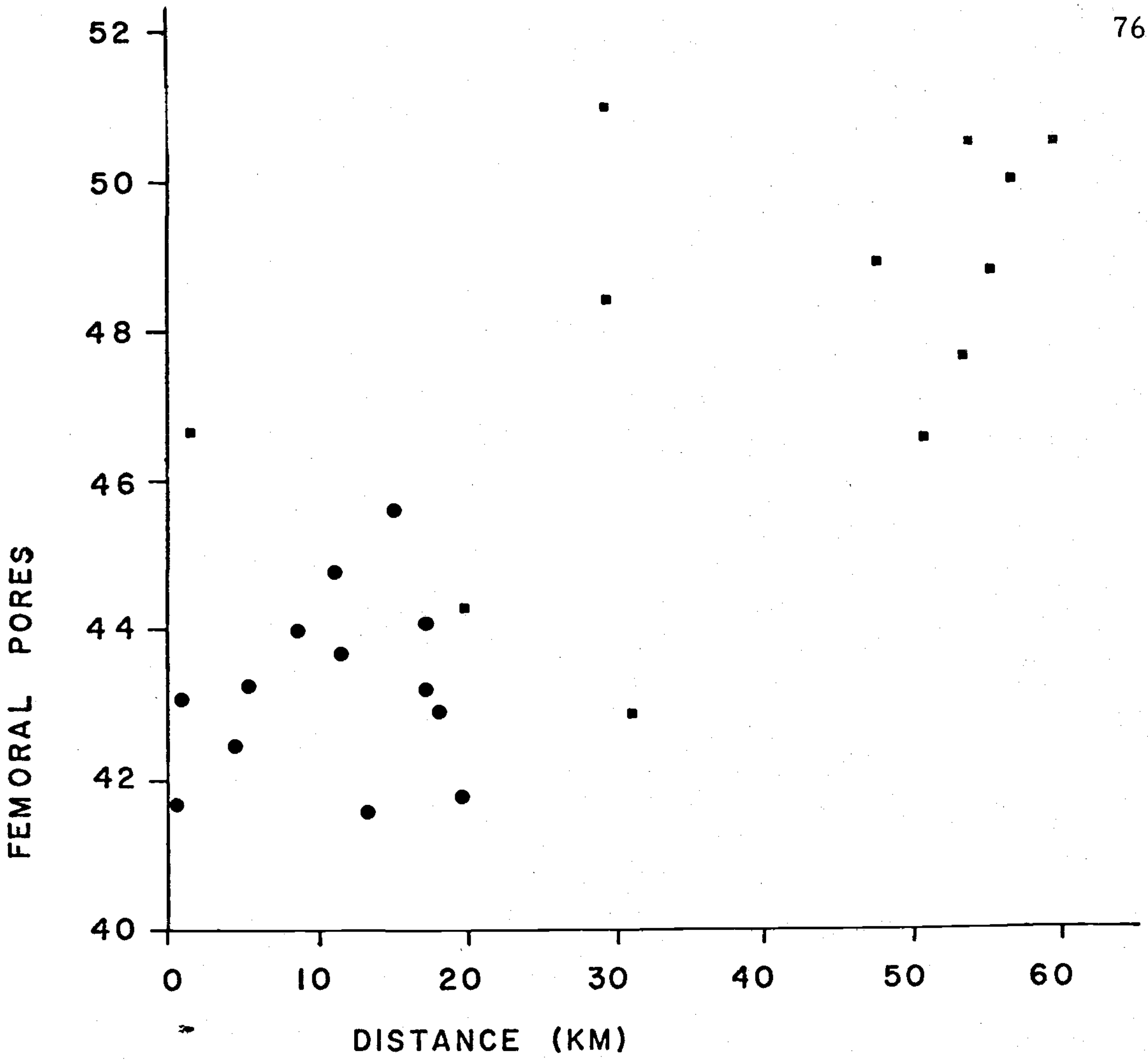

Figure 9. Scatter diagram of average number of femoral pores versus distance of the islands to the mainland. Symbols: circles = northern islands; squares = southern islands.

aggression. In areas where olfactory predators are abundant, lizards with fewer femoral pores would be less likely to be eaten.

Support for this explanation is weak, since direct evidence relating femoral secretions to intra-specific communication is lacking (Cole, 1966). However, it is generally accepted that lizards of the division Autarchoglossa rely on olfaction to a great extent in their social and foraging behavior (Evans, 1967). Rand (1954) noted that an island population of *Cnemidophorus lemniscatus* differed from mainland populations by having more femoral pores and considerably less predation. Burghardt (1971) has demonstrated chemical cue preferences in snakes in which attack behavior is mediated by Jacobson's organ, and experiments with temporarily blinded snakes (Burghardt, 1973) showed that attack behavior still occurred when chemical extracts of prey were offered.

It is obvious that no conclusion regarding the adaptive significance of femoral pore variations can be reached with the available information. It is my hope that the explanation proposed above will stimulate interest in the role of femoral secretions in intra- and interspecific communication.

The fact that patterns of covariation between biogeographic features and lacertid characters exist suggests the importance of natural selection in governing interpopulation variations. Other mechanisms, such as gene flow, founder effects, or genetic drift have undoubtedly played some role in determining the extent of these variations, but it is unlikely that widespread patterns of variation would develop through their actions. The inadequacies of tentative selectionist arguments in explaining these patterns are, in my opinion, due more to the lack of quantitative information regarding ecological conditions and functional morphology than to stochastic processes in the population biology of these lizards. Consideration of patterns of intrapopulation variation provides further evidence for this point of view.

VI. INTRAPOPULATION VARIABILITY

The existence of inter-individual phenotypic differences in a population may be viewed from two extreme viewpoints. One may argue that for any particular environment there exists an optimal phenotype; the level of variation in a population is, under this view, a measure of the deviation of individuals from the theoretical optimum. At the other extreme, one may expect for any particular set of environmental circumstances an optimum distribution of phenotypes, i.e., an optimal level of variation. Levins (1968) suggests that these are two alternative strategies, the optimal strategy being a function of the spatio-temporal variation of the environment and the organisms' abilities to perceive and respond to these variations.

Comparisons of the levels of intrapopulation variability among closely related populations are hampered by the lack of a theoretical framework relating overall variability within a population to causal factors. The reasons for the lack of a general theory are complex. The description of overall variation is fraught with difficulties of quantification, discerning between genetic and environmental contributions to variability, and with a tendency to ignore functional and developmental interrelationships among characters. These difficulties are superimposed on the inability to distinguish among proximate and ultimate causal factors of the levels of variability in a population. Partly because of these difficulties recent attempts to compare and explain different levels of variability in natural populations have led to confusion and controversy.

One controversy revolves around the evolutionary mechanisms for maintaining genetic variation in natural populations and has led some workers to a renewed emphasis on the significance of genetic drift and the maintenance of neutral alleles in evolutionary processes (e.g., Kimura, 1968; King and Jukes, 1969). This emphasis is strongly opposed by "selectionists" who rely on classical formulations of heterosis, frequency-dependent selection, temporal variations in relative fitness, regressiveness, and other mechanisms as explanations for maintaining genetic variation (e.g., Richmond, 1970; Wills, 1973). Related to this controversy is another concerning the relationship between genotype and phenotype. On one hand it is argued that heterozygosity permits phenotypic uniformity through the ability of heterzygotes to buffer the effects of environmental variation during development (e.g., Lerner, 1954). On the other hand, Soulé (1972; Soulé, et al., 1973) found that levels of heterozygosity and levels of phenetic variation in several lizard populations are highly correlated and suggested that phenetic variation is roughly directly proportional to the amount of additive genetic variation in a population. Finally, there is a lack of agreement as to the significance of morphological variation in a population and the relationship of variability to the population's niche breadth (see Rothstein, 1973a). The niche-variation model (Soulé and Stewart, 1970; Rothstein, 1973a) states that the level of variation within a population is an increasing function of the width of the niche exploited by the population. Rothstein (1973a) summarized the recent work of this hypothesis and pointed out some of the conceptual and operational difficulties involved in its evaluation. Related to this model is the phenomenon of "character release" (Grant, 1972) which often accompanies establishment of populations in isolated or depauperate areas. In insular situations where competitors and/or predators are reduced in number or are absent, populations often exhibit a wider range of morphological variation for particular characters than related populations in biotically complex situations (Foster, 1964; Grant, 1965; Keast, 1970; Wilson, 1961). Character release is not universal in these situations, however, since resource arrays may vary independently of competitors and predators. Thus, in an island population a tendency toward increased character variation in the absence of interspecific interactions may be counteracted by a small resource base upon which to diversify.

The lizard populations considered here are from islands of various ages, sizes, geographical positions, and ecological heterogeneity (Tables 2 and 9). At several locations congeners co-inhabited islands while other islands were inhabited by a single species of lizard. Since I have no quantitative data on resource availability, I will examine levels of variability with respect to biogeographic features of islands.

Procedures

Much of the literature regarding the niche-variation model is concerned with the variation of characters which reflect recognizable ecological function (e.g., use of bill by birds in foraging) and since some of the confusion regarding this model is due to the use of characters whose function is unknown, I have examined relative variation in two sets of characters, for two reasons. The first set of characters include ten relatively uncorrelated meristic characters. Using similar characters for *Uta*, Soulé (1972) found that the coefficients of variation showed agreement in their ranking of 18 populations. He hypothesized the existence of a *population variation parameter*, a statistic which the variation of each character estimated. Thus, the *average* of a set of coefficients of variation for a population could be considered an estimate of the *overall variability* of a population. Such a measure could be of great use in developing generalizations of phenetic variation in natural populations. I have examined the data from 24 populations of *L. melisellensis* and 7 populations of *L. sicula* in an attempt to verify the population variation parameter model.

The second set of characters whose relative variation I have examined are three highly intercorrelated measurements of head size and shape. The shape and size of a lizard's head imposes certain restrictions on its dietary intake (Schoener, 1967). Although few data exist to support the assertion that an optimum diet exists for a lizard of a particular size and shape, lack of empirical support may be due primarily to a failure to look for such data rather than an inherent deficiency of the argument. The work of Schoener on several species of Anolis (Schoener, 1967, 1969a; Schoener and Gorman, 1968) indicates that in many cases morphological features of the lizards are highly correlated with food size eaten, providing some evidence for the assertion. Several authors have investigated levels of variability in vertebrate populations under the assumption that natural selection favors an optimal morphology for exploiting a food source array (e.g., Van Valen, 1965; Soulé and Stewart, 1970; Pianka, 1969; Grant, 1967b; Willson, 1969; Rothstein, 1973a, 1973b) and most agree that variation of trophic-related characters is roughly proportional to the range of variation in the food resources used by the populations. Soulé and Stewart (1969) and Willson (1969) disagreed and suggested that the variables commonly used as indicators of food exploitation may not suitably indicate the basis upon which food selection by individuals occurs. I have examined the levels of variation within populations for head width, inter-nasal width, and head length in an effort to determine whether patterns exist which might indicate the validity of the niche-variation model.

Statistics

I have used the coefficient of variation as a measure of the relative variation in characters which are uncorrelated with measures of body size. Kerfoot (1969) showed that coefficients of variation for scale counts reliably characterized relative variation in a number of different reptile groups and recommended their use for these purposes. In small samples the coefficient of variation (CV) may be biased (Haldane, 1955), but fortunately, a simple correction removes most of the bias. For a sample of size n, mean $\bar{x}$, and standard deviation s, the nearly unbiased estimate of the CV is

$$CV = \frac{s}{\bar{x}} \cdot 100(1 + 1/4n).$$

The standard error of a CV is equal to CV/2n, and confidence limits for a CV may be calculated if the CV is derived from a sample of a normal distribution (Sokal and Rohlf, 1969).

For characters whose variations are functionally related to size variations I used the "rel-variance" (RV) (Hansen, et al., 1953) of the ratio between the size dependent character and the snout-vent length in place of the CV of each character to minimize the possibility of incorporating variation due to age differences within the samples.

I used the coefficient of concordance (Tate and Clelland, 1957) to see if the CV's and RV's of several different characters showed agreement in their rankings of populations. The populations were ranked according to the size of the CV for a number of characters, then Kendall's coefficient of concordance was calculated by

$$W = \frac{12 \Sigma d^2}{m^2(n^3-n)}$$

where m is the number of sets of ranks, n is the number of populations ranked, and Σd^2 is the sum of the squares of the differences between observed and expected totals for each sample. A statistically significant value of W would support the hypothesis of a population variation parameter existing for each population.

Multiple regression analyses were used to examine the importance of several island features in explaining the variation in the CV's of some of the characters in L. melisellensis.

Results and Analysis

Overall Variation

The CV's of ten relatively uncorrelated characters (Table 13) in 24 populations of L. melisellensis showed no significant agreement in their rankings of the populations ($W = .128$; $P > .05$). This statistic, incidentally, indicates a lack of significant heterogeneity in overall variation among the populations with respect to these CV's. A high concordance among CV's would suggest that whatever is responsible

Table 13. CV's and RV's. A. Southern populations of *L. melisellensis*; B. Northern populations of *L. melisellensis*; C. *L. sicula*.

Population	Character												
	5	6	7	8	9	10	11	12	13	14	16	17	19
A													
4	6.2	3.6	2.6	11.5	45.1	33.1	10.1	2.7	4.2	6.6	1.3	92.3	.16
5	6.9	7.2	4.9	11.6	24.2	18.8	7.2	3.7	3.1	3.9	.26	5.4	.02
6	3.0	5.8	4.0	13.9	24.4	21.4	11.4	5.5	5.0	3.4	1.6	29.1	.40
7	0.0	2.9	4.5	13.0	24.4	21.4	11.4	5.5	5.8	7.0	.4	36.6	.12
8	4.9	0.0	4.0	31.2	29.3	20.3	13.4	4.8	4.2	3.9	1.0	15.3	.27
9	2.3	0.0	3.3	24.0	32.4	26.4	8.2	4.2	5.5	7.7	1.0	13.6	.09
10	3.0	10.3	6.4	17.0	20.8	21.2	8.9	2.6	4.4	4.9	2.6	18.5	.18
11	3.6	7.2	3.0	23.1	30.0	19.5	10.1	4.0	4.9	8.1	.9	14.2	.10
17	2.5	0.0	8.2	9.6	38.9	25.7	7.1	4.4	3.6	3.8	.4	11.9	.04
26	0.0	0.0	6.3	21.1	26.6	17.5	9.9	4.4	4.2	4.9	.38	9.7	.08
28	6.0	8.7	6.7	14.0	36.3	31.3	8.3	3.9	3.4	5.1	.8	5.0	.11
B													
16	6.5	6.3	9.2	18.6	27.7	25.2	9.6	1.5	5.5	5.4	1.1	10.8	.18
18	3.3	0.0	4.5	17.8	36.8	22.0	10.7	4.8	4.0	4.2	.3	10.6	.16
19	3.1	4.6	7.3	14.2	30.7	23.1	10.3	3.5	3.2	6.3	.2	8.0	.05
20	3.7	0.0	6.9	17.7	23.4	18.0	12.0	2.7	3.9	5.2	.4	3.9	.07
21	4.4	0.0	0.0	14.5	28.6	23.7	12.3	4.4	2.8	5.2	.9	16.7	.16
22	3.1	0.0	4.2	14.7	19.9	26.1	10.1	2.5	3.7	4.1	.6	20.4	.20
23	4.4	0.0	4.8	13.5	31.9	24.3	14.0	3.4	4.1	4.6	.3	7.2	.06
24	7.4	6.1	6.7	14.6	35.5	30.4	11.5	4.3	3.6	3.4	.3	12.5	.06
25	3.1	0.0	4.4	12.6	19.6	20.4	6.5	3.3	4.2	3.8	.3	13.2	.07
27	2.3	0.0	4.4	19.0	20.6	23.3	11.7	3.1	4.1	4.4	.2	5.7	.09
30	0.0	0.0	0.0	24.6	20.0	22.4	7.6	3.1	3.9	6.0	3.0	82.4	.75
31	6.2	9.0	4.1	32.1	24.5	22.9	11.6	5.1	5.6	4.7	3.1	57.8	.58
32	7.5	4.4	5.4	11.9	21.5	22.7	3.4	2.2	4.0	4.9	.7	14.3	.09
C													
1	6.7	0.0	3.5	14.4	40.9	16.2	11.1	4.4	7.9	7.4	1.1	22.4	.07
2	6.8	8.2	8.7	24.7	48.7	24.3	18.2	4.2	5.2	4.7	.9	16.3	.18
3	7.2	4.6	5.2	19.9	45.9	31.5	16.9	6.1	15.8	6.3	.7	20.7	.16
12	4.6	4.1	6.9	35.3	29.9	20.7	13.4	3.4	6.3	6.2	.7	7.0	.05
13	6.4	9.4	2.0	12.4	42.3	39.1	9.4	4.1	4.8	10.0	.7	7.0	.05
14	3.0	2.2	6.1	18.9	28.1	31.5	8.8	4.4	7.3	4.9	.2	7.3	.02
15	4.2	0.0	0.0	10.2	26.0	34.9	6.5	4.2	6.4	7.3	.8	15.2	.13

for differences in variation among populations would be acting throughout the phenome (Soulé, 1967). Lack of concordance might result from sampling bias or from the factors effecting variation acting differentially among characters and populations.

The most likely sources of sampling bias may lie in the lumping of samples which have different evolutionary histories or from the use of characters which exhibit fluctuating asymmetry. For example, it might be expected that the populations of L. melisellensis from the southern region have had a much longer time for adjustment of their phenotypic distributions to insular and local conditions than have the northern populations. Thus, the distributions of some measure of overall variation (i.e., population variation parameters) for the northern and southern groups may be of biological significance, but the individual CV's in the two groups may show different patterns of variation.

Seven of the ten characters whose CV's I examined for concordance are normally bilaterally symmetrical, but frequently individuals differ from one side of the body to the other. The CV of a character which is a total of the left and right sides of the body is due in part to differences among bilaterally symmetrical lizards and in part to differences among symmetrical and asymmetrical lizards. Although the variation due to asymmetry was minimized by using only the total of both sides of each lizard, some of the variation in the totals was due to differences of the latter type.

In accordance with these possible sources of bias, I computed coefficients of concordance for a number of different sets of populations and characters (Table 14). Of the 12 coefficients, 3 are significant at the 95 percent level of confidence; two of these are just barely significant at this level.

These results provide little support for the existence of the hypothetical population variation parameter which reflects the pervasive action of some factor governing overall variation. It seems likely that the factors contributing to variation act differentially among various characters.

Lack of concordance of CV's of diverse characters is to be expected if different characters are more closely related to components of fitness than others. Many of these populations have rapidly diverged from ancestral populations in many respects; some of the divergences exhibit a geographical pattern, others show no such pattern and indeed are not (statistically) significantly different from each other in terms of relative variation.

For any character, the potential rate of divergence of a population is directly related to its additive genetic variation, adjusted for the relationship of the character to fitness (Fisher, 1958). Assuming that characters related to the food relationships of a population are more closely related to fitness than are characters such as scale

Table 14. Coefficients of concordance (W) for CV's or RV's of different sets of characters and populations. The sets are identified in Table 13. Significant coefficients indicate agreement of the CV's or RV's in ranking the populations (see text).

	10 characters		7 characters		3 characters		3 ratios	
	W	X^2	W	X^2	W	X^2	W	X^2
L. melisellensis								
11 southern islands	.064	6.40	.135	9.46	.628	18.85*	.828	24.85**
13 northern islands	.177	21.25*	.306	25.70*	.360	12.97	.803	28.92***
All 24 islands	.128	29.44	.175	28.03	.468	32.29	.823	56.75***
L. sicula								
7 islands	.201	12.03	.230	9.66	.564	10.14		

* $P < .05$

** $P < .01$

*** $P < .005$

size, we would expect that during strong directional selection trophic characters would have lower CV's. To the extent that different populations are subject to different intensities of selection, we should expect consistent patterns of variation in resource-relevant characters while characters more remotely related to fitness should exhibit less consistency in the way in which they vary.

Variation of Resource-Relevant Characters

The coefficient of concordance for the RV's of three measures of head size is highly significant (Table 14). The concordance of these statistics may be largely attributable to the strong correlations among the characters themselves (Table 5), but it is not due to the correlations between these characters and body size because body size effects are minimized by use of RV's.

The multiple regression analyses included as independent variables those features of islands which hopefully include the ultimate sources of the observed variation (Table 9). With all independent variables in the models, 72 to 91 percent of the variation in the RV's of the three characters was explained. Four independent variables were sufficient to account for 62 to 86 percent of the variation. Examination of Table 15 suggests the importance of island size, distance to the nearest land mass of equal or larger size, and elevation in these models.

Table 15. Multiple regression analyses using geographic features in Table 9 as independent variables and RV's as dependent variables. The multiple regression coefficients (R^2) are shown at each step.

Head Width/Snout-Vent Length

Stepwise:	D_2^*	D_2D_2'	D_2-D_2'L'	D_2-D_2'L'-E	D_2-D_2'L'-EC_2
	.19	.32	.42	.85	.87

D_2-D_2'L'-EC-C_2'	D_2-D_2'L'-EC_2-C_2'-A	D_2-D_2'L'-EC_2-C_2'-AL
.87	.88	.89

D_2-D_2'L'-EC_2-C_2'-AL-A'	D_2-D_2'L'-EC_2-C_2'-AL-A'-E'
.89	.89

Reverse Procedure:	D_2-D_2'L'-EC_2-C_2'-AL-A'	D_2-D_2'L'-EC_2-C_2'-AL	D_2-D_2'-EC_2-C_2'-AL
	.89	.89	.88

D_2-D_2'-EC_2-AL	D_2-D_2'-E-AL	D_2-E-AL	D-AL	-AL	L
.87	.87	.78	.58	.50	.04

Inter-Nasal Width/Snout-Vent Length

Stepwise:	L'	L'-A	L'-A-E'	L'-A-E'D_2	L'-A'E'D_2-D_2'
	.37	.52	.54	.58	.68

Table 15 (cont.)

	L'-A-E'D$_2$-D$_2$'A'	L'-A-E'D$_2$-D$_2$'A'-E	L'-A-E'D$_2$-D$_2$'A'-E-L			
	.69	.70	.71			
	L'-A-E'D$_2$-D$_2$'A'-E-LC$_2'$	L'-A-E'D$_2$-D$_2$'A'-E-LC$_2'$-C$_2$				
	.72	.72				
Reverse Procedure:	L'-AD$_2$-D$_2$'A'-E-LC$_2'$-C$_2$	L'-AD$_2$-D$_2$'A'-E-LC$_2'$	L'-AD$_2$-D$_2'$A'-E-L			
	.72	.72	.71			
	L'D$_2$-D$_2$'A'-E-L	D$_2$-D$_2$'A'-E-L	D$_2$-D$_2$'A'-E	D$_2$A'-E	A'-E	A'
	.70	.70	.62	.54	.42	.35

Head Length/Snout-Vent Length

Stepwise:	L'	L'-E	L'-ED$_2$	L'-ED$_2$-D$_2'$	L'-ED$_2$-D$_2'$-A	L'-ED$_2$-D$_2'$-AL
	.16	.44	.57	.78	.82	.89
	L'-ED$_2$-D$_2'$-AL-C$_2$	L'-ED$_2$-D$_2'$-AL-C$_2$-A'	L'-ED$_2$-D$_2'$-AL-C$_2$-A'-E'			
	.90	.90	.91			

Table 15 (cont.)

$L'-ED_2-D'_2-AL-C_2-A'-E'C'_2$

Reverse Procedure:	$L'ED_2-D'_2-AL-C_2-A'-E'$	$-ED_2-D'_2-AL-C_2-A'E'$	$-ED_2-D'_2-AL-A'-E'$
	.91	.91	.91

$D_2-D'_2-AL-A'-E'$	$D_2-D'_2-AL-A'$	$D_2-D'_2-AL$	$-D'_2-AL$	$-AL$	$-A$
.90	.90	.86	.70	.68	.04

Since many of the independent variables in these models are correlated with one another (Table 16), it is difficult to judge the true relationship of any single variable with the RV's of the characters by examining the simple product-moment correlation coefficients. Multiple regression sorts out these relationships to some extent, so that, say, the relationship between island area and the RV of head width can be estimated without the confounding effects of the positive correlation between island area and elevation. Different combinations of the independent variables in the multiple regression models indicate the importance of one variable in accounting for variation in the dependent variable while the effects of the other independent variables are held constant.

The relatively high multiple regression coefficients (R^2) suggest that the independent variables reflect, however obscurely, the important ecological and evolutionary sources of variation in the rel-variances.

Island Size

Levels of variability in the three characters appear to be positively correlated with island length (L' or L), but no significant correlations exist between rel-variances and area. Length appears to be the better measure of island size when the independent variables are in a linear scale, probably because of the skewness of the area data.

Table 16. Correlation matrix of variables used in multiple regression analyses of intrapopulation variability. Refer to Tables 3 and 8 for abbreviations.

	HW	NW	HL	A	A'	D_2	D'_2	C_2	C'_2	E	E'	L	L'
HW		.67	.86	.01	.29	.44	.31	.15	.09	.16	.35	.20	.37
NW			.69	.19	.59	.36	.32	.03	.07	.48	.53	.36	.61
HL				-.01	.32	.19	.07	-.13	-.10	.14	.30	.21	.40
A					.77	.08	.11	.02	.08	.76	.59	.96	.74
A'						.39	.44	.15	.22	.94	.89	.88	.96
D_2							.95	.65	.55	.53	.62	.14	.38
D'_2								.72	.66	.57	.65	.03	.43
C_2									.95	.27	.34	.81	.12
C'_2										.30	.35	.10	.19
E											.70	.81	.91
E'												.70	.90
L													.87
L'													

This is substantiated by the observation that the logarithmic transformation of area (A') does show a positive relationship with the rel-variances. Comparisons of the levels of variation between fringing islands and their parents (Figure 10) indicate the restrictive effect of small size of geographically close islands on the levels of variation in the lizard populations.

Effect of Island Shape

The two variable combinations which best explained variation in the food-related characters were in each case -A+L. This combination suggests that the shape of an island may account for some of the observed differences in levels of variation among islands of very similar area but of different shape. Thus, populations on round, small islands appear to be less variable, on the average, than populations on long, but equally small islands. The regression analyses of Soulé (1972) for overall variability of Uta populations on the islands of the Gulf of California suggest that A' and L (island length was W in his terminology) were, in combination, good predictors, but he ignored the possibility that they may represent island shape. It is apparent here that island shape may be a measure of the amount of lizard habitat, longer islands having more area directly influenced by the sea and more diverse lizard populations.

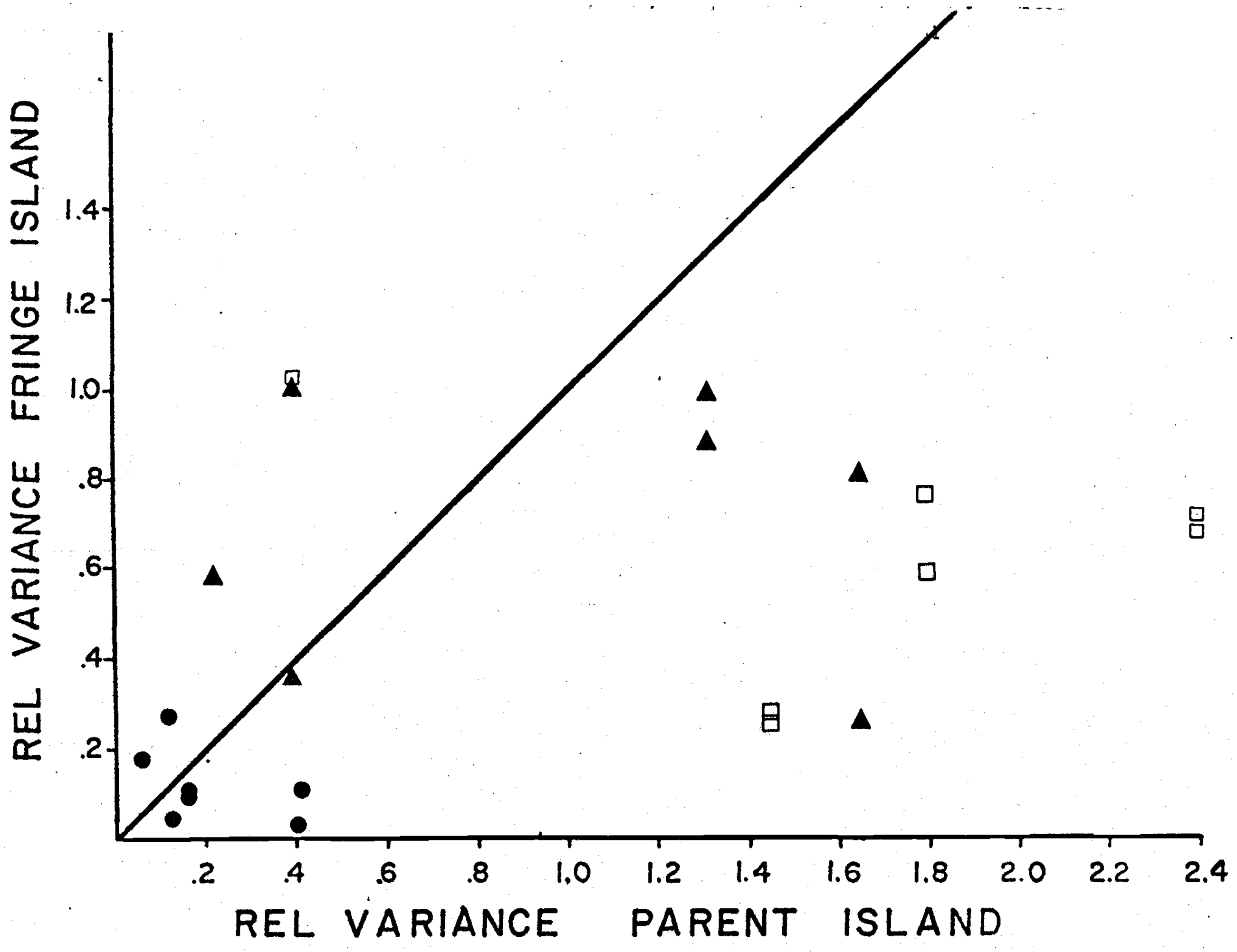

Figure 10. Comparison of RV's on fringing and parent island populations. Symbols: Circles = HL/SV; triangles = HW/SV; squares = NW/SV. The scale for NW/SV is ten times that shown.

Elevation

Elevation heterogeneity may reflect differences in the amount of habitable area on islands which are otherwise similar in size. On larger islands, such as Korcula and Vis, habitat heterogeneity is relatively high and vertical variations in vegetational composition are quite apparent to a visitor to these islands. The relationship between elevation and character variation may represent a response by these populations to habitat heterogeneity on large islands. On small islands no such increase in habitat heterogeneity with elevation is apparent, however. Here, elevation is much more likely to represent some other potential source of population variation, perhaps population size (Fisher, 1937).

Distance

The distance from an island to the nearest land mass of equal or larger size (D_2) is highly correlated with depth (C_2) between the masses, and with elevation of the island. Since D_2 is not correlated with A or L, it, perhaps along with C_2 and E, represents a very different source of variation for the insular populations. The islands considered in this study were probably formed by a gradual sinking of the Adriatic basin and/or a gradual rise in the level of the sea (Radovanović, 1959), so the distance between an island and the nearest large mass of land may reasonably be thought of as a measure of the period of time that the population on that island has been isolated. With the effects of A, L, and E held constant in the regression models, D_2 may be considered to represent the duration of evolutionary isolation of the resident population; the longer islands have been extant, the more diverse are their lizard populations.

Discussion

Interpretation of these results is hazardous in view of the small sample sizes, possible inadequacies of the independent variables in representing significant biological and historical sources of variation, and lack of knowledge concerning the heritability of the characters involved. Yet I proceed with the following speculative examination of the findings because of the similarities to the data of others who have worked with insular populations and because there are implications for general considerations of population variation.

Several theoretical arguments have been presented to explain patterns of morphological and genetic variation in space. In abbreviated form they are as follows:

1. The niche-variation model--natural selection optimizes distributions of phenotypes with respect to resource distributions permitting efficient subdivision of the resource among different phenotypes (Van Valen, 1965).
2. Direct effects of environmental heterogeneity on developing

organisms would be expected to affect morphological variation proportionately; these effects would be particularly evident in organisms with overlapping generations (Rothstein, 1973b).

3. Gene flow among locally adapted populations in large areas enhances variation in recipient populations (Mayr, 1963).
4. Increased homozygosity of the gene pool associated with sampling errors (founder effects, population bottlenecks) may have significant effects upon the phenotypic variation of a population. Genetic variation decreases with accumulating sampling errors and phenotypic variation will decrease proportionately to the additive effects of the loci.
5. Directional selection in novel environments erodes genetic variation, and to the extent that additive genetic variation influences the characters, decreases morphological variation (Soulé and Yang, 1973).

The above list is not exhaustive, but it includes the major paradigms for explaining variation of morphological characters. Other explanations which bear strong resemblance to some of those above are mentioned below where appropriate.

The proposal which has received the most attention recently is that of Van Valen (1965). In essence, this model suggests that "destabilizing selection" (Rothstein, 1973a) in species or populations confronted with a wide range of some potential resource acts to distribute phenotypes along the resource gradient in an optimal manner. Roughgarden (1972) distinguished two components of a population's niche width, the within-phenotype variation in resource use and that variation in resource use due to variation among different phenotypes. Thus, shifts in niche width in the face of changed resource distributions may be achieved at the extreme either by altering resource use patterns of individuals or by changing the distribution of individuals within the phenotype categories. In the latter case, assuming that the morphological traits being considered are closely related to resource use, an increase in niche breadth should be accompanied by an increase in morphological variation. Van Valen (1965) and others (e.g., Fretwell, 1972; Hespenhide, 1973) present data which seem to be in accord with this niche width--between phenotype hypothesis. Roughgarden (1972) predicted that sexually reproducing species would have difficulty in achieving new optimum phenotype distributions in the event of ecological release, and suggested that such conditions would favor an increase in the within-phenotype component of niche width. In this case, behavioral mechanisms of flexibility in resource use would predominate; morphological variation (i.e., character release) may or may not accompany ecological release.

Evidence for within-phenotype flexibility in lizard populations is minimal. Grant (1967) and Soulé (1966) observed island lizards eating foods not normally a part of their diet on the mainland; Ruibal and Philibosian (1970) showed that *Anolis oculatus*, the only anole on Dominica, inhabited a broader "thermal niche" than five species of anoles occurring on Cuba. The latter study suggested that apparent stenothermy of anoles on large islands may be due to interspecific competition for structural aspects of the environment, spatial restrictions leading to less variable thermal environments. Whether the resource is considered to be heat or habitat structural components, the within-phenotype component of niche width was wider on Dominica than Cuba.

Eisentraut (1929, 1949) reported that many island populations of lacertid lizards have taken up herbivorous habits which are rare in mainland populations. Plant material was included in the diets of these lizards most frequently in the late summer when insects were rare, suggesting individual flexibility in omnivory. I have observed individual *Lacerta melisellensis* eating *Pistacia* sp. flowers on the island of Greben, and *L. sicula* as well as *L. melisellensis* have both been seen eating figs which have fallen from trees on several small islands. At the opposite extreme from herbivory, I have observed cannibalism in *L. melisellensis*, and Kramer (1946) as well as Radovanović (1954) implicated this process as having profound effects on populations from small islands, while it has not been observed on the mainland. It is possible, then, that individuals in the *Lacerta* populations I have analysed have increased the range of food item types eaten on small islands.

The lack of agreement between theoretical expectations of ecological release on small islands and increased variability can be explained as the result of increased individual flexibility, i.e., release of the within-phenotype component of niche width. However, this does not explain the decrease in variability found in populations on small islands.

Rothstein (1973a) concluded that selection in response to increased niche width sometimes favors one form of the between-phenotype component of niche width--sexual dimorphism. Since the growth of lizards may be continuous throughout life, I have calculated indices of sexual dimorphism by

$$\frac{\bar{x}\text{ (male) HW}/\bar{x}\text{ (male) SV}}{\bar{x}\text{ (female) HW}/\bar{x}\text{ (female) SV}}$$

where $\bar{x}$ HW is the average head width for each sex and $\bar{x}$ SV the average snout-vent length for each sex. A scatter diagram of RV's for the males and the indices of sexual dimorphism (Figure 11) suggests that in most of the small island populations of _L. melisellensis_ there is little variation among males, but considerably more sexual dimorphism than in populations from larger islands. Two noteworthy exceptions are the populations on Jabuka (10) and Zirje (31). The former island is very small and distantly separated from other islands and is surrounded by deep water (140 m). The latter island is

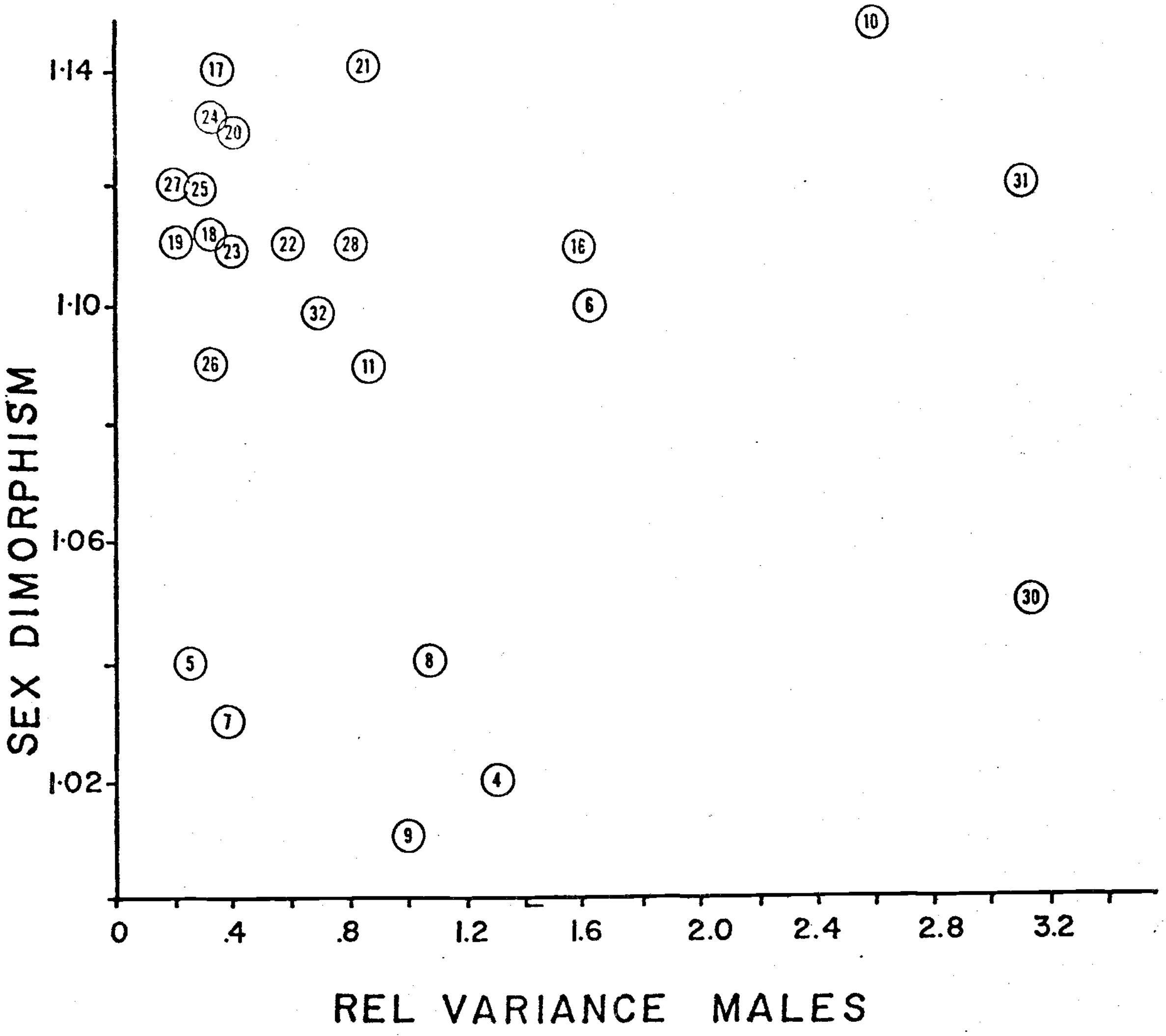

Figure 11. Scatter diagram of index of sexual dimorphism (ordinate) and RV's for HW/SV in L. melisellensis.

relatively large and close to the mainland. Both islands are inhabited by populations which exhibit both high sexual dimorphism and male variation. Zirje, although a large island, is ecologically homogeneous, appearing relatively flat, and consisting of rocks and sparse patches of low lying vegetation. It is unlikely that any other species of lizards live on this island (Radovanović, 1959; personal observation), while on the similarly sized island of Ciovo (30), sexual dimorphism is less pronounced in a population of L. melisellensis which is sympatric with L. sicula and possibly other species.

This suggests that populations not subjected to interspecific competition for food, such as are found on many small islands and on Zirje, often respond by increasing the differences between members of the two sexes. Presumably such sexual dimorphism leads to more efficient exploitation of the food resources through reduced intraspecific competition (Schoener, 1967). The corollary for populations on large islands is that interspecific competition and predation prevents the build-up of dense populations and attendant selection for sexual dimorphism. Why then is intra-sex variation generally lower on small islands than on large islands? The argument that increased diversity of food items and food sizes on large islands leads to destabilizing selection appears to be contradicted by the observation that the two islands which have the least diverse habitats of the large islands (Ciovo, 30 and Zirje, 31) have the highest levels of intra-sex variation. One hypothesis which is not discordant with the niche-width destabilizing selection argument requires consideration of the absolute size of the characters in conjunction with relative variation. On large islands overall size and head measurements are generally small. Thus, the absolute size of food related characters implies a restriction on the absolute size of prey items which can be taken and consequently a smaller range of food sizes. If the food size distribution is limited within this range and unimodal, the range of food sizes may be insufficient to permit subdivision of the resource between two phenotypes (i.e., sexual dimorphism). Since small size may imply both evolutionary and age structure shifts in size to accommodate low prey densities, populations on islands where food is scarce and which have small food-related characters may have a diversity of phenotypes which take advantage of small but important fluctuations in food size distributions.

The direct action of environmental conditions during development may be construed as important in explaining the pattern of intrasex variation found here. Large islands probably have more diverse physical environments while small islands are more buffered against extremes by the surrounding water. However, all collections of lizards were confined to a small area, even on large islands, within which it is doubtful that significant variability in developmental conditions existed. Furthermore, populations from more diverse large islands would be expected to exhibit more variation than populations from less diverse large islands if environmental conditions during development were an important factor causing variation.

Gene flow among locally adapted populations (or among local populations subjected to different developmental environments) on large islands is also unlikely. Populations on the large, diverse islands of Vis (4) and Lastovo (7, 26) should exhibit higher intra-sex variation than those on less diverse large islands such as Ciovo (30) and Zirje (31). However, gene flow between islands (or from the mainland) may be of considerable significance. Vis (4) and Lastovo (7, 26) are rather distinctly separated from the mainland while Ciovo (30) is separated by only a small gap of approximately 40 meters (over which is a bridge). Zirje (31) is only a short distance from the mainland (11 Km) and the interval is filled with numerous islands of varying sizes. The depth of the water is relatively shallow between Zirje and the mainland, and additionally, fishing boats often seek shelter from storms at larger islands which are inhabited, increasing the possibility of man-caused immigration from the mainland. Radovanović (1960, 1965) suggested that transport of L. sicula by man with subsequent competitive exclusion would explain the patchy distribution of these two species of lizards.

Genetic drift, operating through founder effects, population bottlenecks, or consistently small population sizes might reasonably be considered an important phenomenon in determining the expression of intra-sex variation in many of the populations from small islands. Particularly for polygenic traits, genetic drift would result in increased homozygosity and concomitant decreased phenotypic variation.

Three lines of evidence suggest that genetic drift, in some form, has been important in the evolution of these insular populations. First, examination of frequencies of a gene for a recessive trait, "concolor" (Kramer, 1941) in these populations shows that either the dominant or the recessive allele has been fixed in many of the small island populations (Figure 12). On larger islands the populations are polymorphic. Some small island populations are also polymorphic, but in these populations two observations are of interest. First, some of these islands are fringing islands of larger islands whose populations are polymorphic and may have been separated for a much shorter time than more remote small islands. These islands may have been formed without a drastic founder effect such as would be expected when a small propagule colonizes an uninhabited island. The closeness of the fringing islands (e.g., 5, 8, 11) to their parent islands may also increase the likelihood of migration and therefore more frequent input of genes from the parent islands. Second, the tendency toward melanism in populations on small islands results in a phenocopy of the concolor trait in many cases. Thus selection may

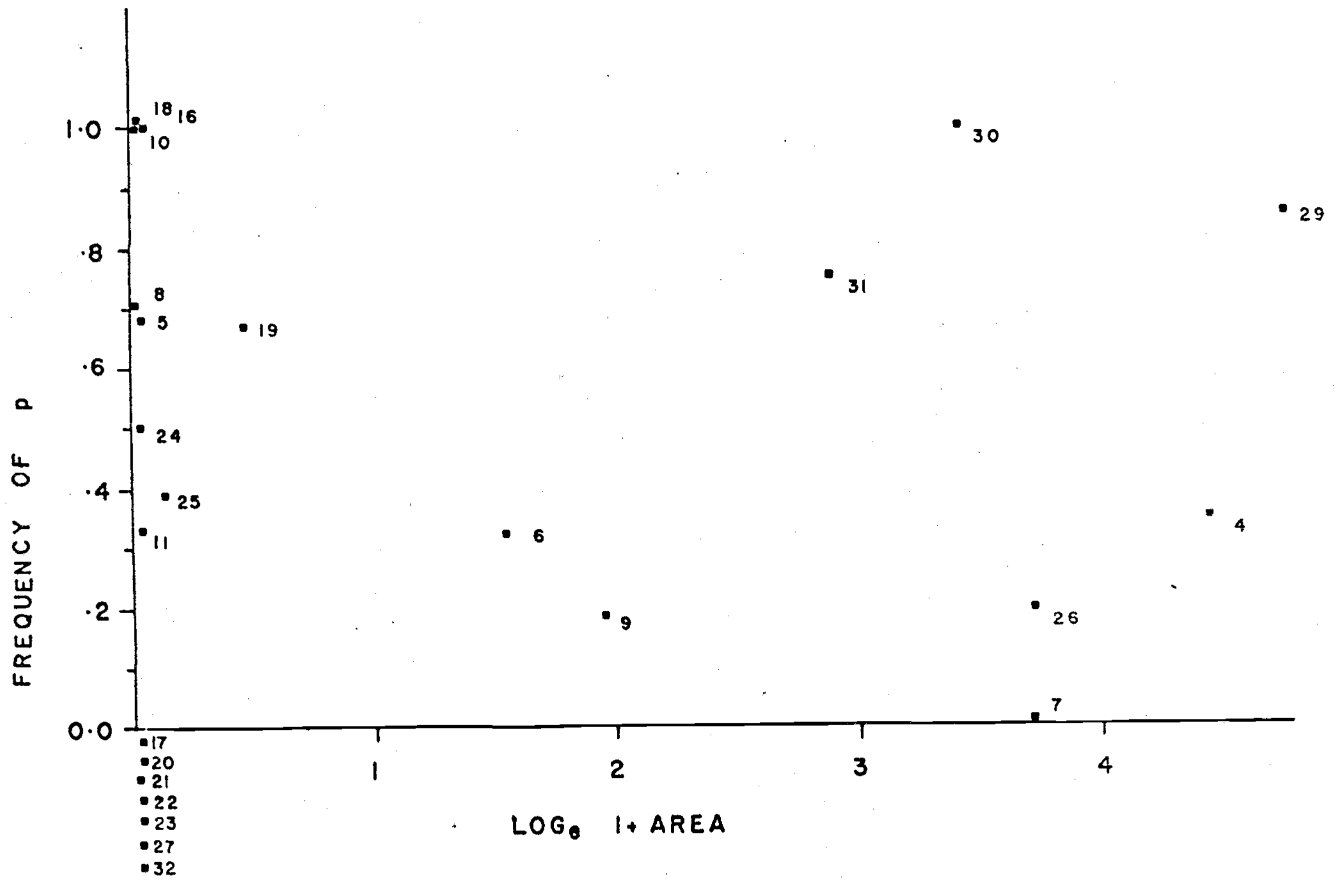

Figure 12. Scatter diagram of frequency of patternless gene (p) in 25 populations of L. melisellensis versus A'.

take alternate directions to the same end, one in which patterned lizards (P_) elaborate their pattern to become increasingly dark (e.g., 17, 20, 24) and another in which patternless morphs (pp) become darker over their entire dorsum (Kramer, 1941). A black dorsal pattern on black lizards would be expected to have little selective advantage over patternless morphs who are also black. Character variations which are virtually selectively neutral would be expected to be more likely to experience genetic drift than those more closely related to fitness.

A second line of evidence for the importance of genetic drift is suggested by interpopulation variations in body size. Some populations on small islands have been characterized as being "dwarf" forms and others "giant" forms. For example, on a very small island near Vis (Mali Barjak) is a population of "dwarf" lizards described as a separate subspecies (Mertens and Wermuth, 1960). On another small island near Vis, Mali Parzanj, is the subspecies _L. melisellensis gigantea_. The extreme variation in average size of these lizards on _small_ islands suggests that the difference may be due to some form of genetic drift.

The third line of evidence derives from allozyme variation detected by electrophoresis. Some of the differences in allelic frequencies in populations on parent and fringing islands can best be explained through some form of genetic drift (Gorman, Soulé, Yang, and Nevo, MS in prep.).

Although it is unlikely that genetic drift would result in fixation at all loci affecting a particular polygenic character, fixation of some of the loci would give qualitatively similar results, namely, a reduction in the potential range of variation for such characters, to the extent that the loci have additive effects.

Soulé (1972, 1973, Soulé and Yang, 1973) has proposed a theory which explains patterns of variation in various groups of organisms. He proposed that populations in ecologically and/or geographically marginal situations are more subject to strong directional selection while central populations are primarily subject to stabilizing selection. The former condition erodes genetic variability, while the latter promotes accumulation of genetic variability through overdominance and continuous testing of new recombinants against a relatively stable but complex set of environmental conditions. Evidence for depletion of genetic variation coincident with strong directional selection comes from numerous artificial selection experiments. In some cases, plateaus of response occur, and upon relaxation no tendency to return toward the original character states is found, suggesting that genetic variation has been depleted (Dobzhansky, 1970:205).

Directional selection has undoubtedly had a strong influence on the evolution of insular populations of Lacerta. Nearly all populations on small islands have undergone rapid changes in average body size, coloration, and to a lesser degree, scalation. Small islands provide unique environments for lizards which evolved in biotically more complex and physically more diverse environments on the mainland. Thus, at least for small or remote islands, an assumption of strong directional selection acting on these populations as they move to new and distinct adaptive peaks with a simultaneous reduction in genetic variation is not unreasonable. On large islands environmental conditions are no doubt less divergent from mainland conditions and directional selection less severe.

Since morphological variation reflects to a large degree underlying genetic variability, this theory may adequately explain the low levels of morphological variation found in populations from small islands. However, this theory predicts larger amounts of variation on Vis and Lastovo than on Ciova and Zirje, a prediction not upheld by the data (Figure 11).

Of the theoretical arguments considered above, the niche width--variation model and the directional selection model appear to have the widest applicability to these populations. Genetic drift, operating through the founder effect or some other manifestation of sampling error, may contribute to decreased morphological and genetic variation on small islands, but the presence of higher levels of sexual dimorphism on small islands provides support for one or both of the selection models. Gene flow from other islands or from the mainland appears to be the best explanation for the high levels of morphological variation on the large but ecologically homogeneous islands of Ciovo (30) and Zirje (31). If gene flow is responsible for the high levels of variation on Ciovo and Zirje, mainland populations should be expected to exhibit both high levels of variation and a high similarity to these populations.

If the effects of genetic drift and gene flow are ignored, we might ask, what selective forces lead to the pattern of increased sexual dimorphism and decreased intra-sex variation on small islands and its inverse on large islands? Discounting Ciova and Zirje, both the niche width-variation model and the directional selection model appear to superficially fit the observations more or less equally. One might reasonably ask, then, what are the differences, if any, between the two models?

The crucial difference between these models is best seen in the following hypothetical example. Imagine a population exploiting a food niche of width W in area A. If a large sample of individuals from this population are introduced to area B in which the range of food types (or size classes) is the same, but are distributed differently, the same food niche width would be available for the colonizing population, but the average phenotype would be shifted according to the new distribution of food items. The niche width--variation model predicts that the variation in the population should not differ from the original source population; the directional selection model suggests that a reduction of variation in the population should take place *as the mean changes position*. Once adjustment to the new distribution of food resources has taken place, variation might be expected to increase through accumulation of advantageous mutations and recombinants. Thus, the essential difference between the models is that one accounts for adjustment of populations through time, while the other is essentially a static model for describing populations which are in equilibrium with their environmental milieu. For populations whose environmental conditions are changing relatively rapidly, the niche-width variation model may be an unsuitable paradigm.

The lizard populations I have considered here represent two kinds of conditions. On large islands, food resources probably aren't too variable in time and populations are limited by a variety of factors, hence selection on trophic characters would be relatively low. On small islands, food resources probably fluctuate strongly in time and probably represent the dominant limiting factor of population sizes (Radovanović, 1952, 1959). Small islands thus represent systems of fluctuating food resources requiring either tracking of changes in food abundance or a general phenotype capable of using a wide range of resources. Either strategy would require strong directional selection (although in different directions), one continually, one until a resistant phenotype had been achieved.

VII. OVERVIEW

An examination of the phenetic relationships of the lacertid lizards from islands near the coast of Yugoslavia demonstrated some of the shortcomings of intraspecific taxonomic categories. A combination of different multivariate analyses indicated that the populations of L. sicula and L. melisellensis could be combined into two distinct groups which correspond to the geologic ages of the islands on which they are found. The northern and southern populations of these species appear to have been isolated on islands which were formed through changes in sea level and sinking of the Adriatic Basin in two different periods. The populations in the southern region were probably isolated as islands were formed by inundation of the coast 20 to 30 thousand years ago, and the northern island populations were cut off by the rising sea only in the last few thousand years. Comparisons of trophic characters in these lizards suggest that convergence may have occurred as a response to similar selective pressures in the southern islands, resulting in a closer phenetic resemblance of L. sicula to southern populations of L. melisellensis than to northern populations. Selection regimes in both regions may be similar, but convergence has apparently progressed further in the southern region due to the longer exposure of these populations. Phenetic similarities in L. melisellensis also roughly correspond to sizes of the islands different populations inhabit. I feel that these trends have been partially obscured by the concentration of previous workers on subspecific categorization.

Multiple regression analyses implicated island length, area, and the distance to the mainland as variables which ultimately incorporate many of the causal factors of interpopulation variations in body size, sizes of trophic structures, and femoral pore numbers in 24 populations of *L. melisellensis*. Larger body sizes and trophic structures in lizards from small and/or distant islands may best be explained by the low abundances of insects and selection for phenotypes capable of using a wider range of food types. Larger numbers of femoral pores in lizards from small and distant islands suggests a role in intraspecific communication since congeners and predators are largely absent in these locations.

Measures of relative variation for ten meristic characters in *L. melisellensis* showed no significant patterns of variation, but levels of intrapopulation variation in ratios of head measurements to snout-vent lengths were generally lower in populations on small islands and higher in large island populations. Island area, length, the distance to potential sources of new colonists, and elevation were shown to be important variables in "explaining" geographic variation in RV's of trophic characters. Low levels of relative variation for trophic characters in populations from small, isolated islands are generally associated with relatively high levels of sexual dimorphism, suggesting that strong directional selection resulting from intraspecific competition for food has depleted genetic variation in these characters. Evidence from gene frequency data and body size distributions shows that genetic drift and/or founder effects complicate possible explanations of these trends.

A number of patterns of variation identified in insular Lacerta from the Yugoslav coast are, to some extent, paralleled in other lizards and island groups. For instance, inverse relationships between body size and island size have been reported in Uta (Soulé, 1966) in the Gulf of California and in Tropidurus in the Galapogos (Carpenter, 1966). Schoener (1969a) reported a tendency in solitary species of Anolis to converge toward an "optimum" body size, involving in many species an increase in body size. Similarly, body sizes of insular populations of chuckwallas (Sauromalus varius and S. hispidus) and whiptail lizards (Cnemidophorus ceralbensis) in the Gulf of California are larger than mainland populations of their relatives (Soulé and Sloan, 1966). Populations of Uta from small islands are less variable than populations from large islands and the mainland (Soulé, 1972), and sexual dimorphism in size is greater in Tropidurus populations from small islands than on larger islands in the Galapogos (Carpenter, 1966). Data from Schoener (1969a) show a remarkable increase in sexual dimorphism in size in several species of Anolis on islands of small size and/or few congeners. Numbers of femoral pores have been found to be higher in insular populations of *Cnemidophorus* (Rand, 1954) and in Italian island populations of *L. sicula* (Kramer and Medem, 1940) than in mainland populations of the same species.

Other patterns observed in insular *L. melisellensis* and *L. sicula* in this study have also been noted in other island lizards. A tendency toward melanism in populations from small, isolated Yugoslav islands is paralleled in *Uta*, *Sauromalus*, and *Cnemidophorus* in the Gulf of California (Soulé and Sloan, 1966). Numerous island populations of *L. sicula*, *L. oxycephala*, *L. tilfordi* and *L. pityuensis* in the Mediterranean are more melanistic (Kramer, 1949; Hartmann, 1953; Eisentraut, 1954) or cyanistic (Lanza, et al., 1971; Lanza, et al., 1972) than mainland populations. Observations of uncommonly high lizard densities in populations of *L. melisellensis* and *L. sicula* from small Yugoslav islands (personal observation; Radovanović, 1952, 1959) are similar to reports in insular *Uta* (Soulé, 1966) and Galapogos iguanas (*Conolophus* and *Amblyrhynchus*--Berrill and Berrill, 1969). Finally, observations of insular lizards feeding on unusual foods (e.g., Soulé, 1966; Grant, 1967) are similar to my observations of *L. melisellensis* and *L. sicula* on small islands feeding on figs, flowers and conspecific lizards. Radovanović (1952) examined stomach contents of Yugoslav *Lacerta* from small islands and reported evidence of cannibalism occurring in nearly five percent of the samples. Grass, land snails and iospods were also found in many of these stomachs.

The fact that different saurians respond to insular environments in similar ways suggests the existence of a general explanation. I believe the fundamental ecological determinant of evolutionary events is isolation. Isolation is difficult to quantify for at least three reasons. First, isolation of an area from colonization (including gene flow) by organisms is a function of the dispersal abilities of the organisms. This restriction is minimized when considering one group of organisms with similar dispersal abilities and similar interspecific interactions. Second, isolation has no units. Third, isolation consists of both spatial and temporal components. The independent variables I used in multiple regression analyses were composite measures of spatial and temporal isolation; the distance of an island to the mainland (D_1), for instance, is a measure not only of the distance over which colonists must travel, but a measure of island age as well, since the continental shelf slopes downward at a fairly constant rate and a rising sea level would have isolated the distant islands earlier than the islands nearer the mainland. Some idea of the importance of the temporal component of isolation can be seen in comparisons of the southern (older) and northern (younger) island populations. Lizards on the southern islands are significantly larger, have wider snouts and longer heads, and more femoral pores than lizards from the northern islands, and since these are widespread trends in insular lizards, I conclude that the response to insular environments is more complete in the older populations. A generalization of this reasoning is that the net intensity of isolation for an island population (or community) is the resultant of vectors describing spatial, temporal and vagility components of isolation.

The ecological effects of isolation are only vaguely recognized. It is clear that spatial isolation is a positive function of disharmony in predator, prey and competitor representations, and that temporal isolation may allow some of the disharmonic effects of spatial isolation to be resolved, since old islands may accumulate "beneficial" combinations of adaptive types through repeated colonization and/or co-evolution. Thus, the presence of L. oxycephala on many of the southern islands could be the result of successful colonization by a food and habitat specialist after L. melisellensis had become more of a generalist in response to insular disharmony. I do not suggest that this is what happened, but present it as an example of the kind of question that needs to be considered. Specifically, the sequence of ecological events leading to the widespread evolutionary patterns in insular lizards needs investigation. Comparative studies of demography, and food relationships of lizards on islands of different ages appear to be the most likely sources of information for understanding causal relationships in the isolation--lizard response patterns.

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APPENDICES

APPENDIX I

In general, four kinds of similarity coefficients have been used to quantify the degree to which two or more groups of organisms are similar in terms of a number of characters considered simultaneously. Coefficients of association have been used most frequently in cases where characters are expressed in only two states (i.e., indicating the presence or absence of a trait). These coefficients generally reflect the number of character matches as a function of the total possible matches. Second, correlation coefficients between the groups may be calculated using the average values of each character being considered to rank the groups according to the degree to which the variation of their characters is correlated. This method allows characters to assume an arbitrary number of character states. A third method involves using the raw data matrix and partitioning groups of organisms on the basis of their contributions to the homogeneity of the original matrix. The coefficients are determined empirically by computing the cumulative probability that a given pair of samples will be as similar or more similar than can be ascertained for each character on the basis of the observed distribution of its states in the set of groups under study. The probabilities of the entire suite of characters are combined to give a probabilistic similarity coefficient for those two groups. Sneath and Sokal (1973) review this subject and provide references for further investigation. The fourth kind of similarity index involves calculating the distance between groups in a multidimensional space whose coordinate axes are the characters. I have used several methods of distance analysis to examine the phenetic relationships in insular Lacerta.

Since the various methods of distance analysis are related to some degree (Goodman, 1972; Gower, 1966), it is important to visualize the structure of the data in multidimensional space so the operations of the various methods I have used are clearly distinguishable. Consider an individual organism on whom several measurements have been taken. If a line is drawn whose length represents the range of values which can be taken by a measurement of a particular character, that individual's position on that line will be designated by the value of the measurement of the character. Similarly, if two lines are drawn so they intersect at right angles, each line represents a different character, and an individual's position with respect to each character can be designated by two points, one on each axis. However, joint consideration of the two characters will place the individual at one point in the space between the two axes. The location of this point is geometrically determined by projecting perpendiculars from the two points to the point of intersection in the two-character space. Similarly, a number of individuals, each represented by a single point, can be located in the space created by considering several characters simultaneously. The distance between any two points in one dimensional space is simply the length of the line separating the two points which fall on the character axis, and is calculated by finding the difference between the values of the measurements, $X_{1i} - X_{1j}$, where i and j refer to individuals, and X_1 is the value each takes with respect to character 1. The distance between two individuals (or means) in k-dimensional space can similarly be calculated by using a generalization of Pythagorus' theorem,

$$D_{ij} = \sum_{k=1}^{n} [(X_{ki} - X_{kj})^2]^{1/2}$$

This represents the "average" distance between two individuals with respect to k axes. This Euclidean distance may include redundant information if the values of some of the characters are linearly dependent, since two correlated characters can be described by a single linear function which encompasses the ranges of variation in the two characters.

When individuals of several populations are plotted in k-space, each population can be visualized as being a cloud of points surrounding a centroid, a direct analogue of the arithmetic mean of a single character. The dispersion of the individual points around their centroid is represented by the within group covariance matrix, which is symmetric, with the variances of the individual characters lying on the diagonal and the covariances of pairs of characters lying off the diagonal. Since some characters are more variable than others they may be unduly emphasized in some treatments of the covariance matrix so it is customary to standardize the data by dividing the difference between each observation and its respective mean by its standard deviation. This kind of standardization converts the covariance matrix into a correlation matrix.

Cluster Analysis

I used a polythetic hierarchical method of agglomerative clustering (Williams, 1971) developed by Ward (1963). This technique, given n distinct sets of Euclidean distances (i.e., the distances between a given population centroid and the centroids of all other populations being considered) will successively consider combining all possible pairs of groups and select the combination which results in the loss of the least information. Maximum information is contained in the matrix of distances prior to clustering By repeating this process until only one group remains, the complete hierarchical structure of the matrix of distances and an estimate of the information loss incurred at each step is obtained. Optimum grouping at each cycle is achieved by the objective function which permits only those two groups to cluster which, when clustered, would have the smallest within group variance. This procedure maximizes the between group variance. This procedure maximizes the between group variance, subject to the restriction that two groups must be combined at each repetition of the cycle.

Principal Component Analysis

This multivariate statistical method is used to describe the variation within a multivariate sample. When some of the characters are intercorrelated, much of the information in a covariance matrix is redundant and can be reduced to fewer linear combinations of the original characters. Principal component procedures find linear combinations of correlated variables which maximize the variance of the weighted sum. The eigenvectors are the weights given the original variables in the derived variables and are solved so that each is independent of every other. Since the new variables, the principal components, are linear combinations of the original variables, most of the total variation in the cloud of data points is accounted for in the first few components. The amount of variation in each component is described by an eigenvalue, and the sum of the eigenvalues is equal to the sum of the variances of the original characters. Thus, principal component analysis simply provides a different viewpoint of the original cloud of data points, one in which the number of dimensions is reduced by a function of the degree of intercorrelation in the original characters.

Canonical Analysis

This method is used to describe the variation within and between multivariate data sets. Standardization of the covariance matrix of means by the pooled within group covariance matrix (a weighted average of the covariance matrices of all the sets) emphasizes factors of variation other than size. The mathematics of the process can be visualized geometrically as finding new uncorrelated axes (canonical axes) on which the centroids of the different clouds of data points would be maximally separated when they are projected onto the line. The new axes are linear combinations of the original characters and they represent the principal axes of the covariance matrix of the means. The vector of weightings given the original characters in these linear combinations indicate the relative importance of each of the characters in defining each of the canonical variates.

All of these procedures are described in detail in numerous texts and papers. For biologists who are inexperienced in multivariate procedures, I recommend Williams (1971) for an introduction to clustering methodology, followed by Sneath and Sokal (1973). Blackith and Reyment (1971) and Jolicoeur and Mosimann (1960) provide the clearest introductions to principal component analyses, and the former reference along with Jolicoeur (1959) provide excellent examples of the uses of canonical analysis. Gower (1966) and Goodman (1972) emphasize the intrinsic relationships of some of these techniques, and Morrison (1967) gives a good balance between theory and application of these and other methods. Cooley and Lohnes (1971) include examples with interpretation of results and list FORTRAN programs for computation, as do Blackith and Reyment (1971).

APPENDIX II

MEANS AND STANDARD ERRORS FOR EACH CHARACTER AND POPULATION

Population	Character						
	1	2	3	4	5	6	7
1	7.54(.19)	2.15(.05)	1.97(.10)	16.16(.37)	12.08(.23)	10.00(.00)	14.33(.14)
2	6.97(.12)	1.92(.03)	1.66(.07)	14.65(.23)	12.06(.19)	10.33(.20)	14.89(.30)
3	7.22(.13)	1.96(.04)	1.80(.06)	15.50(.26)	12.62(.18)	10.15(.09)	14.89(.30)
4	6.29(.32)	1.68(.08)	1.16(.06)	12.70(.72)	12.38(.26)	10.13(.13)	13.88(.13)
5	7.37(.15)	1.99(.03)	.96(.09)	14.68(.24)	12.05(.19)	10.30(.16)	14.75(.16)
6	6.85(.13)	1.86(.04)	1.40(.07)	13.88(.25)	12.00(.09)	10.29(.14)	14.23(.14)
7	7.07(.13)	1.90(.03)	1.56(.11)	14.60(.22)	12.00(.00)	10.08(.08)	14.25(.18)
8	7.39(.15)	2.06(.03)	.44(.12)	14.82(.28)	12.27(.15)	10.00(.00)	14.20(.15)
9	5.94(.27)	1.66(.07)	1.19(.08)	11.68(.59)	12.07(.07)	10.00(.00)	14.29(.13)
10	7.46(.48)	2.04(.11)	.99(.15)	15.09(.80)	12.13(.13)	10.83(.38)	14.25(.33)
11	7.54(.10)	1.97(.03)	1.45(.07)	14.61(.17)	11.80(.11)	9.93(.18)	14.20(.11)
12	8.20(.17)	2.41(.04)	1.68(.07)	16.41(.36)	12.09(.16)	10.18(.12)	14.91(.29)
13	8.30(.30)	2.45(.08)	1.62(.10)	16.92(.60)	12.46(.22)	10.46(.27)	14.07(.03)
14	7.93(.08)	2.09(.02)	1.81(.08)	16.51(.15)	12.14(.08)	10.05(.05)	15.14(.20)
15	8.01(.20)	2.39(.03)	1.73(.28)	17.19(.43)	12.75(.25)	10.00(.00)	14.00(.00)
16	6.81(.11)	1.85(.03)	1.29(.04)	12.91(.14)	12.14(.21)	9.93(.17)	15.00(.36)
17	7.89(.12)	2.13(.03)	1.33(.11)	14.86(.20)	11.92(.08)	10.00(.00)	15.33(.36)
18	7.38(.11)	1.86(.02)	1.45(.05)	13.41(.15)	12.17(.11)	10.00(.00)	14.25(.18)
19	6.76(.11)	1.76(.02)	1.04(.05)	13.58(.17)	12.14(.07)	10.15(.09)	15.23(.22)
20	7.92(.06)	2.08(.01)	1.45(.07)	14.56(.08)	12.25(.10)	10.00(.00)	14.60(.22)
21	7.75(.17)	2.14(.05)	1.57(.11)	15.09(.30)	11.92(.15)	10.00(.00)	14.00(.00)
22	6.58(.10)	1.86(.02)	1.38(.05)	13.31(.15)	11.86(.10)	10.00(.00)	14.21(.16)
23	7.02(.08)	1.79(.02)	1.27(.04)	13.43(.11)	11.95(.08)	10.00(.00)	14.50(.11)
24	7.57(.10)	1.89(.02)	1.36(.06)	14.29(.15)	11.62(.17)	9.96(.12)	14.19(.18)
25	7.23(.10)	1.85(.02)	1.34(.07)	14.06(.16)	11.93(.07)	10.00(.00)	14.45(.12)
26	7.29(.13)	1.95(.03)	1.50(.05)	14.70(.19)	12.00(.00)	10.00(.00)	14.42(.21)
27	7.25(.07)	1.89(.02)	1.46(.04)	13.68(.11)	11.92(.05)	10.00(.00)	14.35(.12)
28	8.21(.11)	2.33(.02)	1.11(.09)	16.03(.15)	12.45(.16)	10.55(.19)	14.86(.21)
29	6.57(.11)	1.77(.02)	0.80(.10)	12.39(.16)	12.36(.17)	10.14(.14)	14.21(.15)
30	6.31(.40)	1.69(.11)	1.10(.12)	11.92(.73)	12.00(.00)	10.00(.00)	14.00(.00)
31	5.31(.31)	1.44(.08)	1.02(.07)	10.04(.62)	11.60(.22)	9.60(.27)	14.10(.18)
32	6.55(.18)	1.85(.03)	1.26(.07)	13.03(.27)	11.75(.25)	10.00(.12)	14.67(.23)

Population	Character 8	9	10	11	12	13	14	15
1	20.75(.85)	11.50(1.33)	11.58(.53)	10.67(.33)	24.67(.31)	66.58(1.49)	44.42(.93)	64.46(1.52)
2	17.17(.98)	5.22(.59)	9.89(.56)	10.50(.45)	25.17(.25)	66.89(.81)	43.78(.48)	58.08(.73)
3	17.27(.67)	7.42(.66)	10.54(.65)	10.81(.36)	25.35(.30)	66.85(2.05)	45.04(.55)	63.44(.96)
4	16.63(.65)	11.00(1.70)	11.25(1.28)	9.38(.32)	24.13(.23)	54.00(.78)	46.50(.78)	53.06(3.29)
5	16.63(.65)	13.70(.73)	11.50(.48)	10.30(.16)	24.55(.20)	56.85(.39)	48.75(.42)	61.83(1.08)
6	16.18(.54)	15.88(.70)	14.94(.96)	9.12(.23)	25.18(.27)	51.94(.62)	50.47(.41)	57.82(.89)
7	15.92(.58)	11.33(.78)	11.92(.72)	10.50(.34)	25.25(.39)	59.58(.97)	51.00(1.01)	60.25(1.14)
8	11.07(.88)	8.67(.64)	10.67(.55)	11.4 (.39)	25.80(.31)	55.47(.59)	42.87(.42)	60.80(.89)
9	19.21(1.21)	13.57(1.14)	12.00(.83)	9.43(.20)	24.50(.27)	55.29(.79)	47.64(.96)	48.93(2.61)
10	14.50(.85)	13.88(.99)	10.88(.79)	10.25(.31)	25.13(.23)	54.75(.82)	50.50(.85)	63.50(3.68)
11	15.87(.93)	9.53(.72)	12.00(.59)	10.20(.26)	24.20(.24)	54.87(.68)	48.87(1.00)	62.33(1.03)
12	27.64(2.87)	7.55(.67)	14.91(.91)	11.55(.46)	24.64(.24)	61.91(1.15)	41.18(.75)	69.00(1.34)
13	21.15(.72)	8.08(.93)	11.23(1.19)	10.46(.27)	24.85(.27)	63.00(.82)	44.31(1.21)	71.58(2.70)
14	17.95(.73)	8.43(.51)	10.95(.75)	13.10(.25)	25.57(.25)	65.43(1.02)	46.76(.49)	67.52(.70)
15	19.75(.95)	8.50(1.04)	11.75(1.93)	9.50(.29)	24.25(.48)	61.50(1.85)	45.50(1.55)	70.38(1.60)
16	25.43(1.24)	19.71(1.43)	15.79(1.04)	11.57(.57)	26.00(.11)	53.00(.77)	43.07(.62)	54.79(.70)
17	15.00(.41)	12.33(1.36)	12.00(.87)	9.58(.19)	26.25(.33)	51.83(.53)	44.33(.48)	63.50(.85)
18	19.50(.98)	14.75(1.53)	9.58(.60)	12.25(.37)	25.75(.35)	53.08(.60)	44.08(.53)	59.92(.80)
19	18.62(.52)	13.89(.83)	13.69(.62)	10.12(.20)	25.62(.18)	53.81(.34)	42.50(.52)	59.00(.91)
20	23.20(.91)	13.25(.68)	14.30(.57)	11.25(.30)	25.65(.15)	53.60(.47)	42.95(.49)	64.65(.50)
21	16.25(.66)	14.42(1.16)	12.17(.82)	10.92(.38)	24.92(.31)	50.25(.39)	43.17(.64)	66.25(1.62)
22	16.43(.64)	16.64(.87)	12.14(.83)	11.64(.31)	25.29(.16)	47.07(.46)	43.21(.46)	58.46(1.16)
23	15.29(.33)	13.74(.71)	14.08(.55)	12.47(.28)	26.42(.14)	53.92(.36)	41.63(.31)	57.43(.48)
24	15.62(.44)	13.92(.96)	12.54(.74)	11.35(.25)	26.62(.22)	50.69(.35)	41.85(.28)	62.14(.84)
25	17.48(.41)	17.90(.65)	12.17(.46)	11.83(.14)	28.07(.17)	53.38(.41)	44.04(.31)	60.90(.76)
26	14.11(.68)	12.58(.76)	12.84(.51)	10.74(.24)	25.84(.26)	55.53(.53)	48.42(.54)	63.11(.99)
27	15.35(.57)	15.89(.64)	11.46(.52)	11.23(.26)	26.19(.16)	52.00(.42)	45.58(.39)	59.14(.69)
28	15.14(.45)	11.09(.85)	11.45(.76)	10.00(.17)	24.91(.21)	52.64(.38)	49.77(.54)	69.80(.70)
29	18.00(.93)	16.14(.84)	9.93(.73)	(Missing)	(Missing)	(Missing)	46.71(.73)	53.00(.68)
30	15.71(1.41)	13.86(1.01)	11.57(.95)	10.29(.29)	25.29(.29)	53.43(.75)	41.71(.92)	49.00(3.89)
31	19.20(.62)	18.10(1.37)	11.60(.82)	11.00(.39)	25.4 (.40)	53.90(.92)	43.70(.63)	41.00(3.22)
32	18.50(.62)	16.83(1.02)	13.08(.84)	13.00(.12)	27.17(.17)	53.75(.61)	44.75(.62)	56.46(1.51)

Population	HW/SV 16	NW/SV 17	Character OW/SV 18	HL/SV 19	HW/HL 20
1	.117	.033	.031	.251	.467
2	.120	.033	.029	.252	.476
3	.114	.031	.028	.244	.466
4	.119	.032	.022	.239	.496
5	.119	.032	.016	.238	.502
6	.119	.032	.024	.240	.494
7	.117	.032	.026	.242	.484
8	.122	.034	.007	.244	.499
9	.121	.034	.024	.239	.508
10	.118	.032	.016	.238	.495
11	.121	.032	.023	.234	.516
12	.119	.035	.024	.238	.500
13	.116	.034	.023	.236	.491
14	.118	.031	.027	.244	.481
15	.114	.034	.025	.244	.466
16	.124	.034	.024	.236	.527
17	.124	.034	.021	.234	.531
18	.123	.031	.024	.224	.550
19	.115	.030	.018	.230	.498
20	.123	.032	.022	.225	.544
21	.117	.032	.024	.228	.514
22	.113	.032	.024	.228	.495
23	.122	.031	.022	.234	.523
24	.122	.030	.022	.230	.530
25	.119	.030	.022	.231	.514
26	.116	.031	.024	.233	.496
27	.123	.032	.025	.231	.530
28	.118	.033	.016	.230	.513
29	.124	.033	.015	.234	.550
30	.129	.034	.022	.243	.530
31	.130	.035	.025	.245	.529
32	.116	.033	.022	.231	.503