*Spea multiplicata.*—(3) Arizona, Cochise Co., Portal; (5) Colorado, Otero Co., 1.2 km S La Junta, Highway 109.

## APPENDIX II

Apomorphies supporting the cladogram in Fig. 1 are given. Changes in allelic arrays are superscripted, primitive to derived shown left to right. The FREQPARS branch length for each stem follows the PAUP optimizations. C = convergence, H = transformation that is reversed, R = reversal.

Node A.—ACCTRAN and DELTRAN: S-Acon-A$^{ee-ee}$, Gpi-A$^{ee-ee}$(H), S-Icdh-A1$^{ee-aa}$(H). FREQPARS: 18.660.

Node B.—ACCTRAN: M-Acon-A$^{bb-aa}$(H), S-Acon-A$^{ee-ee}$, Ga3pdh-A$^{bb-aa}$(H), M-Sod-A$^{bb-aa}$. DELTRAN: M-Acon-A$^{bb-aa}$(H), Ga3pdh-A$^{bb-ab}$(H), M-Sod-A$^{bb-aa}$. FREQPARS: 9.760.

Node C.—ACCTRAN and DELTRAN: Cbp-2$^{aa-bb}$, frontoparietal boss. FREQPARS: 2.000.

Node D.—ACCTRAN: Ga3pdh-A$^{aa-ab}$(R), S-Icdh-A1$^{aa-bb}$, S-Icdh-A2$^{aa-bb}$. DELTRAN: S-Acon-A$^{ee-ee}$, S-Icdh-A1$^{aa-bb}$, S-Icdh-A2$^{aa-bb}$. FREQPARS: 5.500.

*S. multiplicata.*—ACCTRAN and DELTRAN: Ldh-B$^{ee-aa}$, Pgm-A$^{bb-ab}$. FREQPARS: 0.600.

*S. hammondii.*—ACCTRAN: M-Aat-A$^{ee-ed}$, S-Aat-A$^{ee-dd}$(C), S-Acon-A$^{ee-aa}$. DELTRAN: M-Aat-A$^{ee-ed}$, S-Aat-A$^{ee-dd}$(C), S-Acon-A$^{ee-aa}$, Ga3pdh-A$^{ab-aa}$(C). FREQPARS: 6.660.

*S. intermontana* (Oregon).—ACCTRAN: M-Aat-A$^{ee-ab}$, S-Acon-A$^{ee-bb}$, Ck-A$^{ee-dd}$, Gpi-A$^{ee-aa}$, S-Mdh-A$^{ee-aa}$. DELTRAN: M-Aat-A$^{ee-ab}$, S-Acon-A$^{ee-bb}$, Ck-A$^{ee-dd}$, Ga3pdh-A$^{ab-aa}$(C), Gpi-A$^{ee-aa}$, S-Mdh-A$^{ee-aa}$. FREQPARS: 10.000.

*S. intermontana* (Colorado).—ACCTRAN and DELTRAN: S-Aat-A$^{ee-dd}$(C), Ck-A$^{ee-bb}$, Ga3pdh-A$^{ab-bb}$ (R). FREQPARS: 5.500.

*S. bombifrons.*—ACCTRAN and DELTRAN: M-Acon-A$^{aa-ab}$(R), Gpi-A$^{ee-ee}$(R), M-Icdh-A$^{aa-dd}$, S-Icdh-A1$^{bb-be}$(R), S-Icdh-A2$^{bb-be}$, S-Mdh-A$^{ee-be}$. FREQPARS: 7.500.

# MICROGEOGRAPHIC CLINES IN THE SIZE OF MATURE MALE *GALLOTIA GALLOTI* (SQUAMATA: LACERTIDAE) ON TENERIFE: CAUSAL HYPOTHESES

Roger S. Thorpe and Richard P. Brown

*Department of Zoology, University of Aberdeen,
Aberdeen AB9 2TN, Scotland*

ABSTRACT: Microgeographic variation in the size of the Tenerife lizard, *Gallotia galloti*, is studied by recording snout–vent length (SVL) from numerous samples of mature males in breeding color. The reliability of the means is commensurate with those of other morphological characters. When simultaneously tested against several hypothesized causes, by both partial correlations and Mantel tests, SVL was shown to vary in relation to both altitude and topographically determined climate/vegetation (latitudinal categories). Both of these altitudinal and latitudinal elements can also be seen in various characteristics of the scalation and color pattern.

*Key words:* Microgeographic variation; Microevolution; Causal hypotheses; Mantel tests; Lizards; Canary Islands; Within-island variation

LIZARDS, such as lacertids (*Gallotia*) on the Canary Islands, can show substantial microevolutionary differences in size among islands (Thorpe, 1985). In these circumstances, it can be difficult to distinguish between the effects of natural selection and chance consequences of isolation over time. However, the study of differentiation of continuously distributed populations within single islands with marked climatic ecotones (such as Tenerife, western Canaries) can contribute to an understanding of the microevolutionary forces influencing populations of lizards (Thorpe and Baez, 1987; Thorpe and Brown, 1989*a,b*). Even so, when an organism can-

not readily be aged and does not reach its final size early on in its life, then it is particularly difficult to define patterns involving subtle size differences among populations. The differences among individuals due to differences in growth-stage/age can obscure the general geographic trends that are due to, for example, natural selection. The microgeographic variation in the size of the vegetarian lizard on Tenerife, *Gallotia galloti*, may pose this problem.

A previous study of microgeographic variation of generalized (multivariate) size of specimens from this island population of *G. galloti* hints at variation correlated with elevation (Thorpe and Baez, 1987), but this is far from conclusive. The above study excluded juveniles but used a range of sub-adults and adults of both sexes and admitted that clear trends could not be confirmed with the type, number, or size of the samples used.

The current study attempts to minimize the problem of comparing snout–vent length (SVL) among populations when there is non-terminal growth by selecting a relatively narrow growth band: i.e., sexually mature males in breeding color. While the limited growth of sexually mature males could still be a source of confusion, the extent of growth during this period is very small compared to the total amount of growth. Furthermore, the number of individuals and localities used in this study is far greater than previously used by Thorpe and Baez (1987) and so general trends may now be detectable.

The island of Tenerife reaches high elevations (3718 m) and has a diverse range of environmental conditions (Fernandopulle, 1976; Huetz de Lemps, 1969) as well as a complex geological history (Borley, 1974; Mitchell-Thome, 1976). A range of historical/geological (phylogenetic) and adaptational (ecogenetic) hypotheses have been proposed for, or could explain, patterns of microgeographic variation within this island. An observed pattern of microgeographic variation can be statistically compared to a range of hypothesized patterns to elucidate its cause. This is done using several techniques, including partial correlations, Mantel tests, and simultaneous Mantel tests.

## METHODS

### Pattern Description

The SVL was recorded from 501 sexually mature males in full breeding color from 67 localities distributed across the island to represent a complete range of positions and conditions (Fig. 1). These samples were collected over an 8 wk period. The existence of among-locality (geographic) variation is tested by an ANOVA treating each locality sample as a group. The pattern of microgeographic variation is portrayed by contouring (Sampson, 1978) the locality means after they have been scaled on a 0–10 range (0 = 10.2 cm, 10 = 12.8 cm).

### Hypothesis Testing

There are several ways of comparing observed and hypothesized patterns of geographic variation. However, matrices expressing observed and hypothesized similarities among localities cannot be compared directly by correlation, because the elements within a matrix are not independent of one another. Two solutions present themselves: (1) correlate unidimensional observations (single characters or ordination scores) with unidimensional hypotheses (Thorpe and Brown, 1989*a,b*), or (2) compare matrices using a random permutation technique: i.e., Mantel test (Brown and Thorpe, 1990, in press; Cheverud, 1989; Cheverud et al., 1989; Dietz, 1983; Dillon, 1984; Douglas and Endler, 1982; Dow and Cheverud, 1985; Dow et al., 1987*a,b*; Malhotra and Thorpe, 1990; Manly, 1986; O'Brien, 1987; Schnell et al., 1985, 1986; Smouse et al., 1986; Smouse and Wood, 1987; Sokal, 1979; Sokal et al., 1980, 1986; Thorpe, unpublished).

Both of these solutions are complicated by the fact that several hypothesized patterns may be inter-correlated and ought to be simultaneously tested against the observed pattern to reveal which hypotheses are accepted or rejected. In the first solution, this can be readily achieved with partial correlation and multiple regression
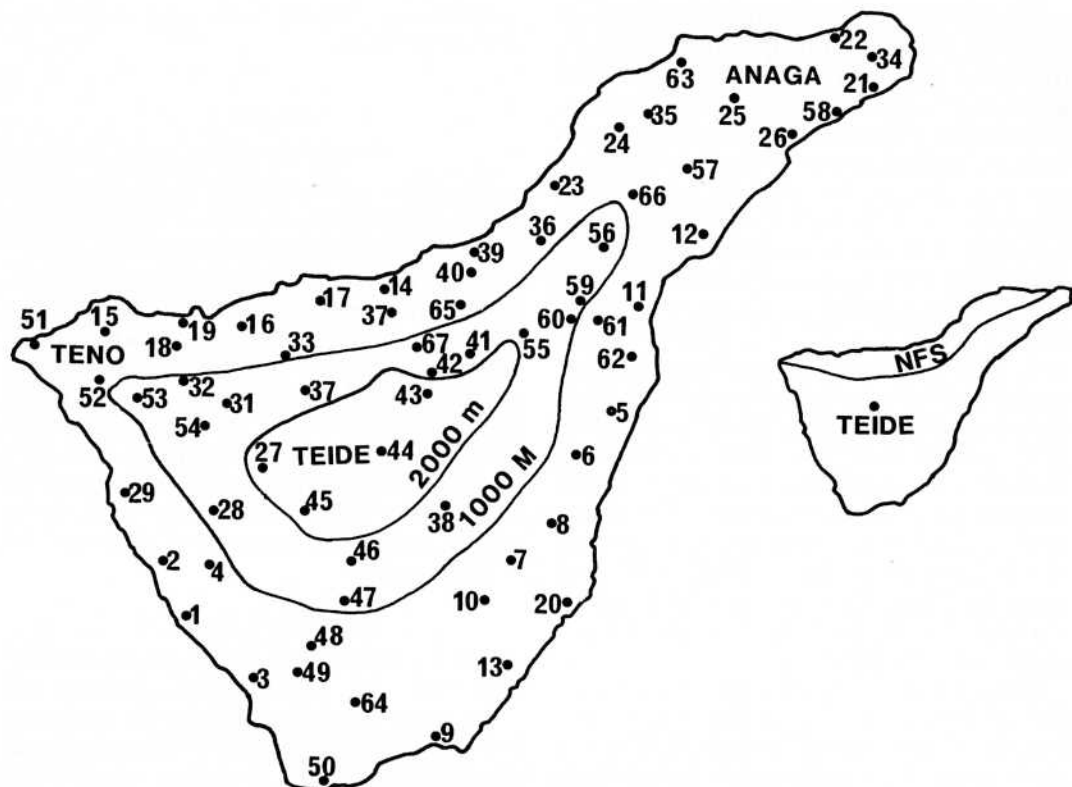
FIG. 1.—Sample localities (numbered 1–67). The locality of a sample is indicated by a dot, the altitudinal contours are indicated by lines, and the positions of the precursor islands (Anaga and Teno) and of the peak of Teide are given. On the inset, the line running approximately latitudinally across Tenerife separates out the north-facing slopes under 1500 m (NFS) from the rest of the island. These two latitudinal ecotones are pertinent to hypothesis 3.

while in the second solution, this may be achieved (with two independent hypotheses) by a simultaneous Mantel test. In any event, the use of these techniques is often only exploratory as there may not be adequate historical, genetic, or ecological information. In this case, the variation in SVL is treated, in relation to the hypothesis testing, as if it has at least some genetic component. However, the possibility of environmental induction is not ruled out.

*Unidimensional comparisons: correlations.*—The observed pattern of geographic variation is represented by an array of locality means (SVL). The following causal hypotheses are represented by unidimensional arrays.

Hypothesis 1a: The precursor islands of Anaga in the east and Teno in the west (Fig. 1) may have been joined by the eruption of Teide (Borley, 1974) between them to form the single present day island of Tenerife. Bischoff (1982) implied that the variation in the color pattern and size of *G. galloti* on Tenerife may be due to predifferentiated populations from these precursor islands (i.e., separate Anaga and Teno lineages) coming into secondary contact after the junction of these islands. This historical/geological (phylogenetic) hypothesis predicts a pattern of geographic variation that is braodly correlated with longitude. Consequently, in the partial correlation analysis, this hypothesis is rep-

resented by the array of locality longitudes.

Hypothesis 2a: Climate changes substantially with altitude (Fernandopulle, 1976; Huetz de Lemps, 1969), and some scalation characters of *G. galloti* have clinal patterns of microgeographic variation correlated with altitude (Thorpe and Baez, 1987). This "ecogenetic" hypothesis predicts a pattern of geographic variation that is correlated with altitude. Consequently, in the partial correlation analysis this hypothesis is represented by the array of locality altitudes.

Hypothesis 3a: The high altitude and prevailing winds (Fernandopulle, 1976; Huetz de Lemps, 1969) result in the north-facing slopes (NFS) below approximately 1500 m being subject to high cloud cover (Fig. 1 inset). These NFS are humid and warm with lush vegetation whereas elsewhere the climate tends to be hot and arid resulting in a barren landscape. Characteristics of the scalation and color pattern of *G. galloti* have patterns of microgeographic variation correlated to these topographically-determined climatic differences (Thorpe and Baez, 1987; Thorpe and Brown, 1989*a,b*). If one assumes a sharp change in ecotones and no gene flow, this "ecogenetic" hypothesis predicts two latitudinal categories as in Fig. 1; hence the hypothesis is represented by an array in which the localities on the NFS are coded zero and those elsewhere are coded as unity.

Hypothesis 4: Some characteristics of the scalation and color pattern of *G. galloti* (Thorpe and Baez, 1987; Thorpe and Brown, 1989*a,b*) are correlated with latitude possibly due to gene flow between, and/or a more gradual change in, the ecotones of hypothesis 3. This "ecogenetic" hypothesis assumes gene flow, and consequently predicts a smooth clinal pattern correlated with latitude rather than the abrupt categories of hypothesis 3. Consequently, in the partial correlation analysis, this hypothesis is represented by the array of locality latitudes.

Partial correlations are computed with the mean SVL as the dependent variable

and the hypothesized patterns as the independent variables.

*Matrix comparisons: Mantel tests.*— The observed pattern of geographic variation is represented by a standard taxonomic distance matrix (Thorpe, 1980) based on locality mean SVL. The following causal hypotheses are represented by dissimilarity (taxonomic distance) matrices.

Hypothesis 2b: This hypothesis is represented by a matrix of dissimilarities in locality altitudes (i.e., the matrix equivalent of the array in hypothesis 2a above).

Hypothesis 3b: This hypothesis is based on the topographically determined climate as in hypothesis 3a above. The dissimilarity matrix among localities is computed from the 0,1 coding attributed to each locality in hypothesis 3a and is referred to as the climatic ecotone hypothesis.

Hypothesis 5: In this study, each locality sample is independent, with no possibility of an individual in one locality being attributable to another locality. Nevertheless, one may still wish to take into account the effects of geographic proximity because of the potential for gene flow. While the unidimensional hypotheses cannot readily represent the two dimensional influence of geographic proximity, it can be represented by a matrix based on geographic distances between each pair of localities (proximity hypothesis).

A measure of association between two matrices is given by a statistic, $G$, where $G = (Z - Exp)/SE$. This is based on Mantel's (1967) original $Z$ statistic which is an unnormalized correlation between the observed and hypothesized distances ($Z = \Sigma X_{ij}Y_{ij}$, where $X_{ij}$ and $Y_{ij}$ are the observed and hypothesized distances (dissimilarities) between localities i and j). The value of $G$ is then compared to those obtained when the first matrix (based on SVL in this case) is randomized. One thousand such randomizations are carried out, and the null hypothesis of no association is rejected if 950 or more of the "randomized" values are lower than the original $G$ value. This procedure is used to test hypotheses 2b, 3b, and 5 by comparing the matrices de-

rived from these hypotheses with the matrix based on means of SVL. This was carried out on a modified version of a FORTRAN program supplied by B. F. J. Manly. This procedure does not take into account the inter-correlation in the hypothesized patterns. To overcome this problem, Manly (1986) developed a FORTRAN program (a modified, IBM compatible microcomputer, version of which is used in this study) for a Mantel test that allows two independent matrices, B and C (hypothesized causes), to be simultaneously compared to the dependent matrix, A (observed pattern of geographic variation in SVL in this case). Five statistics are computed—$g_{AB}$ and $g_{AC}$, the simple regression coefficient between the dependent matrix (A) and independent matrices (B and C) respectively; $g_{AB.C}$, the partial regression between matrices A and B once the effects of matrix C have been regressed out; $g_{AC.B}$, the partial regression between matrices A and C once the effects of matrix B have been regressed out; and $R^2$, the multiple correlation between matrix A and matrices B and C (for a full exposition, see Manly, 1986). Once again, for all five statistics, one can deduce the probability of their differing from zero by comparing the values obtained with the distributions found by 1000 randomizations.

Using this test (1) the relative (dis)-similarity in SVL among localities (matrix A) was simultaneously compared to similarity in altitude (hypothesis 2b) and similarity in geographic proximity (hypothesis 5); (2) the similarity in SVL was simultaneously compared to similarity in climatic ecotones (hypothesis 3b) and proximity (hypothesis 5); and (3) the similarity in SVL was simultaneously compared to altitude (hypothesis 2b) and climatic ecotones (hypothesis 3b).

## RESULTS AND CONCLUSIONS

### Pattern of Geographic Variation

There is significant among-locality (geographic) variation in SVL ($F = 10.2$, $P < 0.001$). When the pattern of geographic variation in the mean SVL of sexually ma-

ture males (Table 1) is portrayed by contouring (Fig. 2), it is apparent that compared to characteristics such as the generalized color pattern (Thorpe and Brown, 1989a,b) and generalized scalation (Thorpe and Baez, 1987), these contours show a greater element of localized mosaic variation. Nevertheless, unlike previous attempts, the type and size of samples enables the contours to reveal some broader trends. That is, the contour values tend to be lower in the high-altitude region of Teide (small animals) and high on the north coast (large animals).

*Unidimensional comparisons: correlations.*—The correlations with the hypothesized patterns confirm this visual interpretation. The longitudinal pattern predicted by secondary contact between precursor populations of Anaga and Teno (hypotheses 1) is not significantly correlated ($r = -0.12$, $P > 0.05$) to the observed pattern nor is there a significant correlation with latitude as predicted by hypothesis 4 ($r = 0.11$, $P > 0.05$). On the other hand, the observed pattern is significantly correlated to altitude ($r = -0.38$, $P < 0.01$) as predicted by hypothesis 2 and to the ecotones ($r = -0.34$, $p < 0.01$) predicted by hypothesis 3.

The two predicted patterns with significant correlations to the observed pattern are not independent: i.e., the northern category has only low altitude ($<1500$ m) localities while the southern category includes all the high altitude ($>1500$ m) localities ($r = 0.29$, $P < 0.05$). The lack of independence among hypothesized patterns can lead to an inability to distinguish among several causes as in Douglas and Endler (1982) if the hypotheses are not considered "simultaneously". Consequently, a partial correlation analysis was run with the altitude (hypothesis 2) and latitudinal categories (hypothesis 3) as independent variables and the SVL as the dependent variable in order to allow for this. Both predicted patterns (hypotheses 2 and 3) are significantly partially correlated to the observed pattern ($r = 0.31$, $P < 0.01$ for altitude; $r = -0.26$, $P < 0.05$ for latitudinal categories; multiple corre-

FIG. 2.—Geographic variation in snout–vent length. Contours based on the mean SVL of sexually mature males at the 67 localities illustrated in Fig. 1. Note that even though there is a mosaic element to this pattern, there is a trend for the smallest lizards to be found at highest altitudes and for the largest lizards to be found at low altitudes on the north-facing slopes.

TABLE 1.—Mean values for snout–vent length (in cm). The difference between a pair of locality (Loc.) means is significant at $P < 0.05$ if they differ by more than 0.53 cm, at $P < 0.01$ if they differ by more than 0.69 cm, and at $P < 0.001$ if they differ by more than 0.89 cm, using least significant differences (Snedecor and Cochran, 1967).

| Loc. | $\bar{x}$ | Loc. | $\bar{x}$ | Loc. | $\bar{x}$ | Loc. | $\bar{x}$ |
|------|-----------|------|-----------|------|-----------|------|-----------|
| 1  | 12.03 | 2  | 11.30 | 3  | 10.75 | 4  | 11.25 |
| 5  | 11.43 | 6  | 10.49 | 7  | 10.93 | 8  | 11.28 |
| 9  | 11.31 | 10 | 11.71 | 11 | 11.48 | 12 | 11.70 |
| 13 | 11.39 | 14 | 12.08 | 15 | 12.83 | 16 | 11.65 |
| 17 | 11.98 | 18 | 11.18 | 19 | 12.23 | 20 | 11.97 |
| 21 | 11.54 | 22 | 11.46 | 23 | 12.10 | 24 | 11.95 |
| 25 | 11.02 | 26 | 10.50 | 27 | 10.39 | 28 | 10.99 |
| 29 | 12.01 | 30 | 10.19 | 31 | 10.69 | 32 | 11.16 |
| 33 | 12.11 | 34 | 12.40 | 35 | 12.37 | 36 | 10.87 |
| 37 | 11.38 | 38 | 10.26 | 39 | 11.81 | 40 | 11.30 |
| 41 | 10.37 | 42 | 10.85 | 43 | 11.41 | 44 | 11.59 |
| 45 | 11.58 | 46 | 11.22 | 47 | 11.57 | 48 | 11.87 |
| 49 | 11.70 | 50 | 11.22 | 51 | 11.69 | 52 | 11.73 |
| 53 | 12.13 | 54 | 11.18 | 55 | 11.09 | 56 | 11.61 |
| 57 | 11.30 | 58 | 11.06 | 59 | 10.92 | 60 | 11.40 |
| 61 | 11.56 | 62 | 10.79 | 63 | 11.71 | 64 | 11.66 |
| 65 | 12.10 | 66 | 10.50 | 67 | 10.60 |    |       |

lation = 0.45). Consequently, there are two elements to the non-mosaic pattern: i.e., clinal altitudinal variation and categorical latitudinal variation, both of which can be detected in Fig. 2.

*Matrix comparisons: Mantel tests.*— The Mantel tests comparing a pair of matrices showed that the relative similarity among localities based on mean SVL is significantly associated with both altitude ($G = 1.75$, $P < 0.05$) and climatic ecotones (hypothesis 3b, $G = 2.08$, $P < 0.05$), but not with geographic proximity ($G = -0.56$, $P > 0.05$). When the effects of proximity are regressed out using the simultaneous Mantel test, then SVL is still significantly associated with both altitude ($g = 0.078$, $P < 0.05$) and climatic ecotones ($g = 0.078$, $P < 0.05$). Proximity is not associated with SVL even when the effects of altitude ($g = -0.02$, $P > 0.05$) and climatic ecotones ($g = -0.03$, $P > 0.05$) are regressed out. Moreover, when the simultaneous Mantel test is used to investigate the relationship among SVL, altitude and climatic ecotones, both of the independent factors (altitude and climatic ecotones) have a significant partial regression with SVL; when the effect of climatic ecotones is regressed out, then the effect of altitude on SVL is significant ($g = 0.083$, $P < 0.05$), and when the effect of altitude is regressed out then the effect of climatic ecotones is significant ($g = 0.079$, $P < 0.05$). The multiple regression between SVL and altitude plus climatic ecotones is significant ($R^2 = 0.02$, $P < 0.05$).

These simultaneous tests are useful in showing that, irrespective of any correlation between altitude and climatic ecotones, they are both related to the pattern of variation in SVL, and that geographic proximity has no demonstrable effect.

## DISCUSSION

Both the partial correlations and the Mantel tests agree in indicating that altitude and climatic ecotones, but not geographic proximity, are related to geographic variation in body length. Because the hypotheses are inter-correlated, simultaneous tests are necessary, and the si-

multaneous Mantel test has the advantage over partial correlations in that it can be used to take into account geographic proximity.

The extent of localized mosaic variation in SVL (Fig. 2) and the rather low, albeit significant, correlations (simple product-moment, partial, and multiple) between the character (SVL) and the hypothesized causes contrast with the situation found in the color pattern characters in which there are generally higher correlations and less localized variation (Thorpe and Brown, 1989$a$,$b$). That is, at least partially, due to the basic difficulty in defining a parameter such as modal, or average, body length in continually growing organisms of indeterminate age. Chance can result in smaller (younger) specimens being sampled in one area while larger (older) specimens are sampled in another area. Chance differences in nutritional status at the locality (environmental induction) are also likely to produce "noise" in the data. Moreover, non-terminal growth can systematically produce high within-locality variance for growth-determined characters and therefore less reliable locality means. However, in this case, a narrow band of growth was sampled, so this is not a major problem. The pooled within-locality standard deviation is 0.49 cm and the 95% standard error is 0.53 cm (Table 1), both of which are approximately a fifth of the range between highest and lowest locality mean scores. This is commensurate with the equivalent values (pooled standard deviation divided by range between highest and lowest locality means) for individual characters of the color pattern (Thorpe and Brown, 1989$b$). Consequently, this indicates the relative reliability of the sampling procedure employed in this study of body length (i.e., use of mature males only).

Both the altitudinal and latitudinal elements are congruent with the variation in several other specific morphological characters of this lizard. The altitudinal element is apparent in the number of dorsal scales and femoral pores, and the latitudinal element is apparent in the number of dorsal scales, number of gular scales

(Thorpe and Baez, 1987), and several characteristics of the breeding colors of males: i.e., the number and size of dorsal yellow cross bars, the number, size and spacing of blue lateral blotches, and the size of the blue chin marking (Thorpe and Brown, 1989*b*). The geographic variation in these characters of the color pattern (except the number of blue lateral blotches) resembles that of the SVL in that the categorical component of the latitudinal variation is stronger than that of the clinal component (Thorpe and Brown, 1989*b*). The extent of congruence among individual characters is, nevertheless, limited, some characters showing altitudinal variation, some latitudinal variation, and some both. This limited congruence typifies "ecogenetic" variation where each genetically independent character is free to respond to different selection pressures. On the other hand, in "phylogenetic" variation, all character systems are subjected to a common process such as a vicariance event, and this should be reflected in greater congruence (Thorpe, 1987, 1990; Thorpe et al., 1991).

The altitudinal and latitudinal elements of the variation are clearly related to variation in the climate and vegetation. The "north-facing slopes" have lush vegetation, and these vegetarian lizards may have a larger body size in this region as an adaptational response. Similarly, the higher altitudes are more seasonal and have a shorter period in the year available for growth, and the lizards may be smaller at higher altitudes due to natural selection for these conditions.

It is also possible that variation in sexual selection may be contributing to the geographic (particularly latitudinal) variation in size. The aggressive territorial males (Borja, 1985) are larger than the females, presumable due to sexual selection, as is the case in some other lizards (Trivers, 1976). While there is no direct evidence to suggest that sexual selection favors larger specimens on the north-facing slopes, it should be noted that the balance between sexual selection and natural selection is clearly implicated as the cause of the char-

acteristic color pattern of males from this part of the island. In adult males in breeding color, there may be a balance between cryptic dorsal markings (to avoid aerial predation) and bright blue lateral markings for conspecific communication. In the north, where lower temperatures may hamper rapid escape and the lush vegetation may offer more opportunity for crypsis, the balance appears to favor crypsis, as the dorsal markings are well developed and the blue lateral markings are lost from the trunk (Thorpe and Brown, 1989*a*,*b*).

One cannot rule out direct environmental induction as the cause: i.e., the areas with less food and shorter growing season have smaller animals directly because they have poorer nutrition. However, it should be noted that the same elements of the pattern are present in some scalation characters which are fixed prior to hatching and are not subject to environmental induction due to post-hatching nutrition. Similarly, the congruent geographic variation in the color pattern of mature males is not readily explained by environmental induction due to nutrition. Consequently, while the congruent elements in the geographic variation of SVL may be due to either natural selection for current environmental conditions, or direct environmental induction, we favor the former explanation. There is no evidence that the pattern of geographic variation is due to historical "phylogenetic" factors.

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# ON THE SPECIES OF THE COLUBRID SNAKE GENUS *NINIA* IN COSTA RICA AND WESTERN PANAMA

JAY M. SAVAGE AND PETE N. LAHANAS

*Department of Biology, University of Miami, P.O. Box 249118, Coral Gables, FL 33124, USA*

ABSTRACT: Variation in scutellation and coloration in snakes of the genus *Ninia* from Costa Rica and western Panama is analyzed to determine the systematic status of named forms. Pacific lowland, upland, and Atlantic lowland *Ninia maculata* show consistent differences from one another in dorsal coloration. The Atlantic lowland population, variously regarded as a distinct species (*Ninia tessellata*) or as a subspecies of *N. maculata* by previous workers, has substantially lower total segmental counts ($\bar{x}$ = 181.5) than other populations ($\bar{x}$ = 195.8). However, examples from geographically intermediate areas show intermediate conditions, and only a single species, *N. maculata* is recognized. The nominal montane species of 17-scale-row *Ninia* (*Ninia cerroensis*, *Ninia oxynota* and *Ninia psephota*) are part of a population system showing clinal variation in segmental counts and differ only in details of coloration. Only a single species, *N. psephota*, appears to be involved, ranging from the Cordillera de Guanacaste of Costa Rica south to western Panama. Data for the two other valid species of the genus found in the region, *Ninia atrata* from upland areas of central Costa Rica and Panama and *Ninia sebae* of the lowlands and adjacent slopes of Costa Rica, are summarized in a key. *Ninia sebae* does not occur in western Panama.

*Key words:* Serpentes; *Ninia*; Systematics; Distribution; Costa Rica; Panama

THE small, semifossorial snakes of the genus *Ninia* (family Colubridae) are an important and locally abundant component of the leaf-litter herpetofauna of the Neotropics. In the most recent summary of the group, Peters and Orejas-Miranda (1970), following Taylor (1951, 1954) as modified by Burger and Werler (1954), recognized eight species of *Ninia*, six of which were listed as occurring in Costa Rica. Savage (1973, 1976, 1980), Savage and Villa (1986), and Villa et al. (1988), however, followed Scott (1969) in regarding three of the nominal montane taxa listed by Peters and Orejas-Miranda (1970) for Costa Rica as representatives of a single species. No evidence for Scott's conclusion was presented by any of the aforementioned authors. Consequently, as the senior

author of the present paper proceeded with work on his comprehensive handbook of the herpetofauna of Costa Rica, it seemed a necessary prerequisite to review the status of *Ninia* in that republic and adjacent areas. Fortunately such a review may take advantage of the considerable accumulation of new material of *Ninia* collected during the last 30 yr and obviously not available for analysis by earlier workers.

The present paper focuses on two major systematic problems: (1) the status of the several populations referred to the species *Ninia maculata* and *Ninia tessellata* by Taylor (1951, 1954) and (2) the status of the montane, 17 scale-rowed *Ninia* placed by Scott (1969) in a single species, *Ninia psephota*, but regarded as comprising three distinct taxa by Taylor (1954) and Peters