

Within-island geographic variation of the dangerous Taiwanese snake, *Trimeresurus stejnegeri*, in relation to ecology

SERGIO CASTELLANO¹, ANITA MALHOTRA² AND ROGER S. THORPE

School of Biological Sciences, University College of North Wales, Bangor, Gwynedd LL57 2UW, UK

Received 4 October 1993, accepted for publication 16 December 1993

Multivariate analysis shows that geographic variation occurs in the scalation and body proportions of the dangerously venomous snake *Trimeresurus stejnegeri*, within the island of Taiwan. Canonical correlation analysis reveals a high correlation between constellations of morphological characters and ecological factors. Numerical hypothesis testing, using partial Mantel tests, provides evidence of a causal relationship with ecology. Head shape was found to be primarily associated with mean annual temperature and altitude, and head scalation with the annual range of temperature. Body scalation was found to be influenced by altitude, mean annual temperature and mean annual rainfall. Tail length is primarily associated with the range of temperature and rainfall and secondarily with the mean annual temperature and altitude. Geographic proximity was found to be less important in the explanation of the observed geographic pattern than some ecological factors, supporting the hypothesis of an ecogenetic origin of morphological variation.

ADDITIONAL KEY WORDS:—Geographic variation – morphology – ecogenesis – partial Mantel test – canonical correlation – Taiwan – venomous snake.

CONTENTS

Introduction	365
The model: <i>Trimeresurus stejnegeri</i> in Taiwan	366
Material and methods	367
Describing geographic variation	367
Testing causal hypotheses	367
Results	368
Pattern of geographic variation	368
Causes of geographic variation	369
Discussion	372
Acknowledgements	373
References	373
Appendix	374

INTRODUCTION

In recent years studies of microgeographic variation within islands have been productive both in the analysis of the pattern of variation and in analysing the

¹Present address: Dipartimento di Biologia Animale, Università di Torino, Via Accademia Albertina 17, 10123 Torino, Italy.

²Author to whom correspondence should be addressed.

possible causes. Many of these studies have employed island lizards as a model (Brown & Thorpe, 1991a, b, Brown, Thorpe & Baez, 1991; Malhotra & Thorpe, 1991; Thorpe, 1991; Thorpe & Baez, 1987, 1993; Thorpe & Brown, 1989a, b, 1991), and have shown the presence of within-island geographic variation in morphology. Partial Mantel tests (Legendre & Fortin, 1989; Mantly, 1991; Smouse, Long & Sokal, 1986; Thorpe & Baez, 1993) have provided support for a natural selection hypothesis as the cause of observed geographic variation. Instances of strong correlations between morphological characters and environmental conditions have been found in a variety of organisms, e.g. insects (Sokal, Bird & Riska, 1980), snails (Dillon, 1984), fish (Douglas & Endler, 1982), mammals (Schnell, Douglas & Hough, 1986), including island lizards (Brown *et al.*, 1991; Malhotra & Thorpe, 1991; Thorpe, 1991; Thorpe & Baez, 1993). Few similar studies have been done on snakes, although the cause of morphological and venom divergence in venomous snakes is of applied importance (Wüster & Thorpe, 1991). Christman (1980) looked at geographic variation in Florida snakes (but his methods did not include rigorous hypothesis testing), Schwaner (1985) showed that differences in body size in island populations of black tiger snakes (*Notechis ater*) is caused by prey size and availability, and Thorpe *et al.* (in press) showed that the pattern of geographic variation in southern Phillipine cobras (*Naja* sp.) is correlated with geological events rather than climate. Since most snakes occur in low numbers, only in exceptional cases do museums holdings contain a good number of any single species with detailed locality records from several localities on the scale required. The bamboo viper (*Trimeresurus stejnegeri*, Serpentes: Crotalidae) in Taiwan is one of these exceptions, and provides the opportunity to test the hypothesis that ecogenetic adaptation can also be a significant factor in the microevolution of snakes.

The model: Trimeresurus stejnegeri in Taiwan

Trimeresurus stejnegeri has an extensive geographical distribution, ranging from Chekiang, China south to Northern Thailand and Burma. It occurs widely in the subtropical island of Taiwan. This island, which is 395 km long and 144 km wide, is extremely mountainous (the highest mountain reaching an altitude of 3950 metres). The mountains rise almost sheer from the east coast, but there is a broad plain on the western side. Because of the mountains, there is considerable climatic variation within the island with the north-east being considerably wetter and colder than the south-west in the winter, and the mountains remaining cool and extremely wet in the summer.

This range of variation in climatic conditions raises the possibility of local adaptation of morphology of *Trimeresurus stejnegeri*. The presence of colour pattern variation within Taiwan was noted by Maki (1931) who described three subspecies. This was later shown by Mao (1962) to be partly (but not entirely attributable) to sexual dimorphism, and later authorities have considered the Taiwanese populations to belong to the same subspecies (*T. s. stejnegeri*) as populations on the adjacent mainland (Regensass & Kramer, 1981). However, this study represents the first quantitative analysis of geographic variation in morphology.

MATERIAL AND METHODS

Describing geographic variation

Thirty-one precisely defined scalation characters (see Appendix for definitions of characters) and eleven body proportion characters (adjusted for size independence by regressing against snout-vent length (SVL) using the pooled within-group slope, as in Thorpe [1976]) were recorded from 71 museum specimens (males only) from 21 localities (Fig. 1). The first objective was to portray the generalized pattern of geographic variation, using canonical variate analysis (CVA). Because some localities were represented by only one specimen, they were grouped with one or more adjacent localities which were similar in altitude; when this was not possible the specimens were excluded. Principal component analysis (PCA) was run on each group to verify internal homogeneity. A total of 61 specimens from seven grouped localities were used for the canonical variate analysis, which included all characters recorded.

Three dimensional isometric plots of the first two canonical variates were drawn using the inverse distance squared weighted averaging technique and smoothed using a cubic spline (Anon, 1990). The eigenvectors obtained from CVA were used to calculate the component scores for those localities that had previously been omitted from the analysis to obtain 15 rather than seven group means to be contoured (as shown in Fig. 2).

Testing causal hypotheses

The next step was to investigate the possible causes of geographic variation. Six geographic and climatic variables were recorded for each locality (1) latitude; (2) longitude; (3) altitude, in metres above sea level; (4) annual rainfall, in millimetres; (5) mean annual temperature, in °C; (6) annual range of temperature, in °C. Latitude, longitude and altitude were obtained from the museum records, while climatic data were obtained from maps (scale 1:10 000 000) in the Climatic Atlas of Asia (Anon, 1981). Two different techniques (canonical correlation analysis and partial Mantel tests) were used.

Canonical correlation analysis was performed on all specimens and characters to investigate the relationships between dependent morphological variables and the independent climatic and altitudinal variables. This technique provides linear combinations of the two sets of variables between which the correlation is as large as possible. Through the interpretation of the canonical variable loadings of the canonical components it is possible to obtain a general overview of the relationships between constellations of the two sets of characters. However, a limitation of canonical correlation analysis is that it does not permit the effects of geographic proximity to be included. This is achieved by using the partial Mantel test of matrix association (using B.F.J. Manly's 'RT-MANT' program). This calculates the partial regression coefficients between a dependent and up to eight independent distance matrices, permitting many causal hypotheses to be tested simultaneously, and giving probability estimates (from 10 000 randomizations) for absolute partial regression coefficients. The partial Mantel test is particularly suitable where the hypotheses are intercorrelated, as is usually the case in such studies.

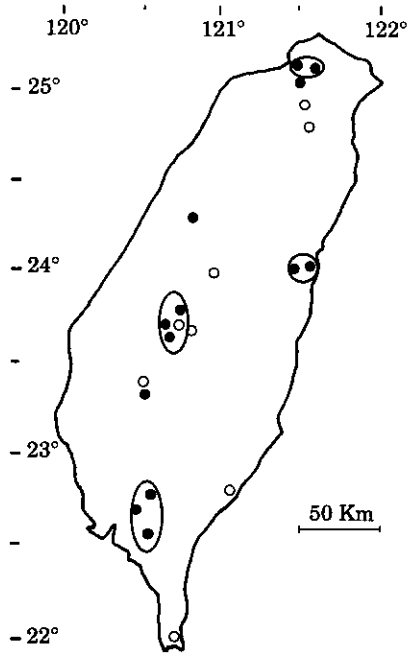


Figure 1. Map of Taiwan showing localities from which specimens were examined. Localities that were used to calculate the canonical variables (see text) are indicated by solid circles, and rings around localities indicates that the individual localities were grouped together because they were insufficient numbers of specimens in any single one.

The dependent distance matrices were obtained by calculating the taxonomic distances between single specimens for all, or a subset of, standardized characters. The independent matrix of geographic proximity was obtained by calculating the taxonomic distance on the latitude and longitude variables previously transformed from sexadecimal to decimal values. The other independent matrices were obtained with a similar procedure using untransformed values. All the distance matrices were finally standardized to obtain standardized partial regression coefficients.

RESULTS

Pattern of geographic variation

The first two canonical variates tend to distinguish between the seven grouped localities (Fig. 2). The east-coast locality is particularly divergent, and the two southern-most are also distinguished from those in the north and central parts of the island. This indicates the presence of interpopulation variability in morphology. The surface contour maps of the first two canonical variates (Fig. 3) provided a more direct representation of the pattern of geographic variation. The first canonical variate (Fig. 3A) shows no clear trend. It might have been deduced from Fig. 2 that an east-west difference was present, as only one east coast locality was represented. However, when the single specimen from the southern part of the east coast is fitted onto the canonical variate, it is seen to be more similar to the other southern localities. It would be valuable to have

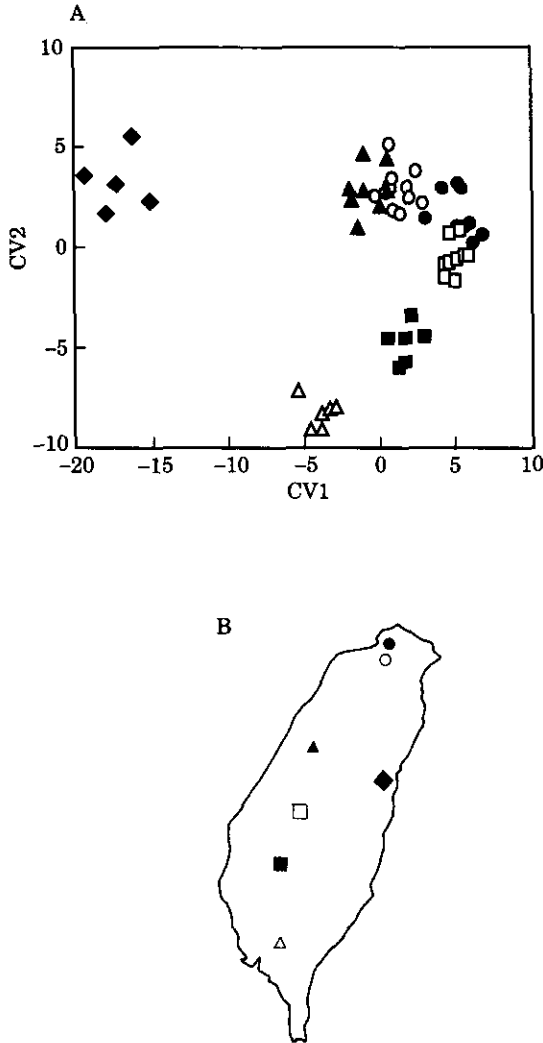


Figure 2. A, Canonical variate analysis: ordination of populations along the first two canonical variates calculated using all body dimension and scalation characters. B, Symbols on the map indicate the geographical position of the populations represented in the CVA plot. Note that the eastern population is particularly distinct from the remaining populations.

more specimens from the east coast to further elucidate this. The second canonical variate (Fig. 3B) unequivocally shows a north-south cline.

Causes of geographic variation

Canonical correlation analysis shows a significant correlation between morphological characters and ecological variables. Table 1 gives the results from an optimized model, using only those morphological characters that had significant squared multiple correlation coefficients with the canonical variables. The two first canonical variates explain 29.7% and 6.8% of the total variance of the ecological and the morphological characters respectively. The proportion of

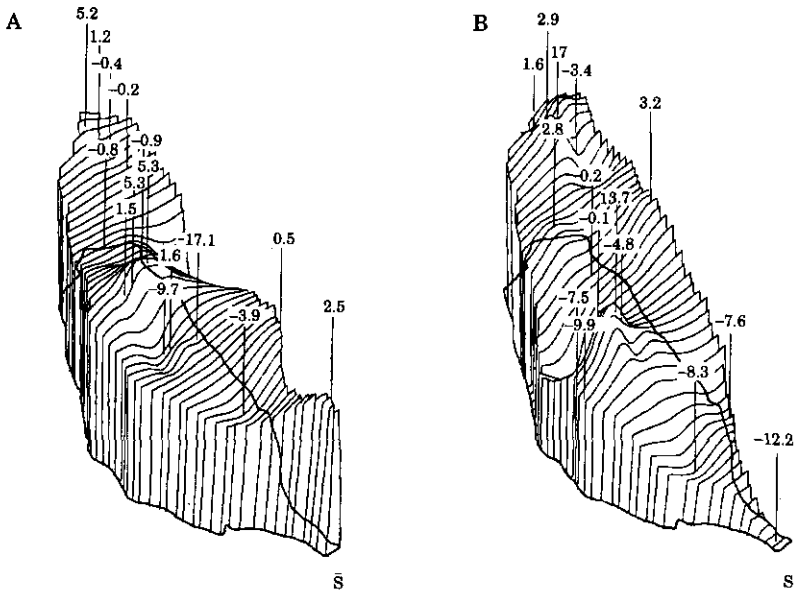


Figure 3. 3-D surface contour plots of the component scores on A, the first canonical variate and B, the second canonical variate. Scores for all the populations shown in Fig. 1 have been included. The second canonical variate shows a particularly clear north-south cline.

remaining variance explained by the second canonical variates is 21.5% and 4.4% for the ecological and morphological characters respectively. The canonical correlation between the ecological and morphological matrices is highly significant (Bartlett's test, $P < 0.0001$). The canonical variable loadings (correlations of canonical variables with original variables) for the ecological variables show that the first canonical variate is predominately and positively influenced by temperature (both mean and range). The interpretation of the corresponding canonical variate for the morphological variables is less straightforward. The first canonical variate is negatively correlated with the width and length of the head as well as with the number of scales between the supraocular scales. It is positively correlated with the length and width of supraocular scales and the shape of the rostral scale. While the length of the tail also has a high loading, the first canonical variable can be interpreted as a head-shape factor.

The second canonical variate is largely positively influenced by rainfall. It is negatively correlated with the number of the ventral scales of the body and the tail, and with the position of scale reductions on the body and the tail. It also has a high negative loading for tail length. The second canonical variate is essentially an expression of the number and pattern of distribution of body scales.

To summarize, canonical correlation analysis reveals some relationships between temperature, head shape and head scalation (specimens from localities with high values of temperature and range of temperature have narrower and shorter heads with larger supraocular scales) and between rainfall and body scalation (a general increase in the number of body scales with decreasing rainfall).

In order to test more rigorously the effects of more than one hypothesis, including the effect of geographic proximity, a partial Mantel test, based on a multiple regression model, was run. A taxonomic distance matrix representing

TABLE 1. Canonical correlations. Canonical variable loadings are the correlation of the original variables of each set with the canonical variables of the other set.

Characters	Loadings	
	CV1	CV2
(A) Ecological characters		
Altitude	-0.390	-0.200
Rainfall	0.220	0.816
Temperature	0.759	-0.022
Range of temperature	0.643	-0.393
(B) Morphological characters		
No. ventral scales (VSC)	-0.259	-0.273
Number of subcaudal scales (SCS)	-0.070	-0.435
Ventral position, 2nd scale reduction (VS2)	-0.053	-0.334
Ventral position, 3rd scale reduction (VS3)	-0.191	-0.298
Ventral position, 4th scale reduction (VS4)	-0.044	-0.247
Dorsoventral position, 4th scale reduction (DS4)	-0.233	0.221
Dorsoventral position, 4th scale reduction (DS6)	0.247	0.309
Ventral position, 7th scale reduction (VS7)	0.165	-0.110
Dorsoventral position, 7th scale reduction (DS7)	0.196	-0.357
Ventral position 9th scale reduction (VS9)	0.116	-0.230
Number of supralabials (SUPLAB)	-0.292	0.214
Number of sublabials (SUBLAB)	0.062	0.256
No. of scales bordering supraocular (BORSUP)	-0.121	-0.172
No. of scales between supraoculars (BTWSUP)	-0.475	0.090
No. of scales bordering subocular (BORSOC)	-0.208	0.075
Width of supraoculars (WSUP)	0.301	-0.058
Length of supraoculars (LSUP)	0.379	-0.300
Width of internasals (WINTNAS)	-0.085	0.044
Ratio of anterior to posterior rostral (ROST)	0.371	0.311
Tail length (TAIL)	0.382	-0.468
Width of head (WHEAD)	-0.487	-0.059
Length of head (LHEAD)	-0.308	0.102
Distance between eye and nostril (EYENOS)	-0.292	-0.096
Distance between the pit and eye (PITEYE)	-0.202	-0.038
Distance between nostril and pit (NOSPIT)	0.168	-0.135

generalized morphology (both scalation and body proportions) was tested against geographic proximity and the four ecological matrices (altitude, rainfall, temperature and range of temperature). The results (Table 2) show that rainfall, annual mean temperature and range of temperature are all significantly correlated with generalized morphology, and are more important than the geographic proximity in the explanation of the morphological differences between specimens.

Subsets of the morphological characters were then used to construct

TABLE 2. Results of a partial Mantel test (in the form of absolute, standardized partial regression coefficients) on generalized morphology (body proportion and scalation characters). The hypothesized matrices are geographic proximity (PRO), altitude (ALT), annual rainfall (RAIN), mean annual temperature (TEMP), mean range of temperature (RANGE); **P* < 0.05.

Character	Hypothesis				
	Pro	Alt	Rain	Temp	Range
Generalized morphology	0.0466	0.0242	0.0625*	0.0654*	0.0794*

TABLE 3. Results of a partial Mantel test (absolute, standardized partial regression coefficients) on groups of morphological characters. The hypothesized matrices are geographic proximity (PRO), altitude (ALT), annual rainfall (RAIN), mean annual temperature (TEMP), mean range of temperature (RANGE). * $P < 0.05$; ** $P < 0.01$.

Character	Hypothesis				
	Pro	Alt	Rain	Temp	Range
Head shape	0.078*	0.098**	0.061*	0.250**	0.023
Head scalation	0.097**	0.008	0.058*	0.053	0.212**
Body scalation	0.040	0.102**	0.064**	0.083**	0.015
Tail length	0.046	0.059*	0.067**	0.061*	0.122**

dependent distance matrices. Four dependent distance matrices were constructed and tested against the five independent matrices: head scalation (consisting of characters SUPLAB, SUBLAB, POSTOC, BORSUP, BTWSUP, DIVSUP, NASPIT, INTNAS, BORSOC and GENIAL); head shape (WSUP, LSUP, ROST, WHEAD, LHEAD, DEYE, EYENOS, PITEYE and NOSPIT); body scalation (VSC, SCS, VS2, VS3, DS4, DS6, VS7, DS7, VS9); tail length (TAIL only). In the case of head shape and head scalation (Table 3) the proximity hypothesis cannot be rejected. However in both cases it is not the variable which best explains the variation in the multiple regression model. Head shape is primarily associated with temperature and altitude, and head scalation with range of temperature. Body scalation is influenced by altitude, temperature and rainfall. Tail length is primarily associated with the range of temperature and rainfall and secondly with the temperature and altitude.

DISCUSSION

This study demonstrates the presence of microgeographic variation in the morphology of *T. stejnegeri* within the island of Taiwan. Both canonical correlation analysis and the Mantel test have supported the hypothesis of an ecological cause. If the existence of a causal relation between morphological characters and environmental factors has been accepted, two different explanations could be proposed. Firstly, the observed morphological differences have a genetic basis and are the result of natural selection and secondly, they are the result of environmental induction. However, studies of environmental effects on the development of scutellation (Osgood, 1978; Fox, Gordon & Fox, 1961) and body proportions (Arnold & Peterson, 1989) in snakes have shown that induction is likely to play only a secondary role in between-populations morphological differences. The alternative hypothesis of adaptation to local environmental conditions cannot be rejected. The results from Mantel tests are consistent with those from canonical correlation analysis. High temperatures at low altitude localities seems to be associated with a smaller head, while the high rainfall areas are associated with a lower number of body scales. Forsman (1991) has shown that head size in adders (*Vipera berus*) is influenced by variation in the size of available prey. The increase in number of body scales with decreasing rainfall has been observed in different lizard species ((Malhotra & Thorpe, 1991; Soule & Kerfoot, 1972; Thorpe & Baez, 1987) and it has been suggested that this is related to thermoregulation and control of water loss. While limited evidence

from aberrant scaleless snakes suggests that scales do not play an important role in limiting cutaneous water loss (Bennett & Licht, 1975; Licht & Bennett, 1972), this is likely to vary according to species and habitats. In any case, temperature, rainfall and especially altitude could be indirect measures of differences in biotic characteristics (such as vegetation and availability of prey types), resulting in variation in selective pressures.

Although the data available for this study is relatively crude, it still gives significant results. This suggests that further more directed, field-based, studies which include a larger number of specimens with a better distribution of localities situated in a wide range of ecological conditions, together with detailed ecological information collected directly from the field, would be rewarding. Lastly the occurrence of geographic variation within a relatively small and well-defined geographic area such as Taiwan raises the possibility of significant variation in venom composition and suggests that it will serve as an ideal model for understanding the evolution of venom variation in dangerously venomous snakes.

ACKNOWLEDGEMENTS

We wish to thank the curators and staff of the following museums for the loan of specimens in their care: the Field Museum of Natural History (Chicago), the Smithsonian Institution (Washington), the California Academy of Science (San Francisco), the Museum of Zoology (University of Michigan, Ann Arbor) and the National Museum of Natural Science (Taiwan). We would particularly like to thank Dr Wen-hao Chou for his efforts on our behalf. Thanks are also due to B.F.J. Manly for making his computer program for partial Mantel tests available to us. This study was funded by a Leverhulme Trust grant to RST.

REFERENCES

- Anon.** 1981. Climatic Atlas of Asia. Geneva: World Meteorological Organisation.
- Anon.** 1990. Surfer reference manual, Version 4. Golden, Colorado, USA: Golden Software Inc.
- Arnold SJ, Peterson CR.** 1989. A test for temperature effects on the ontogeny of shape in the garter snake *Thamnophis sirtalis*. *Physiological Zoology* **62**: 1316–1333.
- Bennett AF, Licht P.** 1975. Evaporative water loss in scaleless snakes. *Comparative Biochemistry and Physiology* **52A**: 213–215.
- Brown RP, Thorpe RS.** 1991a. Within-island microgeographic variation in body dimensions and scalation of the skink *Chalcides sexlineatus*, with testing of causal hypotheses. *Biological Journal of the Linnean Society* **44**: 47–64.
- Brown RP, Thorpe RS.** 1991b. Within-island geographic variation in the colour pattern of the skink *Chalcides sexlineatus*: pattern and cause. *Journal of Evolutionary Biology* **4**: 557–574.
- Brown RP, Thorpe RS, Baez M.** 1991. Parallel within-island microevolution of lizards on neighbouring islands. *Nature* **352**: 60–62.
- Christman SP.** 1980. Patterns of geographic variation in Florida snakes. *Bulletin of the Florida State Museum, Biological Sciences* **25**: 157–256.
- Dillon RT.** 1984. Geographical distance, environmental difference, and divergence between isolated populations. *Systematic Zoology* **33**: 69–82.
- Douglas ME, Endler JA.** 1982. Quantitative matrix comparisons in ecological and evolutionary investigations. *Journal of Theoretical Biology* **99**: 777–795.
- Forsman A.** 1991. Adaptive variation in head size in *Vipera berus*. L. populations. *Biological Journal of the Linnean Society* **43**: 281–296.
- Fox WW, Gordon C, Fox MH.** 1961. Morphological effects of low temperatures during the embryonic development of the garter snake, *Thamnophis elegans*. *Zoologica* **46**: 57–71.
- Legendre P, Fortin MJ.** 1989. Spatial pattern and ecological analysis. *Vegatatio* **80**: 107–138.

- Licht P, Bennett AF. 1972.** A scaleless snake: tests of the role of reptilian scales in water loss and heat transfer. *Copeia* 1972: 702–707.
- Maki M. 1931.** *A monograph of the snakes in Japan*. Japan: Dai-ichi Shobo.
- Malhotra A, Thorpe RS. 1991.** Microgeographic variation in *Anolis oculatus*, on the island of Dominica, West Indies. *Journal of Evolutionary Biology* 4: 321–335.
- Manly BFJ. 1991.** *Randomization and Monte Carlo methods in biology*. London: Chapman and Hall.
- Mao SH. 1962.** Sexual dimorphism of Taiwan bamboo vipers. *Bulletin of the Institute of Zoology, Academia Sinica* 1: 41–46.
- Osgood DW. 1978.** Effects of temperature on the development of meristic characters in *Natrix fasciata*. *Copeia* 1978: 33–47.
- Regenass U, Kramer E. 1981.** Zur Systematik der grünen Grubenottern der Gattung *Trimeresurus* (Serpentes, Crotalidae). *Revue Suisse Zoologie* 88: 163–205.
- Schnell GD, Douglas ME, Hough DJ. 1986.** Geographic patterns of variation in offshore spotted dolphins (*Stenella attenuata*) of the eastern tropical Pacific Ocean. *Marine Mammal Science* 2: 186–213.
- Schwaner TD. 1985.** Population structure of black tiger snakes, *Notechis ater niger*, on offshore islands of South Australia. In: Grigg G, Shine R, Ehmann H, eds. *Biology of Australian frogs and reptiles*. Chipping Norton, New South Wales, Australia: Surrey Beatty and Sons, 35–46.
- Smouse PE, Long JC, Sokal RR. 1986.** Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology* 35: 27–732.
- Sokal RR, Bird J, Riska B. 1980.** Geographic variation in *Pemphigus populicaulis* (Insecta: Aphididae) in Eastern North America. *Biological Journal of the Linnaean Society* 14: 163–200.
- Soule MF, Kerfoot WC. 1972.** On the climatic determination of scale size in a lizard. *Systematic Zoology* 21: 97–105.
- Thorpe RS. 1976.** Biometric analysis of geographic variation and racial affinities. *Biological Reviews* 51: 407–452.
- Thorpe RS. 1991.** Clines and cause: microgeographic variation in the Tenerife gecko (*Tarentola delalandii*). *Systematic Zoology* 40: 172–187.
- Thorpe RS, Baez M. 1987.** Geographic variation within an island: univariate and multivariate contouring of scalation, size and shape of the lizard *Gallotia galloti*. *Evolution* 41: 256–268.
- Thorpe RS, Baez M. 1993.** Geographic variation in scalation of the lizard *Gallotia stehlini* within the island of Gran Canaria. *Biological Journal of the Linnaean Society* 48: 75–87.
- Thorpe RS, Brown RP. 1989a.** Testing hypothesised causes of within-island variation in the colour of lizards. *Experientia* 45: 397–400.
- Thorpe RS, Brown RP. 1989b.** Microgeographic variation in the colour pattern of the lizard *Gallotia galloti* within the island of Tenerife. Distribution, pattern and hypothesis testing. *Biological Journal of the Linnaean Society* 38: 303–322.
- Thorpe RS, Brown RP. 1991.** Microgeographic clines in the size of mature male *Gallotia galloti* (Squamata: Lacertidae) on Tenerife: Causal hypotheses. *Herpetologica* 47: 28–37.
- Thorpe RS, Brown RP, Day ML, Malhotra A, McGregor D, Wüster W.** Testing ecological and phylogenetic hypotheses in microevolutionary studies: an overview In: Eggleton P, Vane-Wright R. *Phylogenetics and Ecology*. Academic Press (in press).
- Wüster W, Thorpe RS. 1991.** Asiatic cobras: systematics and snakebite. *Experientia* 47: 205–209.

APPENDIX: CHARACTERS USED IN THE STUDY

1. Number of ventral scales (VSC).
2. Number of pairs of subcaudal scales (SCS).
3. Ventral scale position of the reduction from 23 to 21 body scales (VS1).
4. Dorsovenral position of the reduction from 23 to 21 (DS1).
5. Ventral scale position of the reduction from 21 to 19 (VS2).
6. Dorsovenral position of the reduction from 21 to 19 (DS2).
7. Ventral scale position of the reduction from 19 to 17 (VS3).
8. Dorsovenral position of the reduction from 19 to 17 (DS3).
9. Ventral position of the reduction from 17 to 15 (VS4).
10. Dorsovenral position of the reduction from 17 to 15 (DS4).
11. Ventral scale position of the reduction from 15 to 13 (VS5).
12. Dorsovenral position of the reduction from 15 to 13 (DS5).
13. Subcaudal scale position of the reduction from 12 to 10 (VS6).
14. Dorsovenral position of the reduction from 12 to 10 (DS6).
15. Subcaudal scale position of the reduction from 10 to 8 (VS7).
16. Dorsovenral position of the reduction from 10 to 8 (DS7).
17. Subcaudal scale position of the reduction from 8 to 6 (VS8).
18. Dorsovenral position of the reduction from 8 to 6 (DS8).
19. Subcaudal scale position of the reduction from 6 to 4 (VS9).

20. Dorsoventral position of the reduction from 6 to 4 (DS9).
21. Number of supralabials (average of left and right hand sides) (SUPLAB).
22. Number of sublabials (average of left and right hand sides) (SUBLAB).
23. Number of postocular scales (POSTOC).
24. Number of scales bordering the supraocular scales (average of left and right hand sides (BORSUP).
25. Number of scales between the supraoculars at the widest point (BTWSUP).
26. Width of the supraoculars measured in mm, at the widest point (WSUP).
27. Length of the supraoculars measured in mm (LSUP).
28. Number of sutures dividing the supraoculars (DIVSUP).
29. Number of scales between the nasal scale and the shield bordering the pit anteriorly (NASPIT).
30. Number of scales separating the internasal scales (INTNAS).
31. Width of the internasals (WINTNAS).
32. Number of scales contacting the subocular (BORSOC).
33. Ratio of the anterior margin of the rostral scale to the posterior margin (ROST).
34. Number of scales between the first ventral and the anterior genial shields (GENIAL).
35. Snout vent length (SVL).
36. Tail length (TAIL).
37. Width of the head measured between the outer edges of the supraoculars (WHEAD).
38. Length of the head measured between the tip of the snout to the posterior edge of the lower jawbone (LHEAD).
39. Diameter of the eye (DEYE).
40. Distance between the eye and the posterior edge of the nostril (EYENOS).
41. Distance between the eye and the posterior edge of the pit (PITEYE).
42. Distance between the posterior edge of the pit and the anterior edge of the nostril (NOSPIT).