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Geographic Variation: Multivariate Analysis of Six Character Systems in Snakes in Relation to Character Number

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With snakes, as with other animal groups, there is a range of character systems available for the study of geographic variation. When multivariate analysis is used to portray the patterns of geographic variation within these various character systems, the resultant patterns can differ. Since the congruence between character systems can be influenced by number of characters, a procedure is developed for comparing the patterns of geographic variation portrayed by various character systems while taking into account the number of characters. The data set used is based on 71 independent characters showing significant variation among 14 populations of the Palearctic snake *Natrix natrix*. The overall pattern of geographic variation in the area under consideration is categorical, i.e., there are two distinct races (one western, the other eastern). A quantitative measure of congruence is computed between the overall pattern and those patterns portrayed by randomly sampled subsets of the six character systems (color pattern, internal morphology, scalation, dentition, body proportions and dermal sense organs). The congruence of character sets selected irrespective of character type gives a benchmark for comparison. The predictivity of the six character systems is thus evaluated. Five of these systems reflect the overall pattern of categorical variation. It is also shown that in ophidian systematics, non-traditional character systems can contribute more (i.e., have higher predictivity per unit character) than widely used conventional character systems.

IN studies of geographic variation, and related topics in snakes, morphological characters from one or more of a range of features including scalation, color pattern, body dimensions, dermal sense (scale) organs, dentition and internal morphology may be used (Christman, 1980; Grobman, 1984; Hughes, 1985; Kramer, 1971; Rasmussen, 1975; Rossman, 1979; Schatti, 1982; Schatti and Agasion, 1985; Thorpe and McCarthy, 1978; and references in Thorpe, 1987). However, these character systems are not used with equal frequency; there being a bias towards the traditional scalation and color pattern and comparative neglect of dentition and internal morphology.

An investigation of geographic variation may

be based on the study of current selection pressures using one type of character (e.g., linear dimensions), whereas others may aim to summarize the general pattern of racial affinities (Thorpe, 1987) and thus have an implied predictivity, i.e., the extent to which the pattern shown by one character set tends to predict the pattern shown by other sets (Bock, 1973; Sneath and Sokal, 1973; Eldredge and Cracraft, 1980). In the case when predictivity is explicit or implicit, it is pertinent to know whether a single character system is adequately predictive and whether the frequent use of some systems such as scalation is justified by them being the most predictive.

An answer to these questions may be attempted by qualitative or quantitative comparison of the patterns resulting from two or more types of characters separately subjected to multivariate on multivariable techniques (see Sokal, 1983; Thorpe, 1983, 1987 for reviews of these techniques in relation to geographic variation). However, if one looks at infraspecific and supraspecific studies which compare character systems (Colless, 1980; Miyamoto, 1983; Yoshiyama and Sassaman, 1983; Lindenfelser, 1984; Patton, 1984; Snell et al., 1984; Thorpe, 1986) a common potential difficulty is apparent. The difficulty arises from the fact that the number of characters within a character system can be low and/or differ between character systems, sometimes very markedly so. This can be a problem because the pattern of geographic variation shown by a character set, and its reliability, can be a function of the number of characters in the set (Thorpe, 1985a, 1985b, 1985c). This can be particularly noticeable when the number of characters within a set is low (Thorpe, 1985a, 1985b). Consequently, the congruence between character sets can depend on the number of characters within the sets. Hence the patterns portrayed by various character types can be perturbed by low and disparate numbers of characters. To overcome this difficulty, the patterns portrayed by the character systems must be compared taking into account the number of characters.

The eastern and western races of the European grass snake (*Natrix natrix*, Colubridae) offer an excellent opportunity to compare the predictivity of the patterns of geographic variation portrayed by various character systems. Six different character systems (described below) offer an atypically large number of character types for comparison, many of which show significant geographic variation. The number of characters within a system showing significant geographic variation ranges from 2–27, embracing the range of characters typically used in studies of geographic variation.

Methods

The materials and basic methods are essentially those used in Thorpe's (1985a) study of character number and congruence in geographic variation. Fourteen populations of the grass snake *N. natrix* representing eastern (seven populations) and western (seven populations) races are chosen (Fig. 1). These races are two distinct categories in that an east-west transect shows a "stepped clinal" pattern of geographic variation (Thorpe 1985a), and a two-dimensional ordination shows two distinct aggregations (with Jersey island as a western outlier) (Fig. 7).

The pattern of geographic variation is summarized by principal coordinate analysis of the normalized population means (Sneath and Sokal, 1973; Thorpe, 1976, 1983). Just the major principal coordinate is used for quantitative comparisons between analyses because the differentiation between two races can be summarized in one dimension (Thorpe, 1985a). It is not necessary to quantitatively compare the scatter of the populations on the first two coordinates and not appropriate to compare the distance matrices from which the coordinates are computed.

The total character set is 71 within-population independent characters showing significant variation between populations (Thorpe, 1985a). The character set is composed of characters from the following six, systems with the number of characters within a system indicated parenthetically: color pattern (27), internal morphology (20), scalation (14), dentition (4), size-adjusted body proportions (4) and dermal sense organs (2).

The comparison of the character types is based on "model B" in Thorpe (1985a) where recurrently randomly sampled subsets of characters yield major principal coordinates that are compared to the major principal coordinate of the total (71 character) data set. This procedure is carried out for each character system. That is, a character set is randomly selected from a specific character system, the major principal coordinate is extracted and compared to the major principal coordinate from the total (71) character set by a product-moment correlation.

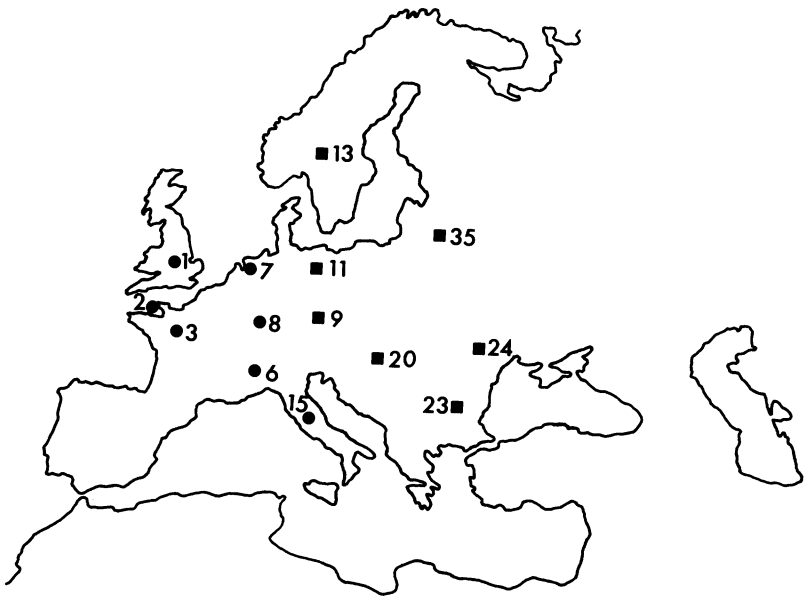

Fig. 1. Map of the sample localities. The circles represent those from the western race while squares represent those from the eastern race. The sample numbers are those used in previous publications of the author.

This gives an assessment of the congruence between the patterns of geographic variation. Even though correlation coefficients are not suitable for comparing matrices they give an appropriate non-probabilistic measure of congruence when the unidimensional pattern is defined by the major principal coordinate.

This procedure is repeated 10 times for a given number of characters and the mean, maximum and minimum congruence (absolute correlation) for analyses based on a given number of characters is found. The number of characters is increased from 1 through progressions 2–4, 6, 8, 10, 12, 14, 16, 20 and 25 where applicable. In addition, a principal coordinate analysis is carried out on the maximum number of characters available for a given character system.

An exception to the procedure of randomly selecting 10 subsets is encountered when the total number of characters in a character system is less than 10 (i.e., dentition, body proportions and dermal sense organs). In these cases, where the number of characters to be selected from a set is one, the absolute correlation between each available character (rather than 10 randomly selected characters) and the major principal coordinate of the total set is computed. The absolute correlations between all the individual characters within a character system and the major coordinate of the total set are also computed for the systems with large numbers of characters (i.e., color pattern, internal morphology and scalation).

The "general" congruence between the pattern of geographic variation portrayed by character sets selected independent of the character system and the pattern portayed by the total 71 character analysis is given in Figure 5 of Thorpe (1985a). This "general" congruence can be used as a benchmark against which to judge the specific congruence of character sets selected from a single specific system.

The mean, minimum and maximum congruence between patterns of geographic variation is plotted against the number of characters in the single system character set. This is done for each character system and the mean "general" congruence irrespective of character system (Thorpe, 1985a) is superimposed on these plots. Also the specific character systems are compared by plotting their mean congruence for a given number of characters on the same congruence-against-character-number diagram.

The above procedure is designed to efficiently test whether a specific character system tends to be predictive of the variation in other character sets. There are various alternatives, but

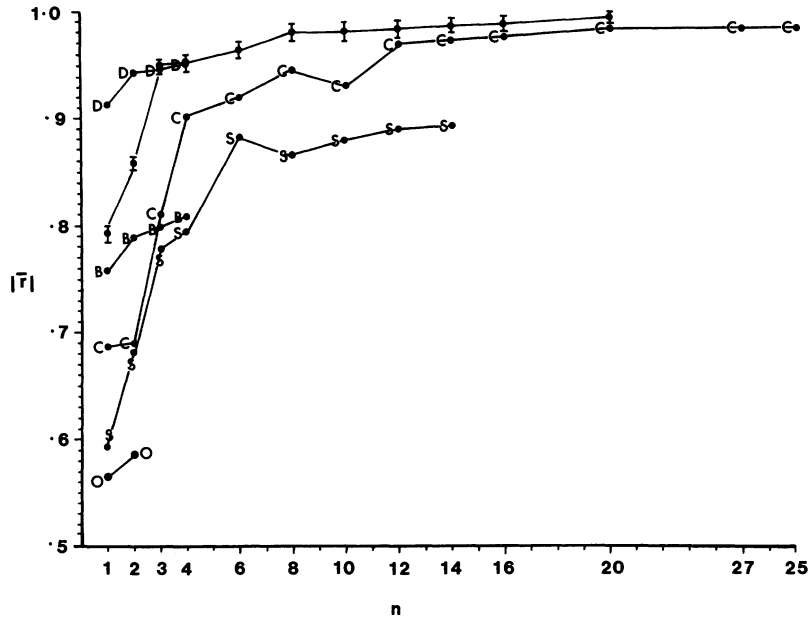

Fig. 2. Mean congruence (|r|, vertical axis) between the pattern portrayed by each character system and the overall pattern based on the total character set, plotted against the number of characters (n, horizontal axis) in the multivariate analysis. When n = 1 then the mean is taken across all available characters within the system; when n is the maximum within the character system then only one analysis need be run but elsewhere the mean congruence (|r|) is based on 10 randomly selected subsets. The character systems are color pattern (C), internal morphology (I), scalation (S), dentition (D), body proportions (B) and dermal sense organs (O).

less efficient, procedures (see Discussion). The "total" pattern is chosen as an end-point against which to judge the predictivity of a character set as it is the best available assessment of the "overall" pattern (Thorpe, 1987) and therefore the likely variation in other "unknown" sets. The existence of such an "overall" pattern is clearly demonstrated by previous work on this large data set (Thorpe, 1985a) which showed that independent character sets exhibit basically the same pattern even when very few characters are used and that a subset shows basically the same pattern as the "total" set when as few as 8–10 characters are used. Of course, since the major coordinate is used to summarize the variation in a character set the similarity in pattern is defined as the similarity in ordination along the major coordinate.

Results

A comparison of the levels of congruence achieved by systems with a large number of characters (i.e., color pattern, internal morphology and scalation) shows that for a given number of characters the internal morphology has the highest congruence, color pattern the next highest and scalation the lowest (Fig. 2). When the congruence levels achieved by these specific character systems are compared (Figs. 3, 4 and 5) to the levels achieved by the subsets selected independent of character system (i.e., the "general" set) then the internal morphology has higher levels of congruence (Fig. 4), the color pattern has comparable levels of congruence (Fig. 3) and the scalation has lower levels of congruence. Nevertheless, all three major systems portray a pattern of geographic variation very close to the "total" pattern, even at low character numbers, such that mean correlation between patterns is greater than 0.85 at two or more internal morphology characters, four or more color pattern characters and six or more scalation characters.

Of the character systems with few (2–4) characters (i.e., dentition, body proportions and der-

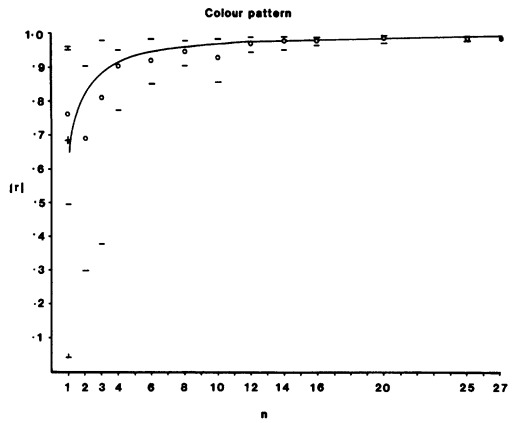

Fig. 3. Color pattern. Congruence (|r|, vertical axis) between the pattern portrayed by a random subset selected from the color pattern and the 'total' pattern for a given number of characters (n, horizontal axis). Mean congruence (hollow circle), maximum and minimum congruence (bars) are indicated for the 10 randomly selected subsets. The analysis based on the maximum number of characters with a character system is indicated by a solid circle while for the univariate analysis the mean across all available characters is indicated by a cross and the minimum and maximum are indicated by horizontal bars with a vertical projection on one side. The line depicting a near hyperbolic curve is the mean congruence of 10 random subsets selected from the total set irrespective of character system from Figure 5 of Thorpe, 1985a.

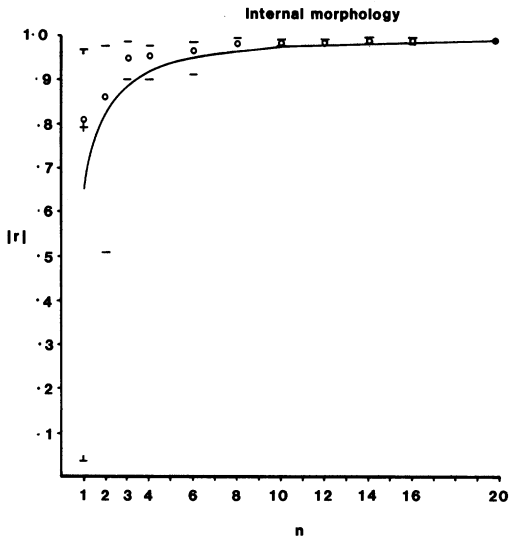

Fig. 4. Internal morphology. Legend as for Figure 3.

mal sense organs), the system with the highest level of congruence with the "total" pattern is dentition, which gives values noticeably higher than the "general" congruence (Fig. 6). The body proportions show levels of congruence similar to the "general" congruence (Fig. 6) whereas the dermal sense organs show the lowest congruence levels of all, well below those of the body proportions and "general" congruence (Fig. 6).

Finally, principal coordinate scatter diagrams based on the maximum number of characters within a system are presented (Fig. 7) for each character system. All of these portray a non-overlapping scatter of the eastern and western races (Fig. 7) except for the principal coordinate derived from the dermal sense organs.

Discussion

The relative levels of congruence have implications for ophidian systematics. Intraspecific ophidian taxonomy and systematics tends to be heavily dependent on scalation, which shows adequate, but unimpressive, predictivity. On the other hand, internal morphology is very rarely used (Thorpe, 1975), although it can supply numerous readily recordable and highly predictive characters. Indeed, Figure 2 shows that, on average, three internal characters give a better portrayal of the common categorical pattern than do any reasonable number of scalation

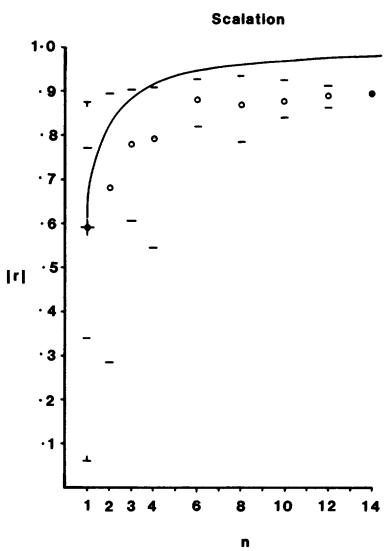

Fig. 5. Scalation. Legend as for Figure 3.

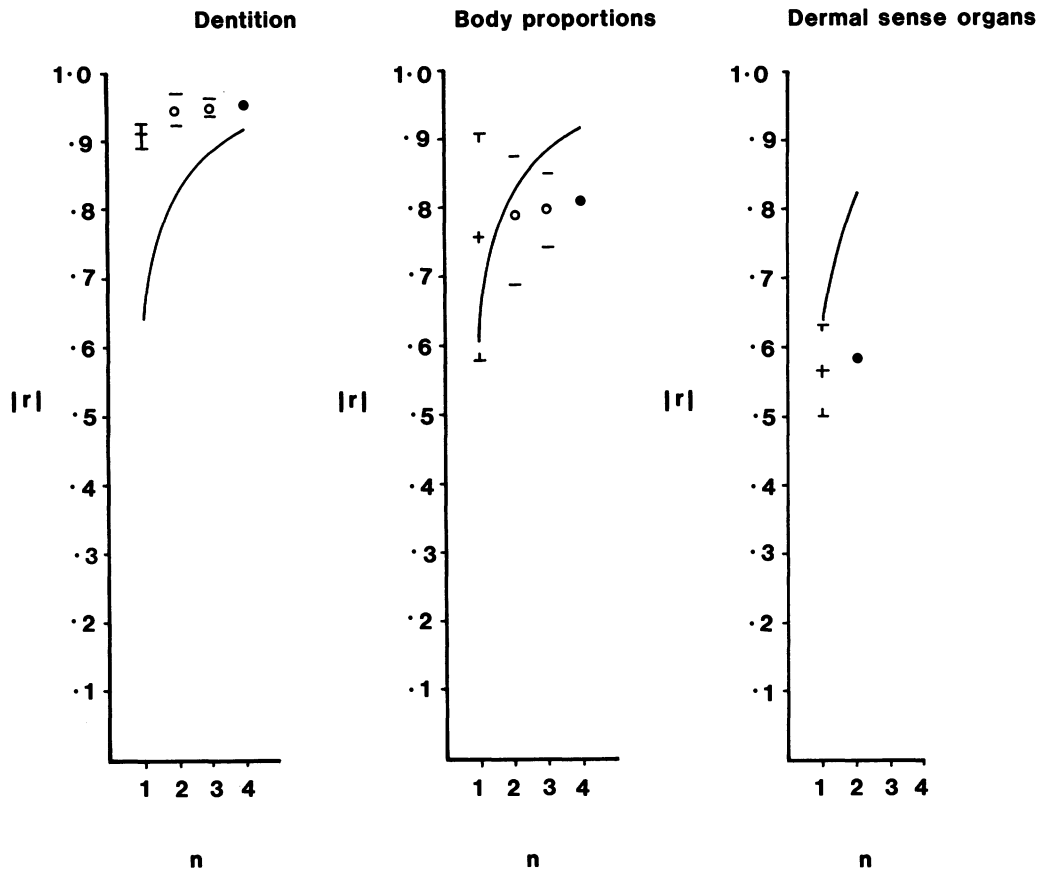

Fig. 6. Dentition (left). Body proportions (size adjusted, middle). Dermal sense organs (right). Legend as for Figure 3.

characters. Even though the levels of congruence achieved with the color pattern are excellent, over twice as many color pattern characters are needed on average, to obtain the same level of congruence with the "total" pattern that internal morphology shows. The dermal sense organ characters were very time consuming to record yet did not prove to be worthwhile from a taxonomic viewpoint for they were unpredictive of the common pattern. However, the reasons for incongruence (that is, their pattern of geographic variation in relation to natural selection, etc.), may be of interest from an evolutionary viewpoint.

The rank congruence of the various character systems is likely to be species-specific, but these results do indicate that non-traditional character systems such as internal morphology of ophidians can supply a considerable array of highly predictive characters that may be more useful than the traditional character systems for evaluation of racial or geographic differences.

With appropriate modifications, the methodology used in this study could be used to compare hierarchical patterns at the supraspecific level. However, use of the "total" character pattern as an endpoint for comparison is not free from difficulties. If the patterns of geographic variation were similar within character systems but differed between systems, then congruence of a specific character system with the "total" pattern would be a function of the proportion of characters it contributed to the total character set. However, in this case there is no correlation, ($r = -0.08$) between the number of characters within a character system and their average congruence to the "total" set.

An alternative based on the comparison of independent sets (as in model A of Thorpe, 1985a) could be used to directly compare sep-

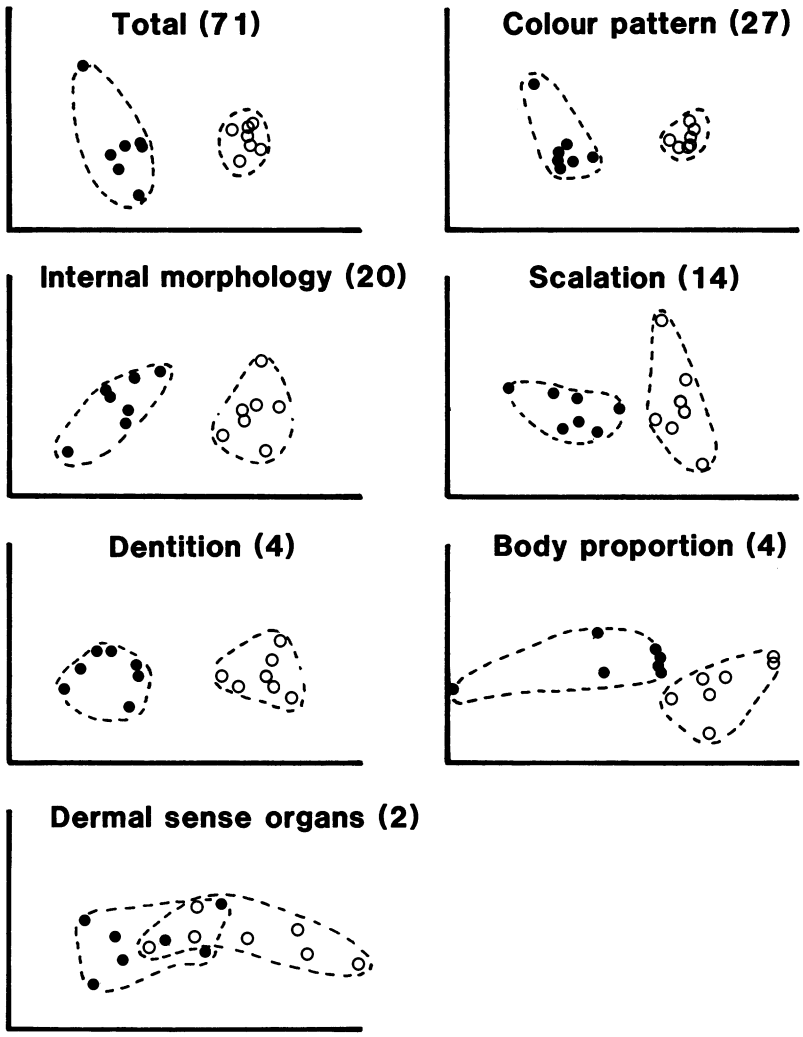

Fig. 7. Principal coordinate scatter diagrams for the total character set as well as for each character system based on the maximum number of characters available within a system (in parentheses). The horizontal axis indicates the first coordinate and the vertical axis the second coordinate while western populations are indicated by solid circles and eastern populations by hollow circles.

arate character systems. However, low congruence could be due to the pattern of one or other or of both character systems. Moreover, the number of characters used for a systematic comparison could not exceed the maximum number within the system with the lowest number of characters (i.e., the dermal sense organs with two characters). Similar difficulties exist with the numerous options and permutations of methodology. Although no efficient methodology pertinent to this study is free of at least minor difficulties, the procedure used in this study provides an adequate basis for comparing character systems while taking into account the number of characters.

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