

Pattern and Function of Sexual Dimorphism: A Biometric Study of Character Variation in the Grass Snake (*Natrix natrix*, Colubridae) Due to Sex and Its Interaction with Geography



R. S. Thorpe

Copeia, Vol. 1989, No. 1 (Feb. 27, 1989), 53-63.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%2819890227%293%3A1989%3A1%3C53%3APAFOSD%3E2.0.CO%3B2-0>

Copeia is currently published by American Society of Ichthyologists and Herpetologists.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://uk.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://uk.jstor.org/journals/asih.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

UEDA, T. 1987. The nucleolus organizer regions in the chromosomes of three species in the genus *Salvelinus* (Salmonidae). Bull. Fac. Educ. Utsunomyia Univ. 37:67–73.

———, AND Y. OJIMA. 1983. Karyotypes with C banding patterns of two species in the genus *Salvelinus* of the family Salmonidae. Proc. Japan Acad. 59, Ser B, no. 10:343–346.

VIKTOROVSKY, R. M. 1978. The evolution of karyotypes in chars of the genus *Salvelinus*. Tsitologiya 207:576–579. (In Russian.)

DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF WISCONSIN—MILWAUKEE, PO BOX 413, MILWAUKEE, WISCONSIN 53201 AND FISHERIES RESEARCH SECTION, ONTARIO MINISTRY OF NATURAL RESOURCES, PO BOX 50, MAPLE, ONTARIO L0J 1E0, CANADA. Accepted 14 June 1988.

Copeia, 1989(1), pp. 53–63

Pattern and Function of Sexual Dimorphism: A Biometric Study of Character Variation in the Grass Snake (*Natrix natrix*, Colubridae) Due to Sex and its Interaction with Geography

R. S. THORPE

Sexual dimorphism and geographic variation in sexual dimorphism were investigated by univariate and multivariate biometric analyses of 139 characters of the grass snake, *Natrix natrix*, represented by populations from throughout its range. Whereas previous investigations have usually only considered one character system, this one is a detailed biometric analysis of sexual dimorphism in six character systems: color pattern; scalation; internal morphology; dentition; body dimensions (size and shape); and dermal sense organs. About half the characters show significant, but sometimes subtle, sexual dimorphism. These characters are not evenly distributed across the character systems, there being a notable paucity of sexual dimorphism in the color pattern indicating that it is not instrumental in sexual recognition. Putative coadapted character constellations appear to adjust female trunk morphology for pregnancy (large size, robust shape, compatible scalation changes and reorganization of the visceral topography) and male tail morphology for accommodating primary sexual organs (large tail, small cloacal gland, and reorganization of tail proportions and scalation). Other character constellations—serially repeated meristic features (e.g., higher scalation and dentition counts in males), anterior internal morphology, head and neck scalation and dermal sense organs—also show sexual dimorphism. Relatively few (i.e., 15) characters show geographic variation in the extent of sexual dimorphism. These characters are mainly from the scalation but a few are from the internal morphology and dermal sense organs. The reorganization of the sexual dimorphism in the Sardinian population is compatible with its “quantum” differentiation via a “bottleneck” whereas the similarity of the sexual dimorphism between the main eastern and western phylogenetic lineages is compatible with their origin without a population bottleneck. The latitudinal nature of the geographic variation in the extent of sexual dimorphism, unlike the primary pattern of geographic variation, may indicate adaptation to current ecological conditions.

THE grass snakes of the *Natrix natrix* species complex are spread over most of the Palearctic west of Lake Baikal. Across its range the complex exhibits considerable local and geo-

graphical variation in the color pattern, scalation, internal morphology, dentition, body dimensions and dermal sense organs (Thorpe, 1979, 1984a). In addition there are mean dif-

ferences between the sexes in numerous characters.

Studies of such secondary sexual dimorphism in snakes have largely concentrated on single character systems, most frequently body dimensions, such as trunk and/or tail length, (Jackson and Franz, 1981; Goddard, 1984; Shine, 1984; Crews et al., 1985; Wynn and Zug, 1985; and particularly Shine, 1978 and Fitch, 1981 and references therein), although scalation (Dixon and Thomas, 1982; Grobman, 1984) and internal morphology (Rossman et al., 1982) have been studied. Some studies have looked at more than one character system (Rossman, 1979; Piak et al., 1979; Kminiak and Kaluz, 1983), but no study, other than Thorpe's (1975) superficial overview of *N. natrix* characters, has to my knowledge undertaken a comprehensive biometric analysis of sexual dimorphism in a wide range of character systems in snakes. Consequently, I have conducted a comprehensive and detailed biometric survey of sexual dimorphism across a wide range of character systems (i.e., scalation, color pattern, internal morphology, dentition, body dimensions and dermal sense organs) of a single snake species throughout its range. My aim is to increase the understanding of the sometimes subtle morphological consequences of primary sexual differences and roles, to reveal coadapted character constellations that may have developed in response to these differences, and to reveal other patterns of secondary sexual dimorphism that may have no very obvious, or indeed any, adaptational advantage. Furthermore, the pattern of geographic variation in the extent and nature of the sexual dimorphism will be investigated. Studies of both geographic variation and sexual dimorphism are available, but the study of their interaction is not so common. Although there have been a few such studies in higher vertebrates (Fonstad and Hogstad, 1981; Ross and Baker, 1982; Ralls and Harvey, 1985; Saether and Haagenrud, 1985), and also lizards and turtles (Fitch, 1981; Iverson, 1985 and references therein), they are rare for snakes.

METHODS

One hundred and thirty-nine quantitative characters from six different character systems (i.e., scalation, color pattern, internal morphology, dentition, body dimensions and dermal sense organs) were measured and are listed

in Appendix 1. The first 82 of these characters are largely independent of one another (i.e., have a low within-group correlation; Thorpe, 1976) whereas the remaining 57 are derived from these (e.g., liver length in number of somites is derived from the somite position of the anterior and posterior tips of the liver).

These characters were recorded from geographic groups throughout the Palearctic. The groups are compound localities which are tested for homogeneity, numbered and mapped in Thorpe (1973, 1979). The 41 groups used in this study are given in List A, Appendix 2. Various subsets of these groups are used throughout the study. Internal morphological characters were not recorded from gravid females, where direct distortion due to displacement by the eggs could have occurred.

The existence of sexual dimorphism, geographic variation, and geographic variation in the extent of sexual dimorphism (i.e., interaction between sex and geography) is assessed for each character by a two-way ANOVA. Statistical significance is taken as $P < 0.01$ of the null hypothesis being correct. In order to maximize the number of characters subjected to this two-way ANOVA, a reduced set of groups was used (24 pairs of groups representing most of the range of all four subspecies; List B, Appendix 2). Even so, several characters (nos. 44–45, 47, 49–50, 54–55) could not be recorded from all of these groups and so were subjected to a two-way ANOVA across a smaller subset of groups (i.e., List C, Appendix 2).

To adjust for size differences prior to the ANOVA the body proportions (95–98) and a linear measurement of the neck scales (22) were regressed against trunk length (93) using the pooled within-group regression slope (Thorpe, 1976). When considering the "size" character (93) it must be borne in mind that individuals are continuously growing and unaged. When the sexual dimorphism is shown by ANOVA to be significant, an indication of its extent and direction is given by the average and SD of the female group mean minus the male group mean across the 24 groups of List B, Appendix 2.

The pattern of geographic variation in the extent of sexual dimorphism was analyzed by taking the set of characters that show significant geographic variation in the extent of sexual dimorphism (i.e., a significant interaction between sex and geography) and computing the Mahalanobis D between sexes per locality using

this character set. The Mahalanobis D between sexes for each group can then be mapped and correlated with variables such as latitude.

The pattern of geographic variation in the nature of the sexual dimorphism was investigated by taking each character in the above set, subtracting the female mean from the male mean, for each group. The normalized character difference $(\bar{x}_\delta - \bar{x}_\text{♀}) \times \text{group matrix}$ is then subjected to a principal component analysis (PCA). The eigenvectors can be investigated for character constellations, the individual principal components (PC) can be investigated for geographic trends and the two main PC can be portrayed as a scatter diagram to illustrate geographic variation in the nature of the sexual dimorphism.

SEXUAL DIMORPHISM

General trends.—The two-way ANOVA reveal that approximately half of the characters (i.e., 67 out of 139) show sexual dimorphism (Table 1) but that they are not evenly distributed across the various character systems. Sexual dimorphism is found in 100% of the four dentition characters, 80% of the underived body-dimension characters, 52% of the underived scalation characters, 50% of the two dermal sense organ characters, 53% of the underived internal morphology characters but only 5 of the color pattern characters. Sexual dimorphism in some character constellations can be explained on functional grounds, whereas sexual dimorphism in other character suites cannot be readily explained. Even when differences between the sexes were statistically significant there was generally a very wide overlap in the character values.

Dimorphism in relation to pregnancy.—Grass snakes lay a large number of eggs (i.e., 30–40) which, even in large snakes with relatively few eggs, may result in a 25% increase in overall volume and a much greater percent increase in the volume of the visceral cavity. It is apparent that the increase in volume and weight due to the eggs results in a substantial additional burden in gravid females that does not have to be borne by males. It is likely that some or all of the following sexual differences reflect functional adaptations related to pregnancy.

The proportion of the body given over to the egg-carrying trunk tends to be greater in fe-

males (102, 159). Moreover, females are, on average, 25% longer (93) than males and have a broader body (98) which would have obvious advantages for carrying a heavy burden of eggs. As is compatible with this more robust build, females have, on average, larger (96–97) heads with more labial scales (26). In order to allow for this increased girth the females have, on average, a greater number of dorsal scale rows at a given somite position because the dorsal scale row reduction (7, 103) generally occurs at a more posterior position.

In advanced snakes (Underwood, 1967) the paired internal organs are displaced so that the right organ is anterior to the left. The gonads are anterior to the kidneys. In females the kidneys are positioned relatively more posteriorly (154, 156, 158) than in males presumably to accommodate the eggs. As a consequence of this relatively posterior position in females, the left kidney has access to less space at the posterior end of the body cavity and is truncated, i.e., shorter (148–149). This tendency for a reduction in length of the left kidney in females is not compensated for by a longer right kidney and consequently the total kidney length (150–151) is, on average, less in females. The right (anterior) kidney is normally larger than the left (posterior) kidney and since the left kidney in females is shorter this generally results in an even greater discrepancy between right and left kidney lengths (152) in females compared to males. There is no evidence for a similar anterior shift of internal organs to the anterior of the gonads (e.g., pancreas; 135) to accommodate the eggs in females. It is apparent that sexual dimorphism in the body dimensions, scalation and internal morphology may be related to functional adaptation to oviparity.

Dimorphism in relation to genitalia.—Sexual dimorphism in the scalation, dimensions and internal morphology of the tail may be related to the accommodation of the hemipenes and their retractor muscles in the proximal region of the tail of males. The paired hemipenes are quite large organs to be accommodated in a relatively slender tail and they extend back about 8–10 somites from the cloaca on average. Their retractor muscles are more slender but extend back into the tail much further (i.e., about 25.5–32 somites on average).

The proximal section of the tail, adjacent to the cloaca, has to accommodate, internally, only

the large paired cloacal glands (86) in females. These glands are used in defense as they emit a foul smelling secretion. In males both the paired cloacal glands and the hemipenes are accommodated in this region of the tail. The cloacal glands are large in females, i.e., a mean of 6.5–7.5 somites long, but in males, in spite of the selective advantage of large defensive glands, they are reduced to a mean of 4–5 somites long to allow for the accommodation of the hemipenes.

The accommodation of the hemipenes and their retractor muscles results in obvious differences in the shape of the proximal part of the tail. In females the proximal part of the tail is tapering whereas in males the accommodation of the hemipenes renders it parallel. This sexual difference in tail shape is reflected in the scalation. The broad proximal section of the tail (accommodating the hemipenes) with 14, 12, 10 and 8 dorsal scale rows takes up a greater proportion of the tail in males (characters 11, 104–112) and the narrow distal part of the tail with 6 and 4 dorsal scale rows takes up a proportionally greater part of the tail in females (characters 114, 117). Furthermore, the accommodation of the hemipenes and their retractor muscles may be a contributory factor in the tendency for the proportion of the body given over to the tail to be greater in males (102, 159).

Sexual dimorphism in serially repeated meristic characters.—Several independent meristic characters from the scalation and dentition show sexual dimorphism with the males having higher mean counts for the serially repeated features. The mean number of trunk somites (ventral scales 3), mean tail somites (pairs of subcaudal scales 4) and the mean total number of somites is higher in males. Furthermore, all dentigerous bones, i.e., dentary, maxilla, pterygoid and palatine (89–92), have higher mean tooth counts in males. The adaptive significance, if any, of this pattern of sexual dimorphism is unclear.

Sexual dimorphism in the anterior internal morphology.—The visceral topography of the anterior internal organs differs slightly between the sexes. It has already been noted that the mid and anterior internal organs do not appear to shift anteriorly to allow space for the eggs in females in the same way that the posterior internal organs have shifted posteriorly.

In males all of the anterior internal organs (e.g., heart, thyroid, left lung, systemic junction

and liver) appear to have a more posterior mean somite position than in females, because the number of the adjacent somite is higher, but this is a product of the greater number of somites in males. Nevertheless, when the relative somite position is considered, the left lung and the anterior tip of the liver (128, 137) are, on average, positioned more posteriorly in males. The relative position of the posterior tip of the liver is the same in both sexes so the liver is, on average, relatively shorter in males (140). If this has any adaptive significance, it is unclear what it is.

Sexual dimorphism in head and neck scalation.—The head and neck scalation differs slightly between the sexes. The mean degree of contact between the temporal and lower post-ocular scales (25) is slightly greater in males, the mean number of supra-labial scales (26) is slightly greater in females and, even taking into account the tendency for greater body size in females, the neck scales (22) are, on average, larger in females. This may not have any adaptive significance but it may possibly be related to the more robust build and larger head of females (see above).

Sexual dimorphism in dermal sense organs.—Up to 20 temporal pits are present in females and up to 40 in males. Since these pits are sensory, their sexual dimorphism may be related to different behavior of the sexes due to sex recognition, or the basking requirements of oviparity.

The comparative lack of sexual dimorphism in the color pattern.—Grass snakes are diurnal and possess a bold and complex color pattern (see Arnold and Burton, 1978, for illustrations) that shows considerable variation between geographic populations and between individuals. Consequently, it is notable that, unlike the other character systems, it shows no obvious sexual dimorphism and only a very subtle, mean difference between sexes in very few (i.e., five out of 30) characters. Moreover, even this very limited dimorphism can be largely explained by the influence of sexual dimorphism in other characters.

The slightly greater mean number of lateral blotches on the trunk (37) of males can be interpreted in terms of their higher trunk somites. Similarly the slight trend for the black nuchal blotches (64) to be further back from the head (in terms of dorsal scales) in females may be related to sexual dimorphism in the neck

scalation. Females grow to a larger size than males and, on average, exhibit greater ontogenetic fading of the color pattern. This may explain the slightly greater mean nuchal streaking (124) and less pronounced white edges to the dorsal scales (36) in females. There is also sexual dimorphism in the number of supra-labial streaks. However, the mean number of streaks is not consistently higher in males or females across the various populations and in any case may be influenced by the sexual dimorphism in the number of supra-labial scales.

These small, and often inconsistent, mean differences would not enable the sexes to recognize one another. Consequently, the color pattern does not appear to play a significant role in sexual recognition in the grass snake complex.

GEOGRAPHIC VARIATION IN SEXUAL DIMORPHISM

Considering that all but 13 characters show geographic variation and about half show sexual dimorphism, it is notable that so few (i.e., 15; Table 1) show significant geographic variation in the extent of sexual dimorphism. Many of the 15 characters are scalation characters where the sexual dimorphism is related to the greatest number of ventral and subcaudal scales (i.e., somite number) in males. For example, the 15 characters include ventral scale (somite) number (3), subcaudal pair (somite) number (4), total somite number (101), 19–17 dorsal scale reduction on the trunk (9, related to 3), and the dorsal scale reduction on the tail (15, 107, 113, 119 related to 4). Other characters, not influenced by somite number, also show geographic variation in the extent of sexual dimorphism (i.e., the relative proportions of the tail with a given number of dorsal scale rows (108–109), the relative position of the liver (137), size of the kidneys (146, 150–151) and the number of dermal sense organs (99).

Although the body proportions and dentition show marked geographic variation and sexual dimorphism, there is no geographic variation in the extent of sexual dimorphism across the groups under consideration. Similarly, geographic variation in the extent of sexual dimorphism is rare in characters from the internal morphology (four out of 50).

The overall pattern of geographic variation in the extent of sexual dimorphism was assessed by mapping the similarity (Mahalanobis D) be-

tween the sexes for each population (Fig. 1). The similarity between the sexes was measured across 14 of the 15 characters showing geographic variation in the extent of sexual dimorphism. The dermal sense organs (99) were excluded because they could not be recorded from all populations. It is notable that the resultant geographic variation does not show the four phenetic/phylogenetic subspecies (sensu Thorpe, 1979, 1984a) (i.e., east, west, Corsica, Sardinia) as being distinct. All four subspecies have broadly similar extents of sexual dimorphism. Although the pattern of geographic variation is not very strong, there is less sexual dimorphism in the north than in the south, i.e., D is correlated to latitude at $r = -0.6$, $P < 0.001$. The most obvious factor here is climate and one also needs to bear in mind the historical factor. I have suggested that grass snake populations expanded northwards from southern refugia in post-Pleistocene times (Thorpe, 1984a, 1984b). The populations in northern, recently colonized areas tend to have less sexual dimorphism than in southern, older populations. If this is the cause then why sexual dimorphism should be lost when new areas are colonized is not apparent. On the other hand natural selection may be the cause and the northern marginal populations such as those of Siberia (Fig. 1) may be subject to more intense selection which somehow militates against the evolution of sexual differences. However, comparison with other species which show geographic variation in the extent of sexual dimorphism, such as sparrows, indicates that the opposite can be true. Behavioral differences between the sexes result in an increase in sexual dimorphism in sparrows (Johnston and Selander, 1973; Fleischer and Johnston, 1982).

The geographic variation in the nature of the sexual dimorphism was investigated by subjecting the male mean minus female mean character values (for the 14 characters) for each group to PCA. The sign and magnitude of the eigenvector coefficients reveal that the PC (Fig. 2) reflect the nature rather than the extent of the sexual dimorphism. This PCA shows that the eastern, western and Corsican subspecies are not discriminated by the nature of their geographic variation just as the D values showed that they were not discriminated by the extent of their sexual dimorphism. Whereas the Sardinian subspecies does not show any difference in the overall extent of its sexual dimorphism (Fig. 1) the PCA scatter diagram does isolate

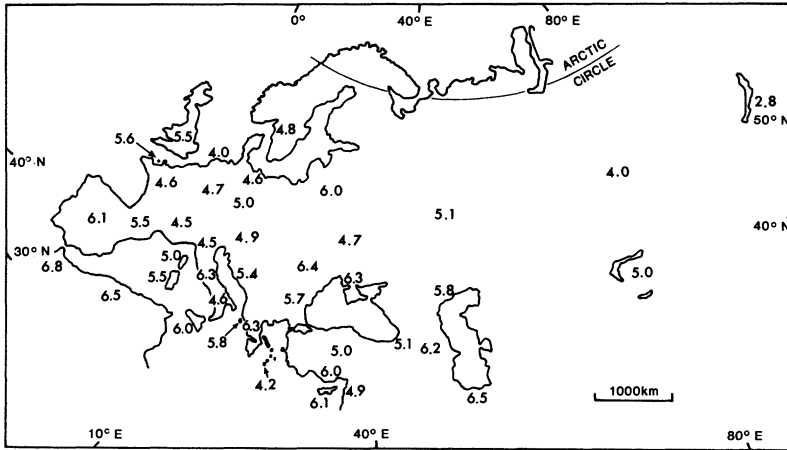


Fig. 1. Map of the Palearctic with Mahalanobis D values between sexes for each group of *Natrix natrix*. This shows the geographic variations in the extent of the sexual dimorphism (i.e., generally less in the north).

the Sardinian population on the nature of the sexual dimorphism.

The direction of the sexual dimorphism can be atypical in the Sardinian population, i.e., mid-tail scalation (108–109) and kidney size (146, 150–151) mean values are higher in Sardinian females whereas normally they are higher in males. In other characters it is the extent of the sexual dimorphism that is atypical; for example, in characters 15 and 107 the Sardinian population is atypical in showing little sexual dimorphism. The peculiar nature of the sexual dimorphism in the Sardinian population is compatible with the origin of the population. It is thought (Thorpe, 1979) that it arose from founder effect colonization from Corsica and underwent a “genetic” revolution (sensu Mayr, 1970) resulting in a reorganized phenotype as exemplified by peculiar lateral blotches and nuchal markings, etc.

DISCUSSION

Sexual dimorphism in putative response to pregnancy.—The constellation of characters possibly forming a coadapted complex in response to this in *N. natrix* includes characters from the body dimensions, scalation and internal morphology. Previous workers have pointed out certain aspects in isolation; for example, the size (Jackson and Franz, 1981 and other references in the introduction; Goddard, 1984) and internal morphology (Rossman et al., 1982) for other snake species. On average, female snakes are larger than male snakes in about two-thirds of species reviewed by Shine (1978). The excep-

tions, in which Shine was particularly interested, were largely explained by male combat. Consequently, in *N. natrix*, like most other snake species, where male combat does not result in selection for large male size, the balance of selection is swung in favor of larger female size due to the extra burden imposed by pregnancy. This does not necessarily assume greater fecundity in larger females within the same species (Trivers, 1972; Shine, 1978) for several reasons. The clutch size may be the same but egg/offspring size may be greater in larger females

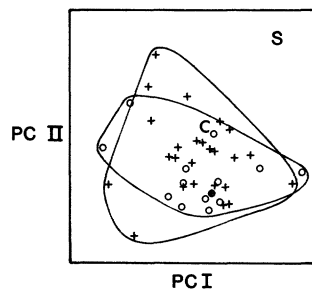


Fig. 2. The nature of sexual dimorphism in groups from the four subspecies of *Natrix natrix* (sensu Thorpe, 1979). Principal component analysis of the difference between sexes ($\bar{x}\delta - \bar{x}\eta$). Note that the groups from the eastern subspecies (+), western subspecies (O) and Corsican subspecies (C) are largely overlapping, indicating that the nature of the sexual dimorphism is broadly similar in each of these taxa. On the other hand the Sardinian subspecies (S) is a distinct outlier indicating that the nature of the sexual dimorphism in this taxon is different from that in the other three taxa.

(Goddard, 1981). Moreover, if the pattern of sexual dimorphism in *N. natrix* is the product of species selection, sensu evolution by punctuated equilibria (Stanley, 1979), then it is not necessary for it to be mirrored by microevolutionary trends within the species. To this end it is notable that this study did not reveal microevolution (in the sense of geographic variation) in the extent of sexual dimorphism in size. However, one must bear in mind the difficulties of analyzing size in an organism with continuous growth.

Other selective factors could contribute towards this size sexual dimorphism. The larger females may attract more males and have a greater chance of reproductive success as in *Thamnophis* (Hawley and Aleksuk, 1976). In some species small males may be more vagile and therefore have greater opportunity to locate females (Shine, 1978). I do not find this latter explanation convincing for *N. natrix* as there is no evidence of smaller adults having greater vagility in *N. natrix* and all else being equal larger animals have greater locomotory powers. Moreover, in neither case (i.e., *N. natrix* or *Thamnophis*) can the explanation be extended to cover all the other characters that can be explained by an increased burden during pregnancy, e.g., visceral topography. In any event it is inconceivable that such a heavy burden as pregnancy, with a 25% or more increase in volume and weight, would not result in selection for some morphological changes in females, unless there were equally strong selective pressures to counter specific changes, as in the influence of male combat on size (Shine, 1978).

Other facets of sexual dimorphism in relation to pregnancy (e.g., visceral topography) have parallels in other snake species. In the tribe *Thamnophini* (Rossman et al., 1982) the females have the anterior and mid-body organs displaced anteriorly and the kidneys displaced posteriorly to allow for space during pregnancy. However, in *N. natrix* the anterior and mid-body organs are not displaced, only the kidneys are displaced. Consequently, the two groups use slightly different means to achieve the same end.

Other facets of the sexual dimorphism also possibly due to adaptation for pregnancy (e.g., shape and scalation differences) have not been studied in a sufficient number of other species to be able to generalize although Singh Bhati and Wadhawan (1974) indicate, in conformity to *N. natrix*, that female sand boas, *Eryx johni*, may have larger heads than males. It would be interesting to know whether the shape, visceral

and scalation dimorphism in the grass snake are widespread in snakes and whether snakes with male combat show the other subtle dimorphisms associated with pregnancy (e.g., reorganization of the visceral topography) even if they do not have larger females.

Sexual dimorphism in response to genitalia.—The constellation of characters showing possibly a coadapted complex in response to the male genitalia in the base of the tail includes characters from the internal morphology, body dimensions and scalation. The greater mean number of subcaudal scales and/or greater proportional length of the tail in male grass snakes is generally true of most snakes except those that are arboreal (Goldsmith, 1984). Tail length and/or subcaudal scale dimorphism has been noted in several species (Branson and Baker, 1973; Singh Bhati and Wadhawan, 1974; Funk and Tucker, 1978; Rossman, 1979; Kminiak and Kaluz, 1983; Goddard, 1984; Grobman, 1984). However, the sexual dimorphism in the dorsal scalation and internal morphology of the tail that occurs in *N. natrix* has not been widely investigated in other species so no generalizations can be drawn. Sexual dimorphism in the post-cloacal vertebral haemopophyses of a range of snakes appears to be in response to the hemipenes and their retractors (Keiser, 1970), but this was not investigated in *N. natrix*.

Sexual dimorphism in other features.—The interesting, but unexplained, sexual dimorphism in the anterior internal morphology, head and neck scalation, dermal sense organs and the lack of sexual dimorphism in the color pattern have not been investigated in a sufficient number of other species to draw any generalizations. The number of ventral scales (a serially repeated meristic feature) has been investigated in several other snake species (Schwarz, 1976; Rossman, 1979; Kminiak and Kaluz, 1983; Grobman, 1984) but no general patterns in the sexual dimorphism emerge. Sexual dimorphism in tooth counts has been investigated in two other species, i.e., *Thamnophis* sp. (Rossman, 1979) and their sexual dimorphism agrees with that of *N. natrix* in showing a greater mean number of teeth in males. If sufficient species and dentigerous bones show parallel trends then this would imply a non-random cause but the functional significance, if any, is unclear.

Sexual dimorphism in the color pattern of the grass snake is largely absent and is not widely reported in other snake species. Sexual dimor-

phism in the number of serially repeated markings on the tail of snakes (Quinn, 1979) is probably a direct consequence of males having longer tails. The paucity of sexual dimorphism in the color pattern of snakes indicates that it is unlikely to play a part in sexual recognition. Since the color pattern is so frequently sexually dimorphic in lizards and often plays an important role in their sexual recognition, its relative absence from snakes may be a product of the possible origin of snakes from a blind fossorial ancestor.

Geographic variation in sexual dimorphism.—Previous studies of this phenomenon, i.e., De Vries' (1976) study of hawks, Fonstad and Hogstad's (1981) study of warblers, Johnston and Selander's (1973) study of sparrows, Ralls and Harvey's (1985) study of weasels, Ross and Baker's (1982) study of starlings, Saether and Haagenrud's (1985) study of moose, Iverson's (1985) study of turtles, and Fitch's (1981) review of the lizards *stansburiana* and *Cnemidophorus tigris* and the turtle *Chrysemys picta*, are all based solely on size and/or shape dimorphisms. Where these studies find geographic variation in sexual dimorphism it is generally explained by the availability of food and/or harshness of conditions influenced by differences in the behavior, role or niche of the sexes. In the grass snake the reorganization of the nature of the sexual dimorphism in the Sardinian population can be interpreted in terms of bottleneck or founder effect differentiations compatible with 'quantum' speciation. On the other hand the similarity in the nature and extent of sexual dimorphism between the two main phylogenetic groups, i.e., the eastern and western lineages (Thorpe, 1984a), is compatible with their origin by vicariance but without population bottlenecks (Thorpe, 1987).

Although the extent of sexual dimorphism is not correlated to the primary, phylogenetic pattern of geographic variation throughout the species complex it does show significant latitudinal variation. This latitudinal pattern in the extent of sexual dimorphism in the scalation and other characters may be related to current ecological conditions but, unlike many of the above studies, is not interpretable in terms of the availability of food.

APPENDIX 1

List of 139 characters used. The characters are numbered from 3–165 as in previous publications and a detailed description is available in Thorpe (1973, 1975). The position of scalation changes and internal

organs and the length of internal organs etc. are measured in somites, i.e., ventral, or pairs of subcaudal, scales. Abbreviations are as follows: ventral scale (VS), pairs of subcaudal scales (SS), position (Pos.), anterior (Ant.), posterior (Post.), dorsal scale rows (DSR), reduction (Red.), lateral blotches (LB), dorsal blotches (DB), ventrolateral blotches (VLB), nuchal markings (NM), separation (Sep.), right (Rt.), left (Lt.), kidney (Kid.), kidneys (Kids.), regression against trunk length (RATL), number (No.).

3, No. VS; 4, No. SS; 5, Pos. of Red. from 23–21 DSR; 7, Pos. of Red. from 21–19 DSR; 8, lower DSR lost at 21–19 Red.; 9, Pos. of Red. from 19–17 DSR; 10, lower DSR lost 19–17 Red.; 11, Pos. of Red. from 14–12 DSR; 12, lower DSR lost 14–12 Red.; 13, Pos. of Red. from 12–10 DSR; 14, lower DSR lost 12–10 Red.; 15, Pos. of Red. from 10–8 DSR; 16, lower DSR lost 10–8 Red.; 17, Pos. of Red. from 8–6 DSR; 18, lower DSR lost 8–6 Red.; 19, Pos. of Red. from 6–4 DSR; 20, lower DSR lost 6–4 Red.; 21, Pos. of Red. from 4–2 DSR; 22, size of neck scales RATL; 23, No. of post-ocular scales; 24, extent of contact between temporal and upper post-ocular scale; 25, extent of contact between temporal and lower post-ocular scale; 26, No. of supra-labial scales; 27, No. of sub-labial scales; 28, No. of sub-labials in contact with anterior chin shield; 29, No. of posterior-temporal scales; 30, No. of rows of gular scales; 32, extent of eye streak; 33, No. of supra-labial streaks; 34, No. of sub-labial streaks; 35, extent of lateral stripes; 36, extent of white edges to dorsal scales; 37, No. of LB; 38, size of LB; 39, No. dispersed LB; 40, lower Pos. of LB; 41, upper Pos. of LB; 42, size of DB; 44, lower Pos. of DB; 45, upper Pos. of DB; 46, N° VLB; 47, size of VLB; 48, extent of occipital line; 49, extent of parietal-occipital marking; 50, extent of temporal occipital marking; 54, overlap of lunar markings on to temporal scales; 55, overlap of lunar markings on to labial scales; 56, size of NM; 57, Sep. of NM; 58, length of NM; 60, upper curvature of NM; 61, lower curvature of NM; 63, fading of NM; 64, Sep. of NM from parietals; 66, thyroid Pos.; 67, heart Pos.; 68, Lt. lung Pos.; 69, systemic junction Pos.; 70, pancreas Pos.; 71, Pos. of Post. of Rt. lung; 72, cystic duct length; 73, Pos. of Ant. of liver; 74, Pos. of Post. of liver; 79, Pos. of Ant. of Rt. Kid.; 80, Pos. of Post. of Rt. Kid.; 81, Pos. of Ant. Lt. Kid.; 82, Pos. of Post. Lt. Kid.; 83, No. of renal arteries; 84, difference in No. renal arteries between Rt. and Lt. Kids.; 85, size of Lt. lung; 86, length of cloacal gland; 89, No. maxillary teeth; 90, No. palatine teeth; 91, No. pterygoid teeth; 92, No. dentary teeth; 93, trunk length; 95, head width RATL; 96, head depth RATL; 97, head length RATL; 98, body width RATL; 99, No. pits on temporals; 100, No. pits on upper post-oculars; 101, total somite No.; 102, trunk somite as % of total somite; 103, % VS Pos. of Red. from 19–17 DSR; 104, No. of SS with 12 DSR; 105, % SS with 12 DSR; 106, % SS Pos. of Red. from 12–10 DSR; 107, No. of SS with 10 DSR; 108, % SS with 10 DSR; 109, % SS Pos. of Red. from 10–8 DSR; 110, No. SS with 8 DSR; 111, % SS with 8 DSR; 112, % SS Pos. of Red. from 8–6 DSR; 113, No. SS with 6 DSR; 114, % SS with 6 DSR; 115, % SS Pos. of Red. from 6–4 DSR; 116, No. SS with 4 DSR; 117, % SS with 4 DSR; 118, % SS Pos. of Red. from 4–2 DSR; 119, No. SS with 2 DSR; 120, % SS with 2 DSR; 122, % of dispersed VLB; 123, VLB as % of LB; 124, % of NM streaked; 126, % VS Pos. of thyroid; 127, % VS Pos. of heart; 128, % VS Pos. of Lt. lung; 129, % VS Pos. of systemic junction; 130, Sep. of heart and thyroid; 131, % VS Sep. of heart and thyroid; 132, Sep. of systemic and heart; 133, % VS Sep. of systemic and heart; 134, Sep. of Lt. lung and heart; 135, % VS Pos. of pancreas; 136, % VS Pos. of Rt. lung; 137, % VS Pos. of Ant. liver; 138, % VS Pos. of Post. liver; 139, length of liver; 140, % VS length of liver; 141, Pos. of mid liver; 142, % VS Pos. of mid liver; 143, % VS Sep. of liver and pancreas; 146, length of Rt. Kid.; 147, % VS length Rt. Kid.; 148, length Lt. Kid.; 149, % VS length of Lt. Kid.; 150, average length of Kids.; 151, average % VS length of Kids.; 152, difference in lengths of Kids.; 153, Pos. of mid Rt. Kid.; 154, % VS Pos. of mid Rt. Kid.; 155, Pos. of mid Lt. Kid.; 155, % VS Pos. of mid Lt. Kid.; 156, % VS Pos. of mid Lt. Kid.; 157, average mid Kid. Pos.; 158, average % VS Pos. mid Kids.; 159, trunk length as % of total length; 164, mid point Sep. of Kids. (i.e., overlap); 165, % VS mid point Sep. of Kids.

APPENDIX 2

Lists of geographic groups used; numbered as in previous publications. (The details of the locations are given in Thorpe, 1979.)

List A. 41 pairs of groups: 1–39 inclusive, 42, 43.

List B. 24 pairs of groups: 1, 3, 5–6, 8–9, 11, 13–15, 18–27 inclusive, 30–31, 33, 42.

List C. 9 pairs of groups: 1, 3, 8–9, 11, 13–14, 20, 23.

LITERATURE CITED

- ARNOLD, E. N., AND J. BURTON. 1978. A field guide to the reptiles and amphibians of Britain and Europe. Collins, London, United Kingdom.
- BRANSON, B. A., AND E. C. BAKER. 1973. Sexual dimorphism in Kentucky queen snakes, *Regina septemvittata*, based on scute counts. Trans. Kentucky Acad. Sci. 34:57-58.
- CREWS, D., M. A. DIAMOND, J. WHITTIER AND R. MASON. 1985. Small male body size in garter snake *Thamnophis sirtalis parietalis* depends on testes. A. J. Physiol. 249:62-66.
- DE VRIES, T. 1976. Prey selection and hunting methods of the Galapagos hawk *Buteo galapagoensis*. Gerfaut 66:3-43.
- DIXON, J. R., AND R. A. THOMAS. 1982. The status of the Argentine colubrid snakes *Liophis sagittifer* and *L. trifasciatus*. Herpetologica 38:389-395.
- FITCH, H. S. 1981. Sexual size differences in reptiles. University of Kansas Mus. Nat. Hist., Misc. Publ. 70:1-72.
- FLEISCHER, R. C., AND R. F. JOHNSTON. 1982. Natural selection on body size and proportions in house sparrows. Nature 298:747-749.
- FONSTAD, T., AND D. HOGSTAD. 1981. Geographic variation and sexual dimorphism in Scandinavian willow warblers *Phylloscopus trochilus*. Fauna Norv. Ser. 4:82-88.
- FUNK, R. S., AND J. K. TUCKER. 1978. Variation in a large brood of lined snakes *Tropidoclonion lineatum* (Reptilia, Serpentes, Colubridae). J. Herpetol. 12:115-117.
- GODDARD, P. 1981. Ecology of the smooth snake *Coronella austriaca* Laurenti in Britain. Unpubl. Ph.D. thesis, Southampton University, Southampton, United Kingdom.
- . 1984. Morphology, growth, food, habitats and population characteristics of the smooth snake *Coronella austriaca* in southern Britain, U.K. J. Zool. Lond. 204:241-258.
- GOLDSMITH, S. K. 1984. Aspects of the natural history of the rough green snake *Ophedrys aestivus* Colubridae. Southwest. Nat. 29:445-452.
- GROBMAN, A. B. 1984. Scutellation variation in *Ophedrys aestivus*. Bull. Fla. State Mus. Biol. Sci. 29:153-170.
- HAWLEY, A. W. L., AND M. ALEKSIUK. 1976. Sexual receptivity in the female red-sided garter snake (*Thamnophis sirtalis parietalis*). Copeia 1976:401-404.
- IVERSON, J. B. 1985. Geographic variation in sexual dimorphism in the mud turtle *Kinosternon hirtipes*. Copeia 1985:388-393.
- JACKSON, D. R., AND R. FRANZ. 1981. Ecology of the eastern coral snake (*Micrurus fulvius*) in northern peninsular Florida. Herpetologica 37:213-228.
- JOHNSTON, R. F., AND R. K. SELANDER. 1973. Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. Amer. Nat. 107:373-390.
- KEISER, E. D. 1970. Sexual dimorphism and ontogenetic variation in the haemophyses of ophidian post-cloacal vertebrae. Herpetologica 26:331-334.
- KMINIAK, M., AND S. KALUZ. 1983. Evaluation of sexual dimorphism in snakes, Ophidia, Squamata, based on external morphological characters. Folia Zool. 32:259-270.
- MAYR, E. 1970. Populations, species and evolution. Harvard University Press, Cambridge, Massachusetts.
- PIAK, N. K., Y. J. KIM AND S. Y. YANG. 1979. Biochemical variation and systematic status of the genus *Aghistrodon* Crotalidae, in Korea. J. Zool. 22:153-164.
- QUINN, H. R. 1979. Sexual dimorphism in the tail pattern of Roman, Oklahoma snakes. Tex. J. Sci. 31:157-160.
- RALLS, K., AND P. H. HARVEY. 1985. Geographical variation in size and sexual dimorphism of North American weasels. Biol. J. Linn. Soc. 25:119-168.
- ROSS, H. A., AND A. J. BAKER. 1982. Variation in the size and shape of introduced starlings *Sturnus vulgaris* Aves, Sturnidae, in New Zealand. Can. J. Zool. 60:3316-3325.
- ROSSMAN, D. A. 1979. Morphological evidence for taxonomic partitioning of the *Thamnophis elegans* complex, Serpentes, Colubridae. Occas. Pap. Mus. Zool. LA State Univ. 55:1-12.
- ROSSMAN, N. J., D. A. ROSSMAN AND N. K. KEITH. 1982. Comparative visceral topography of the New-World snake tribe Thamnophini, Colubridae, Natricinae. Tulane Stud. Zool. Bot. 23:123-164.
- SAETHER, B. E., AND H. HAAGENRUD. 1985. Geographical variation in body weight and sexual size dimorphism of Norwegian moose, *Alces alces*. J. Zool. (Lond.) 206:83-96.
- SCHWARZ, A. 1976. Variation in the colubrid snake *Uromacer frenatus* Gunther (Reptilia, Serpentes, Colubridae). J. Herpetol. 10:319-327.
- SHINE, R. 1978. Sexual size dimorphism and male combat in snakes. Oecologia (Berlin) 33:269-278.
- . 1984. Reproductive biology and food habits of the Australian elapid snakes of the genus *Cryptophis*. J. Herpetol. 18:33-39.
- SINGH BHATI, D. P., AND B. S. WADHAWAN. 1974. Sexual dimorphism in the Indian sand snake, *Eryx johni johni* (Russel). Ann. Zool. (Agra.) 10:71-76.
- STANLEY, S. M. 1979. Macroevolution, pattern and process. W.H. Freeman & Co., San Francisco, California.
- THORPE, R. S. 1973. Intraspecific variation in the ringed snake *Natrix natrix* (L.). Unpubl. Ph.D. dissert., CNA, United Kingdom.
- . 1975. Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snake *Natrix natrix* (L.). Biol. J. Linn. Soc. 7:27-43.
- . 1976. Biometric analysis of geographic variation and racial affinities. Biol. Rev. 5:407-452.
- . 1979. Multivariate analysis of the population systematics of the ringed snake *Natrix natrix*. Proc. Roy. Soc. Edin. 78B:1-62.

- . 1984a. Primary and secondary transition zones in speciation and population differentiation: a phylogenetic analysis of range expansion. *Evolution* 38:233–243.
- . 1984b. Multivariate patterns of geographic variation between the island and mainland populations of the eastern grass snake (*N. n. natrix*). *J. Zool. Lond.* 204:551–561.
- . 1987. Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis. *Boll. Zool.* 54:3–11.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136–179. *In: Sexual selection and the descent of man*. B. Campbell (ed.). Heinemann, London, United Kingdom.
- UNDERWOOD, G. 1967. A contribution to the classification of snakes. Publ. 653. Trustees of the British Museum of Natural History, London, England.
- WYNN, A. H., AND G. R. ZUG. 1985. Observations on the reproductive biology of *Candoia carinata*, Serpentes, Boidae. *Snake* 17:15–24.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ABERDEEN, ABERDEEN AB9 2TN, SCOTLAND.
Accepted 15 Dec. 1987.

Copeia, 1989(1), pp. 63–70

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

R. S. THORPE

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; Schat-

ti, 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