Research Article

A brief review of morphological variation in *Natrix tessellata* in Israel: between sides, among individuals, between sexes, and among regions

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Abstract: After introducing the distribution and biology of *Natrix tessellata* in Israel, on the southern edge of its range, we address its intraspecific variation from the literature and examination of 262 museum specimens. Head pholidosis showed no significant directional asymmetry, but asymmetry in infralabial plates was significantly correlated with frequency of injured tails. Variation in body size showed no clear seasonal growth, presumably due to climatic fluctuations. The variation in number of ventrals (in males, 159-173, mode 165) was not geographical. Females attained 750-800 mm (head and body; mode 600-650) and males 700-750 (mode 500-600) mm. Females had significantly greater relative head length, and males significantly greater eye size relative to head length, counts of ventrals and of subcaudals, and relative tail length. The sexual dimorphism in relative tail length was evident also in juveniles. The sexual dimorphism varied geographically within Israel: that of head size was stronger in the south, that of relative tail length and number of subcaudals stronger in the north. Trunk coloration commonly comprised 6 rows of blackish spots of equal or different size. Head coloration in some individuals extraordinarily resembled that of *Natrix natrix*. We discuss some methodological problems and compare variation within Israel and with Anatolia.

Key words: Feeding behaviour, directional asymmetry, sexual dimorphism, normal variation, geographic variation, caudal injury, *Natrix natrix*, character displacement

Introduction

The distribution and biology of the dice snake, *Natrix tessellata* (Laurenti, 1768), in Israel (*sensu lato*) are of general interest because here this Palaearctic species (Gruschwitz et al., 1999) is at its southern distributional boundary, constrained by the desert that occupies the south of the country (Werner, 1988; Yom-Tov and Tchernov, 1988). The dice snake is of

special local interest because of its aquatic habits (Schreiber, 1912; Boulenger, 1913) in which it is locally unique, and it is known as "water snake" in both Arabic (*ḥayeht ma'*) and Hebrew (*neḥash mayim*). Its local distribution is more or less limited to the northern mesic, Mediterranean *sensu stricto* part of the country but it is found in various places penetrating the arid zone where freshwater resources exist. Figure 1 shows locality records of voucher
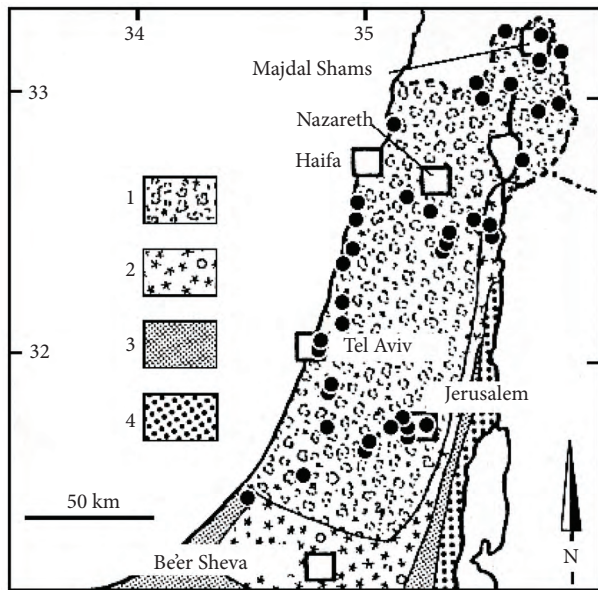
Figure 1. Locality records of voucher specimens of *Natrix tessellata* in HUJR, each point represents one or more specimens. The background pattern shows the ecological regions: 1, Mediterranean; 2, Irano-Turanian; 3, Saharo-Arabian; 4, Sudanian penetration zone (adapted from Werner, 1988).

specimens (sometimes many from a single locality) in the National Collections of Natural History at the Hebrew University of Jerusalem, on the background of a sketch-map of the local geographical regions.

The snake's occurrence in moist habitats (*sensu lato*) of northern "Palestine" (as defined and termed at the time) was already reported by Lortet (1883) and Tristram (1884). Surprisingly it was not mentioned by Hasselquist (1766). It is particularly abundant around fish ponds (mainly raising *Cyprinus* and *Tilapia*) and the fish growers, rightly or wrongly, regard it as an economically harmful pest. At least in the past, they used to trap and kill large numbers (Perry and Dmi'el, 1988).

Natrix tessellata is the only local representative of the genus. As explained elsewhere (Grillitsch and Werner, 2009), the listing of *Natrix natrix* for "Palestine" {Explained above} (Bedriaga, 1879; Boettger, 1880; Tristram, 1884; Aharoni, 1929; Bodenheimer, 1935), was apparently based on the occurrence of the species in the northern environs of Beirut, now in Lebanon (Boettger, 1877). Moreover, *N. tessellata* is the only local representative of the

Natricinae, and thus the only local colubrid whose feeding behaviour is predominantly guided by chemosensation (Wells et al., 1971). In captivity it is easily fed with dead fish or even pieces of commercial frozen fish, facilitating its maintenance in the laboratory, classroom, or amateur home.

Despite these economical and educational aspects, the dice snake has hardly been studied and very little is known of its biology in Israel (see below under Materials and Methods: Study Organism). Against this background we report in this paper on variation in *N. tessellata* in Israel at 4 levels—within individuals, among individuals, between sexes, and geographical—based mainly on material in the National Collection at the Hebrew University of Jerusalem. Additionally we incorporate relevant *N. tessellata* data from our recent studies of directional asymmetry (Faiman et al., 2004; Razzetti et al., 2007) and of sexual dimorphism (Faiman et al., 2005; Razzetti et al., unpublished data).

While almost all of our data are from Israel, some come from other parts of Cisjordan, the area between the Jordan River and the Mediterranean Sea. Our wish to make comparisons with other populations of the species' wide range, as done by Mebert (1993), is curbed by 2 considerations: (1) Scope and time constraints. (2) The recent evidence that *N. tessellata* shows extensive and profound genomic variation across its range and thus perhaps is not homogeneous (Guicking et al., 2009). The Cisjordanian population was not examined in this large project but presumably belongs to the Jordan-Egypt clade. We endeavour to make comparisons with the closest population studied, the Lake District in south-western Anatolia, 37°35′-38°45′N and 30°45′-31°45′E (Dinçaslan, 2005). This area, too, was not genomically examined and it might be populated by the Jordan-Egypt clade or the geographically somewhat closer Turkey clade.

Materials and methods

Abbreviations

DA, directional asymmetry. **%DA,** relative DA. **FMR,** mean ♀ value as percent of mean ♂ value. **HUJR,** Herpetological collection, National Collections of Natural History at the Hebrew University of Jerusalem. **L,** left. **PERCRA,** percents

of rostrum-anus length (Werner, 1971). **R**, right. **RA,** rostrum-anus length (Werner, 1971).

Study organism

Although in principle *N. tessellata* is tied to inland water, it can wander quite far from water bodies. For example, it has been collected in the Judean Hills at least twice at distances of at least 1 km from known water (HUJR 8403, HUJR 20816). On the other hand, in Lake Kinneret (Sea of Galilee) it was photographed by bathers swimming in open water, 7-10 m from the shore, where water depth was approximated 140 cm (south of Tiberias, between Sironit and Shiqmim beaches, 15 September 2006, between 1300 and1500 h, thus on Friday, with bathers few - pers. comm., Orit Levi). Its food is always said to comprise mainly fish and amphibians and according to Amitai and Bouskila (2001), occasionally also dead mice and birds that had drowned, but it is unclear whether these statements derive from observations in Israel (or from European literature, such as Filippi et al., 1996) and they lack quantitative data.

In contrast, some local reproductive data were summarised from assorted sources by Perry and Dmi'el (1988) in what seems to be the only scientific paper on the biology of the species in Israel. According to this summary, during July-September females lay clutches of 6-17 eggs ($\bar{X}$ =12.3 ± 4.58, SD). At 30-31.5 °C these hatch in 34-37 days, and the hatchlings average 220 mm total length. As with the vast majority of Israel's reptiles, the rate of further growth, age at maturity, size and age structure of the population, longevity in nature, and population density are unknown. Longevity of Israeli specimens, presumably in captivity, has been reported as attaining 14 years (Amitai and Bouskila, 2001) but even this means little as it is unknown from what sample size this was the maximum (Werner et al., 1993). As to its local enemies, besides man (Perry and Dmi'el, 1988) and the presumed serious predation by the Egyptian mongoose *Herpestes ichneumon* (Mendelssohn and Yom-Tov, 1988), predation is expected by the locally present ophiophagous short-toed eagle *Circaetus gallicus* (Bakaloudis et al., 1998), grey heron *Ardea cinerea* and purple heron *Ardea purpurea* (Cramp, 1977), seasonally by the white stork *Ciconia ciconia* (Cramp, 1977; Kosicki et al., 2006) and occasionally by the night heron *Nictycorax nycticorax* and great

crested grebe *Podiceps cristatus* (Cramp, 1977). There is an actual report of a Smyrna kingfisher, *Halcyon smyrnensis*, predating a 60-70 cm long *N. tessellata* (Mienis, 1980).

Material

We examined only specimens of *N. tessellata* preserved in alcohol in HUJR: Specimens from Cisjordan and the Golan plateau that had collection data (121 ♂♂, 39 ♀♀, 46 juveniles or sex unknown) and hatchlings, offspring of females caught gravid from the Ha-Zore'a fishponds (N = 56). The latter were excluded from most computations.

Statistics

Thorpe (1973, 1979) has set an example of sophisticated statistical analysis of broad geographical variation in *Natrix* (*N. natrix*). In contrast, herein we summarise data from a small area that could be compared, especially by other researchers, to data from elsewhere. Therefore, except as detailed below, basic parametric statistics were performed using Microsoft Excel, accepting a significance level of P = 0.05. The actual tests used are specified where relevant.

Directional asymmetry

For DA we use the data of Razzetti et al. (2007). Briefly, they tested DA in 3 bilateral cranial characters: numbers of supralabial and infralabial scutes, and eye diameter (i.e. the greatest horizontal diameter of the spectacle) of museum specimens. Measurements were taken 3 times with callipers under a stereomicroscope, and the 3 measurements were averaged. Each character was tested also separately for both sexes, since asymmetry has occasionally been noted only in one sex.

The %DA of a character in an individual was expressed as the individual R – L difference as a percentage of the individual's average of R and L dimensions, %DA = $100 \times 2 \times (R-L)/(R+L)$ (Werner et al., 1991). Negative values indicate L-dominance (more scales, or larger eye, on the L). The significance of the deviation of the sample average from 0 was tested by Student's 1-sample (2-tailed) t-test. The absence of antisymmetry, the co-occurrence of distinctly left-biased and right-biased individuals (Van Valen, 1962), was verified by viewing the distribution of the data in histograms.

Razzetti et al. (2007) explored the relationship between the degree of morphological asymmetry and the rate of injury in male *N. tessellata* (N = 47 from the Levant). First, the material was divided according to tail status (intact vs. injured). For each bilateral character, the averages of these 2 sub-samples were compared, and the hypothesis that injured individuals are more likely to be morphologically L-dominant was tested following Seligmann et al. (2003).

Second, the males were ranked by the level of DA in each of the 3 characters and checked where within the resulting DA gradient (from highly positive to highly negative) the few tail-injured individuals were located. The significance of the deviation of the group's locations from random was tested using c^2 tests for independence in 2 ways: (a) The distribution of the injured males between 2 sections of the asymmetry gradient, L-dominant versus neutral and R-dominant. (b) The distribution of the 2 tail states over the 3 directional asymmetry states, namely L-dominant, neutral, and R-dominant. Since the c^2 test involved small expected frequencies, the c^2 distribution could not be a reliable approximation. Therefore P values were estimated by computer simulations. For each case 1000 simulated samples were drawn under the assumption of the null hypothesis. The proportion of samples that had a c^2 statistic larger than the observed c^2 was taken as an estimate of the real P value.

Sexual dimorphism

Razzetti et al. (unpublished data) examined in 47 ♂♂ and 29 ♀♀ from the Levant the following characters: Sex (males and females excluding juveniles); RA; tail length; head length; eye (spectacle) diameter separately on L and R; ventral scales count; (subcaudal scales (or pairs) count; supralabial scales counts L and R; infralabial scales counts L and R.

From these individual data relative size was computed in PERCRA for tail length and head length; mean eye size in mm, and relative eye size both in PERCRA and in % of head length. The advantage of these units (versus, e.g., residuals of regressions) is that single specimens can be compared to the data. For all characters, meristic, mensural, or proportions, the FMR was computed. The advantage of this is compatibility with literature data, especially Fitch's (1981). Each FMR value is considered statistically significant if female and male means from which it

was derived differed significantly by t-test (P < 0.05, without Bonferroni-type corrections). We sexed the snakes by tail-base thickness.

Coloration

In lieu of undertaking a detailed quantitative study of the many parameters of the variable coloration, as done for *Natrix natrix* by Thorpe (1973, 1979) we endeavoured to classify specimens by visual inspection, guided by the terminology of Werner (1890) and Schmidt and Davis (1941). We examined the body parts visible from above, namely the array of spots on the dorsal and lateral aspects of the trunk, and the lateral aspect of the head.

Results and comments

Variation within individuals: directional asymmetry and its biological correlates

According to Razzetti et al. (2007), asymmetry in one or another character occurred in many *N. tessellata* individuals (e.g., Figure 2). However, no character showed significant directional asymmetry (in either separate or pooled sexes). There was also no significant correlation of the level of individual asymmetry between any 2 characters. Nevertheless there was one case of correlation with injury rate. The
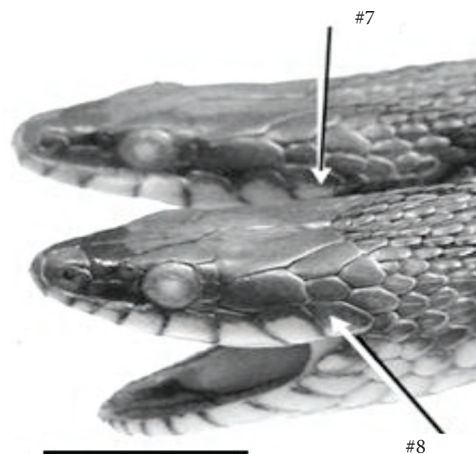

Figure 2. *Natrix tessellata* adult male from Tantura, Israel, HUJR 4540, head from the left and mirror image showing the right side, revealing asymmetry in the number of supralabialia (scale bar, 10 mm).

number of infra-labial plates was more asymmetric (%DA = −6.11 ± 9.31) in individuals with injured tails (N = 5) than in individuals with complete tails (%DA = 1.39 ± 6.59; N = 44). As expected from ample precedents, the asymmetry in the injured specimens was left-biased (Seligmann et al., 2003, 2008; Shacham, 2004). The difference between the injured and unharmed groups was significant (one-tailed Mann-Whitney U-test, P = 0.043).

Variation among individuals

Naturally, the greatest variation among individuals occurs in body size and mainly depends on age and growth. The distribution of body size in our sample is shown in Figure 3. Females are a little larger than males, approximately 50 mm, in terms of both the largest individuals and the mode of the size distribution. The greater number of males reflects only the encounter rate, which is affected by the snake's behaviour, likely to vary seasonally, and is no evidence of sex ratio. The large number of smallest juveniles probably reflects prolific reproduction. With the passage of time, reflected in body size, the numbers of juveniles probably diminish through predation, down to a minimum at 350-400 mm. Thereafter successive size classes probably increase in numbers due to overlapping of cohorts, up to the mode of the sex. At this size presumably many individuals live for years. A similar distribution but of total length of *N. tessellata* in Austria (N = 119) was presented by Zimmermann and Fachbach

(1996). Presumably not all individuals attain their potentially largest sizes as during growth the cohort is decimated by aging and predation. Nishimura (1993) presented a comparable histogram showing the RA distribution of the habu, *Trimeresurus flavoviridis*, from 218 individuals, some of them with known age. He concluded that yearlings were 50-90 cm, the 2-year old 60-100 cm, the 3-year old 70-120 cm, etc. At modal size, 100-110 cm, the oldest snakes were 7 years old. This age group gradually increased in number in groups of increasing RA despite the numerical decline in the larger size classes, and then dropped to rarity at 140-150 cm; the 2 largest snakes, 150-160 cm, were 8 and 10 years old.

Although most of the size variation in Figure 3 (or in Nishimura, 1993) should be due to age and growth, it is expected in principle to include also some individual variation, with genotypic and phenotypic components. The genotypic variation in body size may be correlated with the number of ventrals (Klauber, 1956; Shine, 2000). However, our scatter plot (RA length over ventral count, for N = 42 ♂♂) showed no such phenomenon, and so the investigation of individual size variation must await other methods.

Out of 206 museum specimens with known locality and date, the 2 smallest ones (RA) were 161 mm (8 May 1975, Jerusalem, HUJR 8618) and 162.5 mm (3 June 1912, Gedera, HUJR 4472). The next smallest specimens, 172-176 mm, were collected in March and
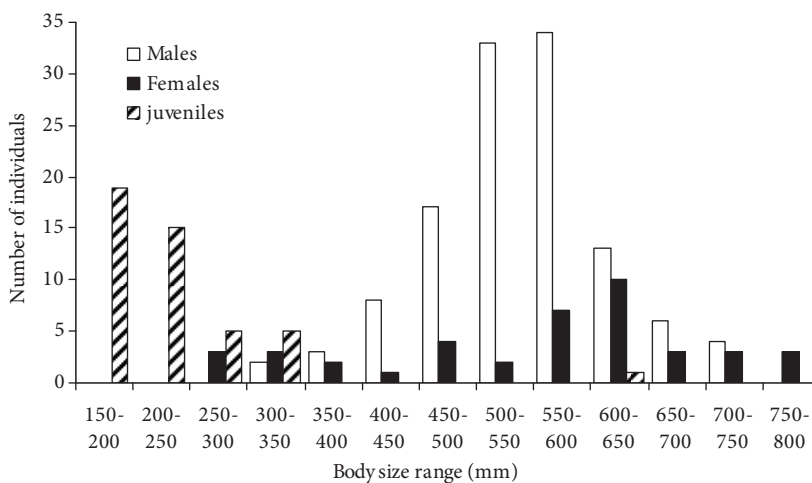

Figure 3. Size (RA) distribution in *N. tessellata* from Israel and Golan (N = 206), specimens from north and south of 32°N pooled (for lack of statistical difference) but data split by sex.

December at different localities. We tried to derive the annual growth of these presumed hatchlings from our museum sample but the scattergram of size versus month yielded no clear indication of annual growth (even when looking in detail at the sex and the geographical origin of specimens). This could be due to climatic heterogeneity across years.

As an example of individual variation in a character that (as far as is known) is not age-dependent and within Israel does not vary regionally, Figure 4 presents the distribution of ventral counts among males.

Sexual dimorphism

According to Razzetti et al. (unpublished data) sexual dimorphism was significant only in the following characters (N = 47♂♂, 29♀♀): tail length PERCRA, males exceeded females (♂♂ $\overline{X}$ = 24.7 ± 2.4, range 17.8-29.5; ♀♀ $\overline{X}$ = 22.8 ± 1.5, range 19.7-25.5; FMR = 91.1); head length PERCRA, females exceeded males (♂♂ $\overline{X}$ = 4.3 ± 0.4, range 3.5-5.5; ♀♀ $\overline{X}$ = 4.5 ± 0.3, range 3.9-5.2; FMR = 105.4); mean eye size relative to head length was greater in males (♂♂ $\overline{X}$ = 14.5 ± 1, range 12.3-16.7; ♀♀ $\overline{X}$ = 13.7 ± 1.1, range 11.7-16.2; FMR = 92); ventral scales count was higher in males (♂♂ $\overline{X}$ = 167.2 ± 4.5, range 159-182; ♀♀ $\overline{X}$ = 162.3 ± 2.9, range 157-170; FMR = 96.9); subcaudal scale pairs count was higher in males (♂♂ $\overline{X}$ = 64.9 ± 6.1, range 48-77; ♀♀ $\overline{X}$ = 57.4 ± 4, range, 51-68; FMR = 88.0).

We reinvestigated the sexual dimorphism of tail length PERCRA in Cisjordan and the Golan; the ♂♂ (N = 104) $\overline{X}$ = 25.72 and the ♀♀ (N = 38) $\overline{X}$ = 22.99 PERCRA; this difference was significant (P < 0.001). Figure 5 shows the fairly normal distribution
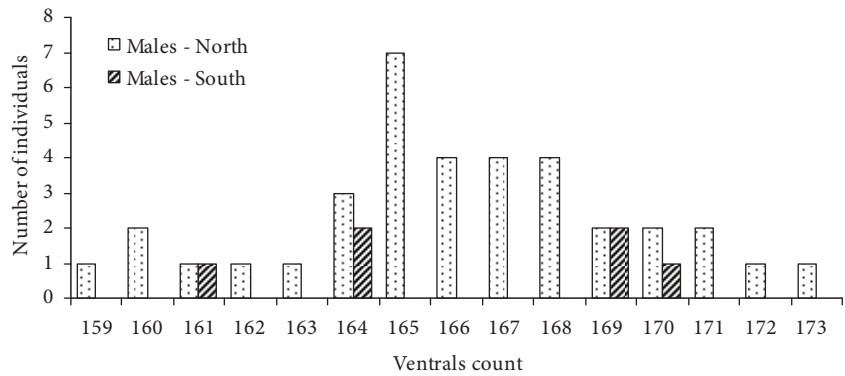

Figure 4. The variation of ventral counts among male *Natrix tessellata* from Israel (N = 42). Specimens marked as from north or south of 32°N.
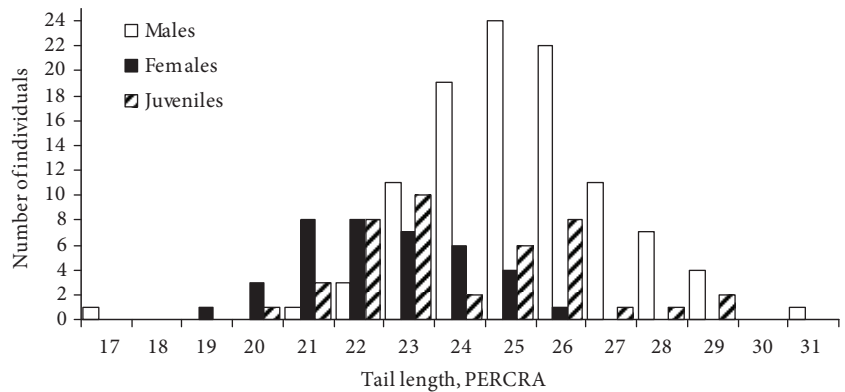

Figure 5. Relative tail length is greater in ♂♂ than in ♀♀, and in each sex shows fairly normal distribution; it is accordingly bimodal in unsexed juveniles.

of relative tail length in ♂♂ and ♀♀, and its bimodal distribution among juveniles of unknown sex (N = 42), presumably reflecting the 2 sexes. The 2 modes of the juveniles occur at higher tail-length-PERCRA values than the modes for adult males and females, presumably due to ontogenetic allometry in tail length (Figure 6).

Indeed, Figure 6 (below) shows the gradual reduction in relative tail length as a function of RA length (hypoallometry), and that the sexual difference does not increase with growth and age. The data of Razzetti et al. (unpublished data) show interesting consequences for eye size. In their data, in RA the ♀♀ ($\overline{X}$ = 577.6 ± 123.6, range 346-792) were only insignificantly larger than the ♂♂ ($\overline{X}$ = 560.1 ± 84.1, range 368-741) but had a significantly relatively larger head. However, the males had significantly, considerably, larger eyes relative to the head. As a result, the absolute size of female eyes ($\overline{X}$ = 3.6 ± 0.5, range 2.4-4.7) was only insignificantly greater than that of the males ($\overline{X}$ = 3.5 ± 0.5, range 2.3-4.5).

Geographical variation

Our sample size precludes a detailed study of geographical variation (such as by GIS) but the climatic and ecological roughly north-south gradient in Israel (Figure 7) enables a preliminary examination by schematically subdividing the Israeli sample at 32°N into northern and southern subsamples. This latitude was chosen somewhat arbitrarily because it is reached by some desert reptiles that penetrate northwards along the Mediterranean coast and in the Jordan Valley (Werner, 1987), and we happen to have no *N. tessellata* specimens from precisely this latitude. The Table compares the north and south samples for 8 characters for pooled and separate sexes. Only the RA and tail length (absolute and relative) characters differed significantly between the regions, possibly because of the smaller sample size of the other characters.

A particularly great regional difference occurred in the sexual dimorphism of relative tail length, which was great in the north but disappeared in the south (Figure 8). Although the north-south differences in most other characters were not significant, in 4 of the 5 characters with FMR values (those with significant sexual difference) the FMR indicated less dimorphism in the south (FMR closer to 100). The exception occurred in relative head length, where the sexual dimorphism, female-biased, was greater in the south.

Coloration

In many specimens the pattern was hardly discernible or indiscernible either because the dark spots appeared too faded or because the background was too dark. Both of these could be preservation artifacts but more likely were biological phenomena as described by Werner (1890). A live apparently melanistic individual had once been found in the Hula Reserve (Mendelssohn, pers. comm.). Two specimens from the Golan in the Natural History Museum, Vienna (NMW 26784) represent a dark unspotted variant (Berger-Dell'mour, 1986). A little
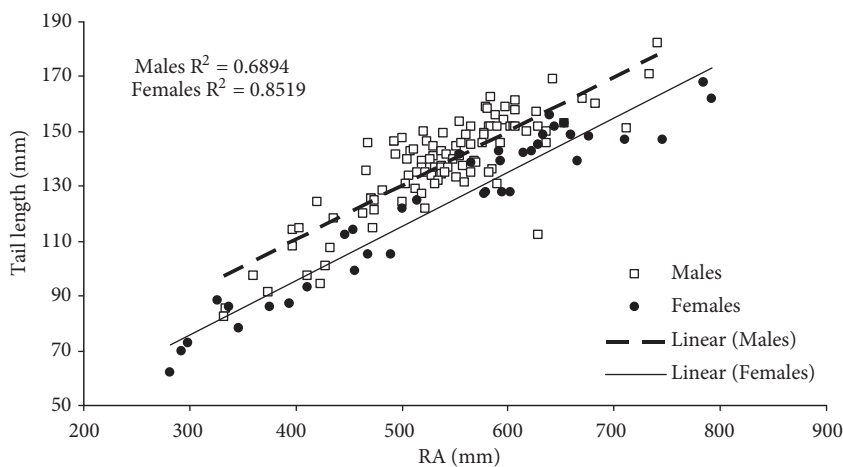

Figure 6. Tail length as a function of RA in *N. tessellata* from Israel and the Golan, in ♂♂ (N = 104, R^2 = 0.6894) and ♀♀ (N = 38, R^2 = 0.8519).
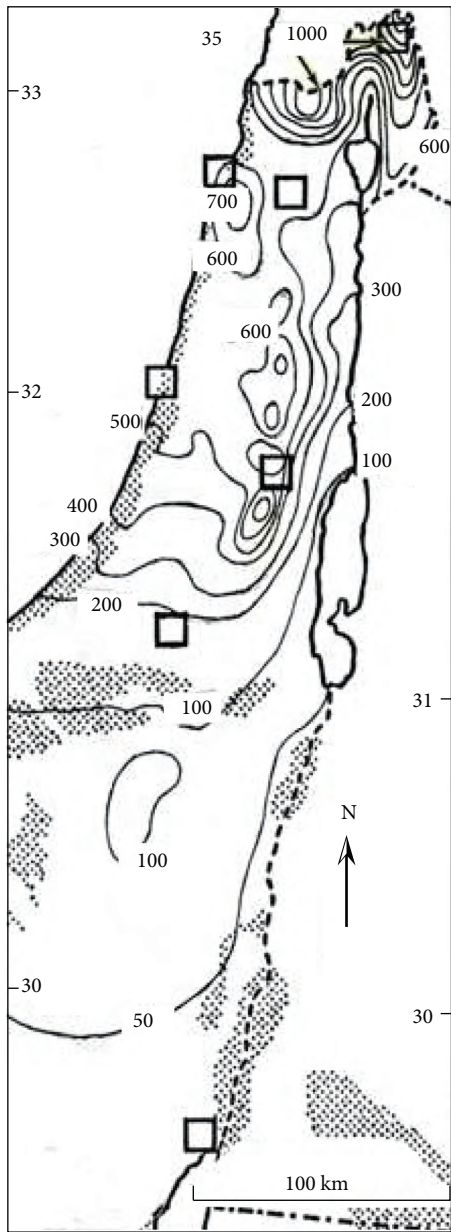
Figure 7. Annual precipitation in Israel, average of the years 1931-1960 (data from Atlas of Israel, 1970).

Usually, when discernible (N = 114), the spaces between neighbouring rows were equal, evidently providing a geometric basis for expansion of the spots that, when more square and touching each other at the corners, would coalesce into the checkered pattern that gave the species its name. In some specimens (16.7%) the mid-dorsal space, separating the 2 dorsal spot rows, was wider, creating a divide between L and R spot systems (Figure 9A).

The number of rows was usually 6, which according to Werner (1890) is the commonest number among snakes (Figure 9B-D). On each side we can term a dorsal row, a dorso-lateral row ("lateral" of Werner, 1890) and a lateral (flank) row ("marginal" of Werner, 1890, but see below). Some specimens with 8 rows had an additional ventro-lateral row, touching the ventral scutes, deserving the term "marginal" (Figure 9E). The 2 dorsal rows were usually not quite symmetrical but a little out of phase with each other, not properly alternating, but laterad the spots of each row were alternating with those of the neighbouring row(s).

The other main variable of the trunk coloration was relative spot size (Figure 9B-D). In some specimens the spots in the dorsal rows were larger than in the other rows (18.7%), a pattern considered by Werner (1890) as the commonest in this species. In others the spots of all rows were of equal (or subequal) size (75.0%), and in yet others the lateral-row spots were enlarged, sometimes into vertical blotches (6.3%). In our material the dorsal spots only rarely fused in pairs to form dorsal cross-bars, as may occur elsewhere in the Middle East (Disi, 2002; Figure 10) and then only on some short section of the body. We observed no specimens with only 4 or 5 rows of spots, a pattern considered typical for this species (Schreiber, 1912; Gruschwitz et al., 1999).

In a small minority of specimens the trunk coloration included small white specks, each covering only a small portion of a scale. If many, specks tended to be arranged in transverse rows alternating with the black spots.

The most interesting variable of the lateral head coloration is the presence, or absence, of a whitish blotch resembling the lunar spot of *N. natrix* ("collar" of Werner, 1890), partly framed above and behind with a blackish marking comparable

north of Israel, in the Ammiq marshes of Lebanon, In den Bosch et al. (1998) saw many melanistic specimens, at least 15 out of 30. Ground colour in the vast majority of specimens was some shade of grey, on which, when discernible, blackish spots with rough edges stood out. The blackish spots were almost always roundish and discrete (not square, not touching) and arranged in orderly longitudinal rows. Werner (1890) stated this to be a primitive pattern in snakes, from which other patterns derived.

Table. Regional differences in *Natrix tessellata* within Israel. For characters with significant sexual dimorphism, FMR values are included.

		N North	N South	Average North	Average South	T-test
RA, mm	F + M	140	21	552.24	502.76	**0.032**
	Males	109	11	540.52	550.45	0.691
	Females	31	10	594.83	450.30	**0.005**
Tail length, mm	F + M	117	21	136.58	121.31	**0.004**
	Males	92	10	138.71	130.90	0.200
	Females	25	11	128.76	112.59	0.132
Tail length, PERCRA	F + M	117	20	25.10	24.46	0.233
	Males	92	10	25.83	24.64	0.069
	Females	25	10	22.43	24.27	**0.001**
	FMR			86.85	98.48	
Ventral scales count	F + M	60	8	164.23	165.63	0.326
	Males	36	6	166.14	166.17	0.985
	Females	24	2	161.38	164	0.132
	FMR			97.13	98.7	
Subcaudals	F + M	56	7	61.16	60.29	0.712
	Males	33	5	64.61	61.4	0.191
	Females	23	2	56.22	57.5	0.588
	FMR			87.02	93.65	
Head length, PERCRA	F + M	60	8	4.35	4.56	0.17
	Males	36	6	4.25	4.43	0.331
	Females	24	2	4.49	4.93	0.086
	FMR			105.47	111.28	
Eye diameter, %HL	F + M	60	8	13.97	14.73	0.074
	Males	36	6	14.3	14.62	0.487
	Females	24	2	13.47	15.03	0.057
	FMR			94.26	102.82	
Eye asymmetry, (R – L)/[R + L)/2]	F + M	100	10	−0.52	−1.85	0.46
	Males	77	7	−0.62	−1.29	0.76
	Females	23	3	−0.16	−3.18	0.376

to the nuchal spot of *N. natrix* ("occipital spot" of Werner, 1890). The pattern occurred distinctively in 5.4% of the specimens (Figure 11) and at various levels of lesser distinctiveness and contrast in additional 6.8% of the specimens. This count may miss some specimens in which the pattern was dubious. In the additional sample of 56 hatchlings, offspring of females from the Ha-Zore'a fishponds, it was distinct in 28.6% and more weakly indicated in 37.5%. Usually the whitish lunar spot of *N. tessellata* continues ventrad to the snake's light ventral coloration (photos in Grillitch and Werner, 2009), in agreement with Werner's (1890) concept, but sometimes it is enclosed by a cranio-ventral extension of the blackish nuchal spot.

Discussion

Variation within individuals: Directional asymmetry and its biological correlates

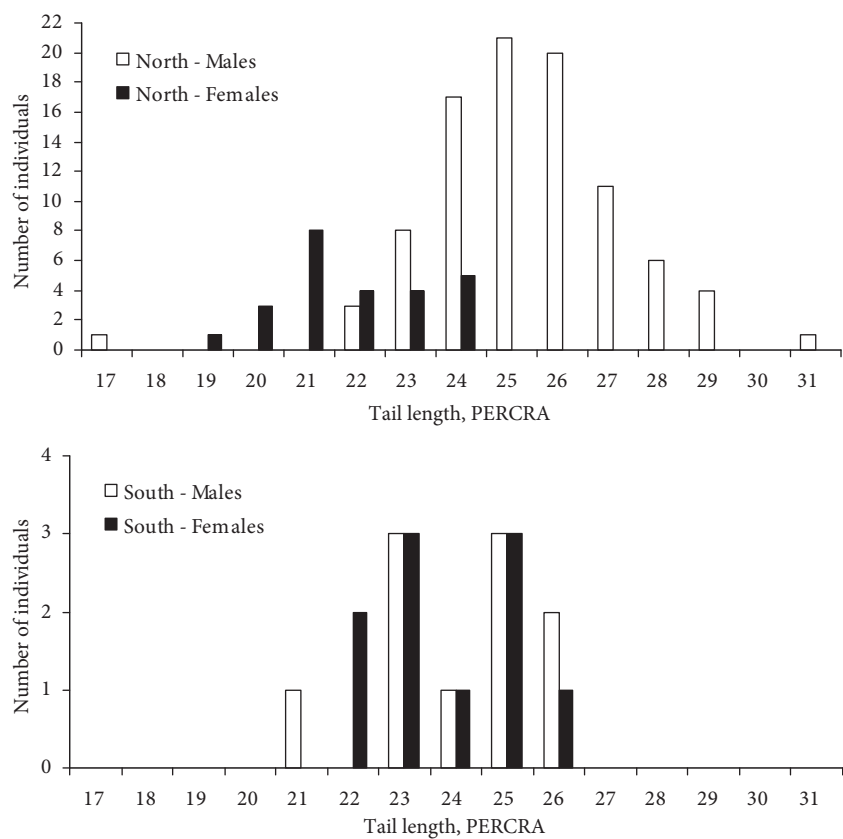In bilaterally symmetrical animals the right–left symmetry is often imprecise. Different types of

Figure 8. Regional difference in sexual dimorphism of relative tail length in *Natrix tessellata* from Israel. In northern Israel (top). In central Israel (bottom).

minor morphological asymmetry can occur (Van Valen, 1962).

Much attention has been paid to fluctuating asymmetry, in which the population average of individual asymmetry is zero. This asymmetry, resulting from imprecision in embryogenesis, is thought to reflect stress on the population. When investigating it, one calculates away the potential other types of asymmetry (Van Valen, 1962; Soulé, 1967; Jackson, 1973; Fox, 1975; Palmer and Strobeck, 1986; Moller and Swaddle, 1997; Graham et al., 1998; Chapman and Goulson, 2000). In a wide-ranging species such as *N. tessellata* it could indeed be interesting to compare the fluctuating asymmetry between populations at marginal locations and environment (e.g., in Israel), and more central populations. Such a comparison was made within Hungary by Herczeg et al. (2005). We lack the data for this.

However, another kind of asymmetry, directional asymmetry (Van Valen, 1962), may occur in reptiles, with assorted implications (Werner et al., 1991). In *N. tessellata* directional asymmetry has not attracted much attention. It may well be rare in this species or distributed unevenly; Mebert (1993) found none in over 400 specimens from Switzerland and northern Italy. The detailed report by Zimmermann and Fachbach (1996) merely mentions the existence of asymmetry, and Gruschwitz et al. (1999) mention the possibility of asymmetry only concerning the pre- and postorbitals, and the source and evidence are unclear. Directional asymmetry was found in the postoculars of *N. tessellata* by Herczeg et al. (2005), who researched fluctuating asymmetry, and therefore excluded the postoculars from further examination. However, the finding of Razzetti et al. (2007) that in this species left-biased asymmetry is correlated with an elevated rate of injuries accords with reports of
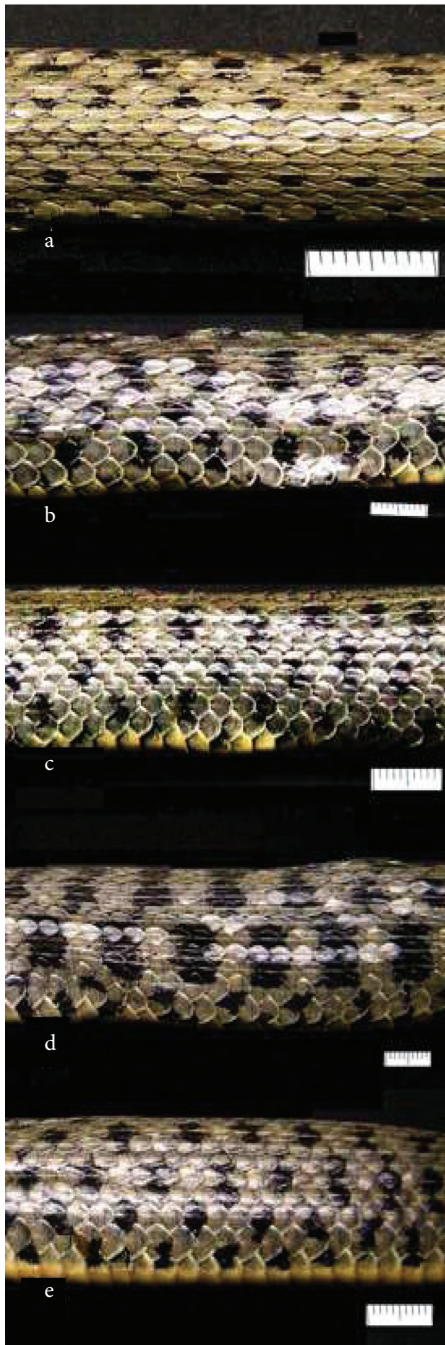
such a link in *Sphenodon*, lizards, and other snakes (Seligmann et al., 2003, 2008; Shacham, 2004). As discussed by Seligmann et al. (2003) and Razzetti et al. (2007), the parallel phenomenon in man has conventionally been explained as resulting from the artificial environment being designed for the right-handed majority.

This attitude should now be reconsidered and it seems more likely that left-handedness expresses some disturbance of organismic harmony. In this case, hypothetically, the left handed individuals would be accident prone, and in the case of squamates, sustain more tail injuries. Alternative hypotheses have been proposed but a full discussion is beyond our scope here (Seligmann et al., 2003; Razzetti et al., 2007).

Variation among individuals

In animals that continue to grow asymptotically after sexual maturity, the character 'body size' is the most difficult character to define and therefore problematic for statistical analysis (briefly reviewed in Meiri, 2007; Seifan et al., 2009). Is the individual considered adult when it stops growing, viz when its growth becomes asymptotic? Or when it is sexually mature (and how is this determined?)? Or already when its sex becomes discernible? Therefore there is a size overlap in our data between the largest "juveniles" (unsexed) and the smallest males and females. We could not define the omnipresent genotypic variation of body size, but could only describe the phenotypic variation within samples defined by sex and district.

The wide variation in the number of ventrals (body segments) observed even within one sex most likely includes a considerable phenotypic effect. The effect of incubation temperature on the number of vertebrae, which operates in all vertebrates and is particularly well known in fish, has long been known in snakes, including Natricinae (Fox, 1948; Fox et al., 1961; Osgood, 1978; Lourdais et al., 2004).

Sexual dimorphism

The expression of sexual dimorphism already in young juveniles, such as tail length in *N. tessellata* (Figure 6), confirmed also in the Alpine region (Mebert, 1993), is rare among squamates, as usually the sexual differences develop during growth (Fitch,

Figure 9. Commonest patterns of dorsal spots in *Natrix tessellata* from Israel.

A, a divide between left and right dorsal spot rows (dorsal view, ♂ HUJR 4553, Tantura Fishponds of Freshwater Fisheries Res. Sta., end April 1959, Ram Moab). B, Six rows, the dorsal row with largest spots. (Lateral view, ♂ HUJR 4517, same data). C. Six rows with spots of roughly equal size (Lateral view, ♀ HUJR 4527, same data). D. Six rows with spots of lateral row largest (Lateral view, ♀ HUJR 3932, En Hamifraz, 28 May 1955, Mary Kabani). E. Eight rows of spots of roughly equal size (Lateral view, ♂ HUJR 4521, data as 4553). (All scale bars, 10 mm).

Figure 10. Live *Natrix tessellata* with dorsal cross bars, the Euphrates Valley in Syria (HUJR 8276, Sabch, 4 km NW of Sabcha, 1 June 1966, Hermann Zinner; photographed by Yitzhak Amit) (scale bar, 10 mm).

Figure 11. *Natrix tessellata* with whitish lunar and blackish nuchal spots from Israel (♂ HUJR 3995, En Hamifraz, 20 June 1955, Grossmann) (scale bar, 10 mm).

1981; Seifan et al., 2009). However, the male-biased sexual size dimorphism of the natricine *Thamnophis sirtalis* is clear already in neonates (Krause and Burghardt, 2007), raising the question of whether this developmental trait is shared by all Natricinae.

Comparison of quantitative characters between samples of adults (such as males versus females) encounters the difficulty that we may wish to compare maximum values that demonstrate the potential of the population but the range and maximum increase with sample size. Hence the data of maximum values

(e.g. of body size or life span) for species and sexes, without sample size, that are so common in the herpetological literature, are scientifically almost worthless (Werner et al., 1993). The routine solution to compare averages is problematic for body size, as explained previously (Seifan et al., 2009). We would therefore prefer the use of the mode, which perhaps best reflects the results of selection, but this is not so common in the literature.

Fatio (1872) already reported measurements of some male and female *N. tessellata* from Switzerland implying that females are larger. Indeed, although many maximum data are invalid, apparently European females attain considerably and probably significantly greater RA than males, have relatively longer heads, shorter tails and lower numbers of subcaudals and (unlike most snakes – Shine 2000) ventrals (reviewed in Gruschwitz et al., 1999). Sexual dimorphism observed in Israel resembles that known from Europe.

Among the characters showing sexual size dimorphism, diergism of head and body size has received some attention. Snakes are gape-limited predators, swallowing their prey whole. Therefore their body size, or at least head size, and the size of their prey are generally correlated (Forsman, 1996 and references therein) to their potential prey (Werner, 1994). This relation of snake and prey sizes is evident among conspecifics of *Natrix* spp. and sometimes expressed in sexual size diergism, females utilising larger prey (Hailey and Davies, 1986; Filippi et al., 1996; Santos et al., 2000; Gregory and Isaac, 2004). Such correlations do not prove causation and in *Nerodia sipedon* (Natricinae) the size of prey consumed by juveniles had a phenotypic effect on the snakes' head and body dimensions (Queral-Regil and King, 1998). However, in *Boa constrictor* the development of sexual size dimorphism was unaffected by the juveniles' prey size (Schuett et al., 2005). In contrast, apparently the generally accepted reproductive role of larger female body size (Cox et al., 2007) has not been addressed for *Natrix*.

Our observations on eye size seem so far unparalleled from Europe, despite the presumed functional importance of eye size. Accepting that eye performance largely depends on its absolute size (Walls, 1942; Werner and Seifan, 2006), and given

that the male *N. tessellata* has a smaller body and a relatively smaller head, the question arises whether males have poorer vision than females (if eye size relative to body or to head is isometric). Similar dilemmas are solved in different ways in different species (Werner and Seifan, 2006; Razzetti et al., unpublished data). In the case of *N. tessellata* the male's eye is enlarged by hyperallometry relative to the head, being only insignificantly relatively smaller than the female's. Unfortunately we lack the data to investigate to what extent the hyperallometry occurs during ontogeny, or is expressed already in juveniles.

Geographical variation

A comparison of some biometric averages between the Israeli population, at the south of the species range, with the next northern population that has been studied, may be of interest. This is the SW Anatolian Lake District population, approx. 6° latitude to the north (or 1100 km overland). This comparison was possible thanks to the doctoral thesis of Yunus Emre Dinçaslan (2005).

When we compare RA length averages of the ♂♂ between Anatolia (N = 22) $\overline{X}$ = 562.3 mm and Israel (N = 121) $\overline{X}$ = 543.4 mm; and RA length averages of the ♀♀ between Anatolia (N = 19) $\overline{X}$ = 562.5 mm and Israel (N = 39) $\overline{X}$ = 556.4 mm, then both sexes appear to be larger in Anatolia. In each population the sexes are of similar size, in Anatolia FMR = 100.04, in Israel FMR = 102.4. This N-S trend is paralleled within Cisjordan (Table 1).

Relative tail length was among ♂♂ in Anatolia (N = 22) $\overline{X}$ = 22.8 PERCRA, and in Cisjordan (N = 104) $\overline{X}$ = 25.72; and among ♀♀ in Anatolia (N = 19) $\overline{X}$ = 22.28 PERCRA, and in Cisjordan (N = 38) $\overline{X}$ = 22.99 PERCRA. Thus while the tail of males was relatively longer in Cisjordan, that of females was similar in both areas, and while in Anatolia FMR = 97.7, in Cisjordan FMR = 89.4. The N-S geographical variation of relative tail length and its dimorphism at the inter-country scale is not paralleled by that seen within Cisjordan (Table 1); rather, they tend to be opposite.

The ventral scales count is among ♂♂ in Anatolia (N = 22) $\overline{X}$ = 174.75 compared with Cisjordan (N = 47) $\overline{X}$ = 167.2, and among ♀♀ in Anatolia (N = 19) $\overline{X}$ = 174.3 compared with Cisjordan (N = 29), $\overline{X}$ = 162.3; in both sexes higher in the north. However, this trend does not continue further to the north and west, and towards Switzerland the number decreases (Mebert, 1993).

Sexual dimorphism occurred only in Cisjordan, and was male-biased. In Anatolia FMR = 99.7, and in Cisjordan FMR = 97.07. Within Israel there was no significant N-S trend in ventral count but the sexes differed a little more in the north (Table 1). Thus body length and the number of segments vary geographically in parallel, as known elsewhere (e.g., Klauber, 1956). In *N. natrix*, too, within most of the southern areas of the wide distribution (in the Iberian Peninsula, in the Balkans, in Anatolia+Cyprus) the ventral counts decrease southwards (Thorpe, 1973).

The subcaudals count is among ♂♂ in Anatolia (N = 22) $\overline{X}$ = 63.45 compared with Cisjordan (N = 47) $\overline{X}$ = 64.9, and among ♀♀ in Anatolia (N = 19) $\overline{X}$ = 60.04 compared with Cisjordan (N = 29), $\overline{X}$ = 57.4; so only in the females did the N-S trend parallel that of the ventrals. In both countries the males had more subcaudals than the females, in Anatolia: FMR = 94.6, and in Cisjordan: FMR = 88.4. Within Israel there was no significant N-S trend in the number of subcaudals but the sexes differed more in the north (Table 1).

In sum, across the Anatolia-Cisjordan N-S gap, *N. tessellata* are larger-bodied in the north and that same trend is indicated within Cisjordan. This appears compatible with Bergmann's rule, according to which mammals are larger at cooler latitudes, applied also to turtles (Ashton and Feldman, 2003; Sacchi et al., 2007). However, at the larger scale Steward (1971) and Zimmermann and Fachbach (1996) have noted that *N. tessellata* is larger in southern Europe than in central Europe. This phenomenon accords with the "reversed Bergmann's rule" that predominates in snakes, viz., conspecifics are larger at the warmer latitudes (Ashton and Feldman, 2003). The difference between the scales of view warrants further investigation.

Coloration

The occurrence of a *N. natrix*-like pattern of whitish lunar and blackish nuchal spots in some

specimens of *N. tessellata* was discovered by Grillitsch and Werner (2009) while investigating whether in the past *N. natrix* had occurred in Cisjordan, from which today it is absent. It transpired that some museum specimens from this area that had been considered to be *N. natrix* were in fact *N. tessellata* possessing this pattern, which had not previously been known in the latter species. The fact that this pattern is absent from *N. tessellata* elsewhere, viz., where it is sympatric with *N. natrix* (Grillitsch and Werner, 2009), generates the hypothesis that initially both sister-species (Guicking et al., 2006) shared this character but in sympatry it disappeared from *N. tessellata* through character displacement (Brown and Wilson, 1956), thus increasing the difference between the 2 species, presumably in the service of reproductive isolation.

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