The northward extension of reptiles in the Palearctic, with the Jordan Valley (Israel) as a model: snakes outrace lizards (Reptilia: Squamata)

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ABSTRACT

The geographical distribution of reptiles is known to be climate dependent. Our analysis of literature data from the Palearctic confirmed that snakes, as a group (186 species), tend to extend further to the north, into cooler climate, than lizards (460 species). This has also been reported for the Nearctic. On a smaller scale, as a model, we investigated the expansion of reptiles from the warm southern desert of Israel northwards along the Jordan valley into cooler climate, based on 587 locality records of 17 species. It transpired that the snakes significantly extend further to the north than the lizards, paralleling and exemplifying the global scale. The ability of snakes to inhabit relatively cooler climates appears to accord with three physiological traits of snakes: lower optimal body temperatures, absence of temperature-dependent sex determination, and ability to thrive on infrequent meals.

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Introduction

The Near East is a meeting place of continents, climate zones, biogeographical regions and ecological regions (Por 1975; Yom-Tov & Tchernov 1988). Especially noticeable is the interface of desert and non-desert. For example, Arnold (1987) pointed out that one of the abrupt boundaries fencing the herpetofauna of the Arabian desert is the one towards the North, where most species do not cross into the more mesic Irano-Turanian region. He listed 11 taxa of lizards (species or whole genera), one amphisbaenian, and one snake genus (Cerastes) as inhabiting the Arabian desert but not penetrating into the more mesic Turkish-Iranian mountains and Tigris–Euphrates system. In the coastal Levant, Cisjordan, or specifically Israel, the gradient from desert to non-desert is particularly abrupt, as the Irano-Turanian is only a scant, sometimes debated, narrow belt between the arid desert and the mesic Mediterranean sensu stricto (Zohary 1962; Danin 1988; Werner 1988). Here the average annual precipitation can drop from >700 mm (near Jerusalem) to <100 mm (near the Dead Sea) over an interval of 20 km (Werner 1987, figure 3).
Consequently within the small area of Israel the local ecological biogeography is rather heterogeneous and complex, and has long attracted the interest of naturalists (Hasselquist 1766; Tristram 1866), botanists (Zohary 1962; Danin 1988) and zoologists (Bodenheimer 1935; Por 1975), including herpetologists (Böttger 1880; Haas 1952; Werner 1988). Squamate reptiles are relatively suitable for eco-biogeographical research because, among vertebrates, they do not fly, are terrestrial and mostly diurnal, and can relatively easily be caught, handled and identified. During 1948–1967, while Israeli scientists could not examine the herpetofauna in Samaria, Judea and most of the Jordan Valley (see map in Werner 1988), a seeming distributional anomaly stimulated much curiosity. Snakes collected or observed on Mt. Gilboa, within the Mediterranean, occasionally included desert species, especially *Echis coloratus*, otherwise recorded only as far north as the Jericho area, 80 km to the south (Mendelssohn 1965, figure 10). It was unknown whether such species truly have disjunct distribution ranges, or whether their ranges continuously extend from the desert northwards into the Jordan Valley all the way to Mt. Gilboa (Wahrman 1959).

After 1967, when the Jordan Valley became accessible, it transpired that indeed the latter was the case and the distribution ranges were not disjunct. Rather, several species of desert squamates have extended their ranges from the Negev desert northwards along the relatively warm Jordan Valley. Of these, the ranges of the arenicolous species were mapped by Werner (1987). However, among the desert herpetofauna extending northwards along the valley, snake records from Mt. Gilboa and vicinity relatively exceeded those of lizards (Werner, unpublished). It was unclear whether this was due to bias in recording (geographical or taxonomical bias, or both) or represented the respective distribution ranges.

The limits of the distribution ranges of animals have long been discussed as being determined by many factors – historical, ecological, and their interactions (Darlington 1957). But on the finer scale, over a small area, biogeography is more likely to be an ecological issue, involving both abiotic and biotic factors, and fine-scale phenomena often exemplify and explain global-scale phenomena (Hengeveld 1990). The biotic factors potentially affecting the distribution of reptiles – predation, parasitism, and, especially, competition – are hard to assess in the Near East due to a dearth of biological information on the relevant species. Among the abiotic factors, temperature has long been emphasized, both in general and specifically for reptiles, these being defined as ‘stenothermal and warmth-loving’ (Hesse 1924; Allee & Schmidt 1951; Cox & Moore 2000). Indeed, temperature emerged as the dominant factor affecting the distribution of snakes in Transjordan, the Hashemite Kingdom of Jordan, when Disi (1987) tested the effects of 14 environmental variables on the spatial distribution of 24 species of snakes.

Therefore this report is aimed at testing the following hypotheses: (1) among desert squamates extending from the Negev desert northwards along the Jordan Valley, the snakes extend farther northwards than the lizards; (2) the different extents of the northwards expansion of the various species along the Jordan Valley can be explained by their respective temperature requirements; (3) the relative distribution of desert lizards and snakes in the Jordan Valley parallels and exemplifies the global distribution of these groups.
Material and methods

Material

For the focal model area, the database of locality records includes all species of Squamata occurring in both the Jordan Valley, within the Great Rift Valley, north of approx. 31.117°N and the Negev desert of southern Israel (Werner 1988), based on the relevant records in the National Herpetological Collection in the Hebrew University of Jerusalem up to HUJ-R 23326 and in Tel Aviv University up to TAU-R 12284. The 17 species are listed in Table 1, with the quantities of records, which total 587 (Sauria, N = 330; Ophidia, N = 257). ‘Records’ refers to voucher specimens in the collections, whose identification can be verified, rather than field notes. The geographical location of these records is mostly based on 1:100,000 topographical maps (Israel Grid = Palestine 1923 Grid) and precise to nearest 100 m; the results are presented in terms of degrees. This material has not been obtained by planned sampling but by opportunistic encounter during the period 1925–2004, including collecting excursions and teaching field-trips.

On the global scale, data on the northward distribution of lizard and snake species (excluding sea snakes) in the Palearctic are from Sindaco and Jeremčenko (2008) and Sindaco et al. (2013). These ‘review’ sources were preferred over the separate genomic taxon revisions in order to maintain more homogeneous and comparable species concepts and accepted as a given sampling project. Comparative comments regarding the Nearctic are based on literature cited where relevant.

Environmental data for the Jordan Valley derive from the Atlas of Israel (1985), and for northern America and northern Eurasia from the Oxford Atlas (Lewis & Campbell 1970) and the Times Atlas (1997).

Table 1. Squamate species in the Jordan Valley, numbers of records of each species, and the northernmost latitude reached by each species.

| Taxon                          | N   | Latitude  |
|--------------------------------|-----|-----------|
| Lizards                        |     |           |
| Acanthodactylus boskianus      | 330 | 32.256°   |
| Mesalina guttulata             | 6   | 31.855°   |
| Pseudotrapelus sinalus         | 200 | 32.174°   |
| Stenodactylus sthenodactylus   | 49  | 31.712°   |
| Tropiocolotes nattereri        | 45  | 31.855°   |
| Uromastyx aegyptia             | 2   | 31.760°   |
| Vauranus griseus               | 3   | 32.046°   |
| Snakes                         |     |           |
| Atractaspis engaddensis        | 52  | 32.489°   |
| Echis coloratus terrae sanctae | 54  | 32.541°   |
| Eirenis coronella              | 32  | 32.785°   |
| Leptotyphlops macrorynchus     | 13  | 32.547°   |
| Platyceps rogeri               | 12  | 31.819°   |
| Platyceps tessellata           | 4   | 32.440°   |
| Platyceps sinai                | 4   | 31.470°   |
| Spalerosophis diadema          | 39  | 32.139°   |
| Telescopus dhara               | 34  | 32.516°   |
| Walterinnesia aegyptia         | 13  | 32.139°   |
Statistics

We used Fisher’s Exact Test for detecting non-random associations between northward extensions of geographic range in the Jordan Valley with relation to the two taxonomic groups (lizards vs. snakes). The same was done for the Palearctic species. Fisher’s Exact Test is used to determine whether there are non-random associations between two categorical variables. It replaces the Chi Square Test, when any square of the contingency table contains too few (<5) data points. Fisher’s Exact Tests were conducted using online resources (Uitenbroek 1997 – http://www.quantitativeskills.com/sisa/).

Results

The northward distribution of desert squamates in the Jordan Valley

The distribution of the locality records of lizards in the study area is shown in Figure 1, and examples for two species are provided in Figure 2: *Mesalina guttulata* (Lacertidae) is the lizard species with the greatest number of individual records (*N* = 200) and shows a clear pattern of extending northwards to approx. isotherm 22°C; *Tropiocolotes nattereri* (Gekkonidae) is based on the greatest sample (*N* = 45) among lizards that extend northwards only to approx. annual isotherm 24°C. The comparable data for snakes are in Figure 3, and two specific examples are shown in Figure 4: *Echis coloratus* (Viperidae) is the snake with most records (*N* = 54) and shows a clear pattern of extending northwards all the way to Mt. Gilboa, approx. isotherm 21°C; *Platyceps rogersi* (Colubridae) (*N* = 12) represents a pattern apparently not extending so far north, approx. to isotherm 23°C. Interestingly the northern population of the former, i.e. that within the study area, was recently described as a distinct subspecies, *E. c. terraesanctae* (Babocsay 2003). Table 1 shows how far north each species was recorded. The most northern record for lizards was approx. 32.222°N, while snakes extended northwards as far as approx. 32.738°N, a difference of approx. 58.7 km. We tested the significance of this difference by Fisher’s Exact Test in two ways. Both at the level of individual records (Table 2) and at the level of species (Table 3), the distributions of lizards and snakes over the areas south versus north of latitude 32.256°N significantly deviated from random.

In statistical sampling, the range grows with the sample size; by the same token, in geographical sampling, the probability to find extreme records may increase as a function of the total number of records. We tested whether the northern limit of the 17 species was correlated with the specific numbers of records (Pearson correlation). There was no correlation (*R* = 0.0808; *P* > 0.05). The result was similar for the lizards alone (*N* = 7, *R* = 0.3023, *P* > 0.05). However, for the snakes alone the correlation was significant (*N* = 10, *R* = 0.5075, *P* = 0.021), and the regression of latitude grid point as a function of sample size was, *Y* = 1969.4*X*+1260.9. Therefore the probability, which always exists, that in the future, as a result of further sampling, yet more northern records will be encountered, appears to be greater for the snakes than for the lizards.
Figure 1. The geographical distribution of all records of lizards in the study area, solid circles. Also indicated are the approximate locations of some key localities for orientation, open squares.
Figure 2. The geographical distribution, in the study area, of the records of two lizard species: *Mesalina guttulata* (Lacertidae), open circles, and *Tropiocolotes nattereri* (Gekkonidae), solid circles. Some key localities for orientation are shown in Figure 1.
Figure 3. The geographical distribution of all records of snakes in the study area, solid circles. Some key localities for orientation are shown in Figure 1.
Figure 4. The geographical distribution, in the study area, of the records of two snake species: *Echis coloratus terraesanctae* (Viperidae), open circles, and *Platyceps rogersi* (Colubridae), solid circles. Some key localities for orientation are shown in Figure 1.
The northward distribution of squamates in the world

Concerning reptile distribution in the Nearctic, it has long been known that squamates are distributed less far to the north in the Nearctic than in the Palearctic due to the different location of the climate zones (Darlington 1957: fig. 28, p.180–182). Within the Nearctic, several authors have agreed that snakes, as a group, extend further northwards than lizards (Darlington 1948: fig. 3; Bleakney 1958: map 6). Logier and Toner (1961) have mapped the locality records of amphibians and reptiles in the northern Nearctic and found that while the lizards, represented by *Elgaria coerulea* (*Gerrhonotus coeruleus*), reach approx. 51°N, the snakes, represented by *Thamnophis sirtalis*, reach about 60°N. Similarly Cook (1984) noted that compared with snakes, lizards have not spread much into northern latitudes in Canada. Indeed, his maps show that of all the Nearctic species only five lizards reach Canada compared with 24 species of snakes.

Our review of the distribution of western Palearctic squamates according to Sindaco and Jeremčenko (2008) and Sindaco et al. (2013) is presented in Table 4. The situation parallels that in the Nearctic. Of the lizards only 7.2%, but of the snakes 11.8%, extend north of 45°N without reaching 50°N, and only 1.5% of the lizards but 4.8% of the snakes extend further northwards. The distribution of the two groups over the latitude belts (Table 5) significantly deviates from the expected (Fisher’s Exact test, \( P = 0.025 \)). However, those with the greatest extent were one lizard, *Lacerta vivipara*, and one snake, *Vipera berus*, both reaching 71°N, both viviparous.

**Table 2.** The distribution of records of lizards and snakes in the Jordan valley over the areas south and north of 32.256°N, compared by Fisher’s Exact Test; \( P \)-value <0.001 (2-tailed).

| Observed specimens | North of lat. 32.256°N | South of lat. 32.256°N | Sum |
|--------------------|------------------------|------------------------|-----|
| Lizards            | 0                      | 330                    | 330 |
| Snakes             | 20                     | 237                    | 257 |
| Sum                | 20                     | 567                    | 587 |

**Table 3.** The distribution of species of lizards and snakes in the Jordan valley over the areas south and north of 32.256°N, compared by Fisher’s Exact Test; \( P \)-value = 0.041 (2-tailed).

| Observed species | North of lat. 32.256°N | South of lat. 32.256°N | Sum |
|------------------|------------------------|------------------------|-----|
| Lizards          | 0                      | 7                      | 7   |
| Snakes           | 5                      | 5                      | 10  |
| Sum              | 5                      | 12                     | 17  |

**Table 4.** The distribution of western Palearctic squamates according to Sindaco and Jeremčenko (2008) and Sindaco et al. (2013) is presented.

**Table 5.** The distribution of the two groups over the latitude belts significantly deviates from the expected (Fisher’s Exact test, \( P = 0.025 \)). However, those with the greatest extent were one lizard, *Lacerta vivipara*, and one snake, *Vipera berus*, both reaching 71°N, both viviparous.

**Thermal requirements of squamates**

One of the general biological attributes by which lizards as a group differ from snakes as a group is their thermal requirements, which tend to be higher for lizards than for snakes. The little that is known of the preferred body temperatures of species included
Table 4. Squamate species in the western Palearctic that extend north of 40°N, and the northernmost latitude limit (full degree) reached by each species, according to Sindaco and Jeremčenko (2008) and Sindaco et al. (2013).

| Lizard species | Limit reached | Lizard species (cont’d) | Limit reached |
|----------------|---------------|-------------------------|---------------|
|                | <50 | <60 | >60 |                | <50 | <60 | >60 |
| Alsophylax laevis | 41 |     |     | Lacerta chlorogaster | 38 |     |     |
| Altiphylax stoliczkai | 41 |     |     | L. lindholm | 46 |     |     |
| Crossobamon eversman. | 49 |     |     | L. parvula | 43 |     |     |
| Cyrtopodion narynense | 41 |     |     | L. portschinskii | 42 |     |     |
| C. kotschyi | 45 |     |     | L. rudis | 44 |     |     |
| C. russowii | 48 |     |     | L. praticola | 45 |     |     |
| C. caspium | 46 |     |     | L. valentini | 42 |     |     |
| C. fedtschenkoi | 42 |     |     | L. saxicola | 46 |     |     |
| Euleptes europaea | 45 |     |     | L. ameniaca | 43 |     |     |
| Hemidactylus turcicus | 46 |     |     | L. rostombekovi | 42 |     |     |
| Tarentola mauritanica | 46 |     |     | L. uzzelli | 41 |     |     |
| Teratoscincus scincus | 48 |     |     | L. dahli | 43 |     |     |
| Laudakia stoliczkana | 41 |     |     | L. unisexualis | 41 |     |     |
| L. caucasica | 44 |     |     | Ophisops elegans | 44 |     |     |
| L. lehmanni | 42 |     |     | Podarcis hispanicus | 46 |     |     |
| L. stellio | 42 |     |     | P. bocagei | 44 |     |     |
| Phrynocephalus mystac. | 49 |     |     | P. erhardi | 43 |     |     |
| P. interscapularis | 47 |     |     | P. melissellensis | 47 |     |     |
| P. guttatus | 50 |     |     | P. lilfordi | 41 |     |     |
| P. melanurus | 50 |     |     | P. taurosurus | 48 |     |     |
| P. persicus | 42 |     |     | P. muralis | 51 |     |     |
| P. saudali | 41 |     |     | P. siculus | 47 |     |     |
| P. ocellatus | 42 |     |     | Psammomromus algerius | 45 |     |     |
| P. strauchi | 41 |     |     | P. hispanicus | 45 |     |     |
| P. rossikowi | 43 |     |     |              |     |     |     |
| Trapelus agilis | 46 |     |     |              |     |     |     |
| Chameleo chamaeleon | 41 |     |     |              |     |     |     |
| Ablepharus bivittatus | 41 |     |     | Typhlops vermicularis | 44 |     |     |
| A. deserti | 47 |     |     | Eryx jaculus | 46.5 |     |     |
| A. kitaibeli | 49 |     |     | E. miliaris | 51 |     |     |
| A. chernovi | 41 |     |     | E. tataricus | 49 |     |     |
| A. pannonicus | 42 |     |     | Boiga trigonta | 41 |     |     |
| Asymblepharus eremch. | 43 |     |     | Coronella austriaca | 62 |     |     |
| A. alaicus | 44 |     |     | C. girondica | 46 |     |     |
| Chalcides chalcides | 45 |     |     | Dolichophis caspius | 49.5 |     |     |
| C. striatus | 46 |     |     | D. schmidti | 43 |     |     |
| C. bedniagai | 43 |     |     | Eirenis collaris | 44 |     |     |
| C. ocellatus | 42 |     |     | E. modestus | 43 |     |     |
| Eumeces schneideri | 43 |     |     | E. punctatolineatus | 41 |     |     |
| Mabuya aurata | 41 |     |     | Elaphe dione | 54 |     |     |
| Mabuya vittata | 41 |     |     | E. quatuorlineata | 45 |     |     |
| Ophiomorus punctatiss. | 41 |     |     | E. sauromates | 50 |     |     |
| Anguis fragilis | 41 |     |     | Hemorrhois hippocrepis | 43 |     |     |
| Pseudopus apodus | 47 |     |     | H. nummifer | 45 |     |     |
| Varanus griseus | 45 |     |     | H. ravernieri | 47.5 |     |     |

(Continued)
in this project is summarized in Table 6 and concerns only five of the 17 species. Among these, the values for the three lizard species are higher than those of the two snake species. However, the body temperature preferences of the two groups have been reviewed by Brattstrom (1965), who from the specific data of 89 lizard species has summarized a group average of 29.1°C (range of specific averages 11–46.4°C) and for 57 snake species derived a group average of 25.6°C (range of specific averages 9–38°C).

Table 4. (Continued).

| Lizard species (cont’d) | Limit reached | Snake species (cont’d) |
|------------------------|---------------|------------------------|
|                        | <50 | <60 | >60 |                        | <50 | <60 | >60 |
| E. szczerbaki          | 42  |     |     | P. rhodorachis          | 46  |     |     |
| E. Stummeri            | 44  |     |     | Rhinechis scalaris      | 45  |     |     |
| E. multiocellata       | 49  |     |     | Rhynchocalamus melanoc. | 41  |     |     |
| E. struchi             | 41  |     |     | Spalerosophis diadema   | 44  |     |     |
| E. lineolata           | 48  |     |     | Telescopus fallax       | 46  |     |     |
| E. pleskei             | 41  |     |     | Zamenis hohenackeri     | 44  |     |     |
| E. scripta             | 49  |     |     | Z. lineatus             | 42  |     |     |
| Lacerta agilis         |     | 62  |     | Z. longissimus          |     | 51  |     |
| L. media               | 46  |     |     | Z. situla               | 47  |     |     |
| L. schreiberi          | 44  |     |     | Natrix maura            | 50  |     |     |
| L. strigata            | 46  |     |     | Natrix natrix           |     | 68  |     |
| L. trilineta           | 46  |     |     | Natrix tessellata       |     | 54  |     |
| L. viridis             | 46  | 53  |     | Malpolon mospessulan.   | 46  |     |     |
| L. lepida              | 46  |     |     | M. insignitus           | 49  |     |     |
| L. danfordi            | 42  |     |     | Psammophis lineolatus   | 49  |     |     |
| L. mosorensis          | 44  |     |     | Naja oxiana             | 43  |     |     |
| L. oxycephala          | 44  |     |     | Glodius halys           | 54  |     |     |
| L. bedriagae           | 43  |     |     | Echis carinatus         | 44  |     |     |
| L. aranica             | 43  |     |     | Macroviper a lebetina   | 44  |     |     |
| L. aurelioi            | 43  |     |     | Montivipera raddei      | 41  |     |     |
| L. bonnali             | 44  |     |     | M. wagneri              | 41  |     |     |
| L. creni               | 42  |     |     | M. xanthina             | 42  |     |     |
| L. horvathi            | 48  |     |     | Vipera ammodytes        | 47  |     |     |
| L. monticola           | 44  |     |     | V. aspis               | 50  |     |     |
| L. parva               | 41  |     |     | V. latastei             | 43  |     |     |
| L. vivipara            |     | 71  |     | V. berus               |     | 71  |     |
| L. alpina              | 44  |     |     | V. seoanei              | 44  |     |     |
| L. clarkorum           | 42  |     |     | V. darevskii            | 42  |     |     |
| L. daghestanica        | 44  |     |     | V. dinniki              | 44  |     |     |
| L. mixta               | 43  |     |     | V. kaznakovi            | 45  |     |     |
| L. caucasic            | 44  |     |     | V. magnifica valid?     | 45  |     |     |
| L. nairensis           | 42  |     |     | V. orlovi valid?        | 45  |     |     |
| L. derjugini           | 45  |     |     | V. altaica              | 48  |     |     |
| L. raddei              | 42  |     |     | V. renardi              |     | 56  |     |
| L. brauneri            | 45  |     |     | V. ursinii             | 48  |     |     |

Table 5. The distribution of lizards and terrestrial snakes over the latitude belts in the western Palearctic.

| Degrees | Species of lizards | Species of snakes |
|---------|--------------------|-------------------|
|         | Number | %     | Number | %     |
| ≤ 40    | 346    | 75.2  | 124    | 66.7  |
| ≤ 45    | 74     | 16.1  | 31     | 16.7  |
| ≤ 50    | 33     | 7.2   | 22     | 11.8  |
| ≤ 60    | 4      | 0.9   | 6      | 3.2   |
| > 60    | 3      | 0.5   | 3      | 1.6   |
| All     | 460    | 100.0 | 186    | 100.0 |
Environmental data for the Jordan Valley and on the global scale

In the Jordan Valley environmental variables show a north–south gradient. Ambient temperature recedes from south to north, so that isotherms approximately parallel the northern limit of the lizards, 32.222°N: In the annual average for 1940–1949, the 23°C isotherm occurs at 32.178°N; in the average of the coldest month, January, the 14°C isotherm is at 32.274°N; and in the average of the hottest month, August, the 30°C isotherm is at 32.206°N. Precipitation increases from south to north. In the average annual rainfall for the years 1921–1950, the 200 mm isohyet passes at 32.136°N and the 300 mm isohyet at 32.500°N. Phytogeographically, it has traditionally been considered that the Saharo-Sindian, with Sudano-Dekanian enclaves, extends northwards up to about 32.183°N (Atlas of Israel 1956).

On the global scale, temperatures drop off towards north such that the climate of northern North America is colder than that of northern Eurasia. For example at latitude 60°N the average monthly temperature of July approximates 10–16°C in America but 16–21°C in Eurasia, hence about 5°C lower in America than in Eurasia (Lewis & Campbell 1970). In other terms, the area of subarctic climate starts in North America around 47°N, but in western Eurasia at around 60°N and in the east around 50°N so in America very roughly approx. 8 degrees latitude further south than in Eurasia (Times Atlas 1997).

Discussion

The results are compatible with all three hypotheses set out in the Introduction and appear to support them: (1) among the desert squamates whose distribution extends northwards along the Jordan Valley, the snakes extend farther northwards than the lizards; (2) this difference between lizards and snakes as groups accords with their respective temperature requirements; (3) the same distributional difference between lizards and snakes occurs also between the global distributions of these groups. This outcome is understandable in the light of the following circumstances.

Reptiles, being ectothermic, physiologically depend on the environmental temperature, on access to insolation, or on both, for attaining and maintaining a body temperature at which their body systems function well (Huey 1982). Ecologically,

### Table 6. Optimum body temperature in the lab or body temperature measured in the field of reptile species occurring in the Jordan Valley.

| Species                  | Body temperature | Source                                |
|--------------------------|------------------|---------------------------------------|
| Acanthodactylus boskianus| 39.2°C           | Duvdevani and Borut, 1974             |
| Pseudotrapelus sinaitus  | 39 ± 0.4°C       | Hertz and Nevo, 1981                  |
| Varanus griseus          | 32.1–38.4°C      | Sokolov et al., 1975                  |
| Echis coloratus          | 30.7°C           | Al-Johany and Al-Sadoon, 1996         |
| Spalerosophis diadema    | 29.9°C           | Dmi’el and Borut, 1972                |

a Outdoor cages – direct sunlight during the day (No heating).
b Mean body temperature in early summer.
c Body Temperature during period of normal activity.
d Body temperature during the day. During the night = 27.6°C.
e Outdoor cages with option of cooler shade, but not in a real temperature gradient.
both the optimal temperature for digestion and growth and a tolerable, workable, temperature for foraging (locomotion and other functions) must be available for a sufficient amount of time during the year (Bustard 1968; Huey 1982). Therefore biogeographically the abundance and diversity of reptiles peak in the world’s warmer regions, both in reality and in public awareness (Darlington 1957). Where reptiles occur in cool, thermally marginal areas, they often fail to sustain an annual reproductive cycle. Thus the European Vipera berus reproduces biennially (Nilson 1981), and in New Zealand Sphenodon punctatus females oviposit only every few years (Newman et al. 1994).

Moreover, for many species of reptiles the survival of populations, and hence of taxa, depends on temperature in an additional and complex way, as the sex of the hatchling depends on the incubation temperature during embryogenesis. One sex is produced at high temperatures, the other at relatively low temperature, and a viable sex ratio at intermediate temperatures. Such environmental sex determination occurs in all crocodiles, many turtles and several lizards of different families (Janzen & Paukstis 1991). For these species the range of distribution is limited by the availability of incubation temperatures at which both sexes are produced, and their survival may be threatened by global climate change (Gibbons et al. 2000).

Among the reptiles, snakes as a group are in three ways relatively preadapted to live also in relatively cooler areas: (1) As a group they tend to have lower thermal requirements than lizards, as detailed above (Brattstrom 1965); (2) They do not have, or are not known to have, environmental sex determination (Janzen and Paukstis 1991; Ciofi & Swingland 1997); (3) As extreme predators, they thrive well on a regime of infrequent large meals, obtained during widely spaced short periods of warmer temperature (Greene 1997). A fourth trait has been suggested by an anonymous referee: the ability of snakes to utilize endothermic prey (predominant in the cold latitudes). But this would not apply to small snakes, including juvenile Vipera berus, nor to Natrix natrix, the second of the two ophidians with greatest northern extent, reaching 68°N.

Given this background together with the results described above, it is not surprising that a wide consensus has long attributed to climate and temperature the limitation to the geographical distribution of reptiles, either generally (Merriam 1894; Hesse 1924) or locally (Guisan and Hofer 2003; Anadón et al. 2006). Nevertheless, depending on location and circumstances, some investigators have reported only moderate effects of climate on reptile distribution (e.g., Licht et al. 1966).

The relationship, mediated by temperature, between the spatial distribution of reptiles and geographical latitude is modulated by altitude. The effect of elevation on reptile distribution has been reviewed before (Nathan & Werner 1999; Fischer & Lindenmayer 2005). It has long been formulated that an altitude difference of 100 m approximates the temperature difference of one degree latitude, 1°C (Allee et al. 1949; Brown & Gibson 1986). To some extent this is an over-simplification. First, the effects of altitude on mountains and of latitude differ in details, for example in the former the conditions are more stable (Darlington 1957). Second, the biological implication of the altitude depends on the latitude (climatic zone) of the mountain (Janzen 1967; Huey 1978; Ghalambor et al. 2006). In the Jordan Valley, from the southern end of the Dead Sea (approx. 31°N; −400 m a.s.l.) to the northern end of the Sea of Galilee (approx. 33°
N; −200 m a.s.l.) the distance is two degrees, and the rise in altitude approx. 200 m. These approximately explain the corresponding decrease in average temperatures, almost 4°C (Atlas of Israel 1985).

**Conclusions**

When the distributions of guilds of lizards and of snakes in the northern hemisphere are compared, the snakes extend further to the north, into cooler climates, than the lizards. This phenomenon is seen both at the global scale and at the more detailed local scale of the Jordan Valley in the Levant. Here the ability of snakes to inhabit relatively cooler climates may clearly be ascribed to three physiological traits: lower optimal body temperatures, absence of temperature-dependant sex determination, and ability to thrive on infrequent meals.

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