Bergmann's and Rensch's rules and the spur-thighed tortoise (*Testudo graeca*)

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Body size is an ecologically important variable in animals. The geographical size variation of most snakes and some lizards counters Bergmann's rule in that, among related taxa, the larger ones live at warmer latitudes. However, exceptions notwithstanding, and despite being ectothermic, turtles as a group tend to obey Bergmann's rule. We examined this idea in *Testudo graeca*, ranging from Morocco to Romania and to Iran with disputed systematics, both at the global scale (using literature) and within the focal area of Israel (using museum specimens). Both globally and locally, carapace length correlated with latitude, in accordance with Bergmann's rule. The scant data on reproduction fully support the hypothesis that Bergmann's rule enables larger clutches where the climate would limit repeated clutches. The sexual size dimorphism (SSD) was approached using two methodologies: (1) 'conventional', using globally literature data and locally museum samples and (2) 'innovated', using photographs of copulating tortoises from Israel and Turkey. By each methodology, SSD emerged as being male biased in the larger-bodied populations and female biased in the smaller-bodied populations, obeying Rensch's rule. Some observations support the hypothesis that the evolution of large males serves intermale combating. Finally, Rensch's rule was found to apply separately within Anatolia and within the Levant, possibly indicating that these populations are separate. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **117**, 796–811.

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INTRODUCTION

Body size is an important variable in animal species where many ecological implications affect both survival and fitness. As an over-simplified review, some implications derive directly from sheer size. Concerning survival, in the interaction with the abiotic environment, body size limits what shelter can be entered and determines what structure of microhabitat can be negotiated. In the interaction with the biotic environment, size decides where the species stands in the gradient between being predator and being prey, affects its performance as both herbivore and carnivore and its food requirements, and directs its predation avoidance. Moreover, the performance of some organs (e.g. the vertebrate's eye and ear) depends on the organ's absolute size (Werner & Seifan, 2006; Werner *et al.*, 2008). Concerning fitness, maternal body size sets the ranges of variation optional for the number and size of the propagulae. Other implications derive from the size-dependent ratios between length of body and limbs, body surface area, and body volume and mass. These range from locomotion through metabolism to thermal relations. The latter differ between ectotherms and endotherms but are influential in both (Peters, 1983). Naturally, species differ in body size and this variation supports their abundance. By the same

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token, size variation occurs of necessity also within species.

Body size variation among related species or among subspecies of a species (some clusters of taxa may be the one or the other) often shows an ecogeographical pattern. In this respect, Bergmann (1847: 648) said 'it is obvious that on the whole the larger species live farther north and the smaller ones farther south' [as translated by James (1970)]. This concerned groups of related species, allopatric and often vicarious, and was preceded by a detailed explanation of the thermal effects of the size-dependent volume-surface relation in endotherms (i.e. mammals and birds). However, later, it transpired that the rule is followed also by many ectotherms (Atkinson, 1994; Atkinson & Sibly, 1997; Partridge & Coyne, 1997), including crustaceans (Sastry, 1983) and certain insects (Arnett & Gotelli, 1999; Angilletta & Dunham, 2003), although some other species appeared to counter the rule (Masaki, 1967, 1978; Mousseau, 1997; Muñoz, Wegener & Algar, 2014).

Concerning vertebrate ectotherms, the validity of Bergmann's rule has been debated for each group. Fish have been reported both to follow the rule (Lindsey, 1966) and disregard it (Belk & Houston, 2002). Similarly, all groups of Amphibians have been found both to obey (Lindsey, 1966) and, with the exception of at least some salamanders, disobey it (Ashton, 2002; Adams & Church, 2007). Lizards have been reported to disregard or even counter the rule, being larger in the warmer latitudes (Lindsey, 1966; Ashton & Feldman, 2003; Pincheira-Donoso, Tregenza & Hodgson, 2007; Muñoz *et al.*, 2014), although some were shown to follow it (Angilletta *et al.*, 2004; Cruz *et al.*, 2005; Olalla-Tarraga, Rodriguez & Hawkins, 2006). Snakes as a group appear to counter the rule (Ashton & Feldman, 2003; Olalla-Tarraga *et al.*, 2006; Feldman & Meiri, 2014) but some do conform with it (Lindsey, 1966). Blackburn, Gaston & Loder (1999) suggested that such controversies may result from different studies having tested the rule at different taxonomic levels. As a redefinition, they stated that 'Bergmann's rule is the tendency for a positive association between the body mass of species in a monophyletic higher taxon and the latitude inhabited by those species'.

Despite the occurrence of some giant species in tropical areas, turtles as a group appear to enjoy a consensus where, although the evidence is poor, overall they conform with Bergmann's rule (Ashton & Feldman, 2003; Sacchi *et al.*, 2007). These observations in the northern hemisphere are mirrored in the southern hemisphere. In South America, the populations (or subspecies) of *Chelonoidis chilensis* constitute a size gradient increasing with increasing latitude (Fritz *et al.*, 2012). In Africa, *Stigmochelys*

pardalis are larger in the Cape area than elsewhere (Boycott & Bourquin, 2000). Moreover, this widespread species is smallest in many of the equatorial populations, and larger both south and north (including Ethiopia and even Somalia) of these (Fritz *et al.*, 2010). These circumstances led us to investigate the widespread, but in this respect almost neglected, *Testudo graeca* Linnaeus, 1758. A preliminary investigation has already indicated that, at least within Israel, this species appears to conform with Bergmann's rule (Meiri *et al.*, 2011/2012).

However, because *T. graeca* is sexually sizedimorphic (Camerano, 1877; Buskirk, Keller & Andreu, 2001), we must also heed another rule concerning the body size of animals. According to Rensch's rule (Abouheif & Fairbairn, 1997; Fairbairn, 1997), among related species, sexual size dimorphism (SSD) is male biased in the larger species, where its magnitude is correlated with species body size (Reiss, 1986, 1989); in the smaller species, it is female biased (Fitch, 1978) and negatively correlated with body size (Fairbairn & Preziosi, 1994). Indeed, as explained by Seifan *et al.* (2009), Rensch himself never formulated this rule; he discussed sexual dimorphism, not SSD (Rensch, 1950). The rule was apparently first expressly formulated by Fitch (1981: 37, 41).

The validity of Rensch's rule has been demonstrated in many assorted animals, from copepod crustaceans through mammals (Abouheif & Fairbairn, 1997), irrespective of thermal physiology. Of the reptiles, overall conformity with Rensch's rule was reported for lizards and snakes in the reviews of Fitch (1981) and Cox, Butler & John-Alder (2007), despite the nonconformity of some subordinate taxa (Nevo, 1981), and despite Abouhaif and Fairbairn (1997) listing Fitch's (1981) review as not supporting the rule.

Regarding turtles, Berry & Shine (1980) noted that, in terrestrial species, the males are the larger sex and the SSD is greater in the larger species, which appears to be compatible with Rensch's rule. Their terrestrial material comprised twenty Testudinidae (eight of them of the genus *Chelonoidis* comprising the giant Galapagos tortoises) and two Emydidae (genus *Terrapene*). By contrast, Gibbons & Lovich (1990) found that, in turtles in general, the SSD tends to be female biased, and its extent is not related to specific body sizes. In a more extensive review, Cox *et al.* (2007) concluded that, of the two turtle lineages in which male-biased SSD and male combat are common, Kinosternidae follow Rensch's rule but Testudinidae do not. Subsequently, Halámková, Schulte & Langen (2013) found that Testudinidae is the only chelonian family following Rensch's rule.

Moreover, specifically for *T. graeca*, the SSD has been reported both as male biased (Camerano, 1877; Berry & Shine, 1980) and as female biased (Buskirk *et al.*, 2001; Meiri *et al.*, 2010, 2011/2012). These additional doubts regarding the geographical and sexual variation of body size in Testudinidae and within *T. graeca* increase the need for clarification of the situation, and justify using *T. graeca* as a model. Knowledge of the patterns of variation is a prerequisite to investigating the function(s) of body size and of its sexual difference.

This present study aimed (1) to examine and confirm the validity of Bergmann's and Rensch's rules for *T. graeca s.l.* as a model testudinine; (2) to pioneer a preliminary exploration of potential implications for the taxonomic structure of the *T. graeca* complex; and (3) to explore the relevance of the main hypotheses on the biological implications of the observed variation in body size.

MATERIAL AND METHODS

Testudo graeca, debatably a species or a species complex, ranges, principally in the Mediterranean, from southern Morocco in the west to Romania in the north, and to Iran and Turkmenistan in the east. Over this wide distribution, much taxonomic splitting has been proposed, although subdivisions to only approximately six subspecies appear to be realistic (Iverson, 1992a; Parham *et al.*, 2006; Fritz *et al.*, 2007, 2009). For the present purpose, we initially consider all of them together as one unit. The identification of individuals as belonging to this unit relies, amongst other things, on the characteristic thigh spurs, despite the rare exceptions when these spurs are missing (Werner, 1985). Where we view regional subdivisions of *T. graeca s.l.*, we lump the African lineages (including their Iberian and island offshoots) under *T. g. graeca s.l.* These are genomically relatively close to each other and together are as far from the various Eurasian subspecies as the latter are from each other (Fritz *et al.*, 2009). Thus, we disregard the finest possible taxonomic subdivision (Fritz *et al.*, 2009; Graciá *et al.*, 2015), for which our data would not suffice.

Body size was represented by straight carapace length (SCL) *sensu* Lovich, Ernst & McBreen (1990). Measurements of all specimens were taken with 500 mm digital calliper rules (Guilin *Guanglu* Measuring Instrument Co. Ltd) when the specimen was resting stably upside down on a trio of adjustably spaced upright pegs anchored in a heavy wood block (courtesy Frank W. Maurer Jr).

Geographically, our material comprised two levels. For range-wide data ('globally'), we used published reports from the assorted locations ($N = 31$) listed in Table 1. For the focal area of Israel, defined for this purpose as the area under the enforcement of the Israel Nature and Parks Authority, we used adult museum specimens (SCL > 80 mm) housed in the Zoological Museum of Tel Aviv University ($N = 47$) and in the National Natural History Collections at the Hebrew University of Jerusalem ($N = 47$). Additionally, three individuals were photographed alive in the field, with a scale, in an informative manner (Fig. 1).

The SCL characterizing and representing each sex of a given 'population' (material reported from a given local project) was defined in two ways. First, as the means of the adult males and females. This had weakness in that both the definition of adulthood and the 'population structure' (size distribution) of the encountered animals varied among projects. Second, as the maximum SCL attained in each sample (of given location and sex). This suffers the obvious statistical constraint that the maximum is a function of sample size, which varied among locations and between sexes. We explain our choices in the Results,.

To explore whether 'globally', throughout its geographical range, *T. graeca* geographically varies in accordance with Bergmann's rule as predicted, we used representative SCL values from 31 research projects between Morocco (31°N) and northern Iran (48°N) (Table 1). We excluded some data from Greece (Willemsen & Hailey, 1989, 2003) as a result of geographical uncertainty and some from Spain (Buskirk *et al.*, 2001) because the unpublished source report (Perez *et al.*, 1998) was not located. We separated the sexes because of the strong and variable SSD. To relate SCL to degrees latitude, we adopted the simplified version, ignoring altitude, where each 180 m difference may approximate a difference of one degree latitude (Masaki, 1967, 1978).

One a priori relatively plausible hypothesis on the biological background to Bergmann's rule relies on the effect of maternal body size on the number and size of eggs (Rothermel & Castellón, 2014). We searched the literature for reproductive data. We derived egg volume from linear measurements and approximated through the formula for the volume of a prolate ellipsoid, V (in ml) $= R_L R_W^2 \pi \, 4 : 3 : 1000$, where R_L is the long radius (in mm) and R_W is a short radius. Using four projects where egg mass was also taken, we verified that this was well represented by the calculated volume ($N = 4$, $r = 0983$, $P = 0.017$).

For quantifying the SSD, we used Fitch's (1976, 1981) female to male ratio (FMR) (i.e. female length as a percentage of male length) to optimize comparisons with previous data. The FMR has been

Table 1. Range-wide samples of *Testudo graeca*, by subspecies, as defined for the present study

Subspecies for the present study	Location	Latitude (N)	Females			Males			FMR based on means	FMR based on maxima	Reference
			N	SCL mean (mm)	SCL maximum (mm)	N	SCL mean (mm)	SCL maximum (mm)			
armeniaca	East Anatolia	39.8	11	192.3	220	15	171	187	112.7	117.6	Türkozan *et al.* (2010)
buxtoni	South-east Anatol	37.8	5	214	273	8	195	205	109.7	133.2	Türkozan *et al.* (2010)
buxtoni	North-west Iran	47.8	12	171.2	300.2	20	223	460	76.9	65.2	Rezazadeh, Alucheh & Kami (2014)
graeca s.l.	Jbilet Morocco	31.8	42	152.2	202.2	40	125	172	121.5	117.4	Carretero *et al.* (2005)
graeca s.l.	Algir	36.8	33	150.7	205	35	138.4	155	108.9	132.3	Rouag *et al.* (2007)
graeca s.l.	Southern Morocco	30.3		184.9	206		145	169	127.6	121.9	Bayley & Highfield (1996)
graeca s.l.	Donana, Spain	37.0	15	175	210.8						Diaz, Keller & Andreu (1996)
graeca s.l.	Essaouira, Morocco	31.8	47	169.7	213.5	44	144	183	117.5	116.4	Carretero *et al.* (2005)
graeca s.l.	Admine, Morocco	30.5	26	182.7	226.2	44	151	184	121.1	122.7	Carretero *et al.* (2005)
graeca s.l.	Donana, Spain	37.0	58	166.1		133	139		119.4		Buskirk *et al.* (2001)
graeca s.l.	Tetuan, Morocco	35.3	10	170.6		14	174		98		Pieh & Perälä (2004)
graeca s.l.	Tarmilete, Morocco	33.2	21	138.5		17	130.4		106.2		Pieh & Perälä (2004)
graeca s.l.	Cyrenaica	32.8	14	172.4		18	149.4		115.4		Pieh & Perälä (2002)
graeca s.l.	Tunisia	35.5	58	129.9		34	121		107.4		Pieh & Perälä (2002)
ibera	Izmir	38.5	9	186.9	205	7	187	242	100.1	84.7	Türkozan *et al.* (2010)
ibera	Epanomi, Greece	40.4	15	189	214						Hailey & Loumbourdis (1988)
ibera	Dobrogea, Romania	44.5	76	196	239	74	196	218	100.0	109.9	Buică, Iosif & Cogălniceanu (2013)
ibera	Central Anatolia	37.7	10	224.8	248	6	211	246	106.5	100.8	Türkozan & Olgun (2005)
ibera	Anatolia	39.0	264	199.4	269	257	184	265	108.7	101.5	Türkozan *et al.* (2010)
ibera	Macin, Romania	45.2				100	200	301			Cogălniceanu *et al.* (2010)
ibera	Romania	44.5		203.2			209		97.2		Fuhn & Vancea (1961)
ibera	Kolchis	45.2			240			210		114.3	Inozemtsev & Pereshkolnik (1994)
ibera	European Thrace	41.5	9	185	233	23	174	199	106.3	117.1	Türkozan & Olgun (2005)
ibera	Anatolian Thrace	40.5	23	173	213	23	167	187	103.6	113.9	Türkozan & Olgun (2005)
terrestris	Jordan	31.5	30	139	178	38	129	185	107.8	96.2	Disi (1998)
terrestris	Israel	31.8	34	137.2	185.1	40	118	157	115.9	117.6	This paper
terrestris	Hatay, S. Anatolia	36.5	8	144.6	188	8	138	155	104.9	121.3	Türkozan *et al.* (2010)
terrestris	Mardin, S. Anatolia	37.3	8	208.6	238	16	204	239	102.4	99.6	Türkozan & Olgun (2005)
terrestris	South-east Anatolia	37.5	37	202.7	248	29	203	240	99.9	103.3	Türkozan *et al.* (2010)
terrestris	Golan	33.1	14	166.9	257.5	9	145	189	115.4	136.3	This paper
terrestris	South Anatolia	36.5	21	211.6	260	30	193	235	109.8	110.6	Türkozan *et al.* (2010)

Figure 1. Photographing a tortoise in the field, with a 10 cm ruler raised on a stone to the level of greatest carapace length. The shell of this individual is healing after an injury, perhaps as a result of fire (Ma'ale Gamla, Golan Plateau, 24 April 2003; photograph by YLW).

criticized, especially for being asymmetrical (Lovich & Gibbons, 1992; Shine, 1994; Smith, 1999). However, the scaling of the fitness gain of a relatively larger male and the scaling of the fitness increase of a relatively larger female cannot be compared.

We checked conformity with Rensch's rule, too, by relating FMR to degrees latitude (North), as a lumping proxy for all SCL values (of females, males, and means), in two ways. First, using the representative FMR values derived from the SCL values for males and females of the various relevant geographical samples. Second, using 'individual' FMR values derived from the SCL measures of naturally matched males and females adequately photographed when copulating (nine pairs from Turkey, six from Israel plus one from Jordan).

Statistical analysis were performed using EXCEL 97–2003 (Microsoft), and, especially to verify significance, SPSS, version 21.0 (IBM Corp.). The tests used are named as appropriate. Some were one-tailed, when the assumption was obviously unilateral; this is always indicated. $P < 0.05$ was considered statistically significant.

RESULTS

Geographical variation of body size

When we represented the SCL by the sample means (regarding the maxima as corrupted by variation of sample size), on the global scale, SCL was significantly correlated with the degrees latitude (for females, $N = 29$, $r = 0.419$, $P = 0.024$, two-tailed; for

males, $N = 28$, $r = 0.747$, $P < 0.000$, two-tailed). When we represented the SCL by the samples' maxima, SCL was similarly correlated with the degrees latitude (for females, $N = 25$, $r = 0.472$, $P = 0.017$, two-tailed; for males, $N = 24$, $r = 0.642$, $P = 0.001$, two-tailed). Thus, *T. graeca s.l.* clearly conforms with Bergmann's rule.

However, it has been noted that, at the lowest taxonomic levels, Bergmann's rule tends to be less apparent (Bergmann, 1847; as translated by James, 1970; Blackburn *et al.*, 1999). Therefore, we segregated the data by subspecies (sometimes considered species) and, within each sex, tested again for correlation of representative (mean) SCL with latitude. Figure 2 shows that the occurrence and level of conformity with Bergmann's rule indeed varied across taxa. Among females, in *T. graeca graeca*, $N = 11$, $r = -0.350$, $P = 0.291$ (two-tailed); in *T. g. ibera*, $N = 8$, $r = -0.159$, $P = 0.706$ (two-tailed); and only *T. graeca terrestris* shows significance, $N = 7$, $r = 0.773$, $P = 0.042$ (one-tailed). Similarly among males, in *T. g. graeca*, $N = 10$, $r = -0.056$, $P = 0.878$ (two-tailed); in *T. graeca ibera*, $N = 8$, $r = 0.250$, $P = 0.551$ (two-tailed); and only *T. g. terrestris* shows significance, $N = 7$, $r = 0.843$, $P = 0.017$ (one-tailed).

To also confirm that, within the small area of Israel, the SCL of *Testudo graeca* geographically varies in accordance with Bergmann's rule, as indicated previously (Meiri *et al.*, 2010, 2011/2012), we subdivided the study area into a south–north series of five latitude zones (Fig. 3), from which we had similarly sized samples of museum specimens augmented by some photographed in the field (Table 2). Because we had similarly sized samples, we could represent them by their maximum values. The correlation of the maximum SCLs per zone with the latitude degrees of the zones from which they originated was significant ($N = 5$, $r = 0.940$, $P = 0.017$, two-tailed).

Variation of reproductive variables

We reviewed the available data on reproduction in *T. graeca* that could relate to the geographical variation in female body size. Although particularly desirable because of the debated systematics, information on *T. graeca* reproduction is scant (Fritz, 2004). The animals are considered endangered and data collection in nature is constrained. Even careful extensive captivity research data are often inadequate for geographical comparison (Lapid *et al.*, 2004; Lapid, 2013). Moreover, although the issue is rare, there is a caveat not to misinterpret extra large eggs that likely contain twins (Jeffrey, Fox & Smyth, 1953; Petty & Anderson, 1989) or Siamese twins (Göçmen, 2012; Lapid, 2013).
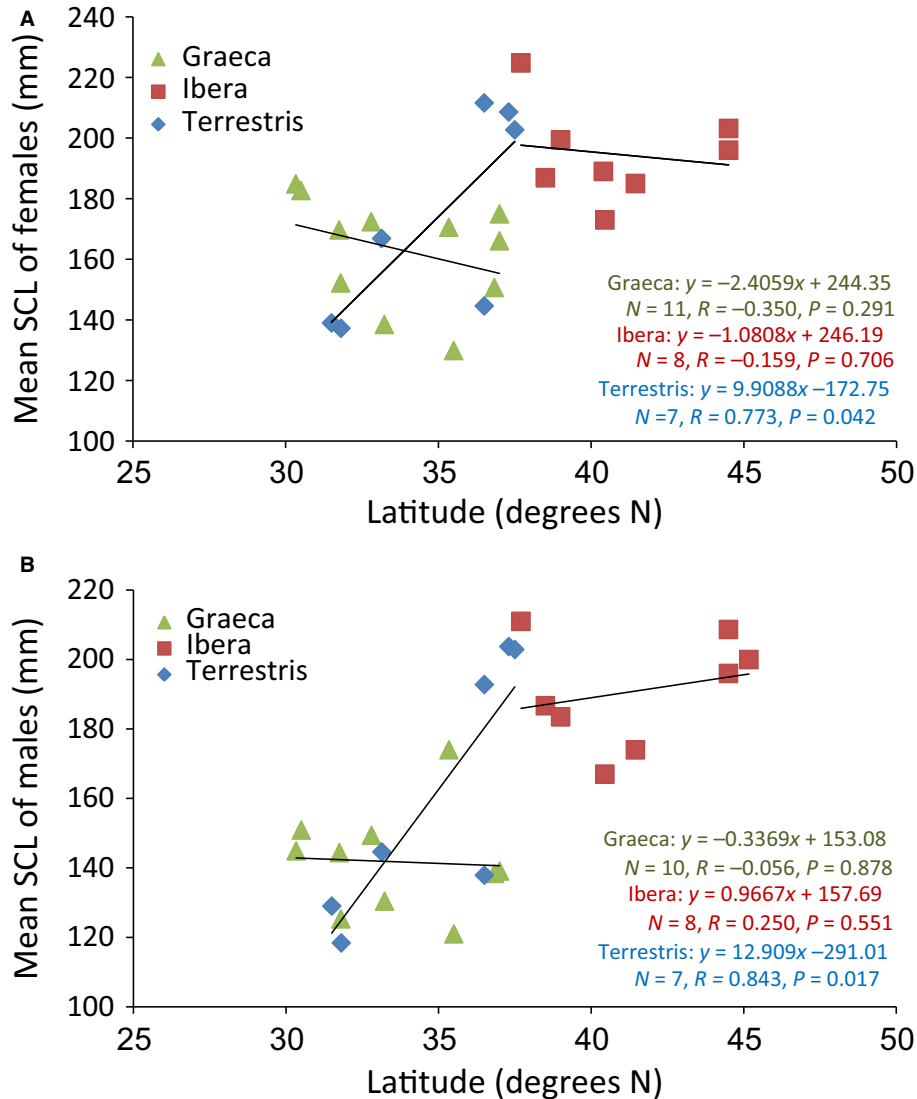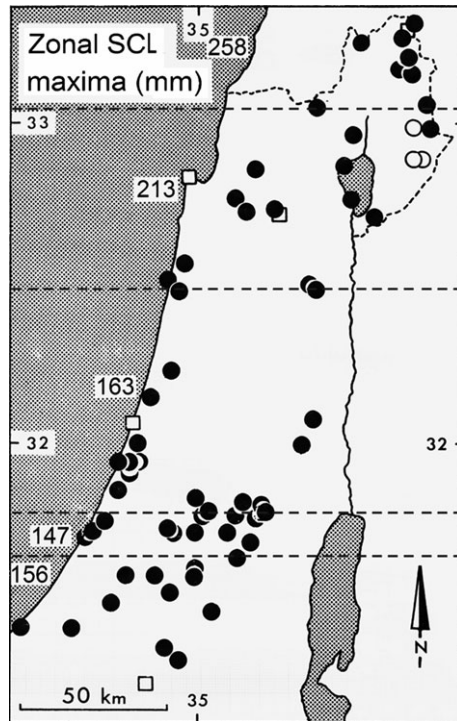
Figure 2. Correlation of straight carapace length (SCL) with latitude, in separate subspecies of *Testudo graeca*. Not every subspecies conforms with Bergmann's rule. A, females; B, males.

In the present study, the reproductive variable that was available in greatest sample size was egg volume (calculated from linear measurements), namely eight data from known latitudes (Table 3). Egg volume was not correlated with mean female SCL ($N = 7$, $r = -0.135$, $P = 0.773$) and not with latitude, viewed as proxy for overall tortoise size, as explained above ($N = 8$, $r = 0.202$, $P = 0.207$). This may result from the interaction of the two phenomena mentioned above. First, larger (and northern) females tend to have larger eggs; indeed, in the present study, unlike egg volume and egg width, egg length did correlate with latitude ($N = 8$, $r = 0.608$, $P = 0.047$). Second, northern (and larger) females tend to have larger clutches, and this is often achieved by reducing egg size. Indeed, although clutch size was known only for five of the samples, it was significantly correlated with latitude ($N = 5$, $r = 0.970$, $P = 0.006$, two-tailed). Finally, relative egg width (regional egg width as a percentage of regional female SCL) was, as expected, negatively correlated with regional female SCL ($N = 7$, $r = -0.735$, $P = 0.030$, one-tailed). (With radiographic measurement of eggs, the width is more accurate than the length.) This fits a hypothetical situation where larger females in the north lay larger clutches of smaller eggs.

GEOGRAPHICAL VARIATION OF SSD

Next, we tested whether the SSD of *T. graeca* varies in accordance with Rensch's rule. Female SCL and

Figure 3. Division of the focal study area into five latitude zones with similar sample sizes, showing the zonal maximum straight carapace lengths (SCLs). Solid circles indicate localities from which specimens originated; some yielded more than one individual. Open circles indicate photographic records. Squares indicate main towns for orientation.

male SCL were different but (naturally) correlated, in terms of both the regional means ($N = 27$, $r = 0.666$, $P = 0.000$, two-tailed) and the regional maxima ($N = 24$, $r = 0.745$, $P < 0.001$, two-tailed). We viewed the variation of SSD at both the global and the local levels, approaching this in three ways. (1) Concerning the global level, comparing the aforementioned equations of female and male SCLs as functions of latitude, we note that the enlargement of SCL towards north is much steeper in males than in females, so that, although in the south (where the tortoises are relatively small), SSD is female biased, north of ~40°N (with the tortoises relatively larger), the SSD becomes male biased. (2) Consequently, for those research projects that had reported SCL data of both sexes, we computed the representative FMR. This correlated negatively significantly with latitude, here serving as a 'proxy' representing the SCL of males, females and the mean (Fig. 4). Thus, at the lower latitudes where the tortoises are smaller, the higher FMRs show more strongly female-biased SSD. Specifically, this was when FMR was based on sample means ($N = 27$, $r = -0.779$, $P < 0.000$, two-tailed) and also when it was based on sample maxima ($N = 23$, $r = -0.433$, $P = 0.039$, two-tailed). However, within each of the three subspecies of which there were sufficient samples, the apparent negative correlation was significant only in *T. g. terrestris* (Fig. 4). FMR based on means also directly (negatively) correlated with SCL but only in males ($N = 27$, $r = -0.648$, $P < 0.000$, two-tailed) and not in females ($N = 27$, $r = -0.152$, $P = 0.450$, two-tailed). (3) Finally, we measured SCL on photographs of mating tortoises (Fig. 5) and calculated their 'individual' (per pair) FMR values. These significantly negatively correlated with latitude ($N = 16$, $r = -0.535$, $P = 0.033$), although the data points clearly aggregated around two regression lines, one for Israel *s.l.* (plus Jordan) and another for Anatolia, with largely overlapping FMR values (Fig. 6). Although, for the Israel + Jordan sample, the negative correlation was not significant ($N = 7$, $r = -0.424$, $P = 0.343$), for the Anatolia sample, the negative correlation was stronger and more significant ($N = 9$, $r = 0.743$, $P = 0.022$) than for the pooled material.

Regarding actual correlation with SCL, pooled geographically, FMR did not correlate with female SCL ($N = 16$, $r = -0.152$, $P = 0.574$) and weakly negatively correlated with male SCL ($N = 16$, $r = -0.445$, $P = 0.042$, one-tailed). Split by geography, in Israel + Jordan, the individual FMR failed to correlate with female SCL ($N = 7$, $r = -0.85$, $P = 0.856$, two-tailed) or with male SCL ($N = 7$,

Table 2. Division of Israel into five latitude zones with similarly sized samples

Zone name	Range of latitude degrees	Number of adults in zone	Maximum SCL in zone (mm)	Latitude of maximum SCL
Golan + North	33.06–33.32	19	258	33.3
North + Golan	32.48–33.03	18	213	32.9
Northern centre	31.78–32.48	20	163	32.2
Southern centre	31.65–31.78	20	147	31.7
South	30.81–31.64	19	156	31.4

SCL, straight carapace length.

Table 3. Reproduction data of *Testudo graeca*

Subspecies in the present study	Locality	Latitude (N)	Female SCL (mm)	Egg total (N)	Egg length (mm)	% Egg length of female SCL	Egg width (mm)	% Egg width of female SCL	Egg volume (ml)	Clutch size (number of eggs)	Clutches per year	Reference
buxtoni	North-west Iran	47.75	171	9	36.89	21.57	31.89	18.65	19.63	9		Rezazadeh *et al.* (2014)
graeca s.l.	Donana, Spain	37	175	31	33.87	19.35	27.97	15.98	13.87	3.48	2.47	Diaz *et al.* (1996)
graeca s.l.	North-west Tunisia	36.5	200		35	17.5	27.75	13.88	14.11	4		Siebenrock (1913)
graeca s.l.	Southern Spain	37.5	175	34	33.2	18.97	26.8	15.31	12.49			Lopéz Jurado *et al.* (1979)
ibera	Romania	44.5	203	9	42	20.69	22	10.84	10.64			Fuhn-Vancea (1961)
Ibera	Epanomi	40.4	189		35.4	18.73	29.2	15.45	15.80	4.5	2.8	Hailey & Loumbourdis (1988)
ibera	Kolchis	45.2	210	10	36.65	17.45	30.65	14.60	18.03	4.9		Inozemtsev & Pereshkolnik (1994)
ibera	Azerbaijan	40.5		9	38.7		30.9		19.33			Nadjafov, Iskenderov & Eminova (1992)

SCL, straight carapace length.

$r = -0.371$, $P = 0.413$, two-tailed). In Anatolia, unexpectedly, the individual FMR positively correlated with female SCL ($N = 9$, $r = 0.677$, $P = 0.045$, two-tailed), although not with male SCL ($N = 9$, $r = 0.014$, $P = 0.971$, two-tailed).

DISCUSSION

BERGMANN'S RULE

Our result, indicating that Bergmann's rule is indeed valid for *T. graeca s.l.*, supports previous claims that Bergmann's rule is valid for Testudines (Ashton & Feldman, 2003) or at least for some Testudinidae (Sacchi *et al.*, 2007; Meiri *et al.*, 2010, 2011/2012), despite these being ectothermic. The rule, initially enacted for the endothermic birds and mammals (Meiri & Dayan, 2003), was also found to be valid for many ectothermic animal groups, including insects and others of small body size (as noted in the Introduction). Therefore, it is hard to accept as omnipotent the initial functional explanation that it derives from the effects of the body's volume/surface ratio on thermoregulation (Bergmann, 1847; as translated by James, 1970). Moreover, it has been claimed that, for ectotherms, Bergmann's rule can be disadvantageous because of the time required for warming up (Pincheira-Donoso *et al.*, 2007, 2008).

If we are willing to consider a functional hypothesis applicable just to tortoises, the effect of body size on thermoregulation warrants further scrutiny. Improved thermoregulation means more activity hours per year, enhancing life history and fitness, and this would be selected for. It appears that the skin of reptiles, and especially the shield of tortoises, has relatively low heat conductance. This strengthens the increased thermal inertia typical of larger bodies (Benedict, 1932; McNab, 1970; King, 1996), climaxing with considerable thermal stability in large reptiles such as the giant lizard *Varanus komodoensis* or the giant Galapagos tortoises *Chelonoidis nigra* sspp. (Mackay, 1964; Brattstrom, 1973; McNab & Auffenberg, 1976; Huey, 1982). This situation has even generated the proposal that dinosaurs could have been physiologically ectothermic and, as a result of thermal inertia, functionally homoiothermic (McNab & Auffenberg, 1976).

This hypothesis does suffer from two weaknesses. First, we still await demonstration of the scope of gain from the different thermal flux of smaller and larger tortoises, either by direct experimentation or by targeted calculation. Second, in some turtles, the geographical variation of body size appears to be affected by other factors, or affected more by other factors. These turtles include *Clemmys guttata* (Litzgus, DuRant & Mousseau, 2004), *Glyptemys*
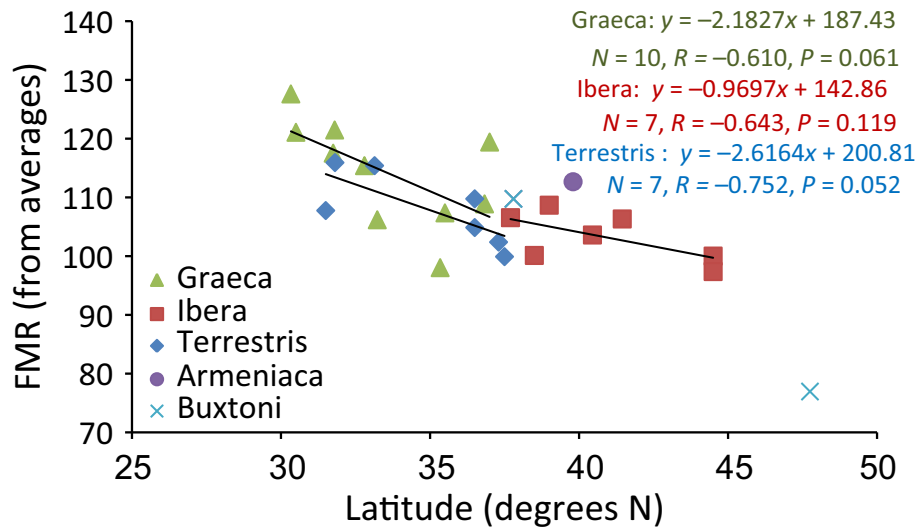
Figure 4. The correlation of female to male ratio (FMR) (based on the means of male and female *Testudo graeca* sspp. in 27 projects) with latitude is significant, total: $N = 27$, $r = -0.779$, $P < 0.000$ (two-tailed). Of the component subspecies with sufficient samples, the correlation is only significant for *Testudo graeca terrestris*: $N = 7$, $r = -0.752$, $P = 0.052$ (two-tailed). For *T. g. gracea* it is: $N = 10$, $r = -0.610$, $P = 0.061$ (two-tailed) and, for *Testudo graeca ibera*, it is: $N = 7$, $r = -0.643$, $P = 0.119$ (two-tailed).

Figure 5. Examples of photographs of mating tortoises providing relative sizes of matched males and females for computing individual female to male ratio (FMR) values. A, Israel: Kefar Szold, 33.2°N, FMR = 105 (photograph by E. Vanuno). B, Israel, Jerusalem, 31.8°N, FMR = 137.5 (photograph by E. D. Reiss). C, Turkey: Ankara, 39.9°N, FMR = 98.5 (photograph by Z. Erbaş). D, Turkey: Marmaris-Mugla, 36.8°N, FMR = 129 (photograph by N. Firtina).

insculpta (Greaves & Litzgus, 2009) and up to four of the 23 species examined in the seminal study by Ashton & Feldman (2003).

Among several potential alternative hypotheses to explain Bergmann's rule (Van Voorhies, 1996, 1997; Blackburn *et al.*, 1999), the most relevant appears to
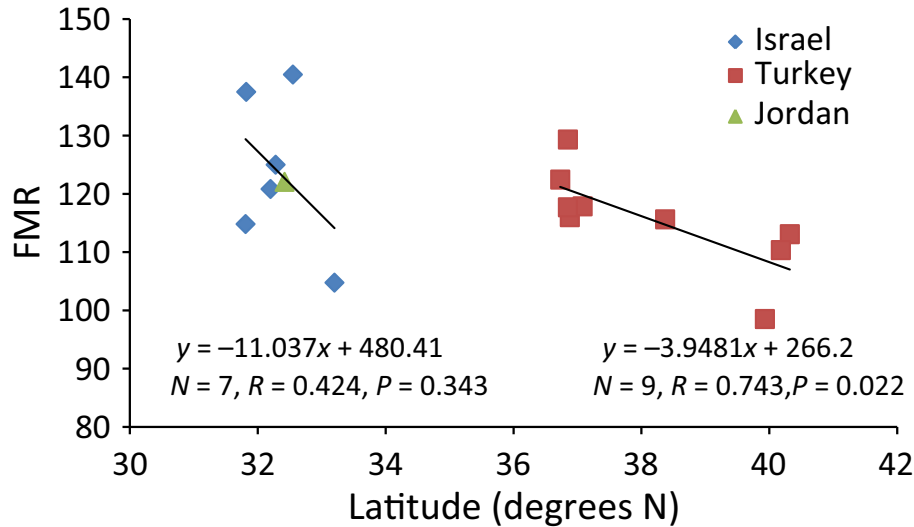
Figure 6. Correlation of 'individual' (per pair) female to male ratio (FMR) values derived from copulation photographs ($N = 16$) with latitude. The data points aggregate to represent one regression line at the latitudes of Israel and Jordan, and another at the latitudes of Anatolia.

be the reproductive one. The shorter reproductive season of the colder northern latitudes, constraining the number of successive clutches (Iverson, 1992b), likely exerts a selection pressure to enlarge the clutches (or litters) and possibly also the offspring (Rothermel & Castellón, 2014). This mechanism is known in mammals and birds (Fitch, 1985) but, in principle, can apply both to endotherms, where it applies compatibly with the thermal hypothesis, and to ectotherms of all groups and sizes.

In Testudines, some clutch enlargement can be achieved at the expense of offspring size; there is widespread negative correlation of clutch size and egg size (Iverson *et al.*, 1993; Charnov & Morgan Ernest, 2006; Warne & Charnow, 2008) but mainly one would expect enlargement of maternal size. Several wide-ranging species of the northern hemisphere indeed have larger bodies in the cooler north. This occurred in 19 of the 23 species sampled by Ashton & Feldman (2003) and was shown in detail in *Chrysemys picta* (Moll, 1973; Iverson & Smith, 1993).

In parallel, many turtle species have larger clutches in their northern populations (Iverson *et al.*, 1993), as occurs also in lizards (Wang *et al.*, 2011). In a commonly ignored study, Fitch (1985) reviewed some 33 600 clutches and litters of 165 species of New World reptiles; all of the six turtles included had larger clutches in the north. This is sometimes known to be accompanied by a reduction of the number of successive clutches in the north, and is considered to compensate for the latter reduction. Such is the case in *C. picta* (Moll, 1973; Iverson & Smith, 1993) and *C. guttata* (Litzgus & Mousseau, 2006).

Indeed, commonly in turtles, as in other ectothermic vertebrates (Frankenberg & Werner, 1992), there is a strong intra-specific correlation of clutch size with maternal size. This occurs, in *Testudo hermanni* (Hailey & Loumbourdis, 1988), *C. picta* (Iverson & Smith, 1993) and *Kinixys spekii* (Hailey & Coulson, 1997). Exceptions do occur, such as *C. guttata* (Litzgus & Mousseau, 2006) and *T. graeca* according to Hailey & Loumbourdis (1988).

Although, in turtles as elsewhere, clutch size and egg size are negatively correlated as a trade-off (Moll, 1973; Iverson *et al.*, 1993), exceptionally, both correlate with maternal size, as in *Gopherus polyphemus* (Rothermel & Castellón, 2014). In other words, egg size can also correlate with maternal size. An

Figure 7. Two male Galapagos tortoises (*Chelonoidis nigra porteri*) interacting (Indefatigable island, Galapagos, January 2010; courtesy of Arlo Midgett).

early reptilian precedent of this phenomenon had been reported from lizards (Frankenberg & Werner, 1992).

On this background, we reviewed the data on *T. graeca* reproduction that could justify the geographical variation in female body size. Our findings fit a hypothetical situation for which the larger females in the north lay larger clutches of smaller eggs. This is compatible with the reproductive hypothesis: presumably, the egg size reduction in the north results from a demographically necessary increase in clutch size that is incompletely enabled by increased body size, and requires augmentation from decreased egg size. More direct proof obviously requires more data.

RENSCH'S RULE

The results concerning Rensch's rule contribute to a clarification of the two controversies noted in the Introduction: (1) Overall, the SSD of *T. graeca* (Testudines: Testudinidae) does vary in accordance with Rensch's rule. (2) Overall, where the *T. graeca* individuals are relatively small, their SSD is female biased but, where the tortoises are larger, the SSD is male biased. We do note the apparent exception shown by the copulation partners: across Anatolia, FMR correlates positively with female SCL, so that the SSD is female biased for the largest females. We interpret this as probably reflecting the Bergmannian selection force enlarging the maternal size, outweighing the Renschian selection force for dominant males. However, the available data do not enable sufficient exploration of a third selection force considered to operate; for example, in lizards, males select large females (Stamps, 1983). Our results appear to be compatible with the conclusions of Berry & Shine (1980) and Halámková *et al.* (2013) but counter those of Cox *et al.* (2007) suggesting that Testudinidae fail to conform with Rensch's rule. More recently, conformity with Rensch's rule was also confirmed for *C. picta* (Emydidae) (Litzgus & Smith, 2010) and Kinosternidae (Cox *et al.*, 2007; Ceballos & Iverson, 2014).

By contrast, Gibbons & Lovich (1990) had concluded that *Trachemys scripta* (Emydidae) failed to conform with Rensch's rule. Moreover, *Emys orbicularis* (Emydidae) may vary in a manner opposing Rensch's rule. Although, in Iberia and North Africa, the sexes are of similar size (Fritz, 2001, 2003), elsewhere, the SSD is female biased. However, in a population where the terrapins are relatively large, the SSD is stronger and the females are much bigger than the males (Fritz, 2001). Such 'converse Rensch's rule' variation has already been reported in some snakes (Cox *et al.*, 2007). The case of *E. orbicularis*

deserves and awaits analysis. Fritz (2001, 2003) has accumulated size data from hundreds of populations, with assorted patterns of variation among neighbouring populations. Altogether, it must be borne in mind that inter-subspecific or geographical differences in SSD and FMR can occur, also in Testudines, without relation to Rensch's rule (Yasukawa, Ota & Iverson, 1996; Carretero *et al.*, 2005; Lovich *et al.*, 2010).

Exceptions notwithstanding, the frequent realization of Rensch's rule requires a functional explanation. The statistical reviews of Abouheif & Fairbairn (1997) and Dale *et al.* (2007) indicate that the hypothesis best fitting the kingdom-wide phenomena is the one attributing Rensch's rule to sexual selection for male size. The conclusions of Berry & Shine (1980) regarding the SSD of Testudines, predating the era of Rensch's rule and linking male-biased SSD with male combat, are in accordance with the above.

Male combat is not ubiquitous in Testudines. As noted by Berry & Shine (1980), it occurs mainly where SSD is male biased; in Testudinidae, mainly in the large species: the African *Geochelone sulcata* and *S. pardalis* and the Galapagos tortoises (*C. nigra* sspp.) (Fig. 7).

Testudo graeca males have long been known or considered to vie with rivals over females. Brehm (1878) quoted Dumeril saying that each male would bite the other in the neck and endeavour to turn him over. According to Schreiber (1912) the combatants would knock and push each other. At those times (i.e. before 1925–1926), *T. graeca* meant what today is *T. hermanni* (Fritz & Bininda-Emonds, 2007) but, by implication, the observations appears to apply also *T. graeca* as considered currently because the two share the same combat behaviour (Auffenberg, 1977). *Testudo graeca* was specifically listed by Berry & Shine (1980) as one of the species having male-biased SSD, with males engaging in combat. For these character states in this species, they provided three sources, which, to be on the safe side, we pursued. (1) Loveridge & Williams (1957) listed, presumably as maxima, a male of 145 mm carapace length (MCZ 18161) and a female of 192 mm (MCZ 1498) and quoted Flower (1945) for three females of 276, 298 and 365 mm. Regarding combat, they only describe captivity observations of two males with a female, saying, 'Owing, perhaps, to the difference in age and size of the males, no combats were observed between them'. (2) Watson (1962) described the courting and mating of an male approximately 22 cm in length with an female approximately 25 cm in length on Kos island (near south-west Anatolia), without mentioning combat. (3) Auffenberg (1977) reviewed the display behaviours in tortoises, listing *T. graeca* as employing the tactile signals of ramming and pushing in both courtship and combat.

However, he provided no sources concerning tactile signals (Table 3), although he did for vocal signals (Table 1) and for biting (Table 2). This leaves us with meager evidence of male dominance and male combats in *T. graeca*. Yet the male combat of ramming attributed by Auffenberg to *Stigmochelis pardalis* has indeed been described from that species by Archer (1948).

Quotations and misquotations notwithstanding, the situation in *T. graeca* is in accordance with our survey: heterogeneous. In Anatolia, the males are relatively large and males have been observed combating: with two males approaching a female. For a short time, the smaller male repeatedly rammed the bigger one (approximately as large as the female) until the latter gave up following the female (Mt Nemrut, Tatvan, Bitlis province, East Anatolia, 13 August 2011; B. Göçmen, unpubl. data). In Israel, the males are relatively small; we have never encountered male combat, nor has our questioning of other reserachers yielded any report. Moreover, during an extensive field study, two separate cases were observed in which two males courted one female, only one male copulated with her, and no combat occurred (Ramat HaNadiv Park, Israel, 2013–2014, M. Bernheim, unpubl. data). It remains unknown, and will not be easy to determine, how this situation arose. However, as in the case of Bergmann's rule, our data review is compatible with the prevailing hypothesis on the proximal cause for Rensch's rule: male combat exists in large Testudinidae, and perhaps only or mainly in the large-bodied populations within *T. graeca s.l.*. Convincing proof awaits more data.

Finally, it is interesting that, by the yardstick of individual mate selection, Rensch's rule appears to manifest itself separately in Anatolia and in the Levant. If confirmed by larger samples, this might support considering these populations as separate entities, each with its set of selection forces and local gradients.

GENERAL COMMENTS

First, we must repeat and emphasize that many samples were small, relative to the within-sample variation. Often, this appeared to prevent significant results. However, a small random sample of individuals could also generate spurious significant results. Moreover, it is unclear to what extent the bulk of tortoises facilitates observation in the field or depresses collection for the museum. Clearly, additional data are desirable, particularly of reproduction.

Our conclusions suggesting that our results are compatible with both Bergmann's and Rensch's rules, and with their prevailing explanations, are not annulled by the fact that, in some other testudinate species, one rule or the other has been found invalid. However, as explained above, the alternative, original, hypothesis on the functional basis of Bergmann's rule, invoking the thermal inertia of larger bodies, has still not been examined exhaustively. This hypothesis has not been supported but, by the same token, it has not yet been failed. If this hypothesis were examined and revived, it might, speculatively, apply also to Rensch's rule. Males and females differ. Conceivably, males (of some species) may have greater need for the improved thermoregulation provided by an enlarged body because of their greater activity, as beyond foraging they seek females. This may be unlikely because the biggest tortoises, with the relatively largest males, live in warm areas. However, the balance and trade-off between assorted factors may differ in different cases (Lovich *et al.*, 2010; Ceballos *et al.*, 2013; Halámková *et al.*, 2013). Thus, in some cases, in the context of seeking females, males might benefit from larger bodies because the speed of locomotion is a function of body size.

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