Population biology and ontogenetic allometry of *Testudo hermanni boettgeri* Mojsisovics, 1889, in a marginal population in Bulgaria
(Testudines: Testudinidae)

Zur Populationsbiologie und ontogenetischen Allometrie bei einer Randpopulation von *Testudo hermanni boettgeri* Mojsisovics, 1889 aus Bulgarien
(Testudines: Testudinidae)

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KURZFASSUNG

Untersucht wurden biologische Charakteristika einer freilebenden *Testudo hermanni boettgeri* MOJSISOVICS, 1889 Population aud dem Eminska Gebirge, dem östlichsten Teil des Balkan-Gebirgszuges (Stara Planina Berge), einschließlich von Individuen, die im Inkubator ausgebrütet wurden. Die Größenverteilung und altersmäßige Zusammensetzung der *T. hermanni* Population im Eminska Gebirge wiesen darauf hin, daß die Individuenzahl in dieser Population langsam abnimmt: nur 18,6% der Tiere waren unter 10 Jahren alt; die Größenklasse von 161-180 Millimeter Karapaxlänge und die Altersklasse von 16-20 Jahren dominierten in der Population. Das Geschlechterverhältnis war etwa ausgeglichen (57,6% männliche Individuen: 42,4% weibliche Individuen). Die männlichen Individuen herrschten in den kleineren Größenklassen vor und in den großen gab es nur weibliche Individuen. Das lineare Wachstum wurde durch die VON BERTALANFFY - Gleichung $L = 287\,(1 - e^{-0{,}0436\,(t + 3.26)})$ beschrieben. Die Regressionen der Körpermasse (W, g), der Karapax-Breite (Wd, mm) und der Karapax-Höhe (H, mm) auf die Karapax-Länge (L, mm) wurden durch folgende Gleichungen beschrieben: $\ln W = -3.7452 + 2.0939 \ln L$; $\ln Wd = 0.3635 + 0.8792 \ln L$ und $\ln H = -0.2151 + 0.9088 \ln L$. Bei gleicher Karapax-Länge hatten die weiblichen Individuen im Durchschnitt höhere Massen und Karapax-Höhen aber niedrigere Karapax-Breiten als die männlichen Individuen. Eine Methode zur Abschätzung der Korpulenz (body mass condition) wurde überprüft.

ABSTRACT

Biological characteristics were studied of a free ranging *Testudo hermanni boettgeri* MOJSISOVICS, 1889, population in the Eminska Mountains – the easternmost part of the Balkan Range (Stara Planina Mountains), as well as of specimens hatched in incubators. The size and age composition of the *T. hermanni* population in the Eminska Mountains suggest that this population is slowly declining: only 18.6% of the animals in the population were under the age of 10 years; the size class of 161–180 mm and the age class of 16–20 years dominated in the population. The sex ratio was approximately balanced (57.6% males: 42.4% females). Males dominated in the smaller size classes, and in the big size classes were only females. The linear growth was described by VON BERTALANFFY's equation $L = 287\,(1 - e^{-0.0436\,(t + 3.26)})$. Regressions of the tortoise body mass (W, g), carapace width (Wd, mm), and carapace height (H, mm) on the carapace length (L, mm) were described by the following equations: $\ln W = -3.7452 + 2.0939 \ln L$; $\ln Wd = 0.3635 + 0.8792 \ln L$, and $\ln H = -0.2151 + 0.9088 \ln L$. At a given carapace length, the females had on the average higher masses and carapax-heights, but lower carapax-widths than the males. A method for estimating the body mass condition was tested.

INTRODUCTION

Although, only a few decades ago *Testudo hermanni boettgeri* MOJSISOVICS, 1889, was found almost everywhere in the territory of Bulgaria, currently, its occurrence is very limited and its abundance is drastically reduced. At present, the species is of conservation concern. In Bulgaria, the tortoise is protected by the Biological Diversity Act (2002), and internationally it is included in the Berne Convention, EU Directive 92/43 (1992), IUCN Red List and CITES (BEŠKOV & NANEV 2006; PETROV 2007).

The investigations on the species in Bulgaria so far refer mainly to its occurrence and relative abundance, evaluated by the inquiry method (Beškov 1984, 1993). Ivanchev (2007) was the first to regularly observe a population in Bulgaria (in the region of the Eminska Mountains).

The aim of the present paper is to describe the population structure as indicated by size, age and sexual composition, as well as growth pattern, body mass condition and ontogenetic allometry of the *T. hermanni boettgeri* population in the Eminska Mountains, Bulgaria.

MATERIALS AND METHODS

The Eminska Mountains, the easternmost part of the Balkan Range (Stara Planina Mountains), comprises a territory of approximately 80 km². It is bordered by the Black Sea to the south and east, the main highway Burgas–Varna to the west, and the Ghin River to the north (Fig. 1). The area lies within the Black Sea coastal climatic zone with an average annual precipitation of 550-600 mm and an average annual air temperature of 12°C. There are neither mineral resources nor industry. A small population of *Testudo hermanni boettgeri* was discovered on a two km² south-facing slope, to the south of the village of Banya, approximately 8 km west of Cape Emine (Ivanchev 2007).

Data were analyzed from both field and experimental laboratory studies carried out from April to October in the period 2003-2006 (Ivanchev 2007; Živkov et al. 2007). In total, 102 adult and subadult individuals were examined in this period. However, in different analyses, different numbers of specimens were used. In addition, the growth rate and the ontogenetic early growth allometries were studied over the period of the first 175 days after hatching in 53 specimens developed in incubators, and 14 specimens hatched in natural nests, all reared under equal conditions. The mean monthly temperature (June-September) in natural nests was 25.8°C (Ivanchev 2007). The temperature was 31-33°C in incubator No. 1, and 28-29 °C in incubator No. 2. The humidity in both incubators was 60-80% (Ivanchev 2007; Živkov et al. 2007).

The following carapace parameters were measured to the nearest 1 mm: maximum straight length (L), maximum median width (Wd), and maximum height (H). In females, H was measured from the medial plastron to the highest point of the carapace; in male specimens, from the mid–plastral concavity to the highest point of the carapace (Ivanchev 2007). The sizes reached in the first 24 hours after hatching were accepted as initial, since before that, their dimensions were highly variable, and age in the first 24 hours was set as age 0 (Ivanchev 2007).

The approximate age was determined by counting scute annuli. Tortoises showing less than 9 annuli and less than 10 cm of carapace length were considered juveniles (Ivanchev 2007). Only three juvenile specimens had slightly higher lengths. The field techniques and ageing were based on the methods described by Stubbs et al. (1984).

Fig. 1: Location of the study area, the Eminska Mountains in Bulgaria (□).
Abb. 1: Lage des Untersuchungsgebietes, dem Eminska Gebirge in Bulgarien (□).

Table 1: Size, age, and sexual composition in a population of *Testudo hermanni boettgeri* MOJSISOVICS, 1889 in the Eminska Mountains, Bulgaria (after ŽIVKOV et al. 2007). n – number of specimens.

Tab. 1: Länge, Alter und Geschlechterverhältnis in einer Population von *Testudo hermanni boettgeri* MOJSISOVICS, 1889 im Eminska Gebirge, Bulgarien (nach ŽIVKOV et al. 2007). n - Zahl der Individuen.

Size classes Größenklassen [L, mm]	Age classes [years] / Altersklassen [Jahre]												n	%
	1-5 juv.	1-5 juv.	6-10 ♂♂	6-10 ♀♀	11-15 ♂♂	11-15 ♀♀	16-20 ♂♂	16-20 ♀♀	21-25 ♂♂	21-25 ♀♀	26-30 ♂♂	26-30 ♀♀		
61-80	5												6	5.9
101-120		3											4	3.9
121-140		1	1	1	1	1							5	4.9
141-160			2	2	15	5		3					27	26.5
161-180				3	3	1	13	2	4		2	1	33	32.4
181-200							2	9	9	4		1	17	16.7
201-220								3	1	3		2	9	8.8
221-240												1	1	0.98
n	5	5	3	6	19	7	15	14	14	7	2	5	102	100
%	100	35.7	21.43	42.9	73.1	26.9	51.7	48.3	66.7	33.3	28.6	71.4		100

The statistical analyses were made according to the standard methods used in biostatistics (PLOKHINSKII 1961). The parameters of VON BERTALANFFY's equation were calculated according to HOHENDORF (1966), and the parameters of the FORD-WALFORD equation according to RICKER (1975).

RESULTS AND DISCUSSION

Size and age composition

The size (straight carapax length, L) – frequency distribution of the sample is shown in Table 1. The size classes, which dominated in the population were: 141–160 mm, 161–180 mm, and 181–200 mm (26.5%, 32.4%, and 10.7%, respectively). There was a clear sexual dimorphism, with females on the average larger than males (females 183 ± 3.7 mm : males 158 ± 1.7 mm). This phenomen was also described in *T. hermanni* from Greece (STUBBS et al. 1985) and France (STUBBS & SWINGLAND 1985) (Table 2).

The characteristic feature of the population structure was the lack of juveniles. (IVANCHEV 2007). Only 10 specimens (9.8%) were juveniles (Table 1, ŽIVKOV et al. 2007). Similar results were reported for the Massiv des Maures in France (STUBBS & SWINGLAND 1985) and for Alyki in Greece (STUBBS et al. 1985).

The age composition was also in favor of the older adults (Table 1). The age classes 11-15 years, 16-20 years, and 20-25 years (25.5%, 28.4%, and 20.6%, respectively), were predominant in the population. Only 18.6% of animals (19 animals) in the study population were under the age of 10 years, compared with 60% and 23% in two populations in Greece (STUBBS et al. 1985) and 18% in a population in France (STUBBS & SWINGLAND 1985).

The characteristics of the size and age composition of the *Testudo hermanni* population and the very unfavourable juveniles-adults ratio strongly suggest that this population is slowly declining. Potential threats include human pressure, increased pressure of released domestic and wild animals and intensified agriculture (IVANCHEV 2007).

Table 2: Carapace lengths of adult *Testudo hermanni* from France, Greece and Bulgaria. The values of the average carapace length are means ± standard error, with the number of specimens in parentheses.

Tab. 2: Karapax-Längen erwachsener *Testudo hermanni* aus Frankreich, Griechenland und Bulgarien. Die Werte der durchschnittlichen Karapax-Länge sind Mittelwerte ± Standardfehler, die Zahl der Individuen steht in Klammern dahinter.

Country / Land (Source / Quelle)	Average carapace length Mittlere Karapax-Länge		Maximum carapace length Maximale Karapax-Länge	
	♂♂ (*L*, mm)	♀♀	♂♂ (*L*, mm)	♀♀
France / Frankreich (Stubbs & Swingland 1985)	138 ± 0.5 (141)	159 ± 0.7 (154)	154	191
Greece / Griechenland (Stubbs et al. 1985)	151 ± 1.0 (978)	156 ± 2.0 (397)	191	201
Bulgaria / Bulgarien (our data, diese Arbeit)	158 ± 1.7 (53)	183 ± 3.7 (39)	181	229

Sex ratio

The total adult sample sex ratio was 53 males : 39 females, and the differences (57.6% : 42.4% or 1:0.85) were not significant ($\chi^2 = 2.1$, $P > 0.05$), i.e. the over-all sex ratio was approximately balanced. The differences between males and females within the various age classes were not significant either. Significantly more males (73.1%) were solely in the age class of 11-15 years ($\chi^2 = 5.5$, $P < 0.05$) (Table 1). Changes in the sex ratio between different size classes were observed more regularly. Males dominated in the smaller size classes: 141–160 mm and 161–180 mm (85.2% and 75.8%, respectively) ($\chi^2 = 13.4$, $P < 0.001$ and $\chi^2 = 8.8$, $P < 0.01$, respectively), and females dominated in the bigger size classes: 181–200 mm (82.3%) ($\chi^2 = 7.1$, $P < 0.01$); the two largest size classes (201–220 mm and 221–240 mm) being represented only by females.

According to Gibbons (1970), the sex ratio of chelonians usually deviated from equal numbers of males and females. Pieau (1971) and Yntema (1976) considered that chelonians showed environmental sex determination (ESD), which was affected by the incubation temperature. Hailey (1990) investigated the adult survival and recruitment, as well as the explanation of an imbalanced sex ratio in a *T. hermanni* population in Alyki in northern Greece. He found that the average sex ratio (males/females) in the population was 3.45:1; the recruitment of adult males was greater than that of females due to the males' lower age of maturity (9 vs. 11 years); and the mean survival rate was 0.914% in males and 0.877% in females equivalent to average adult longevity values of 11.6 y and 8.1 y, respectively. Hailey & Coulson (1999) assumed that different mortality rates can not account for a bias of the sex ratio. According to these authors, "the larger shells of females are more robust, and so persist longer in the environment" which could cause a female bias if carcasses were involved in the assessment.

When studying the sex ratio in a number of fish species, it was found that usually, up to four periods characterized by specific sex ratios can be distinguished in a spawning population. Males dominate in the younger year classes (period A), since they mature earlier. The following period (B) is of balanced sex ratios. In the older year classes (period C), females dominate because of their longer life span. In the fourth period (D) there are only females (Živkov & Yankov 1987; Yankov & Živkov 1988; Hamwi & Raikova-Petrova 2005). Evidence suggests that regularities in variation of the sex ratio within different size and age classes and within different populations which are valid for fishes, could be valid for reptiles as well. The tortoises may provide an example. Our results and the results of other authors showed that**:** (i) males of *T. hermanni* mature earlier than females; (ii) the quota of males in smaller size and age classes is higher than of females; (iii) the females predominate in bigger size and age classes; (iv) only females are present in the biggest size classes; and (v) the sex ratio in some populations is approximately 1:1 (Table 1, Stubbs & Swingland 1985; Swingland & Stubbs 1985).

Table 3: Average carapace length (*L*, mm) of *Testudo hermanni* during the first 175 days (*t*, days), calculated for given ages (0, 30, 60, …etc. days) (L_0, L_{30}, L_{60},…etc, mm). L_1, L_2, L_n - the average lengths of specimens hatched in incubators No. 1 (L_1), and No. 2 (L_2), and in natural nests (L_n). *n* – number of specimens.

Tab. 3: Durchschnittliche Karapax-Länge (L, mm) von *Testudo hermanni* während der ersten 175 Tage (*t*, Tage), berechnet für Alter von 0, 30, 60 … usw., Tagen (L_0, L_{30}, L_{60}, … usw., mm). L_1, L_2, L_n - die durchschnittlichen Längen der Individuen aus Inkubator No.1 (L_1), No. 2 (L_2) und natürlichen Nestern (L_n). *n* - Zahl der Individuen.

Regression $\ln L = a + b \ln t$	L_0	L_{30}	L_{60}	L_{90}	L_{120}	L_{150}	L_{180}	n
$\ln L_1 = 3.5524 + 0.0021t$	34.9	37.2	39.6	42.2	44..9	47.8	50.9	27
$\ln L_2 = 3.5732 + 0.0021t$	35.6	37.9	40.4	43.0	45.8	48.8	52.0	26
$\ln L_n = 3.5442 + 0.0022t$	34.6	37.0	39.5	42.2	45.1	48.1	51.4	14

Growth rate

With the aim to determine the pattern and rate of growth of *T. hermanni*, first, the linear growth (*L*, mm) was monitored in 67 hatchlings for 175 days (*t*, days) (IVANCHEV 2007; ŽIVKOV et al. 2007). It was found that the carapace length of the hatchlings (L_0) ranged from 32.5 to 40 mm (mean 35.2 ± 0.33 mm), and the body mass (W_0) ranged from 10 to 17 g (mean 13.44 ± 0.15 g). The growth was best described by the exponential function (Table 3). The differences are not significant in the growth of the tortoises, hatched at different conditions, as well as in the values of parameters *a* and *b* in the three equations in Table 3 .

The linear growth of *T. hermanni* from 0 to 30 years (*t*, years) was described by PLOKHINSKII's (1961) asymptotic equation and by the VON BERTALANFFY's equation, most frequently used in biology for this purpose (Fig. 2). The relationship L_{t+5} - L_t is a straight line (Fig. 3). This indicates the validity of VON BERTALANFFY's growth model for *T. hermanni*.

The growth rate was higher in females than in males (Table 4). However, the difference in the values of *b* in the equations for both sexes was not significant ($t = 1.34$, $P > 0.05$), because of the comparatively small number of adult specimens studied (53:39).

When comparing the growth of the study population of *T. hermanni* from Bulgaria with the growth of other populations from Greece and France, similar or even identical parameters were determined (Table 5): noticeable retardation of the growth rate after the 12th-13th year; sexual size dimorphism; similar growth rates of the Bulgarian and the Greek populations from Kastoria and Alyki; and identical L_6 values of the Bulgarian population and the population from Keramoti (Greece) – 95 mm, etc. However, some substantial differences did exist. In the graphic representations of the growth models of *T. hermanni*, suggested by other authors, the following was shown: after the age of 8, 9, 12, 16 years, the growth rate decreased quickly and growth almost ceased, even at very low values of *L* – usu-

Table 4: Equation statistics of correlations between the average carapace length (*L*, mm) and age (*t*, years) in *Testudo hermanni*. L_1, L_2, L_n – the average lengths of specimens at the age of 0 to 175 days (t_d), hatched out in incubator No. 1 (L_1), No. 2 (L_2), and in natural nests (L_n). S.E. – standard error, *r* – correlation coefficient, *P* – probability, *n* – number of specimens.

Tab. 4: Gleichungen der Korrelationen zwischen durchschnittlicher Karapax-Länge (*L*, mm) und Alter (*t*, Jahre) bei *Testudo hermanni*. L_1, L_2, L_n - die durchschnittlichen Längen der Individuen im Alter von 0 bis 175 Tagen (t_d) aus Inkubator No. 1 (L_1), No. 2 (L_2) und natürlichen Nestern (L_n). S.E. - Standardfehler, *r* - Korrelationskoeffizient, *P* - Wahrscheinlichkeit, *n* - Zahl der Individuen.

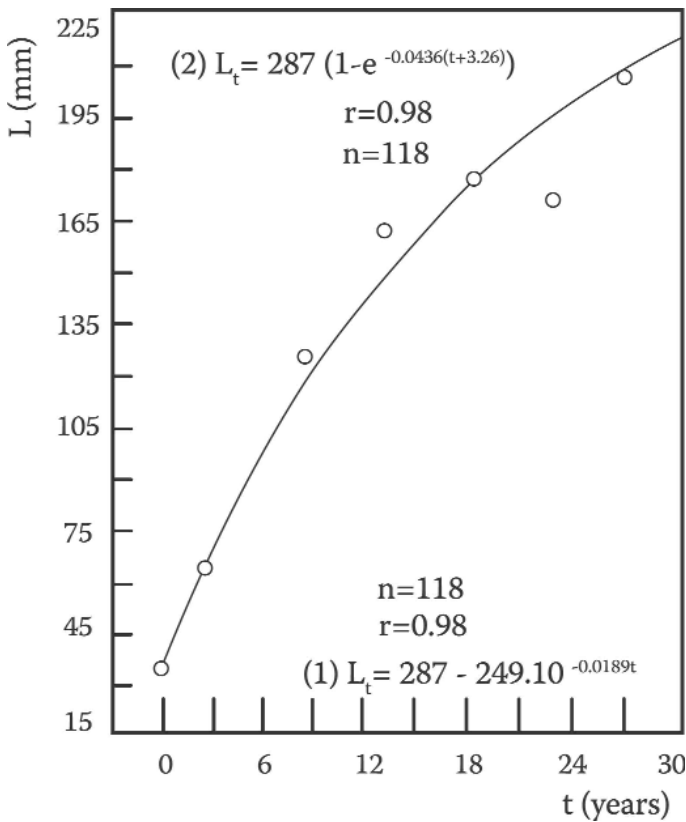| Regression	$a \pm$ S.E.	$b \pm$ S.E.	r	$P <$	n
$\ln L_1 = a + bt_d$	3.5524 ± 0.0043	0.0021 ± 0.0004	0.94	0.001	113
$\ln L_2 = a + bt_d$	3.5732 ± 0.0531	0.0021 ± 0.0005	0.91	0.001	108
$\ln L_n = a + bt_d$	3.5442 ± 0.0518	0.0022 ± 0.0006	0.91	0.01	32
♂ $\ln L = a + b \ln t$	4.3506 ± 0.1093	0.2587 ± 0.0395	0.96	0.001	53
♀ $\ln L = a + b \ln t$	4.0789 ± 0.2779	0.3997 ± 0.0972	0.94	0.001	39

Fig. 2: Regression of the average carapace length (*L*) on the age (*t*) in *Testudo hermanni* described by Plokhinskii's asymptotic equation (1) and von Bertalanffy's equation (2).

Abb. 2: Regression der durchschnittlichen Karapax-Länge (*L*) auf das Alter (*t*) bei *Testudo hermanni* beschrieben durch Plokhinskiis asymptotische Gleichung (1) und von Bertalanffys Gleichung (2).

ally 145-165 mm (Fig. 5 in Stubbs & Swingland 1985; Fig. 5 in Hailey 1988; Fig. 7 in Willemsen & Hailey 2001). If the Bulgarian populations of *T. hermanni* grew according to these models, the longest specimens of this species caught in Bulgaria (for instance, *L* = 357 mm, in Beškov 1997), would never have reached this size. Therefore, we assume that the curve in our Fig. 3 is closer to the real growth curve of *T. hermanni* (at least for the population in the Eminska Mountains, and until the specimens reach the age of about 30 years and the length of 230 mm). This curve, unlike the curves of other authors, does not show a drastic decrease of growth rate after the age of 12-16 years and at lengths over 145-160

mm, not even after the age of 30 years and at lengths over 230 mm (Fig. 3).

Most authors considered the growth patterns in fishes, amphibians and reptiles as similar, because of the physiological similarity between these animals, expressed mainly by their poikilothermy. Therefore, the variations in growth rate of these animals were related to changes in ambient temperature (Mina & Klevezal 1976; Avery et al. 1993; Hailey & Coulson 1996), as well as quantity and quality of the diet (Pough 1973; Wood & Wood 1981; Hart 1983; Troyer 1984; Avery et al. 1993). Hailey & Coulson (1999) supported the hypothesis that the pattern of growth of chelonians depended on nutrition. In
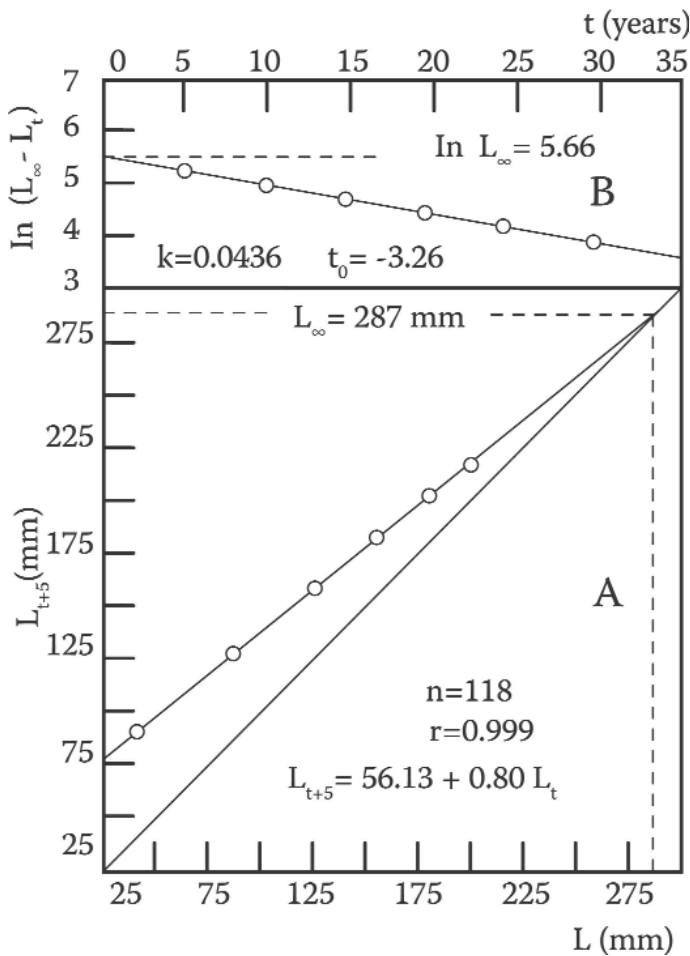
Fig. 3: WALFORD graph of carapace length growth of *Testudo hermanni* in the Eminska Mountains, Bulgaria. A - relationship between carapace length at the age of t years (L_t) and $t+5$ years (L_{t+5}), calculated by PLOKHINSKII's equation ($L_t = 287 - 249.10^{-0.0189t}$). B - relationship between age (t) and $\ln(L_\infty - L_t)$. L_∞, k, t_0 – parameters of VON BERTALANFFY's equation.

Abb. 3: WALFORD Diagramm des Karapax-Längenwachstums von *Testudo hermanni* im Eminska Gebirge, Bulgarien. A - Verhältnis zwischen Karapax-Länge im Alter von t Jahren (L_t) und $t+5$ Jahren (L_{t+5}), berechnet nach der Gleichung von PLOKHINSKII ($L_t = 287 - 249.10^{-0.0189t}$). B - Beziehung zwischen Alter (t) und $\ln(L_\infty - L_t)$. L_∞, k, t_0 - Parameter in VON BERTALANFFYs Gleichung.

their Table 4, a total of 32 species of chelonians were listed and the growth pattern of these species (both BERTALLANFFY and non-BERTALANFFY growth) was related to nutrition (carnivorous, herbivorous or omnivorous). In 15 species, the growth rate could be described by VON BERTALANFFY's equation. The species *T. hermanni* was considered having a "non-BERTALANFFY" growth pattern based on STUBBS et al. (1984, 1985). However, our Fig. 3 shows that the growth rate of *T. hermanni boettgeri* from the Eminska Mountains can be described fairly well by VON BERTALANFFY's equation.

Based on our results and published data on growth of vertebrate animals, it can be concluded that the following facts, regularities and conventions should be consid-

Table 5: Linear growth rate of *Testudo hermanni* in different localities according to different authors. L_0, L_6, L_{10}...etc., t, years, calculated by the equations or graphs published. BG - Bulgaria, F - France, GR - Greece.

Tab. 5: Lineare Wachstumsrate von *Testudo hermanni* in unterschiedlichen Gebieten nach verschiedenen Autoren. L_0, L_6, L_{10}, ... u.s.w., mm durchschnittliche Karapax-Längen im Alter von 0, 6, 10 ... etc., t, Jahren, berechnet auf Grundlage publizierter Gleichungen bzw. Diagramme. BG - Bulgarien, F - Frankreich, GR - Griechenland, years - Jahre.

Locality, country (source) Gebiet, Land (Quelle)	Equation or graph Gleichung oder Graph	Average carapace length age Mittlere Karapaxlänge Alter				
		L_0	L_6	L_{10}	L_{14}	L_{18}
Epanomi, GR (HAILEY 1988)	$L = 21 + 12.9t$, t_{max} = 8 years	21	98			
Keramoti, GR (HAILEY 1988)	$L = 26 + 11.5t$, t_{max} = 8 years	26	95			
Alyki, GR (HAILEY 1988)	Graph, t_{max} = 30 years	30	100	145	161	170
Alyki, GR (HAILEY 1988)	$L = 37 + 10.0t$, t_{max} = 8 years	37	97			
Alyki, GR (HAILEY 1988)	$L = 38 + 10.9t$, t_{max} = 8 years	38	103			
Eminska Mts., BG (our data / diese Arbeit)	$L = 287 (1 - e^{-0.0436(t + 3.26)})$, t_{max} = 30 years	38	95	126	152	173
Kastoria, GR (WILLEMSEN & HAILEY 2001)	Graph, t_{max} = 26 years	40	90	125	160	187
Massif des Maures, F (STUBS & SWINGLAND 1985)	Graph, t_{max} = 30 years	40	90	118	141	145
Kalamata, GR (WILLEMSEN & HAILEY 2001)	Graph, t_{max} = 26 years	42	115	155	162	164
Alyki, GR (STUBS & SWINGLAND 1985)	Graph, t_{max} = 30 years	43	99	133	156	166

ered when studying the growth pattern of chelonians:

1. The necessity to determine and analyze the growth pattern over the whole life cycle, at least until the age of 50-60 years. We agree with the opinion of STUBBS et al. (1985) that "growth studies and analysis of population structure depend on accurate estimating of age, yet scute ring counting has not been found to be reliable".

2. The conclusion of SCHNUTE (1981), that (i) VON BERTALANFFY's equation, (ii) the equation of GOMPERTZ and (iii) the logistic curve are all expressions of the same growth pattern, which is characterized by asymptotic length (L_∞) and mass (W_∞) at age t. It can be added that the great diversity of functions and equations, which describe the relation L–t, is just apparent. The lines (HAILEY 1988), the exponential curves (our Fig. 2) and the asymptotic curves (Fig. 3 in WILLEMSEN & HAILEY 2001) that were used by different authors to describe the relation L–t in different periods of the life of chelonians, could be assumed as different segments of one and the same common sigmoid curve, which describes the growth pattern of most animals. The selection of the equation to describe the corresponding segment of the curve will depend mostly on the pattern of growth in the particular period studied, or in the period which is the best represented by empirical material.

3. The necessity of establishing preliminary goals when describing the relation L–t by an equation, i.e., the application aspect of this equation must be considered. The equation can be applied to mathematically describe the growth curves, i.e. for calculation and comparison of mean sizes (masses) at a definite age in different populations (Table 5, MEDAWAR 1945; RICKLEFS 1967; KNIGHT 1968, 1969), or to express physiological/biological regularities, (SCHMALHAUSEN 1935; VON BERTALANFFY 1938, 1957, 1960; TAYLOR 1962; WINBERG 1966). According to other authors, growth is specific to every ontogenetic stage, and therefore, it must be described by different equations (BRODY 1927, 1945; SCHMALHAUSEN 1935; VASNETSOV 1934; PARKER & LARKIN 1959).

4. The pattern and the rate of growth are genetically programmed. Changes in environmental conditions could provoke
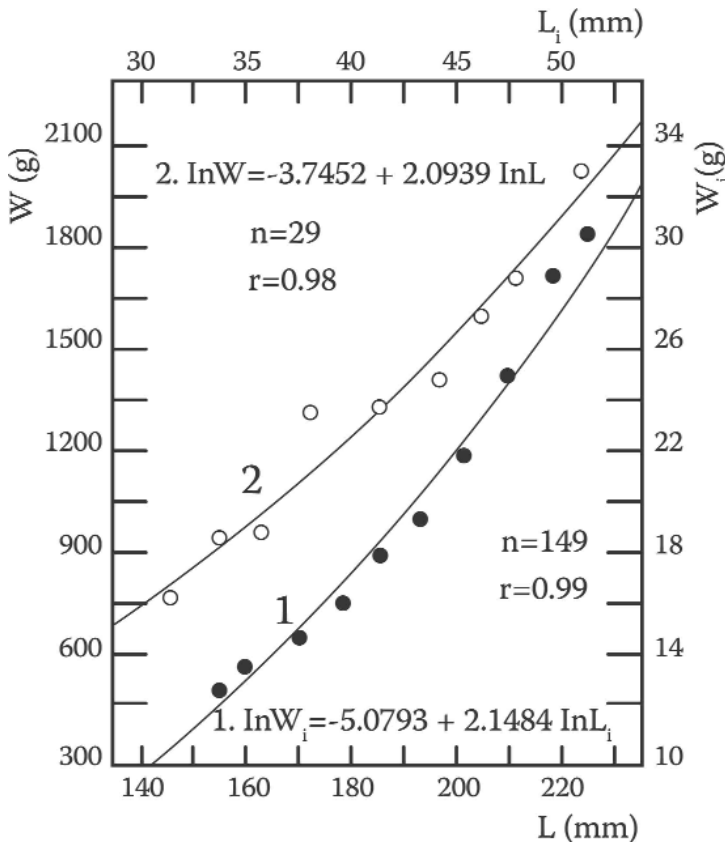
Fig. 4: Regressions of average tortoise mass of specimens of *Testudo hermanni* at the age of 0 to 175 days, hatched in incubators (1, W_i) and of specimens at the age of 1 to 25 years, hatched in natural nests (2, W) on average carapace length (L_i and L, respectively).

Abb. 4: Regressionen der durchschnittlichen Schildkrötenmasse von *Testudo hermanni* Individuen im Alter von 0 bis 175 Tagen, aus dem Inkubator (1, W_i) und von Individuen im Alter von 1 bis 25 Jahren, aus natürlichen Nestern (2, W) auf die durchschnittliche Karapax-Länge (L_i bzw. *L*).

variations in growth only within a certain range under continuous genetic control. For this reason, many authors study and take into consideration the effect of the natural process of growth self-regulation (growth compensation, or "Äquifinalität" in VON BERTALANFFY's, 1957 terms of growth) (WILSON & OSBOURN 1960; ZAMAKHAEV 1967; RICKER 1975; MINA & KLEVEZAL 1976; ŽIVKOV 1982, 1996; DOBSON & HOLMES 1984; MIGLAVS & JOBLING 1989; QUINTON & BLAKE 1990; RUSSEL & WOOTTON 1992; ŽIVKOV et al. 1999; XIE et al. 2001; ZHU et al. 2001, 2003; ALI et al. 2003).

Relationship of carapace length and body mass; condition coefficient

The regression of the tortoise body mass (W) on carapace length (L) of *T. hermanni* was best described by the power equation $W = aL^b$ (Fig. 4, Table 6). Although the relative mass growth rate in relation to length of juvenile specimens in the first 175 days ($b = 2.1484 \pm 0.1097$) was higher than that of the adult specimens ($b = 2.0939 \pm 0.1608$) (Fig. 4), this difference was not significant ($t = 0.26$, $P > 0.05$).

Table 6: Equation statistics of correlations of average tortoise masses (W, g) and average carapace lengths (L, mm) of specimens of *Testudo hermanni* at the age of 1 to 25 years. L_1, L_2, L_n and W_1, W_2, W_n - symbols for specimens at the age of 0 to 175 days, hatched in incubator No. 1 (L_1, W_1), No. 2 (L_2, W_2), and in natural nests (L_n, W_n). S.E. – standard error, r – correlation coefficient, P – probability, n – number of specimens.

Tab. 6: Gleichung der Korrelationen der durchschnittlichen Schildkröten-Massen (W, g) und der durchschnittlichen Karapax-Längen (L, mm) der *Testudo hermanni* - Individuen im Alter von 1 bis 25 Jahren. L_1, L_2, L_n und W_1, W_2, W_n - Symbole für Individuen im Alter von 0 bis 175 Tagen aus Inkubator No. 1 (L_1, W_1), No. 2 (L_2, W_2) und natürlichen Nestern (L_n, W_n). S.E. - Standardfehler, r - Korrelationskoeffizient, P - Wahrscheinlichkeit, n - Zahl der Individuen.

Regression	$a \pm$ S.E.	$b \pm$ S.E.	r	$P <$	n
$\ln W = a + b\ln L$	-3.7452 ± 0,8494	2.0939 ± 0.1608	0.98	0.001	29
♂ $\ln W = a + b\ln L$	-7.6952 ± 3.0044	2.8754 ± 0.5940	0.84	0.05	10
♀ $\ln W = a + b\ln L$	-3.5136 ± 1.0792	2.0497 ± 0.2043	0.93	0.001	19
$\ln W_1 = a + b\ln L_1$	-3.8511 ± 0.7488	1.8192 ± 0.1952	0.96	0.001	48
$\ln W_2 = a + b\ln L_2$	-4.3047 ± 0.1961	1.9259 ± 0.0527	0.999	0.001	53
$\ln W_{1+2} = a + b\ln L_{1+2}$	-5.0793 ± 0.4107	2.1484 ± 0.1097	0.99	0.001	101
$\ln W_n = a + b\ln L_n$	-3.3288 ± 1.2763	1.6409 ± 0.3497	0.93	0.001	19

This shows that in the process of postembryonal development (ontogeny), the tortoise *T. hermanni boettgeri* does not strongly change its body proportions (length, height, width), in contrast, for example, to fishes, whose values of slope b in the juvenile period are much different from those in the adult period (e.g. see PROKEŠ 1993).

There were no significant differences between the values of b for individuals hatched in incubators No. 1 ($b = 1.8192 \pm 0.1952$) and No. 2 ($b = 1.9259 \pm 0.0527$), ($t = 0.55$, $P > 0.05$), and for individuals hatched in incubator No. 2 and in natural nests ($b = 1.6409 \pm 0.3497$), ($t = 0.8$, $P > 0.05$); as well as for males ($b = 2.8754 \pm 0.5940$) and females ($b = 2.0497 \pm 0.2043$), ($t = 1.31$, $P > 0.05$) (Table 6). In comparison to the population of *T. hermanni* in

Alyki, Greece (HAILEY 2000), the population in the Eminska Mountains had higher mean masses at any given carapace length (Table 7).

When analyzing the length–mass relationship of *T. hermanni,* we found similar regularities and characteristics as in fishes (ŽIVKOV 1993; RAIKOVA-PETROVA & ŽIVKOV 1998; ŽIVKOV & RAIKOVA-PETROVA 2001; ŽIVKOV et al. 2003). The mass/length ratio, like any other morphological ratio of organisms, is genetically programmed. Changes in environmental conditions can provoke variations in this ratio only within a certain range and under continuous genetic control. The inverse relation between the intercept a (or initial mass at the same length) and slope b in the equation $W = aL^b$, in fact, parallels the process of correction of mass deviation

Table 7: Average body mass of *Testudo hermanni* from different localities and of different sex, calculated for carapace lengths of $L = 140, 160, \ldots$ etc., mm (W_{140}, W_{160}, \ldots etc., g). r – correlation coefficient, n – number of specimens. BG - Bulgaria, GR - Greece.

Tab. 7: Durchschnittliche Körpermasse von *Testudo hermanni* aus unterschiedlichen Gebieten und unterschiedlichen Geschlechtes berechnet für Karapax-Längen von $L = 140, 160, \ldots$ etc., mm (W_{140}, W_{160}, \ldots etc., g). r - Korrelationskoeffizient, n - Zahl der Individuen. BG - Bulgarien, GR - Griechenland.

| Locality, country (source) Gebiet, Land (Quelle)	Equation Gleichung	Average body mass / Mittlere Körpermasse						
		W_{140}	W_{160}	W_{180}	W_{200}	W_{220}	r	n
Alyki, GR, ♂ (HAILEY 2000)	$\log W = -3.1031 + 2.7199\log L$	542	780	1074	1430		0.96	746
Alyki, GR, ♂ + ♀ (HAILEY 2000)	$\log W = -3.1160 + 2.7290\log L$	551	793	1093	1457		0.97	1465
Alyki, GR, ♀ (HAILEY 2000)	$\log W = -3.0636 + 2.7103\log L$	556	813	1209	1490		0.98	361
Eminska Mountain, BG, ♂	$\log W = -3.3420 + 2.8754\log L$	676	961	1310			0.84	10
Eminska Mountain, BG, ♂ + ♀	$\log W = -1.6265 + 2.0939\log L$	736	974	1247	1555	1899	0.98	29
Eminska Mountain, BG, ♀	$\log W = -1.5259 + 2.0497\log L$	746	981	1249	1551	1855	0.93	19
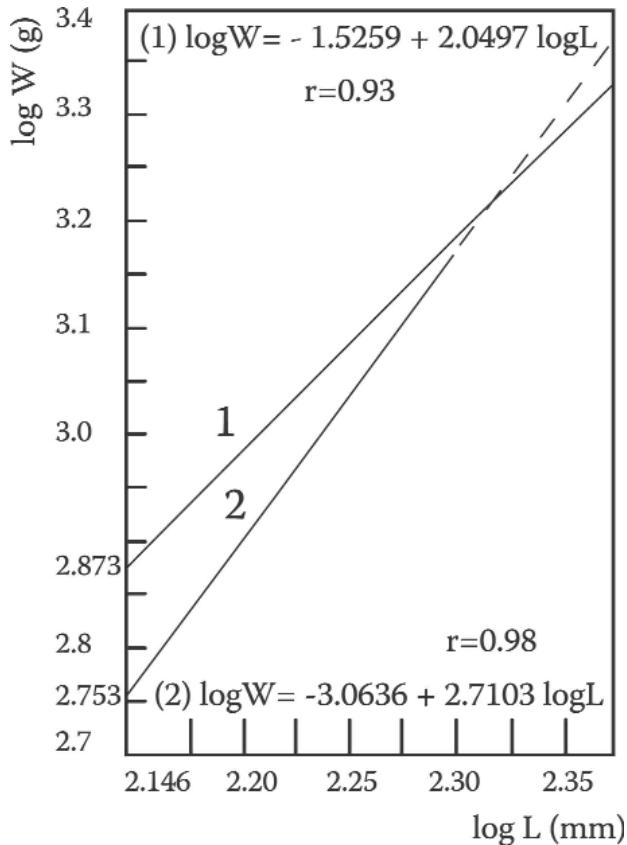
Fig. 5: Differences in log carapace length (*L*) – log body mass (*W*) regression lines of females in two populations with different average initial masses (W_1 = 746 g, log 746 = 2.873; W_2 = 566 g, log 566 = 2.753) at the same length (140 mm, log 140 = 2.146). 1, 2 - regression lines of *Testudo hermanni* in the Eminska Mountains (Bulgaria) (1) and in Alyki (Greece) (2).

Abb. 5: Unterschiede in den Regressionslinien von log Karapax-Länge (*L*) – log Körpermasse (*W*) der weiblichen Individuen in zwei Populationen mit unterschiedlichen durchschnittlichen Ausgangsmassen (W_1 = 746 g, log 746 = 2.873; W_2 = 566 g, log 566 = 2.753) bei gleicher Karapax-Länge (140 mm, log 140 = 2.146). 1, 2 - Regressionslinien von *Testudo hermanni* aus dem Eminska Gebirge (Bulgarien) (1) und aus Alyki (Griechenland) (2).

from the normal (genetically programmed) values of a given length, i.e. the process of ontogenetic growth self-regulation. For instance, the relation between average log*a* and *b* parameters in the equations log*W* = log*a* + *b*log*L* describing the length (*L*, mm) – mass (*W*, g) relationship in females and males of *T. hermanni* in Alyki (Greece) (HAILEY 2000), and in the Eminska Mountains at different months, can be expressed by the equation $b = 1.3969 - 0.4275 \log a$, $r = -0.99$, $n = 18$. In this case log*L* – log*W* re-gression lines gradually approach each other and in most cases intersect (Fig. 5). The fact that the lines cross, makes it impossible to use the parameters a (= W/L^b) or b as body mass condition coefficients. Also, it is not possible to distinguish the influence of the two factors (self-regulation and environmental conditions), which determine individual and population specificity of the *W-L* relation. Therefore, it is suggested to use the mean masses calculated for standardized carapace length values, according to the

Table 8: Equation statistics of correlations of average carapace width (Wd, mm) and carapace height (H, mm) on average carapace length (L, mm) of *Testudo hermanni* specimens at the age of 1 to 25 years. L_i Wd_i H_i and L_n Wd_n H_n - symbols for specimens at the age of 0 to 175 days, hatched in incubators (i), and in natural nests (n), respectively. S.E. – standard error, r – correlation coefficient, P – probability, n – number of specimens.
Tab. 8: Gleichungen von Korrelationen der durchschnittlichen Karapax-Breite (Wd, mm) und Karapax-Höhe (H, mm) zur durchschnittlichen Karapax-Länge (L, mm) bei *Testudo hermanni* - Individuen im Alter von 1 bis 25 Jahren. L_i Wd_i H_i und L_n Wd_n H_n - Symbole für Individuen im Alter von 0 bis 175 Tagen, aus Inkubatoren (i) und natürlichen Nestern (n). S.E. - Standardfehler, r - Korrelationskoeffizient, P - Wahrscheinlichkeit, n - Zahl der Individuen.

Regression	$a \pm$ S.E.	$b \pm$ S.E.	r	$P <$	n
$\ln Wd = a + b\ln L$	0.3635 ± 0,0590	0.8792 ± 0.0120	0.999	0.001	99
♂ $\ln Wd = a + b\ln L$	0,0084 ± 0,1617	0.9564 ± 0.0320	0.997	0.001	45
♀ $\ln Wd = a + b\ln L$	0,5593 ± 0,0900	0.8383 ± 0.0175	0.998	0.001	39
$\ln Wd_i = a + b\ln L_i$	0,6723 ± 0,1280	0.7831 ± 0.0390	0.99	0.001	218
$\ln Wd_n = a + b\ln L_n$	0,2901 ± 0,1388	0.8825 ± 0.0371	0.99	0.01	32
$\ln H = a + b\ln L$	-0,2151 ± 0,1273	0.9088 ± 0.0255	0.96	0.001	99
♂ $\ln H = a + b\ln L$	0,5329 ± 0,6283	0.7562 ± 0.1246	0.95	0.001	45
♀ $\ln H = a + b\ln L$	0,1828 ± 0,3505	0.8325 ± 0.0683	0.97	0.01	39
$\ln H_i = a + b\ln L_i$	0,3564 ± 0,2262	0.7359 ± 0.0601	0.97	0.001	215
$\ln H_n = a + b\ln L_n$	0,3784 ± 0,3472	0.7275 ± 0.0928	0.94	0.01	32

equation $W = aL^b$, as a body mass condition coefficient for different populations within species (Table 7).

The method for studying the body mass condition of tortoises, suggested by Hailey (2000), is close to our assumption. He assessed the body mass condition of *T. hermanni* using the ratio of observed mass (W) to predicted mass (W') based on the term $W = aL^b$. A condition index ($CI = \log W/W'$), which ranged from approximately -0.1 to +0.1 was suggested. However, we do not recommend this method, because it did not take into account the natural self-regulation process of the allometric ontogenetic W-L growth, and because it used relative indices (-0.1 to +0.1) instead of absolute ones (i.e., mass, g, at given lengths, mm). The curves in Hailey's (2000) Fig. 3, which expressed the seasonal (monthly) variation in the con-

dition index, were not quite precise. It was shown that both in male and female tortoises the body mass condition index was lowest in September, when, according to the author, the index values were unusually low as compared to those in all other months. This is, however, not quite correct. We recalculated the body masses at given lengths (140, 160, etc., mm) (W_{140}, W_{160}, etc., g), for the months March and September, using the equation $W = aL^b$ from Table 2 in Hailey (2000). The results showed, that the values of W (i.e., body mass condition) for the months March and September were rather close, whereas the values of W_{140} of females and the values of W_{180}, W_{200}, etc., of males were higher in September than in March (which was to be expected for the pre-overwintering period).

Table 9. Sexual differences in average carapace width (Wd, mm) and average carapace height (H, mm) of *Testudo hermanni* at carapace lengths of L = 130, 150, … etc, mm (Wd_{130}, Wd_{150}, … etc, mm; H_{130}, H_{150}, … etc, mm, respectively).
Tab. 9: Geschlechterunterschiede in den durchschnittlichen Karapax-Breiten (Wd, mm) und Karapax-Höhen (H, mm) von *T. hermanni* bei Karapax-Längen von L = 130, 150,… usw., mm (Wd_{130}, Wd_{150}, … usw., mm; bzw. H_{130}, H_{150}, … usw., mm).

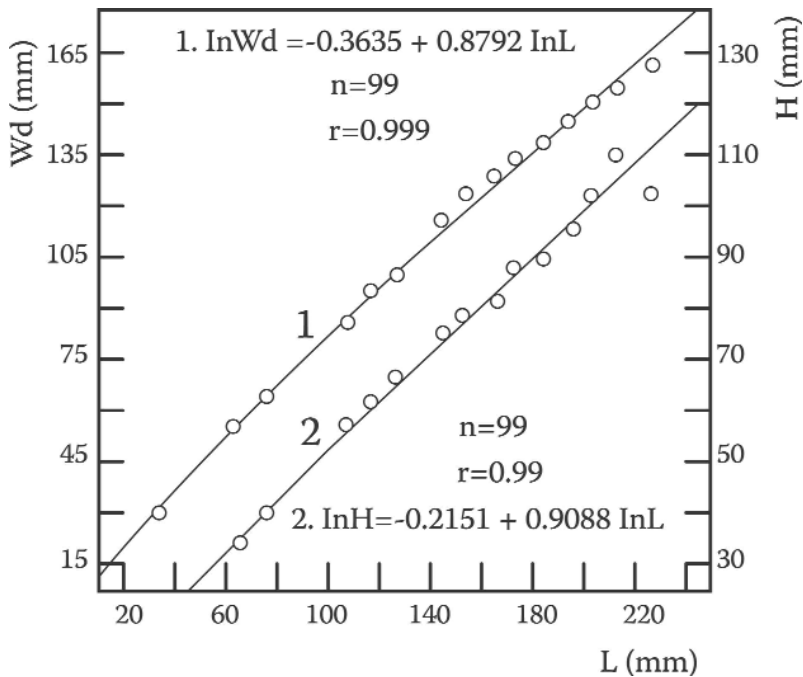| Sex	Regression	Wd_{130}/H_{130}	Wd_{150}/H_{150}	Wd_{170}/H_{170}	Wd_{190}/H_{190}	Wd_{210}/H_{210}
♂	$\ln Wd = 0.0084 + 0.9564\ln L$	106.0	121.6	137.0	152.4	167.7
♀	$\ln Wd = 0.5593 + 0.8383\ln L$	103.5	116.7	129.6	142.3	154.7
♂	$\ln H = 0.5329 + 0.7562\ln L$	67.6	75.3	82.8	90.1	97.2
♀	$\ln H = 0.1828 + 0.8335\ln L$	69.4	78.2	86.8	95.2	103.5

Fig. 6: Regressions of average carapace height (1, *H*) and average carapace width (2, *Wd*) on average carapace length (*L*) in *Testudo hermanni* in the Eminska Mountains (Bulgaria).

Abb. 6: Regressionen der durchschnittlichen Karapax-Höhe (1, *H*) und der durchschnittlichen Karapax-Breite (2, *Wd*) auf die durchschnittliche Karapax-Länge (*L*) von *Testudo hermanni* aus dem Eminska Gebirge (Bulgarien).

Relationship of carapace length and carapace width

The regression of average carapace width (*Wd*) on average carapace length (*L*) was best described by the power equation $Wd = aL^b$ (Fig. 6 and Table 8). The correlation between *Wd* and *L* was extremely high ($r = 0.99$). The difference (0.0994) between slopes *b* of the regression log*Wd*–log*L* straight lines for tortoises hatched in incubators (i) and in natural nests (n) was not significant ($t = 1.84$, $P > 0.05$) (Table 8). However, the difference (0.1181) between slopes *b* of these lines for males and females was significant ($t = 3.2$, $P < 0.01$). The mean carapace width of females (138.3 ± 2.7 mm) was significantly higher than that of males (127.5 ± 1.18 mm), ($t = 3.36$, $P < 0.01$). Moreover, at the same carapace length, the carapace width in males was higher compared to that of females (Table 9).

Relationship of carapace length and carapace height

The regression of the average carapace height (*H*) on the average carapace length (*L*) was also described by a power equation (Fig. 6 and Table 8). The correlation between *H* and *L* was very high ($r = 0.99$). The difference (0.0084) between slopes *b* of the regression log*H*–log*L* straight lines for the tortoises hatched in incubators (i) and in natural nests (n) was not significant ($t = 0.08$, $P > 0.05$). The difference (0.0738) between slopes *b* of these lines for males and females was not significant either ($t = 0.5$, $P > 0.05$). Moreover, the mean carapace height of females (92.04 ± 1.81 mm) was significantly higher than that of males (80.04 ± 0.64 mm) ($t = 6.25$, $P < 0.001$). The relative growth rate of the carapace height towards the carapace length in adult specimens ($b = 0.9088 ± 0.0255$)

was significantly higher than the growth rate in juvenile individuals, hatched in incubators ($b = 0.7359$), ($t = 2.64$, $P < 0.01$). This difference, however, was not significant with regard to the juvenile individuals, hatched in natural nests ($t = 1.88$, $P > 0.05$). At any given carapace length, the carapace height of females was higher than of males (Table 9). There were no investigations available on carapace length – carapace width and carapace length – carapace height relationships of *T. hermanni* in order to compare the obtained results with that of other authors.

ACKNOWLEDGMENTS

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