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THE COMPARATIVE POPULATION ECOLOGY OF HERMANNS TORTOISE, *TESTUDO HERMANNI* IN CROATIA AND MONTENEGRO, YUGOSLAVIA

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ABSTRACT

Following initial studies on the population ecology of *Testudo hermanni* in Montenegro, Yugoslavia (Meek, 1984; 1985; 1988a) new demographic observations have been made on additional populations of these tortoises in Croatia and Montenegro. Results indicate that Montenegren males attain a greater size than Croatian males, but there were no significant differences between the sizes of females. Adult sex ratios were in good agreement with equal numbers of males and females in Croatia; in Montenegro the ratio was 1.33:1. A large proportion of individuals in both populations exceeded 19 years although the proportion was higher in Montenegro as a result of Montenegren males attaining greater age than Croatian males. Equations to describe growth trends indicate that in general females grow faster than males and that Montenegren females grow faster than Croatian females. Population and biomass densities, biomass production and relative biomass turnover were higher in Croatia. Survivorship was higher and mean annual recruitment lower in Montenegro but males have a higher survivorship than females in both regions. Females sustained greater shell damage and physical injuries than males although generally Croatian tortoises of either sex sustained injuries at earlier ages. Sexually active males were smaller than their female partners and there were no inter-population differences between the sizes of males or females. Allometric equations describe morphometric characters, confirming sexual dimorphic trends found earlier in Yugoslavia and additionally show that males have longer tails. Only male plastron length, which was relatively greater in Croatian males showed inter-population differences.

INTRODUCTION

Studies on the ecology of Mediterranean tortoises have developed principally out of a concern that commercial exploitation for the food and pet trades may have detrimental effects on wild populations (Lambert, 1980). The earliest work examined the impact of pet trade collection on *Testudo graeca* in North Africa and indicated serious declines in population levels over large areas of its range (Lambert, 1980, 1982). Further studies concerned *Testudo hermanni* in Europe. In Greece the effects of deliberate burning and ploughing of the habitat resulted in a dramatic reduction in numbers (Stubbs *et al.*, 1985) and in southern France a slow decline in population levels was attributed to the abandoning of traditional agricultural practices by the local people (Stubbs and Swingland, 1985). Clearly many factors could be involved in a species decline and thus demographic information concerning Mediterranean tortoise populations are important conservation tools, since it is conceivable that the dynamics of each population may differ even when these are closely situated to one another; indeed, distinct differences in the thermal ecology of *T. hermanni* have already been found between various populations (review in Meek and Avery, 1988). This paper presents new observations on the comparative population ecology of *T. hermanni* in Yugoslavia and compares a Montenegren population living in close association with humans with one living in a relatively undisturbed area in Croatia. The paper forms part of a series of field studies on the ecology of *T. hermanni* which have to date after an initial general survey in Montenegro (Meek and Inskeep, 1981), examined thermal ecology (Meek, 1984, 1988a, 1988b) and population ecology (Meek, 1985).

STUDY AREAS

The observations were obtained from tortoise populations inhabiting scrubland areas with partly wooded perimeters on the Adriatic coast. The northern site was in Croatia where the dominant vegetation, *Quercus pubescens, Agrimonia eupatoria, Paliurus spina-christi, Ficus carica, Prunus domestica* and *Olea europaea* were used by *T. hermanni* as shade plants. Typically there were open grass covered clearings with limestone rocky outcrops (Fig. 1b) where growth of *Hedera helix* was also found. Such clearings in the summer months could experience air temperatures around 41°C. Wet Autumn weather saw the appearance of fungi (*Basidiomycetes*) on the clearings.

The main feature of the Montenegren site was the agricultural activities (e.g. cabbage, lettuce and olive cultivation) which accounted for about 30 per cent of the land area (Fig. 1a). In the remaining natural zones the dominant vegetation was *Vicia, Arundinkria, Rubus, Pteridium* and *Pistacia*. The whole area was covered by a series of irrigation ditches (mostly of concrete construction) about 1 metre wide.

The adults were mostly found in scrub habitat generally in both areas. In contrast, hatchlings and

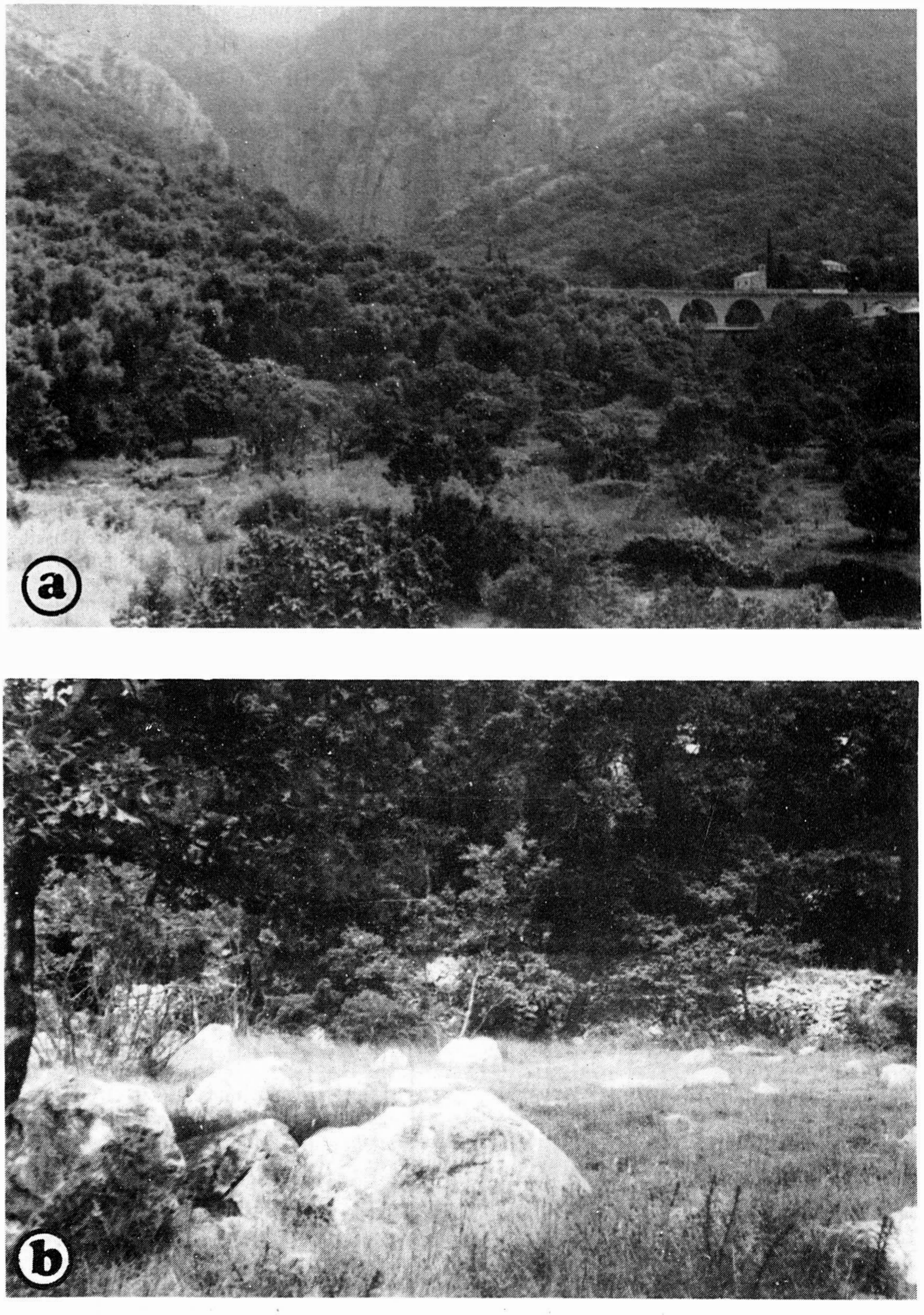

Fig. 1 Views of study areas in Montenegro (1a) and Croatia (1b). Fig. 1a shows the cultivated areas in the foreground and the heavily wooded eastern section. Fig. 1b shows an open clearing with characteristic limestone outcrops.

very young tortoises (<5 years) were when found, usually in association with *Spartium juniceum* (Croatia) and *Brachypodium* sp (Montenegro). These tall (app. 1 m) narrow stemmed plants provide the benefits to small tortoises of both cover and sunlight penetration.

METHODS

Field work was carried out in Montenegro over an eight day period in late May 1986 and over a two week period in early June 1986 in Croatia. Additional general information was gathered over a three week period in Croatia from late September to mid-October 1984. When located each tortoise was given a unique mark using the method of scute notching; also noting the date and time of capture. Other procedures in the field, that is methods for gathering plant samples, body measurements, assessment of age and physical condition are those given in Meek (1985). Sampling was carried out throughout the daily period, by making daily routine patrols of the study area usually by two observers, but each working alone. Most tortoises were located by sight although a small number of individuals, particularly juveniles were located by sound when moving through dense vegetation.

Population Density Estimates

Density estimates have been made using the triple catch method in which recaptures are grouped according to the time at which they were marked. In this system the three samples were taken at short intervals of time and although it is not required that the time intervals between sampling should be equal (Ricker, 1958) in this study two day sampling periods were separated by one day non-sampling intervals.

Statistical Analysis

Regression analysis has been used for calculating mathematical models of age related and relative growth after transforming the data into logarithmic form (Sokal and Rohlf, 1981). To estimate the number of growth annuli on the coastal scutes from carapace length Model (1) regression has been used which treats y, the number of annuli, as dependent on carapace length (x). To describe relative growth Model (2) regression (geometric mean) has been used. This is considered a more appropriate method for relating variables when neither can be regarded as truly

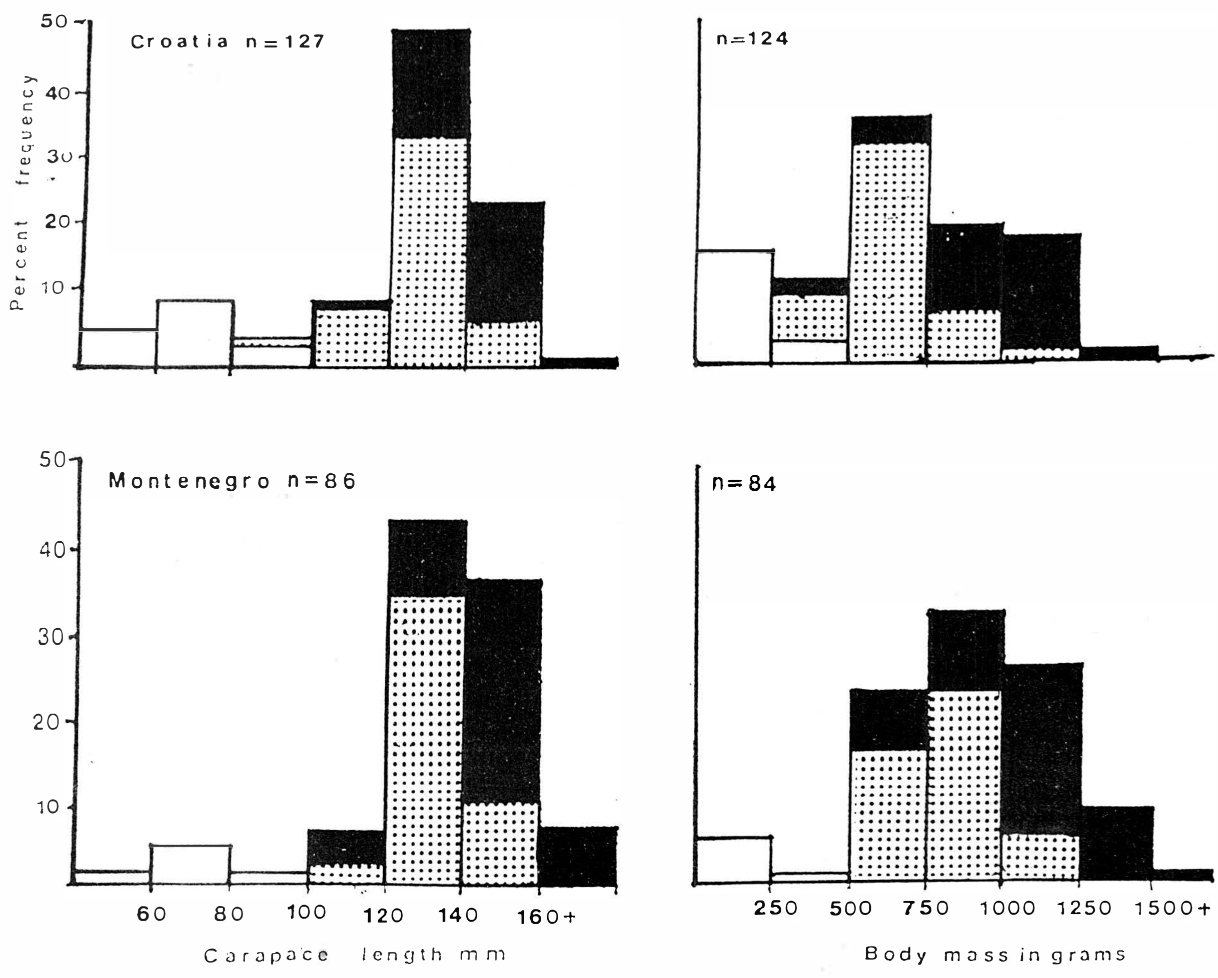

Fig. 2 Size frequencies of *T. hermanni* in Croatia and Montenegro. Solid histograms represent females, stippled bars males and open bars immatures.

	Mean and (maximum) carapace length ± 1 S.E. in mm		Mean and (maximum) body mass ± 1 S.E. in grams	
	males	females	males	females
Mont. (1)	135.4 ± 7.8 (148)	147.6 ± 16.8 (190)	822.9 ± 136.6 (1038)	1075.7 ± 276.5 (1680)
Mont. (3)	126.4 ± 8.6 (143)	147.0 ± 12.1 (170)	609.0 ± 105.3 (740)	989.0 ± 208.9 (1410)
Mont. (4)	140.9 ± 11.3 (170)	159.3 ± 14.6 (175)	— — —	— — —
Croa. (2)	127.7 ± 9.8 (145)	141.7 ± 9.6 (164)	631.9 ± 144.8 (1025)	990.9 ± 184.8 (1300)
Cor. (5)	140.6 ± 7.9 (150)	164.6 ± 19.6 (190)	724.3 ± 131.4 (879)	1056.0 ± 276.5 (1417)

TABLE 1: Details of size characteristics of *T. hermanni* populations in this study in Yugoslavia (1,2) and also data from (3) Budva (Meek, 1985) (4) Petrovac (Wallace and Wallace, 1985) and (5) Corfu (Wallace and Wallace, 1985). The calculations are based on tortoises exceeding 100mm carapace length.

independent. A basic description of the differences between the two methods has been given in Meek (1987).

Confidence intervals have been calculated for the constants in the equations at the 95 percent interval. In Model (2) regression the confidence limits are expressed for b and y_0, in Model (1) regression for b and a. The expression x/÷ in the intervals for a and y_0 indicates for example in equation (1) in Table 2, from 0.0004 x 1.07 to 0.0004 ÷ 1.07. Tests for significant differences between exponents have been made using the t-distribution in the way described by Bailey (1981). Other population characters have been analysed at the 95 per cent interval using the t and F-distributions at appropriate degrees of freedom.

RESULTS

Population Structure

The frequency distributions of carapace lengths and body masses of both populations are shown in Fig. 2 with details of the means and ranges given in Table 1. The samples were skewed towards larger animals with females larger than males in both populations: Carapace lengths (Croatia) $F\{1,103\} = 48.74, P<0.0001$ and (Montenegro) $F\{1,78\} = 16.05, P<0.001$; body masses (Croatia) $F\{1,100\} = 118.59$, $P<0.0001$ and (Montenegro) $F\{1,76\} = 25.53$, $P<0.0001$. Males from Montenegro had significantly longer carapace lengths $\{F\{1,99\} = 15.51, P<0.001\}$ and greater body masses $(F\{1,95\} = 41.59$ $P<0.001)$ than Croatian males, but there was no significant difference between the carapace lengths or body masses $(P>0.05)$ of females from the two populations.

Sex Ratios

From a total of 127 identified tortoises in Croatia, 60 were males 45 were females and 22 immatures or hatchlings. This indicates an adult sex ratio of 1.33:1 in favour of males and an adult: immature ratio of 4.77:1. Eighty six tortoises were identified in Montenegro of which 41 were males, 39 were females and 6 immatures. This gives an adult sex ratio of almost parity (1.05:1) and adult: immature ratio of 13.33:1.

Age Structure

Based on the limitations of growth ring number as a means of determining age (Castanet and Cheylan, 1979). Age structure has been limited at 19 years with older animals shown as more than 19 years. The age distributions are shown in Fig. 3. In both populations most tortoises were above 16 years (Croatia 75.5 per cent; Montenegro 87.1 per cent). However, whilst in Croatia 42.5 per cent exceeded 19 years a much larger proportion (67.4 per cent) of Montenegren tortoises exceeded 19 years. In animals aged more than 19 years males predominated (Croatia, males 27.5 per cent, females 14.9 per cent; Montenegro, males 39.5 per cent, females 27.9 per cent), although in both

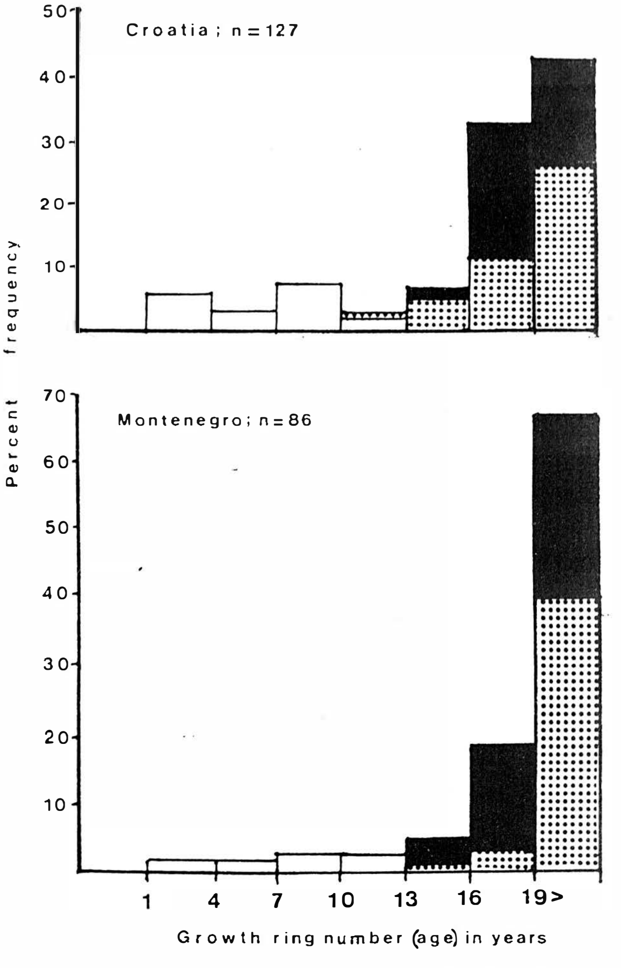

Fig. 3 Age frequencies of *T. hermanni* in Croatia and Montenegro. Other details are given in Fig. 2.

Eqn. No.	Independent variable x	Pop.	Factor a	95% con. interval	Exponent b	95% con. interval	n
(1)	C. length (males)	C	0.0004	1.07	2.23	0.18	82
(2)	C. length (females)	C	0.0011	1.07	1.99	0.16	67
(3)	C. length (males)	M	0.0011	1.06	2.02	0.29	47
(4)	C. length (females)	M	0.0096	1.05	1.54	0.25	45

TABLE 2: Allometric equations of the form $y = ax^b$ relating the number of growth annuli on the coastal scutes y with the straight length of the carapace x in mm in *T. hermanni* from Croatia (C) and Montenegro (M). The 95% confidence intervals attached to factor a are the x/÷ type, to the exponent b the ± type. The number of observations on which the equations are based (n) are also given.

populations females were more numerous between 16-19 years. Based on growth ring counts there was no significant difference between the ages of females in the two populations (Croatia $\bar{x}$ = 20.2; Montenegro $\bar{x}$ = 20.3: $F\{1.82\} = 0.01$, $P>0.05$) but Montenegren males ($\bar{x}$ = 23.6) were apparently older than Croatian males ($\bar{x}$ = 21.3) with the difference significant ($F\{1.99\} = 4.07$, $P<0.05$). Immatures from Croatia ($\bar{x}$ = 5.7) were younger than those from Montenegro ($\bar{x}$ = 7.6) but the differences was not significant ($P>0.05$).

AGE MODELS

The simplest model which relates the logarithms of carapace length y in mm with the logarithms of growth ring number x, is a model I allometric equation of the form:

$$y = ax^b$$

where a and b are constants. Data for these variables are shown in Table 2. The highest correlations were found for Montenegren tortoises (males r = 0.94;

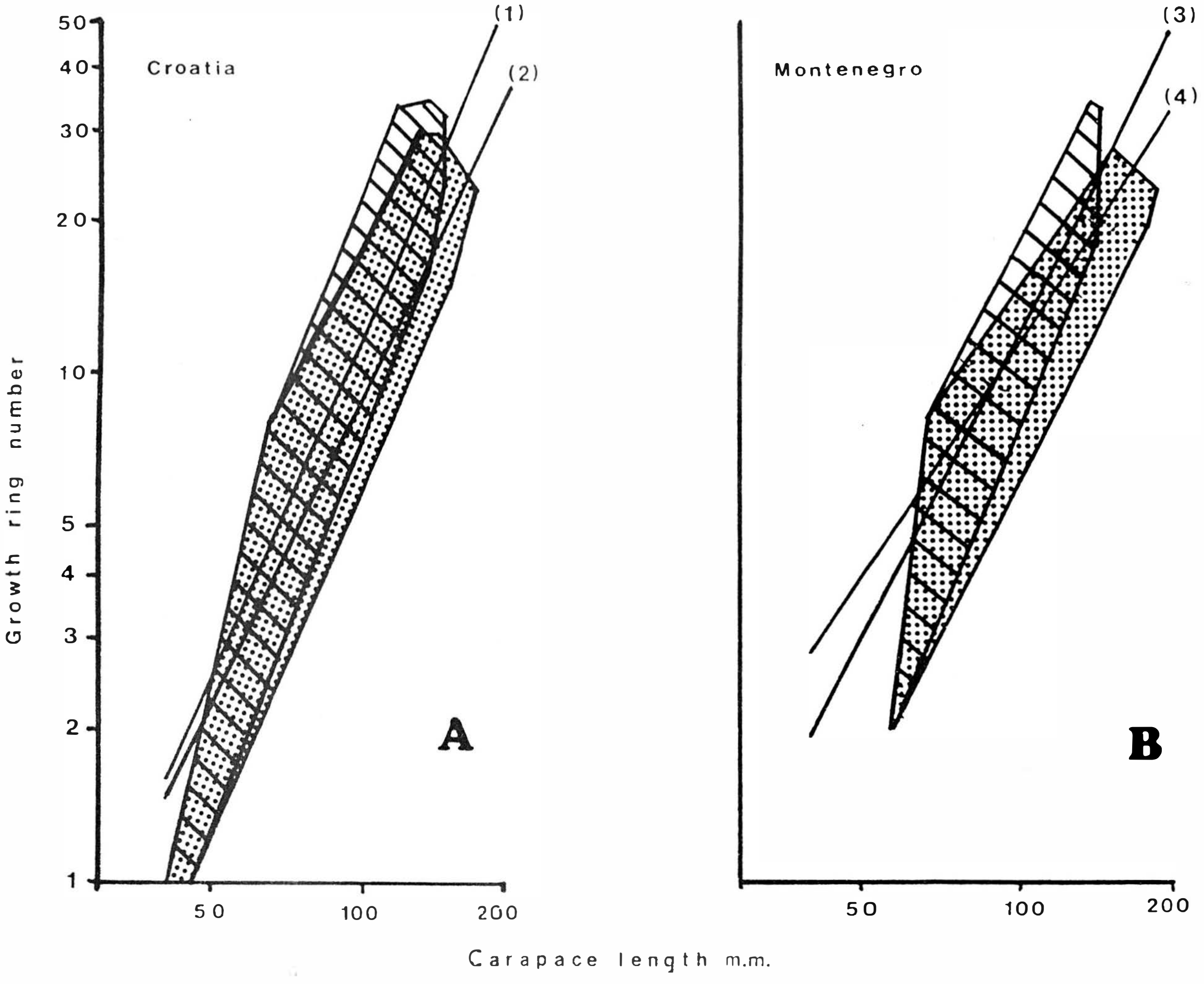

Fig. 4 Graphs on logarithmic coordinates of growth ring number plotted against carapace length in *T. hermanni* from Croatia (A) and Montenegro (B). The data have been converted into the smallest convex polygons which will enclose all the data points with male and female data treated separately. Hatched polygons represent females, stippled polygons males. The lines running through the polygons are derived from equations given in Table 2: these are explained in the text.

females r = 0.95) although good correlations (males r = 0.89; females r = 0.90) and better confidence intervals were found in Croatian animals. These equations indicate that in general, females grow faster than males, and that Montenegren females grow faster than females from Croatia (t = 2.25, P<0.05). Montenegren males appeared to grow faster than Croatian males but the equations describing the data are not significantly different (P>0.05). Fig. 4 is a graph of the data plotted as convex polygons on logarithmic coordinates and are shown with lines calculated from the four equations. These suggest that (for example) a female from Montenegro would require 33 years to achieve a carapace length of 200mm whereas this would take 56 years for a Croatian male.

SURVIVORSHIP

The age structures of the populations have been used to infer survivorship on the assumption that there were no conspicuous gaps in the age distributions of either population which would suggest periods of low recruitment or possible sampling error, i.e. annual recruitment rates and age structures have been assumed constant. Survivorship curves have been calculated by the method described by Deevey (1947). The survivorship curves in Fig. 5 have thus been calculated by taking the number of tortoises present at the beginning of each age class as a percent of the total population sample. Survivorship is higher in the Montenegren population which until 19 years is 67.4 per cent (Fig. 5b); in Croatia the corresponding value is 42.5 per cent (Fig. 5a). Both populations have a higher survivorship until 19 years than a population from central Montenegro (Fig. 5a) described by Meek (1985). Male survivorship is higher than females in both areas with major departures in the male-female curves beginning around 16 years (Fig. 5b).

Mean annual recruitment has been calculated from the mean annual population increment until 19 years and expressed as a percentage of the total using the equation:

$$R_p = \frac{(T_n - t_o)18\ (100)}{T_n}$$

where R_p is the percent recruitment, T_n the total number of tortoises in each study area sample and t_o the total number of tortoise over 19 years. This method gives a recruitment value that may only be empirical but it is useful in estimating mortality for the first 18 years. The calculations indicate that mean annual recruitment is lower in Montenegro (males 1.3%; females 2.7%; $\bar{x}$ = 1.8%) than Croatia (males 3.1%; females 4.0%; $\bar{x}$ = 3.2%).

MORTALITY

A total of six dead tortoises were found on the study area none of which appeared to be recent deaths since there were no soft tissue remains. Of these four (two males, one female and one unsexed) were from Croatia. Based on the number of growth annuli on the scutes these were all old animals with at least 24 annuli on the males (c. lengths 148 and 150mm) and 20 annuli on the female (c. length 144mm) with the unsexed animal showing adult size. The dead animals from Montenegro appeared to be males with at least 21 and 25 annuli (128 and 148mm carapace lengths). The skeletal remains of the shells and many other bones of these and the three sexed Croatian tortoises were intact suggesting perhaps mortality during the winter dormancy. The percentage of dead tortoises to the *total* field samples (*total* = dead plus living tortoises) was 3.05 per cent in Croatia and 2.3 per cent in Montenegro.

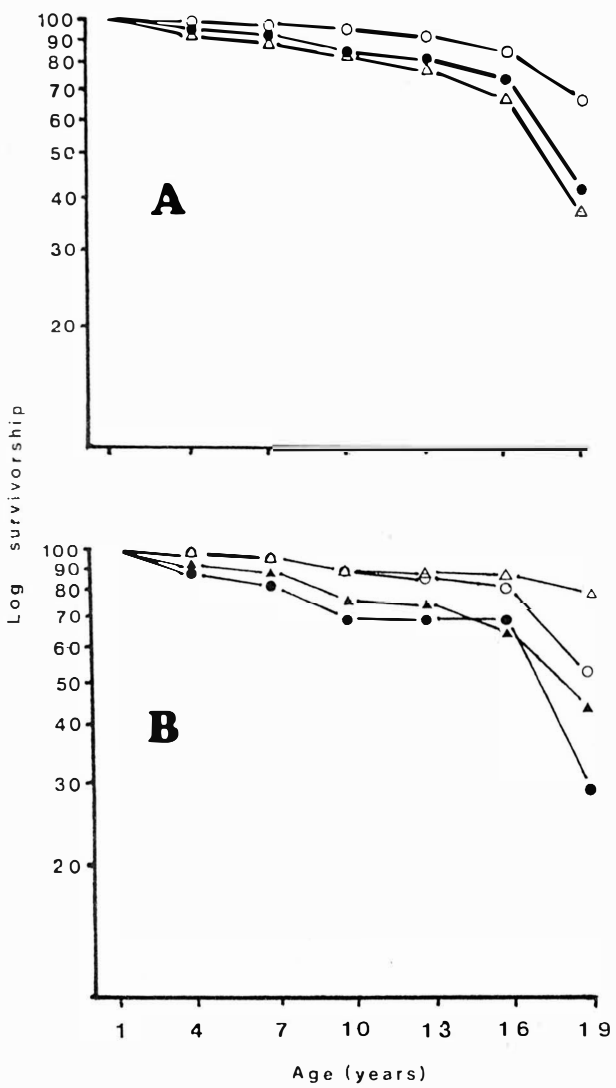

Fig. 5 General survivorship curves for *T. hermanni* in Montenegro and Croatia until 19 years (Fig. 5a). Open circles represent Montenegro, solid circles Croatia and triangles data for Montenegro from Meek (1985) for comparison. Fig. 5b shows distinct male-female survivorship curves for Montenegro (this study) where males are open triangles, females open circles and Croatia where males are solid triangles and females solid circles.

INJURIES

Eighteen tortoises (14.2 per cent) in Croatia and eight tortoises (9.3 per cent) in Montenegro were found to have sustained injuries. These included, in Croatia, carapace scutes absent (probably from fire damage), cracked shells, dents in the carapace and one animal with the right rear limb absent. In Montenegro they consisted principally of dented or cracked shells. One female (c. length 178mm) in addition to having lost part of the anterior section of the carapace, had also lost the left rear limb. Fig. 6 shows the frequency distributions of damaged tortoises in relation to their age. Figs. 6a and 6b show the simple numerical frequencies; Fig. 6c and 6d the frequencies when corrected for the bias in age class frequency. Fig. 6 demonstrates two main points 1) In both areas females sustained more injuries than males and 2) Croatian tortoises sustained injuries at earlier ages (although no animal in Croatia had serious injuries below 14 years).

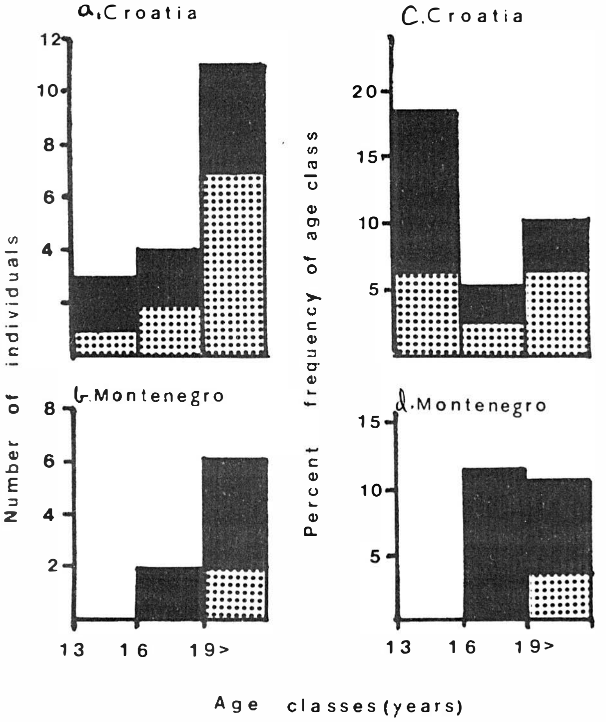

Fig. 6 Histograms showing shell damage and injury distribution in relation to age in *T. hermanni*. Upper histograms show data for Croatia, lower histograms data for Montenegro. See text for discussions and Fig. 2 for bar keys.

Densities

Population densities have been estimated using the 'triple catch' method (Ricker, 1958) where sampling was divided into three periods each of two days duration with one day non-sampling intervals between. On the first occasion tortoises were marked and released and after the one day interval a second sample was taken with recaptures noted and unmarked animals given new distinguishing marks. On the third sampling period recaptures from the first and second samples were recorded with unmarked tortoises. Density has been calculated using:

$$D_2 = \frac{(N_2 - M_{1.2})(N_2 + 1) M_{1.3}}{(M_{1.2} + 1)(M_{2.3} + 1)}$$

where N_1 are the total captures on day one, N_2 the total captures on day two, N_3 the total captures on day three, $M_{1.2}$ the recaptures on day two of tortoises marked on day one, $M_{1.3}$ the recaptures on day three of animals marked on day one and $M_{2.3}$ the recaptures of animals on day three of the animals marked on day two. Table 3 shows the numbers for the sampling periods for both areas. In Croatia this indicated 226.6 tortoises in 2.8ha and in Montenegro 58.3 tortoises in a 1.3ha area. Thus population density estimates were 80.92ha^{-1} in Croatia and 44.83ha^{-1} in Montenegro (although in Montenegro the area sampled included the agricultural zones, so the densities in natural zones would be somewhat higher).

	Period 1	Period 2	Period 3
Montenegro	N1 = 25	N2 = 23	N3 = 19
	—	M1. 2 = 6	M1. 3 = 6
	—	—	M2. 3 = 5
Croatia	N1 = 40	N2 = 39	N3 = 37
	—	M1. 2 = 5	M1. 3 = 4
	—	—	M2. 3 = 3

TABLE 3: Triple catch analysis to estimate population density of *T. hermanni* in Croatia and Montenegro. Further details are given in the text.

Biomass Density

Using the results from population density estimates, biomass density has been calculated. In this paper density has been estimated by taking the mean biomass of the population in g times the population density. Thus in Croatia where the mean biomass was 681.93g, a biomass density of 55.2kg ha^{-1} is indicated. In Montenegro mean biomass was 892.0g which gives a biomass density estimate of 39.9kg ha^{-1}. These values exceed the density calculated by Meek (1985) for a population of *T. hermanni* at Budva but the mathematics used in that study underestimated biomass density since it is based on the allometric relationship of body mass with carapace length. A more accurate (and simpler) method if mass is known is the one used in this paper. This would give an estimate of 26.8kg ha^{-1} in Budva which is in slightly better agreement with the results of this study.

Annual Biomass Production

Biomass production has been calculated by the method described by Iverson (1982). It is based principally on the assumption that the population is stable, and therefore that biomass lost to mortality is an approximation of biomass production. Annual biomass production is thus found by estimating the number of tortoises in each age class per hectare and the number of tortoises lost each year from the age classes. The resulting estimate is found by:

$$ABp = \Sigma (ACm \times ACb)$$

where annual biomass production (ABp) is derived from the annual age class mortality (ACm) and the mean biomass of each age class (ACb).

The calculations indicate that in Croatia biomass production is 4.367kg/ha annually and in Montenegro 2.413kg/hg annually. The ratios of biomass production to biomass density (i.e. relative annual turnover in biomass) are therefore 0.07 in Croatia and 0.06 in Montenegro. These values exceed the ratios of 0.034 and 0.042 for *Geochelone gigantea* Coe *et al.*, 1979) but are lower than the 0.21 calculated for *Chrysemys picta* (Iverson, 1982).

Mate Selection

The mean carapace lengths of males observed courting, attempting to mount or copulating with females were significantly shorter than their corresponding female partners in both areas: Croatia, males $\bar{x}$ = 126mm females $\bar{x}$ = 150mm, $F\{1,10\}$ = 10.76, $P<0.01$; Montenegro males $\bar{x}$ = 128.5mm females $\bar{x}$ = 147mm, $F\{1,18\}$ = 15.71, $P<0.001$. There were no significant inter-population differences $\{P>0.05\}$ between the sizes of males or between the sizes of females involved in sexual activity. Neither population showed evidence ($P>0.05$) for the 'Big Male' effect (O'Donald, 1983), that is that males from either population involved in sexual activity had greater mean carapace lengths than their population means, which is in agreement with the data for *T. hermanni* in Greece and France (Swingland and Stubbs, 1985).

Nests and Hatchlings

Two nesting females were observed in Croatia on the morning of 2 June. Both females had selected sites about 1 metre from deep shade and each deposited 3 eggs. The mean egg length of both clutches was 30.3mm (range 26-33mm) and mean width 23.3mm (range 23-24mm). Three other nests where the young had apparently recently emerged were found on the Croatian site in late September. Four hatchlings were found near one of these nests and these had carapace lengths ranging from 31-45mm ($\bar{x}$ = 38.5mm) and body masses from 10-19g ($\bar{x}$ = 15g).

Food Plants

The largest food plant sample was collected in Croatia (n = 22). The majority of these were from the Leguminosae (n = 11;5%) although other families were also collected (Table 4). However, the samples were collected over two seasons and as can be seen in Table 4 the Leguminosae were not present in the Autumn sample and were thus an exclusive summer food plant (78.6 per cent) with, interestingly, mushrooms forming part of the Autumn diet. The Montenegren sample was smaller (n = 11) and consisted only of any early Summer collection. Here the Leguminosae although present, are less prominent (n = 2; 18.8 per cent).

It is recognised that these are small samples but the data do appear to suggest two points worth considering. The first is the possibility of a seasonal shift in diet in Croatian *T. hermanni* with a more restricted diet based on Leguminosae in Summer shifting to a broader range of plant food in Autumn. The second is that the Leguminosae are less important in the Summer diet of Montenegren *T. hermanni* although whether the close proximity of human activities has some influence here is unclear. An earlier food plant sample from *T. hermanni* in Montenegro also living in close association with humans (although in rather less close proximity) showed 33.3 per cent to be Leguminosae (Meek, 1985).

Morphometrics

The morphometric analysis has been based on body mass (the x variable) since this is the only variable

	Family	Genus	Species	n	Comments
Croatia (summer)	Leguminosae	Medicago	—	6	
	Leguminosae	Medicago	echinata	1	
	Leguminosae	Trifolium	campestre	3	
	Leguminosae	Vicia	—	1	
	Compositae	Composite	picris	1	
	Plantaginaceae	Plantago	—	1	
	Rosacea	Prunus	cerasus	1	fruits (plum)
Croatia (autumn)	Umbelliferae	—	—	2	
	Compositae	—	—	1	
	Labiatae	Thymus	—	2	
	Rosaceae	Malus	domesticus	1	fruits (apple)
	Basidiomycetes	Agaricus	arvensis	2	mushrooms
Montenegro	Araliaceae	Hedera	helix	2	
	Chenopodiaceae	Chenopodium	—	2	
	Aristolochiaceae	Aristoluchia	—	1	
	Plantaginaceae	Plantago	—	1	
	Leguminosae	Medicago	echinata	2	
	Scrophulariaceae	Pedicago	—	1	
	Cruciferae	Brassica	oleracea	1	cabbage

TABLE 4: Food plants of *T. hermanni* in Croatia in summer and autumn and in Montenegro in summer. The number of observations of feeding on a particular plant (n) are also shown.

Eqn. No.	Sex	Pop	y	y_0	95% C.lim.	x_0	b1	b2	95% C.lim.	P	r	n
(5)	P	M	C.L.	133.78	1.01	790.24	0.33	0.33	0.01	n.s.	0.98	84
(6)	P	C	C.L.	116.14	1.02	511.43	0.33	0.34	0.01	n.s.	0.97	124
(7)	M	M	S.W.	45.64	1.04	631.31	0.46	0.47	0.03	0.05	0.98	45
(8)	F	M	S.W.	42.97	1.02	779.05	0.39	0.40	0.03		0.97	45
(9)	M	C	S.W.	35.97	1.04	359.39	0.47	0.49	0.03	0.01	0.96	80
(10)	F	C	S.W.	33.99	1.05	442.03	0.41	0.42	0.02		0.97	61
(11)	P	M	4V.S.	33.46	1.02	790.24	0.29	0.32	0.03	n.s.	0.90	84
(12)	P	C	4V.S.	28.89	1.02	511.43	0.29	0.31	0.02	n.s.	0.91	124
(13)	M	M	P.L.	102.59	1.01	631.31	0.28	0.28	0.01	0.001	0.99	45
(14)	F	M	P.L.	119.48	1.01	779.05	0.34	0.34	0.03		0.99	45
(15)	M	C	P.L.	86.99	1.01	359.39	0.32	0.32	0.01	0.05	0.98	80
(16)	F	C	P.L.	97.30	1.02	425.33	0.34	0.34	0.01		0.99	66
(17)	M	M	T.L.	37.54	1.06	631.31	0.72	0.77	0.09	0.001	0.93	45
(18)	F	M	T.L.	23.71	1.07	779.05	0.42	0.51	0.09		0.82	45
(19)	M	C	T.L.	22.10	1.14	414.14	0.74	0.84	0.14	0.001	0.89	43
(20)	F	C	T.L.	15.17	1.05	614.32	0.42	0.46	0.06		0.92	45

TABLE 5: Model 2 allometric equations of the form $y/y_0 = (x/x_0)^b$ relating selected dimensions of the shell or tail length y in mm with body mass x in grams by the geometric mean of y (y_0), geometric mean of x (x_0) and exponent b. Confidence intervals for y_0 are the x/÷ type, for b the ± type. Correlation coefficients r, number of observations n and significant differences P (when applicable) between equations for males and females are also given. For comparative purposes corresponding exponents that would be found by Model 1 regression (b1) are shown. Montenegren data are indicated as M, Croatian data as C, other abbreviations are: C.L. (carapace length) S.W. (supracaudal scute width) 4V.S. (4th vertebral scute width) P.L. (plastron length) T.L. (tail length).

which can be regarded as representing the whole body. However, body mass be subject to error and thus Model 2 regression has been used in the analysis. Model 2 equations have the form:

$$y/y_0 = x/x_0)^b$$

where shell dimensions or tail length y in mm are related to body mass x in g by the geometric means of $y(y_0)$ and x (x_0) and exponent b. The differences between the two methods are only minor when the correlation coefficient (r) for the data are high; when r is low Model 2 equations produce steeper slopes.

The results are shown in Table 5 where the separate male and female equations have been calculated by including the data from immatures although when the exponents are not significantly different the data sets have been combined and comprehensive equations produced. High correlation coefficients have been found for most of the data sets and thus there would be little difference between the exponents had they been calculated by Model (1) regression, the exponents for which are also shown in Table 5. The lowest correlations concerned 4th vertebral scute width and tail length giving some disagreement between regression exponents (see Table 5). The widest confidence intervals were for tail length (0.06-0.14) suggesting rather greater variation in size than in the other characters measured.

The sexual dimorphic trends found earlier in a central Montenegren population of *T. hermanni* (Meek, 1985) are confirmed here; principally the relatively wider supracaudal scute in males Montenegro, $t = 2.05$, $P<0.05$, Croatia, $t = 3.04$, $P<0.01$ and relatively longer plastrons in females, Montenegro $t = 3.3$, $P<0.01$; Croatia $t = 2.06$ $P<0.05$. Tail length which was not measured in the earlier study (Meek, 1985) also differed between males and females with that of males being relatively longer (Montenegro $t = 3.02$ $P<0.01$; Croatia $t = 4.12$, $P<0.001$). Inter-population differences in morphometric characters were found only in male plastron length which was relatively longer in Croatian males ($t = 3.09$, $P<0.01$).

DISCUSSION

The differences observed in survivorship, age spans and growth rates in Yugoslavian *T. hermanni* are important life history characteristics but were they primarily related to the close proximity of the Montenegren population with humans? Stubbs and Swingland (1985) have already suggested that the ecology of *T. hermanni* in woodland areas in southern France was linked to the traditional horticultural practices of the local people. Apparently the key factors were the establishment and maintenance of clearings in the forest for crop growing which provided nesting areas for the females and also the control of mammalian predators thus reducing nest predation. It is unlikely that in Montenegro crop growing areas were important in increasing tortoise nesting success since extensive natural clearings were a regular feature of scrubland areas in the region (Fig. 1) and were used by the females for nest sites. Control of mammalian predators did occur and this could increase tortoise survivorship but additionally and perhaps more importantly the areas was extensively irrigated which may improve both the quality and availability of food plants during the hot dry Summer. However, agricultural activities could be involved in reducing the densities of tortoises by confining the animals to natural zones within such areas, since although tortoises were observed on the perimeters of crop growing areas, there was no movement onto these areas apart from one instance of a tortoise feeding on cabbage.

Previous studies on the population ecology of *T. hermanni* have indicated low numbers of both immatures and hatchling tortoises (e.g. Meek and Inskeep, 1981; Meek, 1985) and several theories have attempted to explain this, i.e. low detectability or differences in habitat selection between adults and immatures. Recently however Stubbs and Swingland (1985) have suggested, from recapture data on juveniles, that immature *T. hermanni* do indeed constitute only a small proportion of the population. This would be in agreement with the general population dynamics of *T. hermanni* which operates at the 'K-endpoint' of the r-K continuum where densities are high and inter- and intra-specific competition intense leading to a highly efficient utilisation of environmental resources. Such a strategy invariably leads to the channelling of all available energy into the production of a few extremely fit offspring (Pianka, 1970). Female *T. hermanni* produce only small numbers of offspring which suffer high mortality at the egg stage (Stubbs and Swingland, 1985) and probably also within the months following hatching. The results in this paper of the adult-juvenile ratios in Croatia appear indirectly to support a high mortality of hatchlings, which were relatively more common in Autumn than in Spring. Predators probably contribute to hatchling mortality (e.g. rat snakes *Elaphe* and mammals in some areas) but perhaps more important is mortality from environmental factors such as late Summer droughts or winter-kill.

Intra and inter-population differences in growth and maximum sizes have been observed in other species of chelonians from within a single geographical area (e.g. Cagle, 1946; Gibbons, 1967; Hulse, 1976). In certain chelonians food quality has been cited as an explanation for differences in growth rates and this could explain the faster growth rates of Montenegren females compared with females from Croatia. The constant irrigation of the Montenegren study site, if it does indeed improve the quality of the wild plants may be important in this respect since it could provide this population with an overall superior diet through the active year. The larger size of Montenegren males in comparison to males from Croatia is also interesting and appeared to be related to the Montenegren males living longer and also their slightly faster rates of growth but it is not immediately obvious as to why only males and not females from Montenegro have significantly longer life spans than Croatian tortoises. Cagle (1946) attributed differences in size and growth between populations of *Pseudemys scripta* to age differences between populations but Gibbons (1967) believed that inter-population differences in size in *Chrysemys picta* could not be explained in this way and suggested that food quality was the primary controlling factor.

Shell damage and injuries are common in Mediterranean tortoise populations (e.g. Lambert, 1982; Meek, 1985) but it is not clear how important these are in contributing to mortality rates. For example, can they be used in the way lizard tail loss has been used as a mortality index? The data in Fig. 6 appears to show that there was an increasing likelihood of injury with age and increases in size in *T. hermanni* but whether these were the result of accidents or predator attacks is not known. Potential predators on large tortoises are probably few particularly in the Montenegren population although the fact that Croatian tortoises suffered injuries at earlier ages is interesting and may indicate at least some degree of predation from carnivorous birds or mammals. Nevertheless although based on only a small sample size it is somewhat surprising that most of the remains of the dead *T. hermanni* on the study areas showed little or no signs of physical injury suggesting that other factors also contribute to mortality rates, perhaps heat death as found for *Geochelone gigantea* (Bourne and Coe, 1978).

The biomass densities of Yugoslavian *T. hermanni* found in this and a previous study (Meek, 1985) are in good agreement with those found for other terrestrial chelonians (see Iverson, 1982 for a review) although they are greatly exceeded by the biomass densities of certain Island species (e.g. *Geochelone gigantea*, Coe *et al.*, [1979]). Scrub habitat, whether in Argentina (Auffenberg, 1969), United States (Auffenberg and Weaver, 1969) or Europe appears to support high densities of herbivorous tortoises, much higher, for example, than are found in desert areas (Iverson, 1982) and thus appears generally to be important habitat for terrestrial chelonians. Herbivorous tortoise biomass densities also greatly exceed the biomass densities of herbivorous lizards, (which have the highest biomass densities of any group of lizards), and also exceed the biomass densities of snakes (Iverson, 1982). Such data appear to suggest that tortoises are particularly successful in utilising environmental resources and indeed *T. hermanni* is often the most abundant or at least the most conspicuous vertebrate species in the ecosystems where it occurs apparently exceeding the density of the most common lizard species (Meek, 1986). However, Iverson (1982) has drawn attention to the possibility that in long lived species with high standing crop biomasses, the annual biomass production may be low (e.g. *T. hermanni* in Yugoslavia) rendering such species susceptible to population disturbances, and recovery from (for example) the effects of large scale collection will be slow or may not occur if at all.

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