ASPECTS OF THE ECOLOGY OF TESTUDO HERMANNI IN SOUTHERN YUGOSLAVIA

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SUMMARY

In 1978 a preliminary study was made on a population of Hermann’s tortoise Testudo hermanni in southern Yugoslavia (Meek & Inskeep, 1981). New observations have now been made on this population and information mainly concerning size and age frequencies, sex ratios, population densities, food plants, injuries and shell abnormalities and morphometrics have been gathered. Female T. hermanni grow significantly longer (carapace length) and heavier than males. Male tortoises in 1978 were significantly heavier than those sampled in 1983. Males outnumber females by 2:1; adults outnumber immatures by 9:2:1. Eighty-six percent of tortoises were 14 years or more in age. Mathematical models of tortoises age predict that large tortoises (>200 mm) may exceed 40 years in field populations. Survivorship until 19 years was 38.3% and mean annual recruitment estimated at 3.4%. The Schnabel formula has been used to calculate population densities and indicates a mean density of 39.2 ha⁻¹. The principal food plants included the families Leguminosae (33.3%) and Ranunculaceae (25%), the latter and Araceae comprised species containing toxic alkaloids (41.6%). In a sample of 82 tortoises, 14.6% showed abnormalities to the shell scutellation and physical injuries. Allometric equations have been produced from the measurements of shell dimensions and body mass. It has been found that most of the allometric exponents are close to the 0.33 required for geometric similarity, except those relating supracaudal width and plastron length to body mass in males. This can be explained by smaller growth increments of male plastrons and larger increments in male supracaudal scute width. Plastron length has also been related to carapace length: the relationship is isometric and the regression equations for males and females are significantly different.

INTRODUCTION

Hermann’s tortoise (Testudo hermanni) constitutes one of the three species of European terrestrial cheloniens (Arnold, Burton & Ovenden, 1978). In the form of two races, T. h. hermanni and T. h. robertmertensi, it is found in a variety of habitats principally in the warmer southern regions of Europe. Until recently, however, field data on the species was virtually non-existent, despite its large scale collection for the pet and food trades (Lambert, 1980). The first field study of T. hermanni was made by Chelazzi & Francisci (1979) who investigated movement patterns and homing behaviour of an Italian population of T. h. robertmertensi. This was followed by two, almost simultaneous studies of populations of T. h. hermanni in Greece (Stubbs, Hailey, Tyler & Pulford, 1981) involving large scale ecological work; and in Yugoslavia (Meek & Inskeep, 1981) where the general field biology of the species was investigated. More recently (Meek, 1984) thermoregulatory behaviour in this Yugoslavian population has been studied adding to the earlier laboratory studies of T. hermanni thermoregulation by Cherchi (1956, 1960). Auffenberg & Weaver (1969) when working with the North American tortoise Gopherus berlandieri drew attention to the possibility that demographic information generated for one tortoise population may not always be applicable to others, even when these may be in close proximity. Comparative ecological information on tortoise populations is therefore not only of general interest but is also a necessary practical conservation tool. This paper is a contribution to the field studies of T. hermanni and examines certain aspects of the species ecology in southern Yugoslavia.

METHODS AND MATERIALS

Field work was initially carried out in 1978 on a population of T. hermanni from Montenegro in southern Yugoslavia, and the preliminary results of this work have been published (Meek & Inskeep, 1981). Additional data were gathered in May 1983 on this population. Further information, mainly growth ring counts and carapace lengths, were gathered from tortoises imported into Britain in May–June 1983, which were reported to have been collected in the southern Yugoslavian province of Macedonia.

Habitat and Food Plants

Samples of the principal shade and food plants of the habitat were collected. Food plants were those actually observed being consumed by the tortoises. The specimens were pressed and later identified at the Department of Plant Sciences, University of Leeds.

Body Measurements

Carapace length. A straight line between the leading edges on the supracaudal and nuchal scutes.
*Plastron length.* A straight line from the leading edge on the gular to the notch on the anal scute. This measurement is shown in Fig. 1.

*4th vertebral scute.* A straight line on the width.

*Supracaudal scute.* A straight line on the leading points on the width. This measurement is shown in Fig. 1.

*Body mass.* This was determined by weighing in a cloth bag suspended from a spring balance.

**Assessing Sex**

Male and female tortoises were distinguished by the concave plastron in males and shorter tails in females; this is shown in Fig. 1. Tortoises of less than 110 mm carapace length could not be sexed confidently.

**Physical Condition**

Records of physical injuries and shell damage were made in both written and photographic form. Only major injuries were noted, minor shell damages (which were quite common) were ignored.

**Population Density Estimates**

A five day mark-release-recapture survey was carried out to estimate population densities. Tortoises were collected and given codes specifying date and time of capture. The coding was painted on the carapace of each animal using Tippex fluid, which was found suitable for a short term survey. To estimate population densities a variation on the Lincoln Index, the Schnabel method (1938) has been used. This method
allows calculation on a daily basis, smooths the data by accumulation and renders the estimates uniform (Davis, 1963). Graham (1979) has demonstrated the mechanics of this method, discussing its problems and the various basic assumptions that should be taken into account; these are believed to have been satisfied for this survey.

**Statistical Analysis**

From the measurements of the shell dimensions, the number of growth annuli on the costal scutes and body mass allometric equations have been obtained by the method of least squares regression after transforming the data into logarithmic form (Bailey, 1959). Since body mass represents the whole animal this measurement has been treated as the independent variable in the morphometric analysis; growth annuli have been treated as dependent on carapace length or 4th vertebral scute width. The method of Kermack & Haldane (1950), which makes no distinction between independent and dependent variables, would produce only slightly different equations when the correlation coefficients are 0.92 or higher. The exponents would be found by calculating \(1/r_b\), where \(r\) is the correlation coefficient and \(b\) the exponent given here (Alexander et al., 1979). Using non-transformed data the least squares method has been used to relate carapace length to plastron length. The \(t\) distribution has been used to assign 95% confidence intervals to the exponents in the allometric equations and to factor \(m\) in the regression equations. Tests for significant differences between equations have been made by analysis of variance.

**Results**

**Habitat**

In the study area (typical Mediterranean mixed scrub), *T. hermanni* was found in association with *Clematis viticella*, *Rubus fruticosus*, *Cornus sanguinea*, *Berberis vulgaris*, and *Paliurus spina-christi*, which were utilized as shade plants. Tortoises were also found moving through extensive growth of bracken, *Pteridium aquilinum*, when these bordered major shade plants.

A preliminary survey of the herpetofauna recorded on the study area has been reported (Meek & Ingskeep, 1981). Further searches revealed *Triturus vulgaris dalmatica* and *Rana ridibunda*, and one reptile *Mauremys caspica rufata*. Few truly wild mammals have been observed, but in recent years, clearly as a result of a large scale killing programme on the study area and subsequent human population influx, there has been an increase in the number of feral cats and domestic goats.

**Population Structure**

Size (carapace length) and body mass frequency distributions of tortoises in 1978 and 1983 are shown in Fig. 2. In both sampling periods the frequency distributions were skewed towards larger animals, the majority of animals had carapace lengths above 120 mm (1978 = 74%; 1983 = 76%) and body masses greater than 500 g (1978 = 68%, 1983 = 79%). Female *T. hermanni* attained longer carapace lengths (1978 = 174 mm, \(\bar{x} = 145\) mm, 1983 = 170 mm, \(\bar{x} = 147\) mm) than males (1978 = 160 mm, \(\bar{x} = 124\) mm; 1983 = 143 mm, \(\bar{x} = 126\) mm). The differences were significant: 1978, \(F(1, 34) = 4.25\), \(P < 0.05\); 1983, \(F(1, 72) = 7.29\), \(P < 0.001\). Female tortoises also attained greater body mass (1978 = 1160 g, \(\bar{x} = 861\) g; 1983 = 1410 g, \(\bar{x} = 989\) g) than males (1978 = 1000 g, \(\bar{x} = 637\) g; 1983 = 740 g, \(\bar{x} = 609\) g). The differences were significant: 1978 \(F(1, 34) = 10.43\), \(P < 0.005\); 1983 \(F(1, 72) = 108.5\), \(P < 0.001\). There was no significant difference between the carapace lengths of females measured in 1978 against those in 1983, \(F(1, 37) = 0.21\), \(P > 0.05\) or between their masses, \(F(1, 37) = 2.77\), \(P > 0.05\). There was also no significant difference between the carapace lengths of males, \(F(1, 69) = 0.82\), \(P > 0.05\), but the 1978 males were significantly heavier \(F(1, 69) = 10.5\), \(P < 0.005\).

**Sex Ratios**

If sex ratios are based on tortoises caught on a daily basis, this gives an average daily ratio of 1.8:1 in favour of males, varying from 1.1:1 to 2.6:1. Based on the total number of identified tortoises measured on the study area (82) a male/female ratio of 2:1 was recorded and an adult-juvenile ratio of 9:2:1.

**Age Structure**

Age frequencies of *T. hermanni* are shown in Fig. 3. Figure 3b is based on estimated ages by use of
growth annuli count for the total sample \( n = 82 \) including juveniles was 18.3 (S.D. = 5.6). Juveniles and immatures were well represented in the 1978 sample but mostly absent in the 1983 data. It is not known whether this is a natural situation or a function of sampling error; smaller tortoises being more difficult to locate particularly in dense vegetation.

**Age Models**

The number of growth annuli on the costal scutes are generally correlated with carapace length \( r = 0.96 \) and with 4th vertebral scute width \( r = 0.95 \). For carapace length the correlation is slightly higher for males \( r = 0.98 \) than females \( r = 0.97 \) and for 4th vertebral scute width also higher for males \( r = 0.96 \) than females \( r = 0.95 \). The relationships can be described by the allometric equation

\[
y = ax^b
\]

where the number of growth annuli \( y \) is related to the length of the carapace or width of the 4th vertebral scute \( x \) by the constants \( a \) and \( b \). Figure 4 shows the data plotted on logarithmic coordinates; Table I the equations derived from the data. The results indicate that males grow more slowly than females since (for example), equations (1) or (4) for males will at any given measurement predict higher numbers of annuli than equations (2) or (5). However, there is no significant difference \( P > 0.05 \) between equations (1)

Table I. Allometric equations of the form \( y = ax^b \) relating the number of growth annuli on the costal scutes \( y \) with either carapace length or 4th vertebral scute width \( x \) in mm by the constants \( a \) and \( b \). The equations for males and females have been calculated by including the data from juveniles. These equations are derived from field and recently imported *T. hermanni*

<table>
<thead>
<tr>
<th>Eqn. number</th>
<th>Independent variable ( x )</th>
<th>( a )</th>
<th>( b )</th>
<th>95% confidence interval on ( b )</th>
<th>( n )</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>Carapace length (males)</td>
<td>0.0003</td>
<td>2.29</td>
<td>0.53</td>
<td>72</td>
</tr>
<tr>
<td>(2)</td>
<td>Carapace length (females)</td>
<td>0.0005</td>
<td>2.12</td>
<td>0.62</td>
<td>46</td>
</tr>
<tr>
<td>(3)</td>
<td>Carapace length (pooled)</td>
<td>0.0005</td>
<td>2.15</td>
<td>0.42</td>
<td>98</td>
</tr>
<tr>
<td>(4)</td>
<td>4th vertebral scute (males)</td>
<td>0.005</td>
<td>2.37</td>
<td>0.57</td>
<td>61</td>
</tr>
<tr>
<td>(5)</td>
<td>4th vertebral scute (females)</td>
<td>0.009</td>
<td>2.20</td>
<td>0.66</td>
<td>40</td>
</tr>
<tr>
<td>(6)</td>
<td>4th vertebral scute (pooled)</td>
<td>0.008</td>
<td>2.25</td>
<td>0.44</td>
<td>91</td>
</tr>
</tbody>
</table>

equations (1) and (2) in Table I. The age distributions were skewed towards older animals in both periods with 40% and 36.6% in the 1978 and 1983 samples respectively of 19+ years. There was an approximate equal distribution of males and females in the 19+ years age class during both periods but males predominate between 16–19 years. The growth annuli counts of males averaged 19.2 (S.D. = 3.6), females 21 (S.D. = 8.8). The differences between the sexes were not significant, \( F(1, 54) = 1.03, P > 0.05 \). The average
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Fig. 5. Survivorship of Yugoslavian T. hermanni field populations until 19+ years. This graph is based on the pooled data from the 1978 and 1983 field samples (n = 129).

and (2) or between equations (4) and (5). The lines taken through the data in Fig. 4 are derived from equations (3) and (6). These general equations predict that large tortoises (i.e., >200 mm carapace length) may exceed 40 years in field populations.

SURVIVORSHIP

Age determination in T. hermanni has enabled the construction of a survivorship curve (Fig. 5). This curve has been calculated by taking, as a percent of the total population sample (1978 and 1983, n = 129), the number of tortoises present at the beginning of each age class (Deevey, 1947). Survivorship until 19 years is 38.3% and the mean annual recruitment based on the pooled 1978–1983 age data estimated at 3.4%.

POPULATION DENSITIES

Population densities have been calculated using the Schnabel formula.

\[ \hat{p} = \frac{\sum (m(u + r))}{\sum r} \]

where the population density \( \hat{p} \) is estimated from the number of tortoises captured, marked and released \( m \), the number of marked individuals recaptured each day \( r \) and the number of unmarked animals captured each day \( u \). The summations are over the number of days, thus \( m \) and \( \sum r \) become progressively larger. Table II shows the results and the arithmetic involved in the survey as it was applied to an area of 0.8 ha. Overt (1971) discusses the methods of averaging the results. However, in this short term survey the estimates become uniform only after the second day of sampling. Extrapolation of the average of the third, fourth and fifth days results for 0.8 ha give a population density estimate of 39.2 ha\(^{-1}\).

When mass is unknown, biomass density can be estimated from,

\[ \delta = (0.0013\delta^{12.7})N \]

where the biomass density \( \delta \) in g is determined from the mean carapace length of the population \( \delta \) in mm and the population density \( N \). This gives a biomass density estimate in T. hermanni of 24 183 g ha\(^{-1}\).

FOOD PLANTS

A total of twelve plant specimens of several species were collected from feeding T. hermanni (Table III). In agreement with the 1978 sample (Meek & Inskip, 1981) the family Leguminosae (33.3%) persists with the family Ranunculaceae (25%) as the principal food plant groups of T. hermanni and both samples combined formed 58.3% of all the food plants that were collected. The Gramineae are also again represented (8.3%) but two new families, the Araceae and Rubiaceae which were not recorded in the earlier survey formed 16.6% and 8.3% of collected plants respectively. One additional specimen was not identified. Also indicated in Table III is the presence of toxic alkaloids in five (41.6%) of the food plants of T. hermanni.

ABNORMALITIES AND INJURIES

In a total of 82 tortoises examined, twelve (14.6%) showed abnormalities in scutellation. Two of these (2.4%) appeared to be congenital peculiarities arising during growth. Of those that appeared to have resulted from injuries almost all (12.2%) involved the carapace.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Alkaloids present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leguminosae</td>
<td>Medicago polymorpha</td>
<td>—</td>
</tr>
<tr>
<td>Leguminosae</td>
<td>Vicia sativa</td>
<td>—</td>
</tr>
<tr>
<td>Leguminosae</td>
<td>Vicia seplum</td>
<td>—</td>
</tr>
<tr>
<td>Leguminosae</td>
<td>Trifolium campestre</td>
<td>—</td>
</tr>
<tr>
<td>Ranunculaceae</td>
<td>Chloris vicicella</td>
<td>Yes</td>
</tr>
<tr>
<td>Ranunculaceae</td>
<td>Clematis sp.</td>
<td>Yes</td>
</tr>
<tr>
<td>Araceae</td>
<td>Arum sp. (italicum, maculatum or orientalis)</td>
<td>Yes</td>
</tr>
<tr>
<td>Araceae</td>
<td>Arum sp. (italicum, maculatum or orientalis)</td>
<td>—</td>
</tr>
<tr>
<td>Gramineae</td>
<td>Dactylis glomerata</td>
<td>—</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Galium sp.</td>
<td>—</td>
</tr>
</tbody>
</table>
Table IV. Allometric equations of the form $y = ax^b$ relating selected dimensions of the shell $y$ in mm to body mass $x$ in g by the constants $a$ and $b$. The $t$ distribution has been used to assign 95% confidence limits to the exponent $b$. The $r$ value is the correlation coefficient, $n$ the number of measurements on which the equations are based.

<table>
<thead>
<tr>
<th>Eqn. number</th>
<th>Dependent variable $y$</th>
<th>$a$</th>
<th>$b$</th>
<th>Confidence limits on $b$</th>
<th>$r$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(8)</td>
<td>Carapace length (males and juveniles)</td>
<td>11.92</td>
<td>0.37</td>
<td>0.06</td>
<td>0.81</td>
<td>78</td>
</tr>
<tr>
<td>(9)</td>
<td>Carapace length (females and juveniles)</td>
<td>14.31</td>
<td>0.35</td>
<td>0.10</td>
<td>0.90</td>
<td>57</td>
</tr>
<tr>
<td>(10)</td>
<td>Carapace length (pooled)</td>
<td>14.20</td>
<td>0.34</td>
<td>0.06</td>
<td>0.96</td>
<td>126</td>
</tr>
<tr>
<td>(11)</td>
<td>Plastron length (males)</td>
<td>26.20</td>
<td>0.22</td>
<td>0.07</td>
<td>0.71</td>
<td>32</td>
</tr>
<tr>
<td>(12)</td>
<td>Plastron length (females)</td>
<td>13.26</td>
<td>0.33</td>
<td>0.04</td>
<td>0.95</td>
<td>19</td>
</tr>
<tr>
<td>(13)</td>
<td>Plastron length (pooled)</td>
<td>13.50</td>
<td>0.32</td>
<td>0.08</td>
<td>0.96</td>
<td>59</td>
</tr>
<tr>
<td>(14)</td>
<td>4th vertebral scute (males and juveniles)</td>
<td>4.07</td>
<td>0.32</td>
<td>0.08</td>
<td>0.91</td>
<td>63</td>
</tr>
<tr>
<td>(15)</td>
<td>4th vertebral scute (females and Juveniles)</td>
<td>4.33</td>
<td>0.30</td>
<td>0.11</td>
<td>0.97</td>
<td>39</td>
</tr>
<tr>
<td>(16)</td>
<td>4th vertebral scute (pooled)</td>
<td>5.84</td>
<td>0.27</td>
<td>0.05</td>
<td>0.92</td>
<td>91</td>
</tr>
<tr>
<td>(17)</td>
<td>Supracaudal width (males and juveniles)</td>
<td>3.33</td>
<td>0.41</td>
<td>0.13</td>
<td>0.94</td>
<td>41</td>
</tr>
<tr>
<td>(18)</td>
<td>Supracaudal width (females and juveniles)</td>
<td>4.36</td>
<td>0.35</td>
<td>0.16</td>
<td>0.95</td>
<td>18</td>
</tr>
<tr>
<td>(19)</td>
<td>Supracaudal width (pooled)</td>
<td>6.56</td>
<td>0.30</td>
<td>0.07</td>
<td>0.81</td>
<td>57</td>
</tr>
</tbody>
</table>

![Graph](image)

Fig. 6. A graph on logarithmic coordinates of body mass plotted against 4th vertebral scute width, supracaudal scute width and carapace length. Lines taken through the data represent allometric equations given in Table IV. For comparative purposes the lines predicted by the allometric equations for Testudo graeca calculated by Lambert (1982) and T. marginata based on Hines (1983) data are shown with that from the general equation (10) for T. hermanni calculated in this study. Details of the symbols are as follows: When body mass vs. 4th vertebral scute width: males = □, females and juveniles = ◊; when body mass vs. supracaudal width: males = ◇, females and juveniles = ○; when body mass vs. carapace length: males = ●, females and juveniles = △.

Although two tortoises showed damage to both the carapace and the plastron. One animal had plastron damage only. Another tortoise had a break in the lower jaw at the anterior junction of the dentary bones to the effect that both sides of the lower jaw worked independently. However, this disability did not appear to affect its ability to feed since it was observed feeding successfully on three occasions.

Morphometrics

Allometric equations describing the relationship between the various shell dimensions and body mass in T. hermanni are shown in Table IV. The equations are of the same basic form as those relating growth annuli with shell measurements except that here a shell character $y$ in mm is related to the body mass $x$ in g by
with the slopes significantly different ($P < 0.001$). Pooling the data also gives a high correlation ($r = 0.94$) and reduced the confidence interval thus,

$$y = 0.84 \pm 0.21x + 3.07 \ (n = 64) \ (22)$$

Figure 7 is a graph of carapace length plotted against plastron length with lines derived from equations (20) and (21) taken through the data. The broken line extrapolates the equation for males (20) to the general maximum carapace length for *T. hermanni* (Arnold et al., 1978).

**DISCUSSION**

Of the ecological factors which govern the stability of tortoise populations one of the most critical is undisturbed habitat. The movement into the study area of parts of the local human population from areas destroyed by the earthquakes of 1979–80 and the inevitable land changes that have subsequently taken place has notably reduced the numbers of tortoises generally encountered on the study site. These developments have mostly had the effect of restricting the remaining tortoise population to small isolated pocket communities separated by extensive housing areas. The introduction of goats into the remaining habitat is an additional factor that may ultimately influence the stability of the remaining population since these have already been shown to affect the survival of Galapagos giant tortoises *Geochelone elephantopus* by competing with the tortoises for food and trampling the nest sites (MacFarland, Villa & Toro, 1974). Goats may also compete with certain other tortoise species for food plants (Morafka, 1982). However, feral cats could have a more immediate effect by preying on the eggs and hatching tortoises.

Skewed size and age frequency distributions towards large or older individuals have been found in a number of populations of terrestrial chelonians. The size and age frequencies of Yugoslavian *T. hermanni* closely approximate those recorded for Greek *T. hermanni* (Stubbs et al., 1981) and North African and Turkish populations of *T. graeca* (Lambert, 1982), although the tortoises recorded in this study did not attain the size of the animals measured in these earlier works. A bias towards large or adult tortoises has been found in North American *Gopherus agassizii* (Reyes Osorio & Bury, 1982) and *G. berlandieri* (Rose & Judd, 1982) and also in giant tortoises *Geochelone gigantea* (Grubb, 1971; Bourn & Coe, 1978). Information on the age structures of Mediterranean tortoises has revealed low recruitment rates varying from 1–5% (Stubbs et al., 1981; Lambert, 1982 and this paper) and late maturity (13–14 years, Castanet & Cheylan, 1979). These data indicate that Mediterranean tortoises operate at the $K$ end of the $r-K$ continuum maintaining stable populations.

Males predominate in *T. hermanni* field populations (Stubbs et al., 1981 and this study) although not necessarily in all Mediterranean *Testudo* where females may be more numerous (Lambert, 1982). Mortality in female *T. hermanni* may differ from males since females incur greater energy costs in egg production.
This would not of course explain why greater numbers of females are sometimes found in *T. graeca* populations (Lambert, 1982). Sex in *Testudo* is known to be temperature dependent (Bull, 1980) where high incubation temperatures of the eggs produce females and lower temperatures males. Lambert (1982) has drawn attention to environmental sex determination as a possible explanation for differences between the sex ratios of Turkish and North African populations of *T. graeca*.

A method of assessing the age of tortoises in field studies when growth annuli are worn smooth is of particular importance in order that the population dynamics can be more fully understood. The mathematical models of age assessment presented in this paper are dependent on two factors. The first is that the number of growth annuli on the carapace does indeed reflect a tortoise's age and secondly that age can be correlated with carapace length or 4th vertebral scute width. These conditions are satisfied by the high correlations for the data and also by the work of Castanet & Cheylan (1979) who examined osseous growth marks of the long bones of *T. hermanni* and *T. graeca* and found that these were in good agreement with shell annuli at least until 19 years. The equations relating growth annuli to carapace length have better confidence intervals and slightly higher correlation coefficients than those relating growth annuli to 4th vertebral scute width. Nevertheless, there is little disagreement in the predictions made by the corresponding sets of equations. However, it should be noted that Kirsch (1979) found differences in age related growth in captive bred *T. hermanni* but Bourn & Coe (1978) found a valid relationship between age and size in a population of *Geochelone gigantea*. With their equations, Bourn & Coe estimated that *Geochelone* may attain between 50–70 years which considerably exceeds the 40 years predicted in this paper for the much smaller *T. hermanni*.

Growth studies of Mediterranean tortoises include those of *T. hermanni* (Meek & Inskeep, 1981; Stubbs et al., 1981), *T. graeca* (Lambert, 1982) and captive *T. hermanni* and *T. graeca* (Meek, 1982). Hine (1982) gathered information on carapace length and body mass in wild *Testudo marginata* in Greece but did not quantify his measurements. However, from his data it is calculated that

\[ y = 17.66x^{0.34} + 0.14 (r = 0.98, n = 24) \]  

(23)

The exponent is in agreement with those for field *T. hermanni* (this paper) and *T. graeca* (Lambert, 1982), thus identical exponents, close to a geometric similarity model have been found for all three species of European *Testudo*. However, the equations have different intercepts (factor a). Figure 6 shows lines predicted by the equation for *T. graeca* calculated by Lambert (1982) and that calculated for *T. marginata* for comparison with the equation for *T. hermanni* demonstrating the effects of the different intercepts on the elevation of the lines predicted by the equations. This shows that Yugoslavian *T. hermanni* appear to be relatively heavier than either *T. graeca* or *T. marginata* which is possibly a function of the quality or quantity of food available in each species habitat, rather than some inherent difference in mass status. Yugoslavian *T. hermanni* also appear to be heavier than specimens from Greece (Stubbs et al., 1981; b = 0.35, a = 16.00 estimated in Meek, 1982) but it is interesting that rather different exponents have been calculated for captive *T. hermanni* (b = 0.38) and *T. graeca* (b = 0.30) by Meek (1982). This might be explained by the differences in diet and activity levels between captive and free-living tortoises.

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