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# Growth and population structure of the Moorish Tortoise (*Testudo graeca graeca*) in Westcentral Morocco: possible effects of over-collecting for the tourist trade

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## Abstract

We studied growth of 284 live Moorish tortoises (*Testudo graeca graeca*) from the central Jbilet Mountains, the Admine Forest, and near Essaouira in westcentral Morocco in 2001. Size structures, but not age structures, differed significantly among populations. No very old tortoises were found at any site. Most populations of tortoises suffered over-collecting for the tourist trade in the past, and some collecting still continues, which probably explains the lack of older tortoises. Of tortoises remaining in the populations we studied, both males and females grew relatively quickly for 10–12 yr in all three populations, after which their growth rates decreased markedly. Females in all three populations had greater asymptotic sizes than males, and CL and log mass differed significantly between sexes by age 9 yr for the three populations, except for log mass of tortoises from Essaouira, which differed by age 6. Mean CLs and log masses were significantly greater in Admine and Essaouira tortoises than in tortoises from Jbilet. Estimated mean age at maturity varied from 5.8 to 7.6 yr for males and 7.7–10.5 yr for females. Although past over-collecting of tortoises has probably depressed population abundances and eliminated the larger, older tortoises at all three sites, the current

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differences in population structure and growth pattern may be the result of geographic variation in environmental conditions, suggesting different selective mechanisms for the three populations.

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**Keywords:** North Africa; *Testudo graeca*; Growth; Population structure; Tortoises; Age at maturity; Over-collecting

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## 1. Introduction

Understanding growth and life-history traits across a species' range can be important to protecting declining species. In North Africa, populations of the Moorish land tortoise, *Testudo graeca graeca*, are declining in the majority of their habitats, particularly in Morocco and northwestern Algeria (Lambert, 1985). *T. g. graeca* is officially considered globally threatened, is listed in Annex II (Appendix II) of The Washington Convention, and is considered "Vulnerable" by the CITES (Groombridge, 1982; Baillie and Groombridge, 1996). It is also in Annex C1 (Appendix II) of the European Union Wildlife Trade Regulation 3626/82 owing to the extensive collecting for the pet and souvenir products trade to tourists (Lambert, 1969, 1979, 1984; Highfield, 1994; Fretey, 1995). Despite these designations, large numbers of Moorish tortoises are still being removed from the wild in Morocco every year, mainly for European pet shops. In addition to the problem of direct over-collecting of individuals, habitat destruction as a result of agricultural intensification, overgrazing, and deforestation is threatening the tortoise (Bayley and Highfield, 1996). Only a few Moroccan populations of *T. g. graeca* can be currently considered abundant and free from human disturbance (Lambert, 1982).

The Moorish land tortoise is one subspecies of the wide-ranging Mediterranean spur-thighed tortoise, *T. graeca* L., which occurs in a large geographic range around the Mediterranean region from Spain and Morocco east to the semi-arid plains of Turkey, Turkmenistan, and Iran, usually in association with dry, open scrub habitats (Loveridge and Williams, 1957; Iverson, 1994). The nominate sub-species, *T. g. graeca*, is native to north Africa from Morocco, northern Algeria, and Tunisia, to northern Libya, and is also found in southern Spain and some Mediterranean Islands (Lambert, 1983; Iverson, 1994; Harris et al., 2003). It is the only tortoise occurring in Morocco, where it occupies varied habitats from the seacoasts and the northern fringe of Sahara Desert up to 2000 m above sea level in the High Atlas Mountains (Lambert, 1983; Bons and Geniez, 1996; Schleich et al., 1996). This expanse across a wide range of environmental conditions could affect growth of this species.

Growth rate can affect a variety of life-history traits. Most reptiles begin reproducing before they reach maximum body size. Prior to maturation, energy is allocated to maintenance and growth, whereas after maturation, energy is allocated also to reproduction. Theoretical life history models predict that this differential energy allocation affects survival and reproductive traits, such as age at sexual

maturity, clutch size and frequency, and size at hatching (Stearns, 1992; Charlesworth, 1994). Growth rate is intimately tied to these traits and therefore can be under strong selective forces (Schaffer, 1974; Case, 1978; Arendt, 1997; Bronikowski and Arnold, 1999). A consistent relationship between growth patterns and other life history traits has been established in several reptile taxa (Charnov and Berrigan, 1991; James, 1991; Shine and Charnov, 1992). In turtles, age and size at maturity have been shown to be determined by growth rate (Germano, 1994; Shine and Iverson, 1995; Germano et al., 2000; Lagarde et al., 2001).

Threats to populations of *T. g. graeca* in Morocco, such as tourist trade over-collecting and habitat loss, in conjunction with fluctuating environmental conditions, could affect the structure and ultimately the persistence of these tortoise populations. Accurate information about the biology and life history of *T. g. graeca* will help provide guidance in establishing plans for the conservation and sustainable management of wild populations. Although previous studies have dealt with various aspects of the ecology of *T. graeca* populations in southwestern Spain (Andreu, 1987; Cobo and Andreu, 1988; Díaz-Paniagua et al., 1995, 1996, 1997, 2001; Keller et al., 1997, 1998; Andreu et al., 2000), Greece (Hailey, 1988; Hailey and Loumbourdis, 1988), Turkey (Lambert, 1982), and the Caucasus region (Bannikov, 1951; Nadjafov et al., 1992; Inozemtsev and Pereshkolnik, 1994), only a few populations have been studied in Morocco (Lambert, 1981, 1982, 1983; Meek and Jayes, 1982; Bayley and Highfield, 1996), and apart from earlier data from Lambert (1982), there are no recent studies of growth. The present study was aimed at comparing age and size structure of three geographic populations of free roaming *T. g. graeca* in westcentral Morocco, years after major over-collecting for the tourist trade and at a time when some collecting is still occurring. We also computed the population structure of a large sample of *T. g. graeca* from the tourist-trade markets in Marrakech of tortoises taken from surrounding areas of this city. Additionally, we determined growth rates that allow comparisons among these populations, between sexes, and with other tortoise species.

## 2. Material and methods

We examined 284 juvenile and adult *T. g. graeca* from three localities in westcentral Morocco: the central Jbilet Mountains (JM) 25 km north of Marrakech (Salas village, El Kalaa Seraghna Province,  $n = 106$ ), the Atlantic coast 30 km north of Essaouira (ESS) (Moulay Bouzerktoun beach,  $n = 100$ ), and Admine Forest (AD) 30 km east of Agadir (Chtouka Plain, Souss Valley,  $n = 78$ ) (Fig. 1). The localities are separated from each other by 170–200 km and are located within the most active tourist areas in Morocco where an important pet trade occurs in the main cities. Tortoises were captured from mid May to early July 2001, although most tortoises were captured after mid-June when females no longer were carrying eggs. They were returned to capture sites and released unharmed after morphological data were collected. In addition, we collected data on 692 tortoises found in 24 tourist-trade shops July–August 2001 in Marrakech.

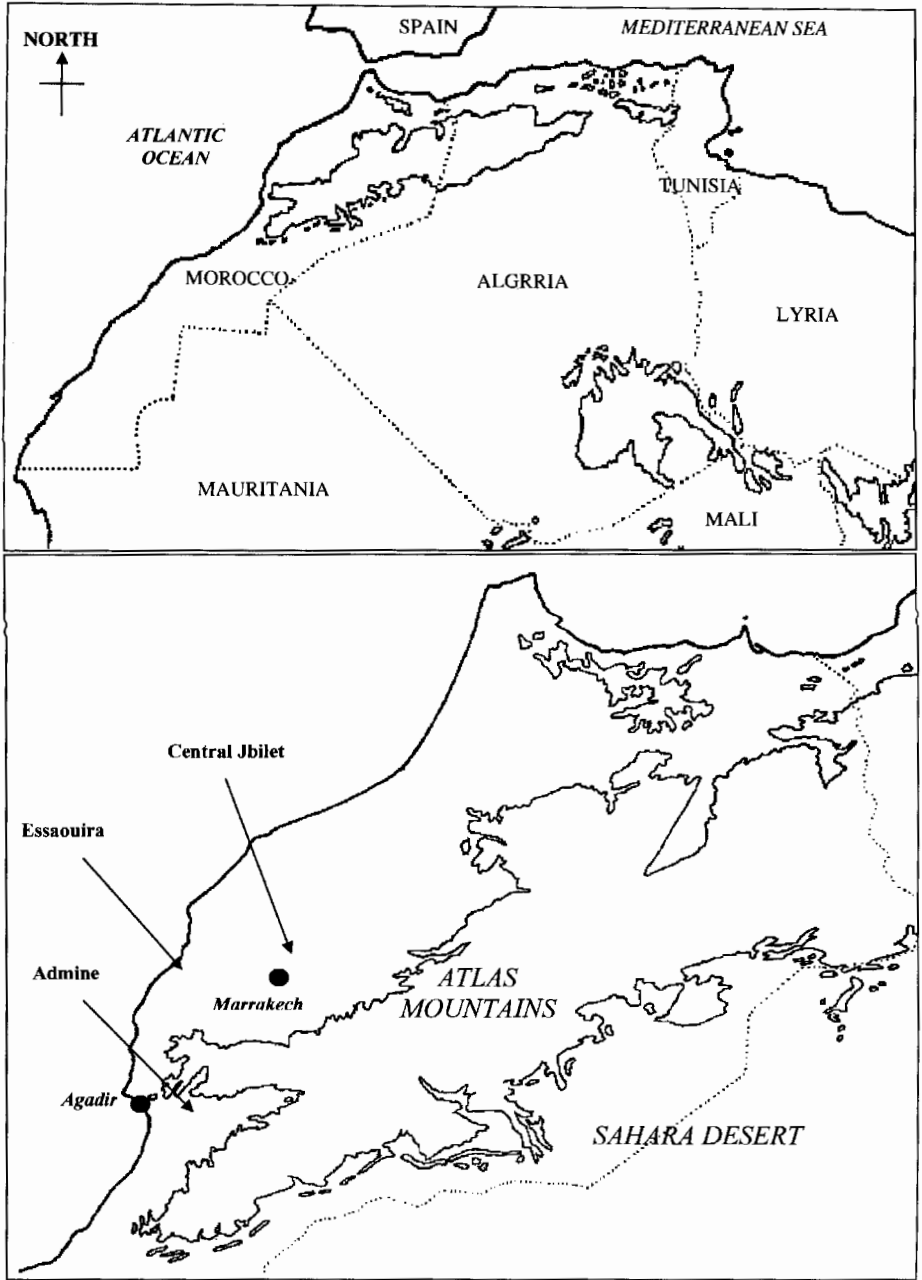


Fig. 1. Areas in Morocco where populations of *Testudo graeca graeca* were studied in 2001.

For each tortoise captured, we recorded its mass (g) after voiding of the bladder, whole shell measurements in mm (straight-line carapace length [CL], maximum plastron length [PL], etc.), and sex. Tortoise age and growth history were estimated using counts of scute rings from the right costal scute on the carapace (Castanet and Cheylan, 1979), and counts were crosschecked with other scutes (Germano and Bury, 1998). Scute rings have been found to match age (= annuli) in *T. g. graeca* up through 15–19 yr, although scute ring formation is less reliable after tortoises attain sexual maturity, which occurs at the latest when tortoises are 12–13 yr old in both sexes (Benedetti, 1926; Castanet and Cheylan, 1979). We only used tortoises with <13 annuli in our analyses of growth. We compared size distributions among populations using Chi-square analysis ( $\alpha = 0.05$ ) of CL categories 35–64, 65–94, 95–124, 125–154, 155–184, and  $\geq 185$  mm. Similarly, we compared age distributions among populations using Chi-square analysis ( $\alpha = 0.05$ ) of age categories 0–3, 4–6, 7–9, 10–12, and  $\geq 13$  yr. We did not collect the same data for tortoises found in Marrakech shops. Because of time constraints, we only made estimates of CL of tortoises by 20-mm size classes, and age was not determined. Size estimates were based on recent experience measuring tortoises in the field the month before. We compared CL distributions of tortoises from the three natural populations to tortoises from Marrakech shops using Chi-square analysis ( $\alpha = 0.05$ ) of CL categories 35–100 and >100 mm.

Growth curves were constructed by fitting age and CL, and age and log mass data to the Richards' growth model (Richards, 1959). The model equation is

$$\text{CL/Mass} = A(1 + (M - 1)e^{-K(T-I)})^{1/(1-M)}$$

where  $A$  is the asymptotic size,  $M$  the shape of the curve,  $K$  the growth constant,  $T$  the age in years, and  $I$  is the inflection point of the curve. For both CL and log mass, the Richards' growth-model was superior to the best-fitting three-parameter model (e.g., Logistic, Gompertz or von Bertalanffy models). The three-parameter models have fixed growth forms and are special cases of the flexible four-parameter Richards' model. This latter model has a variable point of inflection specified by the shape parameter of the growth curve ( $m$ ) (Richards, 1959; Causton, 1969). The Richards' model produces less biased estimates of the growth function if the shape of growth curve differs from that of a fixed-curve model (Leberg et al., 1989).

Following recommendations of Bradley et al. (1984), we used mean upper deciles sizes of adults as asymptotic sizes because of the high values predicted from growth data with large confidence intervals. We also included sizes of juvenile tortoises in male and female growth analyses because juvenile chelonians must grow rapidly to reach sizes that minimize predation risk (Wilbur and Morin, 1988), such that male and female juveniles are expected to have similar growth rates prior to maturity (Gibbons and Greene, 1990). Comparisons of growth rates among tortoises were also made using mean and upper decile CL of adults and calculated carapace lengths (CCL) by 3-yr intervals from ages 0 to 12 yr. We used the log transformation of body mass because this homogenised the residual variances and increased the explained percentage of variation, which is a useful selection criterion for the best-fitting model.

We estimated age at maturity using growth equations for each sex from each region. We converted the mean, minimum, and maximum size at maturity determined by Benkaddour et al. (2003) for *T. g. graeca* from the Jbilet region of Morocco into age estimates for each sex. They found that the mean CL of females exhibiting reproductive activity was 146.2 mm (114.6–171.8 mm) and the mean CL for males was 109.7 mm (91.4–131.4 mm).

### 3. Results

We captured 106 tortoises from the Jbilet Mountains (40 males, 42 females and 24 juveniles), 78 from Admine (44 males, 26 females and 8 juveniles) and 100 from Essaouira (44 males, 48 females and 8 juveniles). Carapace lengths of tortoises varied from about 50 up to 226 mm across populations (Fig. 2). Most captures were from 90 to 170 mm CL for Jbilet, 140–190 mm CL for Admine, and 110–210 mm CL for Essaouira. The mean CL of males varied from 125 mm in Jbilet to 151 mm in Admine (Table 1). Similarly, the smallest mean CL of females was from Jbilet (152 mm) and the largest from Admine (183). Mean mass of males and females showed the same pattern as for CL (Table 1). Both mean CL and mass of female *T. g. graeca* in the three populations were significantly larger than those of males (ANOVA: CL:  $F_{[1, 70-92]} = 18.62-37.40$ , Mass:  $F_{[1, 70-91]} = 28.28-50.99$ ,  $P < 0.001$  in all cases). The largest CLs for males were 172 mm for Jbilet, 183 mm for Essaouira, and 184 mm for Admine. The largest CLs for females were 202 mm for Jbilet, 214 mm for Essaouira, and 226 mm for Admine. Size distributions differed among populations ( $X^2_{[0.05, 10]} = 44.43$ ,  $P < 0.001$ ,  $n = 283$ ): the distribution of CL from Essaouira had a significantly greater proportion of larger tortoises than the distribution from Jbilet ( $X^2_{[0.05, 5]} = 29.43$ ,  $P < 0.001$ ,  $n = 205$ ) and Admine ( $X^2_{[0.05, 5]} = 11.49$ ,  $P = 0.042$ ,  $n = 179$ ), and the distribution of CL from Admine also differed significantly from that of Essaouira ( $X^2_{[0.05, 5]} = 35.31$ ,  $P < 0.001$ ,  $n = 182$ ). There were a large number of small ( $< 100$  mm CL) tortoises found in the shops in Marrakech (Fig. 3), and the size structure of this group was significantly different than those of the natural populations ( $X^2_{[0.05, 3]} = 218.7$ ,  $P < 0.001$ ,  $n = 977$ ). The percentages of tortoises  $< 100$  mm from the natural populations ranged from 7.9% to 22.6%, whereas small-sized tortoises from the tourist-trade shops constituted 65.5% of the population ( $X^2_{[0.05, 1]} = 70.10-119.9$ , all  $P < 0.001$ ,  $n = 770-798$ ).

Sexual size dimorphism index (SDI) calculated as the ratio of the size (mean CL or CCL) of the larger sex divided by the size of the smaller sex (Lovich and Gibbons, 1992) was almost constant in the three populations and averaged 0.83 (or  $-0.17$  when we subtract 1.0 from SDI in the case where females were larger for inter-specific comparison [Lovich and Gibbons, 1992; Germano, 1994]). Mass of all tortoises (juveniles, males and females combined) from the three populations studied were highly correlated to CL ( $r^2 = 0.990-0.994$ ,  $P < 0.0001$  in all cases) and was best described as the following power function for the combined

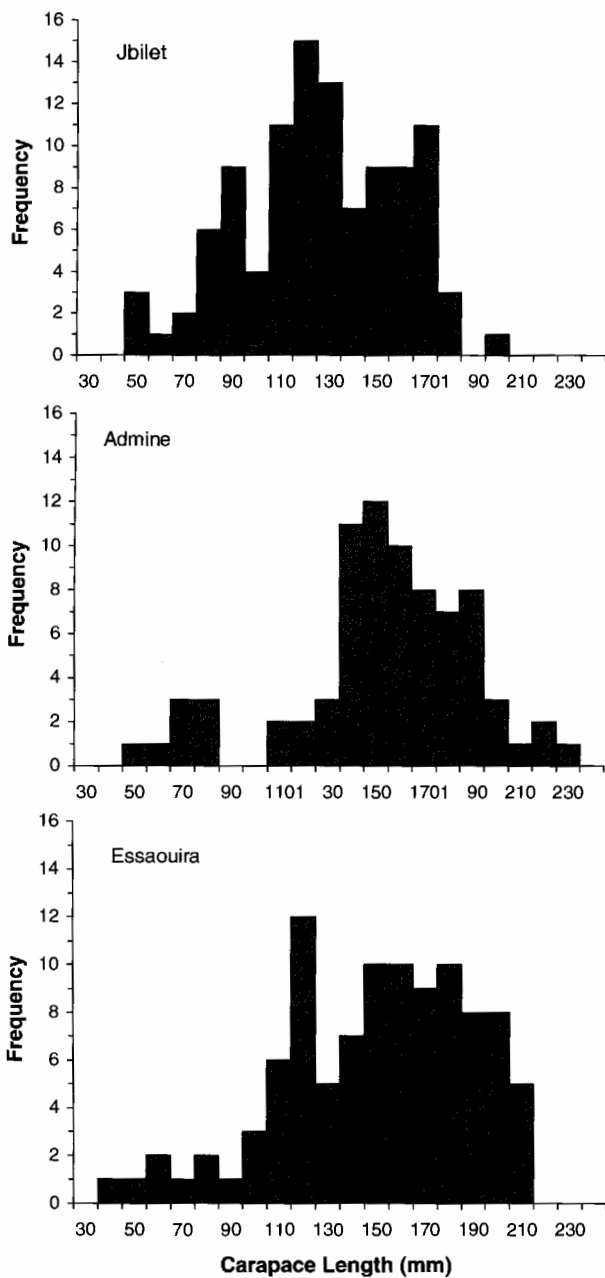


Fig. 2. Population structure based on carapace length of *Testudo graeca graeca* from the Jbilet Mountains (top), Admine Forest (middle), and near Essaouira (bottom), Morocco.

Table 1

Mean and upper decile carapace lengths and mass ( $n$ ,  $\pm 1$  standard error) in mm of male and female *Testudo graeca graeca* from three populations in Morocco

Population		Mean carapace length/ mass	Upper decile carapace length/mass
Central Jiblet Mountains	Male	125.3 (40, $\pm 2.30$ )	155.7 (4, $\pm 5.98$ )
		<i>494.1 (39, <math>\pm 4.40</math>)</i>	<i>682.5 (4, <math>\pm 80.59</math>)</i>
	Female	152.2 (42, $\pm 3.69$ )	182.7 (4, $\pm 6.54$ )
		<i>761.9 (42, <math>\pm 4.14</math>)</i>	<i>1040.8 (4, <math>\pm 88.12</math>)</i>
Admine Forest	Male	150.9 (44, $\pm 2.17$ )	176.1 (4, $\pm 2.83$ )
		<i>657.9 (44, <math>\pm 3.61</math>)</i>	<i>924.0 (4, <math>\pm 21.92</math>)</i>
	Female	182.7 (26, $\pm 5.98$ )	213.2 <sup>a</sup> (6, $\pm 3.57$ )
		<i>1255.9 (26, <math>\pm 12.35</math>)</i>	<i>1650.0<sup>a</sup> (6, <math>\pm 63.29</math>)</i>
Essaouira	Male	144.4 (44, $\pm 3.05$ )	173.6 (5, $\pm 2.46$ )
		<i>676.0 (44, <math>\pm 4.26</math>)</i>	<i>969.3 (4, <math>\pm 48.68</math>)</i>
	Female	170.8 (46, $\pm 5.04$ )	209.6 (5, $\pm 1.09$ )
		<i>1205.5 (45, <math>\pm 7.27</math>)</i>	<i>1655.0 (5, <math>\pm 49.70</math>)</i>

Mass values (g) are in italics below values for carapace length.

<sup>a</sup>Upper quartile carapace length.

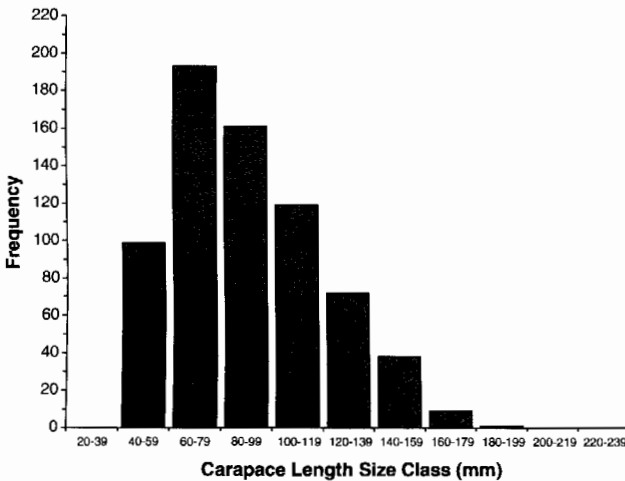


Fig. 3. Population structure based on carapace length size classes of *Testudo graeca graeca* from tourist shops of Marrakech, Morocco in 2001.

three populations:

$$\text{Mass} = (0.000408 \pm 0.000105) \text{CL}^{2.841 \pm 0.015}$$

$$n = 283, r^2 = 0.992, P < 0.0001.$$



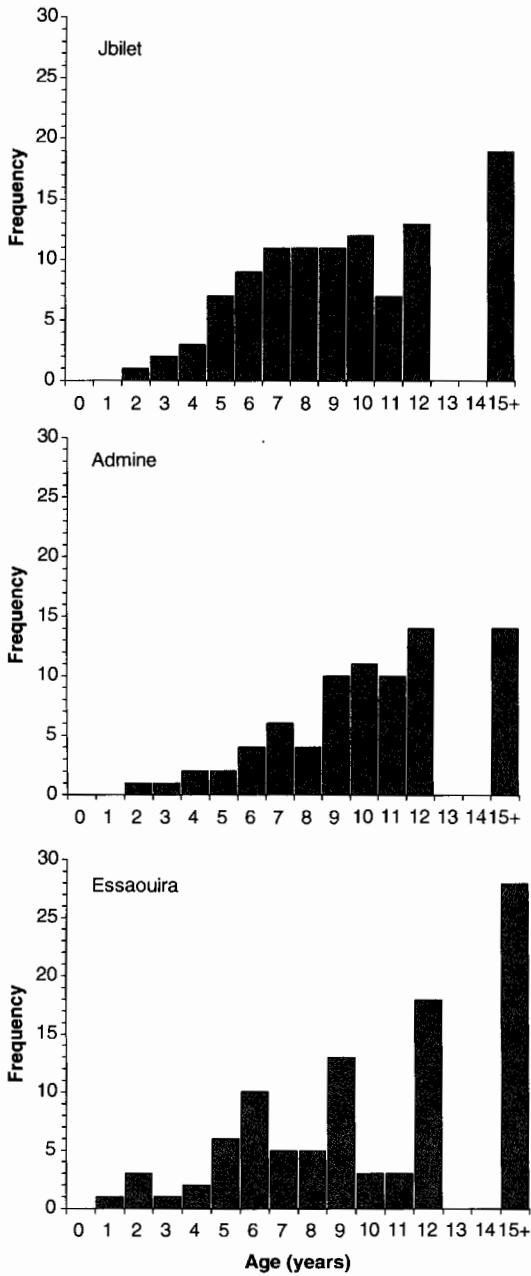


Fig. 4. Population structure based on age of *Testudo graeca graeca* from the Jbilet Mountains (top), Admine Forest (middle), and near Essaouira (bottom), Morocco.

Ages ranged from 2 to 18 for Jbilet tortoises, 2–16 for Admine tortoises, and 1–17 yr for tortoises from Essaouira (Fig. 4), but tortoises >12 yr may have been older than the number of scute rings counted. Juveniles (age <7 yr) constituted 20.7% and 23% of the population for Jbilet and Essaouira, respectively, but only 14% for Admine. Adults 7–12 yr were less frequently encountered in Essaouira (47%) than in Jbilet (61%) and Admine (68%). Conversely adults older than 12 yr were more frequently encountered in Essaouira (28%) than in Jbilet and Admine (18% each). Total age distributions, however, did not differ significantly among populations ( $X^2_{[0.05, 8]} = 15.38$ ,  $P = 0.052$ ,  $n = 280$ ). Sex-ratios (males:females) were not significantly different from 1 (or 1:1) for both Jbilet ( $X^2 \text{ Yates}_{[0.05, 1]} = 0.012$ ,  $P = 0.912$ ,  $n = 82$ ) and Essaouira ( $X^2 \text{ Yates}_{[0.05, 1]} = 0.044$ ,  $P = 0.834$ ,  $n = 91$ ) populations, whereas for Admine, the sex-ratio was male biased (1.69 or 1:0.59;  $X^2 \text{ Yates}_{[0.05, 1]} = 4.13$ ,  $P = 0.042$ ,  $n = 70$ ).

Females reached greater asymptotic sizes than males in all populations, based on either CL (Fig. 5) or log mass (Fig. 6). Means of CL and log mass were significantly greater in tortoises from Admine and Essaouira than for tortoises from the Jbilet Mountains (Table 1). Both CL and log mass fit the Richards' growth model well, based on closeness of data points to predicted lines (Figs. 5 and 6), standard deviations of parameters being <30% of their mean values, and coefficients of determination close to 1.0 (Table 2). The mean values of the shape parameter,  $M$ , were >1 in both males and females from the three localities. There were no significant differences in any of the model parameters, either between males and females within the same site or between tortoises of the same sex among sites (Table 2). The point of curve inflection ( $I$ ), the shape parameter ( $M$ ), and the growth

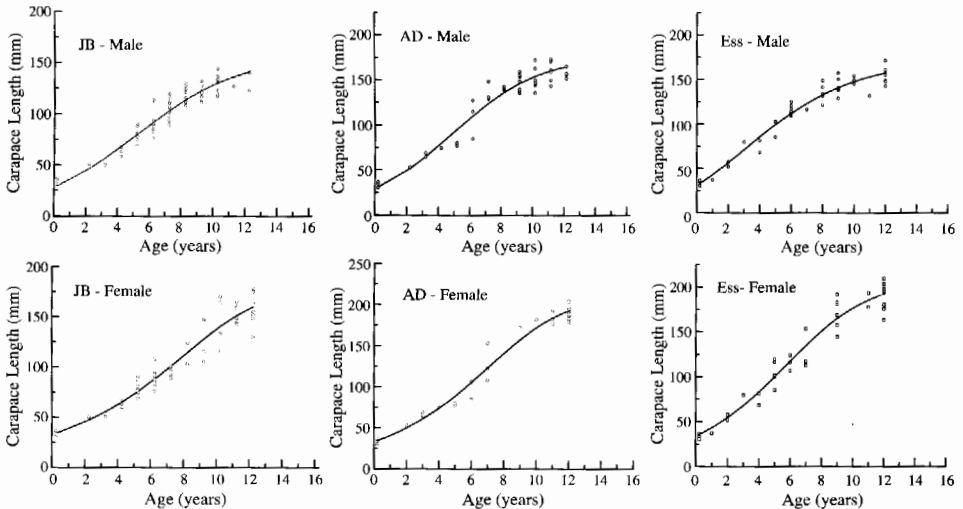


Fig. 5. Growth curves of male (top) and female (bottom) *Testudo graeca graeca* from the Jbilet Mountains (left), Admine Forest (middle), and near Essaouira (right), Morocco based on carapace length. Curves were produced using the Richards' growth model.

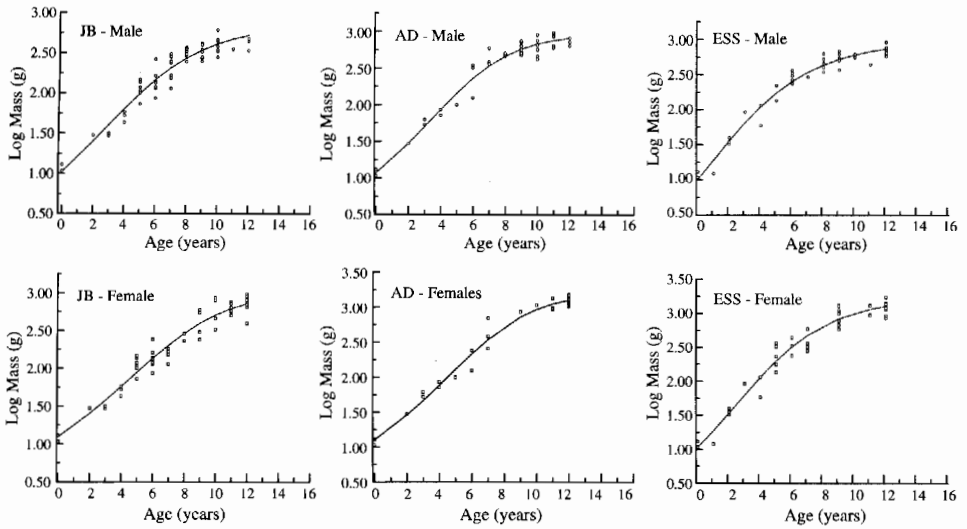


Fig. 6. Growth curves of male (top) and female (bottom) *Testudo graeca graeca* from the Jbilet Mountains (left), Admine Forest (middle), and near Essaouira (right), Morocco based on mass. Curves were produced using the Richards' growth model.

Table 2

Growth parameters (95% confidence intervals) of Richards growth curves for carapace length and log mass of male and female *Testudo graeca graeca* from three populations in Morocco

		Parameters			
		COD	<i>M</i>	<i>K</i>	<i>I</i>
Central Jiblet Mountains	Males	0.904	2.126 (0.356–3.897)	0.320 (0.168–0.472)	4.998 (2.677–7.320)
		<i>0.915</i>	<i>2.530 (0.291–4.768)</i>	<i>0.332 (0.199–0.465)</i>	<i>2.701 (0.262–5.140)</i>
	Females	0.918	3.579 (0.353–6.805)	0.436 (0.143–0.729)	7.774 (5.140–10.41)
		<i>0.941</i>	<i>3.873 (1.063–6.682)</i>	<i>0.384 (0.221–0.546)</i>	<i>4.675 (2.405–6.946)</i>
Admine Forest	Males	0.926	2.149 (0.266–4.032)	0.366 (0.192–0.541)	4.722 (2.352–7.092)
		<i>0.956</i>	<i>3.569 (1.167–5.971)</i>	<i>0.461 (0.294–0.628)</i>	<i>3.464 (1.660–5.269)</i>
	Females	0.971	3.048 (0.864–5.231)	0.438 (0.217–0.659)	7.055 (4.943–9.167)
		<i>0.977</i>	<i>4.016 (1.356–6.675)</i>	<i>0.448 (0.256–0.641)</i>	<i>4.649 (2.685–6.612)</i>
Essaouira	Males	0.954	1.231 (0.048–2.414)	0.225 (0.157–0.353)	2.974 (0.515–5.434)
		<i>0.966</i>	<i>1.305 (–0.201–2.811)</i>	<i>0.292 (0.198–0.386)</i>	<i>0.878 (–1.407–3.163)</i>
	Females	0.945	2.448 (0.518–4.378)	0.382 (0.185–0.579)	5.743 (3.541–7.945)
		<i>0.958</i>	<i>2.159 (0.131–4.188)</i>	<i>0.349 (0.201–0.498)</i>	<i>2.469 (0.097–4.842)</i>

Parameters describing model fit and growth curves are coefficient of determination (COD), shape of curve (*M*), growth constant (*K*), and inflection point of curve (*I*). Values for log mass are in italics below values for carapace length.

constant ( $K$ ), however, were lower for the tortoises of Essaouira than for those of the Jbilet and Admine, which showed values close to each other for both CL and log mass. The equations of CL and log mass growth are as follows:

JB—female:

$$\begin{aligned} \text{CL} &= 182.7(1 + (3.579 - 1)e^{-0.295(T-7.77)})^{1/(1-3.579)}, \\ \text{Log mass} &= 3.017(1 + (3.873 - 1)e^{-0.384(T-4.68)})^{1/(1-3.873)}; \end{aligned}$$

JB—males:

$$\begin{aligned} \text{CL} &= 155.7(1 + (2.126 - 1)e^{-0.320(T-5.00)})^{1/(1-2.126)}, \\ \text{Log mass} &= 2.834(1 + (2.530 - 1)e^{-0.332(T-2.70)})^{1/(1-2.530)}; \end{aligned}$$

AD—female:

$$\begin{aligned} \text{CL} &= 213.2(1 + (3.048 - 1)e^{-0.438(T-7.06)})^{1/(1-3.048)}, \\ \text{Log mass} &= 3.218(1 + (4.016 - 1)e^{-0.448(T-4.65)})^{1/(1-4.016)}; \end{aligned}$$

AD—male:

$$\begin{aligned} \text{CL} &= 176.1(1 + (2.149 - 1)e^{-0.366(T-4.72)})^{1/(1-2.149)}, \\ \text{Log mass} &= 2.966(1 + (3.569 - 1)e^{-0.461(T-3.46)})^{1/(1-3.569)}; \end{aligned}$$

Ess—female:

$$\begin{aligned} \text{CL} &= 209.6(1 + (2.448 - 1)e^{-0.382(T-5.74)})^{1/(1-2.448)}, \\ \text{Log mass} &= 3.219(1 + (2.159 - 1)e^{-0.349(T-2.47)})^{1/(1-2.159)}; \end{aligned}$$

Ess—male:

$$\begin{aligned} \text{CL} &= 173.7(1 + (1.231 - 1)e^{-0.255(T-2.97)})^{1/(1-1.231)}, \\ \text{Log mass} &= 2.986(1 + (1.305 - 1)e^{-0.292(T-0.88)})^{1/(1-1.305)}; \end{aligned}$$

where CL is in mm, mass is in g and  $T$  is age in years.

The growth period  $T$ , equivalent to the age at which 90% of the asymptotic CL is obtained, was delayed by approximately 3 yr in females relative to males in *T. g. graeca* from Jbilet (males 14.9 yr; females 11.8 yr) and Admine (males 12.0 yr; females 9.0 yr), but not in *T. g. graeca* from Essaouira (males 11.4 yr; females 11.8 yr). Growth was relatively fast for the first 7–10 yr of life for tortoises in all three populations whether based on CL (Fig. 5) or log mass (Fig. 6). Growth decreased rapidly after about 10–12 yr. Based on calculated CL and calculated mass, tortoises from Admine became larger than tortoises from Jbilet between 3–6 yr and tortoises from Essaouira exceeded the size of tortoises from Jbilet between 1 and 3 yr (Tables 3 and 4). A significant sexual size dimorphism occurred by 9 yr of age for the three populations based on calculated CL (Table 3). Based on calculated mass, male and female tortoises from Essaouira diverged in size by 6 yr of age, whereas sexes did not diverge in mass until 9 yr of age for tortoises from Jbilet and Admine.

Table 3

Calculated carapace lengths (95% confidence interval) in mm of male and female *Testudo graeca graeca* from three populations in Morocco

	Age (yr)	Calculated carapace lengths (mm)	
		Male	Female
Central Jiblet Mountains			
	0 (hatchling)	29.3 (20.4–38.1)	33.8 (24.1–43.4)
	3	56.5 (51.6–61.3)	55.4 (48.7–62.1)
	6	91.6 (88.3–94.9)	87.9 (83.1–92.8)
	9	122.2* (119.0–125.5)	127.9* (122.7–133.0)
	12	140.8* (136.4–145.2)	160.0* (154.1–165.9)
Admine Forest			
	0 (hatchling)	30.6 (19.4–41.7)	32.9 (23.3–42.5)
	3	64.7 (57.5–72.0)	60.7 (53.6–67.8)
	6	109.9 (103.5–116.3)	105.2 (97.6–112.8)
	9	146.1* (142.0–150.1)	156.9* (150.0–163.8)
	12	164.7* (160.6–168.8)	192.3* (186.5–198.2)
Essaouira			
	0 (hatchling)	30.6 (22.1–39.2)	33.9 (23.0–44.8)
	3	71.0 (65.5–76.5)	67.8 (60.4–75.1)
	6	112.0 (107.8–116.1)	117.5 (110.2–124.8)
	9	140.8* (137.2–144.4)	164.8* (158.5–171.0)
	12	157.4* (153.4–161.3)	192.3* (185.8–198.9)

Calculated carapace lengths at various ages were determined from growth equations for each sex.

\*Significant difference based on mean value not within confidence interval of opposite mean.

The estimated age at maturity varied by region. Age at maturity of males was lowest for tortoises from Essaouira (mean = 5.8 yr, range: 4.4–7.9 yr) and Admine (mean = 6.0 yr, range: 4.8–7.6 yr), but was almost 2 yr greater for males from Jbilet (mean = 7.6 yr, range: 6.0–10.2 yr). Similarly, youngest age at maturity of females was for tortoises from the Essaouira population (mean = 7.7 yr, range: 5.8–9.6 yr). Age at maturity was slightly higher for females from Admine (mean = 8.3 yr, range: 6.5–10.0 yr) and was highest for Jbilet females (mean = 10.5 yr, range: 8.0–14.0 yr).

#### 4. Discussion

We found significant differences in size structure of *T. g. graeca* from three populations in westcentral Morocco. These differences did not follow a latitudinal gradient, but the population with the greatest proportion of larger tortoises was Essaouira, which was close to the coast. There were no significant differences in age structure, though, indicating that size differences were based on differing growth rates and not because of older tortoises. Few small (<90 mm CL) or young (<5 yr) tortoises were found in any of our populations. Small, young turtles of any species

Table 4

Calculated mass (95% confidence interval) in g of male and female *Testudo graeca graeca* from three populations in Morocco

	Age (yr)	Calculated mass (g)	
		Male	Female
Central Jiblet Mountains			
	0 (hatchling)	10.5 (7.53–14.8)	12.5 (8.99–17.3)
	3	40.3 (34.6–47.0)	37.6 (32.1–44.1)
	6	145.8 (133.1–159.9)	134.3 (119.4–151.1)
	9	340.0* (309.6–373.5)	392.2* (351.7–437.3)
	12	515.4* (468.2–567.4)	716.6* (638.6–804.1)
Admine Forest			
	0 (hatchling)	11.8 (8.73–15.9)	12.7 (9.44–17.0)
	3	49.8 (42.7–58.9)	46.0 (39.0–54.3)
	6	227.6 (199.8–259.4)	214.0 (180.8–253.4)
	9	574.2* (525.1–627.8)	722.2* (623.1–837.1)
	12	806.2* (758.9–856.5)	1278.1* (1137.2–1436.5)
Essaouira			
	0 (hatchling)	10.1 (7.56–13.5)	10.7 (7.48–15.3)
	3	67.1 (55.3–76.6)	62.9 (51.5–76.8)
	6	252.9* (228.9–279.5)	319.2* (275.0–370.4)
	9	527.7* (480.5–579.5)	836.0* (722.6–967.2)
	12	744.3* (686.5–806.9)	1280.4* (1137.7–1440.9)

Calculated mass at various ages were determined from growth equations of log mass for each sex.

\*Significant difference based on mean value not within confidence interval of opposite mean.

are rarely encountered in the field (Germano et al., 2000), and this is generally true of *T. graeca* (Lambert, 1982; Hailey et al., 1988; Bayley and Highfield, 1996). Tortoise searches were done during the dry summer season also, and young tortoises in Morocco are generally less active in summer compared to spring and fall (Znari et al., unpublished data). In addition, tortoise hatchlings and small juveniles are particularly vulnerable to predators (Diemer, 1992; Morafka, 1994), and a study of small *Gopherus flavomarginatus* from North America showed that hatchling tortoises spent 85–98% of their time under vegetation (Tom, 1994). Even in protected reserves in Spain, few young tortoises are found (Díaz-Paniagua et al., 2001). It is not surprising, therefore, that small tortoises are generally not found in population searches.

It is interesting to note, however, that virtually all the tortoises we found had detectable rings, even those that we classified as > 12 yr. We found no tortoises with smooth shells and for which we could not count rings. This indicates that even the older tortoises for which we did not estimate age are not very old. This may mean that the much older (and probably larger) tortoises in these populations were lost years ago to the souvenir trade (Lambert, 1979, 1984; Highfield, 1994; Fretey, 1995). Even though this species is protected from over-collecting, our reconnaissance of shops in Marrakech showed hundreds of tortoises still being collected for sale. Most

of these tortoises were small sized, and were likely fairly young tortoises. These tortoises were not likely collected from the populations we studied; rather they probably came from areas of the Atlas Mountains near Marrakech. Although we do not know for sure the impact collecting has on native populations, it appears that older, larger tortoises may have been removed in the past and now smaller tortoises are being taken. This has obvious negative consequences for these tortoise populations because not only are the large, most fecund females mostly absent, but now the younger tortoises that could take their place are being removed. We do not think that heavy collecting is still occurring at the sites we studied, but any additional collecting could lead to the extinction of these populations.

We found that adult female *T. g. graeca* were significantly larger than adult males, which is similar to what most others have found. Maximum CL recorded for male and female *T. g. graeca* from northwestern Africa were 151 and 198 mm, respectively, with corresponding body masses of 775 and 1675 g (Lambert, 1982). In the same Admine Forest where we worked, Bayley and Highfield (1996) reported larger maximum CL in females (206 mm) than males (169 mm) with corresponding body masses of 1840 and 980 g. However, we found greater maximum CL for both sexes in the same area (184 mm for males, 226 mm for females), although our maximum CL for tortoises from our Jbilet populations were similar to those found by Bayley and Highfield (1996). In contrast, Diaz-Paniagua et al. (2001) found maximum CL of males (210.8 mm) exceeded that of females (191.2 mm) for *T. g. graeca* in southwestern Spain. Interestingly, the largest *T. graeca* ever recorded for Morocco (female, 255.2 mm CL and 2990 g; male 200.3 mm CL and 1250 g) were recently found in northeastern Morocco at Tagourast, about 15 km south of Misour (Znari et al., unpublished data). This area is far from where tortoises are collected and may represent the potential sizes tortoises can reach if not impacted by collecting.

The growth equations reported here are the first calculated for *T. graeca*. As in other chelonians, *T. g. graeca* showed a sigmoidal pattern of growth, with rapid growth during the juvenile period (i.e., prior to 10–12 yr) after which rates decreased markedly in adults (Davenport and Scott, 1993; Germano, 1994; Germano et al., 2000; Lagarde et al., 2001). Lagarde et al. (2001) found that growth of *Testudo horsfieldi* was best described using a von Bertalanffy model curve type, whereas Germano (1994) found that in three of four species of North American tortoises of the genus *Gopherus* a mean shape parameter is close to 1, which corresponds to the logistic model. We found that growth curves for *T. g. graeca* did not correspond to any of the defined fixed-parameter models (the shape parameter was higher than 1) and that size at point of inflection (at which the absolute growth rate is the highest) exceeded 50% of asymptotic size. This seems to be determined by the time of sexual maturity acquisition relative to the growth time and asymptotic size.

As suggested by Lagarde et al. (2001) for *T. horsfieldi*, the decrease in growth prior to maturation in *T. g. graeca* may be due to physiological preparation for first reproduction, especially for females. Lambert (1982) found that male *T. g. graeca* could be distinguished from females and juvenile tortoises by year 9, and by year 11 in *T. g. ibera*. We could distinguish male from female tortoises at about 110 mm CL.

Based on our growth curves, this corresponds to an age of 5.6 yr for males and 5.8 yr for females from Essaouira, 6.0 yr (males) and 6.3 yr (females) for tortoises from Admine, and 7.7 yr for both sexes from Jbilet. However, estimated ages at maturity of females were 2–3 yr older than the ages at which the sexes could be distinguished (and, therefore, 2–3 yr older than males for each population). In Spain, Díaz-Paniagua et al. (2001) found that sexes of *T. g. graeca* could be distinguished after 6 yr. Based on a marked decrease in growth rate using widths of scute rings, they estimated mean sexual maturity of male tortoises at 6.9 yr (5–9 yr) and of females at 8.5 yr (6–14 yr). For *T. graeca* from Greece, Willemsen and Hailey (2003) could distinguish sexes at about 130 mm CL, and based on courtship behaviour of males and egg production of females, the minimum CL of mature males was 134 mm and of mature females 170 mm. Although no ages were estimated, males became sexually active about the size at which sexes could be distinguished and females kept growing past this size. These results are similar to what we found in Morocco, except that tortoises from our populations matured at a smaller size and younger age.

Rapid juvenile growth without early sexual differentiation even if sexes become dimorphic later in life is typical of turtles and may be the result of the need to attain large size to minimize predation risk as quickly as possible (Wilbur and Morin, 1988). However, precocial sex differentiation in growth patterns may occur in some tortoises (Andrews, 1982; St. Clair et al., 1994; Lambert et al., 1998). In addition to predation considerations, females may also be confronted with minimal size constraints on producing optimal clutch size. This may be the case of female *T. graeca*, which, similar to other tortoise species, mature relatively later than do males.

The removal of large tortoises from a population will markedly affect population structure, but probably has little effect on growth rates of tortoises that remain. Growth rate is likely most affected by environmental factors and genetics characteristics of individuals. We found that *T. g. graeca* from the Admine Forest and Essaouira showed more rapid growth than those from the Jbilet Mountains. The pattern of precipitation is fairly similar at recording stations near these study sites (Fig. 7), although annual rainfall at Essaouira ( $298 \text{ mm yr}^{-1}$ ) is a little greater than the other two localities (approximately  $240 \text{ mm yr}^{-1}$ ). Both Essaouira and the Admine Forest experience much more moderate average temperatures in the summer than in the Jbilet Mountains (Fig. 7), but we are not certain that this accounts for the differences in growth that we found. Growth rate variations of tortoises also have been recorded for *Geochelone gigantea* (Grubb, 1971; Swingland, 1977; Bourn and Coe, 1978), *Geochelone pardalis* in eastern Africa (Lambert, 1995; Lambert et al., 1998), and for four distinct population segments of *Gopherus agassizii* (Germano, 1994), although the particular effect of the environment on growth differences were not certain. Ultimately, we found that despite past over-collecting, and some level of current exploitation of tortoises, the populations we studied in westcentral Morocco were experiencing a healthy rate of growth and exhibited a fairly normal population structure for tortoises. If these populations do not experience any additional collecting, particularly of younger individuals, the populations likely will be self-sustaining. However, a return to over-collecting could cause these populations to become extinct.



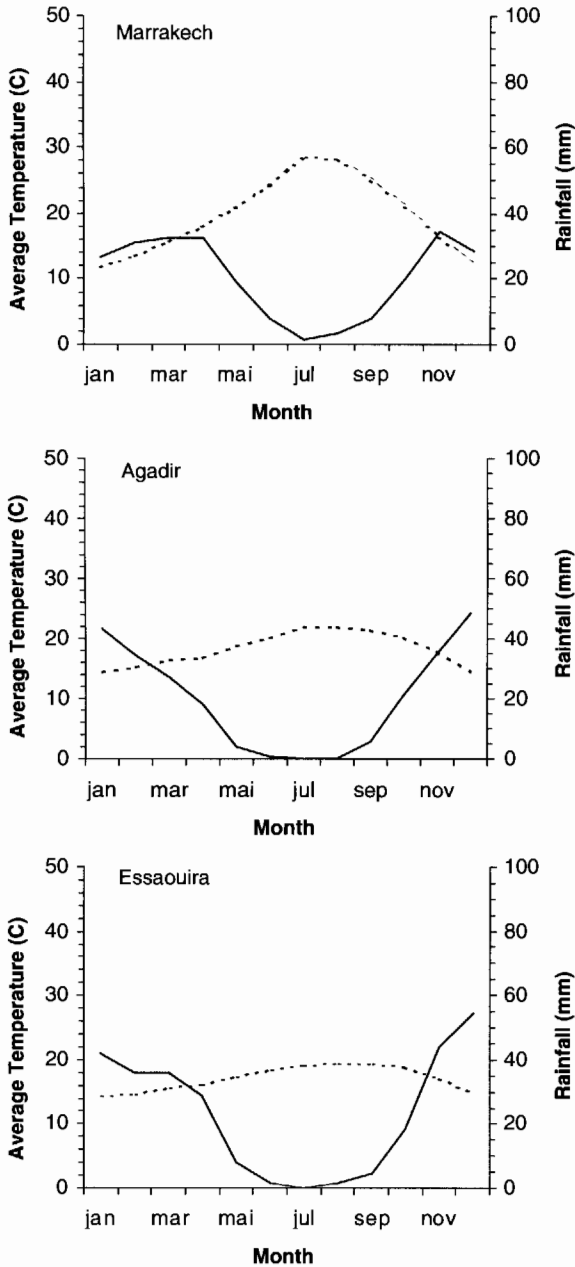


Fig. 7. Rainfall (solid line) and average temperatures (dotted line) for three areas near sites where *Testudo graeca graeca* were studied. See Fig. 1 for locations of sites.

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