

Variation in Shell Morphology and Color of Hermann's Tortoise, *Testudo hermanni*, in Southern Europe

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ABSTRACT. – Shell measurements and color were compared among four populations of *Testudo hermanni* in Greece, mainland France, Corsica, and Spain. Significant differences in adult body size, shell morphology, and color were detected. Females were larger than males in the western populations but not in the Greek population. Females in Corsica were the largest; Spanish males were the smallest. The trapezoidal shell form of males is most pronounced in the Greek population, in which the back of the shell is greatly broadened. This character is highly variable in Corsica but did not differ between French and Spanish males. The western populations differed in yellow shell color shades and plastral pattern, whereas the Greek population was highly variable in these characters. Due to pronounced variation among populations, it is essential that wildlife management considers the conservation of local adaptations in relocation programs by careful selection of individuals and stringent attention to locality of origin.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Testudo hermanni*; tortoise; morphology; allometry; color; conservation; France; Spain; Greece; Corsica

Hermann's tortoise, *Testudo hermanni*, is one of several species of *Testudo* found in Mediterranean Europe (Bour, 1986, 1995). The species has a fragmented distribution, extending from western Turkey to Spain. It occurs on many Mediterranean islands, from the Balearics to the Greek islands (Stubbs, 1989; Iverson, 1992). Two subspecies are currently recognized: *T. h. hermanni* and *T. h. boettgeri*. A key diagnostic feature is the relatively longer pectoral and shorter femoral seams in *T. h. hermanni* (Bour, 1986).

Most allometric studies of *Testudo hermanni* have dealt with sexual dimorphism or growth patterns in single populations (Meek and Inskeep, 1981; Stubbs et al., 1984) or compared different sympatric tortoise species (Meek, 1982). Allometry (length/weight ratio) was also used to assess the health of Hermann's tortoises (Jackson, 1980). Only a few studies have compared different populations of *T. hermanni*; Meek (1985, 1989) compared two geographically close populations in Yugoslavia. Cheylan (1981) suspected that plastral color and the trapezoidal shape of the shell might vary locally but did not present a rigorous analysis. These studies, however, indicated that interpopulation variation in morphology and color of *T. hermanni* are more pronounced and widespread than the current recognition of just two subspecies suggests.

In western Europe many populations of *T. hermanni* are threatened by habitat alteration through increasing urbanization, fires, and changes in agricultural practices. Collection by humans is another cause of their decline (Swingland et al., 1986). For several years France, Italy, and Spain have based management actions for the conservation of Hermann's tortoise on captive breeding and relocation operations (Stubbs, 1988; Devaux, 1990; Montori et al., 1993). These already include the collection of pet tortoises in central Europe, their

designation to one of the two subspecies, and their release into wild populations in southern Europe (Ballasina, 1992, 1996). However, in order to preserve local distinct populations of this patchily distributed species, it is imperative to define the basic morphometric and genetic differences among these populations.

The emphasis of the present study is comparison of a few selected populations of *T. hermanni* across its range (Spain, mainland France, Corsica, and Greece; Fig. 1) in order to evaluate characters which are useful for the analysis of interpopulation variation. In addition to standard morphometric measurements, we present data on femoral and pectoral scute width as indices for trapezoidal shell shape. We also quantify shell color and plastral pattern for the first time.

METHODS

Data Collected and Site Details. — Four populations of *Testudo hermanni* were studied in the field during summer and autumn of 1994 (Fig. 1). We only used adult individuals with a straight carapace length > 115 mm. Immatures were not included because morphology and color may change during growth. Tortoises were located in their habitat during daylight hours (0900–1800 hrs). Each tortoise handled was sexed according to Stubbs et al. (1984), measured (with calipers accurate to 1 mm), and weighed (with a Pesola scale accurate to 20 g). Body measurement included straight carapace length (SCL), maximum carapace depth (D), carapace width across the middle of the pectoral scutes (PW), carapace width across the middle of the femoral scute (FW), and lengths of the femoral and pectoral scutes.

As the color of *T. hermanni* is composed of yellow and black, the yellow tendency of the shell was evaluated by comparing it with a range of colors (Fig. 2) defined as: greenish

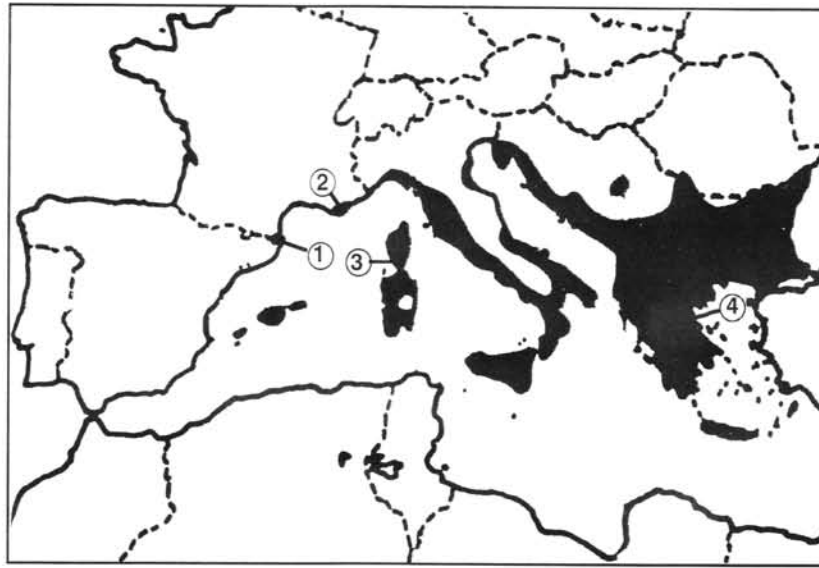


Figure 1. The overall range of *Testudo hermanni* (Bour, 1986) and the locations of the four populations studied: 1) Les Albères, Spain, 2) Le Cannet des Maures, mainland France, 3) Calvi, Corsica, 4) Alyki, Greece.

yellow (1A6), yellow (11/2A6), ochre yellow (2 1/2A6), and orange (3A6), using the Methuen method (Kornerup and Wanscher, 1967). The extent of plastral black pigmentation was also measured by comparing each specimen to a range of five ventral patterns (Fig. 3). These ventral patterns differed from one another in overall size and fragmentation of the black pigment.

We intentionally chose populations spread across the species' range. In Spain, data from 47 tortoises (34 females, 13 males) were collected during the first week of August 1994 in the "Albères," a dry shrubland around Gariguella, western Figueras. For the French mainland sample, 99 tortoises (42 females, 57 males) were captured during August and September 1994 at the Cannet des Maures in shrubland and meadows near a river. In Corsica, 30 tortoises (20 females, 10 males) were collected in late August 1994 near Calvi in an open forest and a shrubland. The Greek sample of 49 tortoises (12 females, 37 males) was collected during one week in October 1994 at Alyki near Thessalonikii (see Stubbs et al., 1985, for description of the site). The first three samples form part of the western subspecies *Testudo hermanni hermanni* Gmelin, 1789; the Greek population belongs to *T. h. boettgeri* Mojsisovics, 1889.

Statistical Analysis. — We first checked whether sexual size dimorphism occurred in a selected parameter, and distinguished sex of individuals in later analysis where necessary.

We compared morphometric values among sites with analysis of variance on body length (SCL) and slopes of allometric equations with t-tests using the following equations:

$$Z = ((SCE_{YX})_1 + (SCE_{YX})_2) / (n_1 + n_2 - 4)$$

$$A = (a_1 - a_2) / (Z * ((1/n_1 S_{X1}^2 + 1/n_2 S_{X2}^2))^{1/2})$$

A followed t-tests (with $(n_1 + n_2 - 4)$ df), where n_1 and n_2 represent sizes of the samples compared, a_1 and a_2 coefficient directors, SCE_{YX} residual variation of linearity tests, S_{X1} and S_{X2} standard deviation. The t-distributions were used to assign 95% confidence limits to the coefficients of the regression equations. For allometric equations between SCL and PW, FW, and D, we used non-transformed data, while the relationship between SCL and body mass was obtained after transforming data into natural logarithmic form. Finally, we analyzed values of color using chi-square tests. The statistical analyses were conducted with the computer package SPSS/PC+ (Norusis, 1986a, 1986b).

RESULTS

Morphometry. — The ratio between the lengths of femoral and pectoral scutes, which is usually used to distinguish the subspecies of *T. hermanni* (Bour, 1986), was 1.65

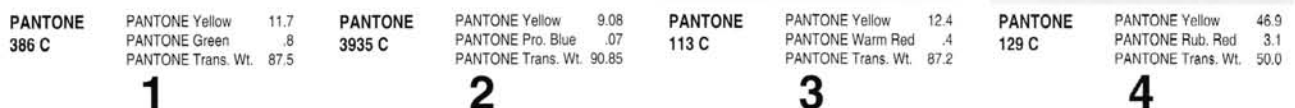


Figure 2. Range of yellow coloration of the shell: 1) greenish yellow, 2) yellow, 3) ochre yellow, 4) orange.

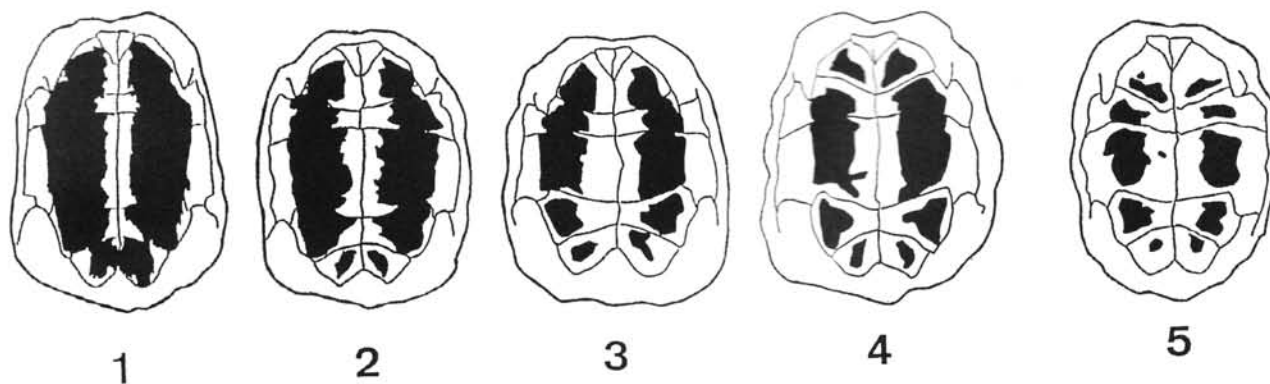


Figure 3. Range of black plastral pigmentation: 1) continuous black pigmentation, 2) black spots on anal scutes are isolated, 3) black spots on anal and femoral scutes are isolated, 4) black spots on anal, femoral, and humeral scutes are isolated, 5) black spots are isolated on each scute and reduced in size.

± 0.40 for the Spanish samples, 1.58 ± 0.44 for the mainland French samples, 1.60 ± 0.40 for the Corsican samples, and 0.75 ± 0.20 for the Greek ones.

Females and males differed greatly in body size (SCL) in the Spanish and the two French samples: Spain $F_{1,28} = 45.92$, $p < 0.01$, mainland France $F_{1,97} = 78.95$, $p < 0.01$, Corsica $F_{1,45} = 45.08$, $p < 0.01$. In most cases females were larger than males (Fig. 4), except in the Greek sample, where no sexual dimorphism was observed ($F_{1,46} = 0.38$, $p > 0.05$). Since sexual dimorphism occurred in most samples, males and females were analyzed separately in the following tests.

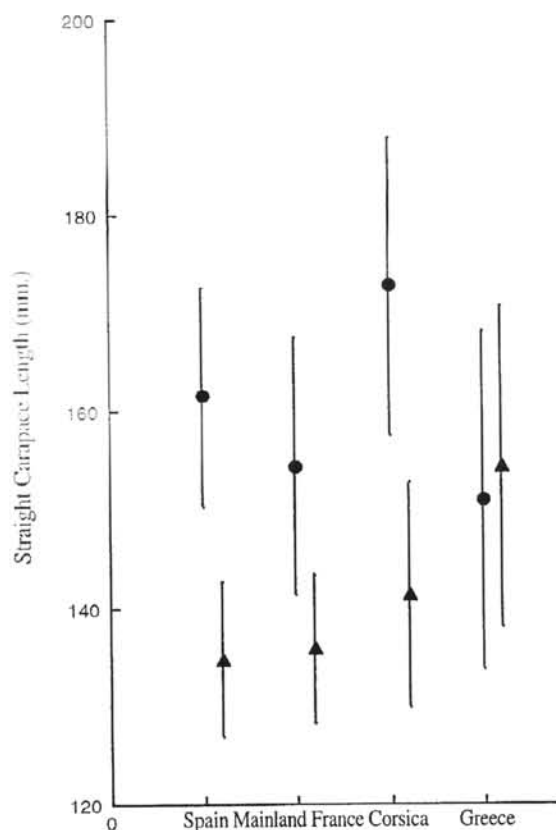


Figure 4. Comparison of body size (mean and standard deviation) in relation to sex and sampling sites. Triangles = males, spots = females.

ANOVA tests on SCL revealed that differences occurred for both sexes among the four sites (males $F_{3,112} = 20.85$, $p < 0.01$; females $F_{3,104} = 13.16$, $p < 0.01$). Comparisons between sites, done two by two, showed that the Spanish and mainland French groups of males ($F_{1,65} = 0.14$, $p > 0.05$) and also the Greek and mainland French groups of females ($F_{1,52} = 0.56$, $p > 0.05$), had similar mean carapace lengths. The Corsican females were the largest individuals, whereas Spanish males were the smallest ones (Fig. 4). Moreover, the large size of Greek males explains the lack of sexual dimorphism, which was only observed in this population.

No differences between sites could be detected for males in the SCL/FW and SCL/D allometric regressions (Table 1). However, for female samples, slopes of the SCL/D equation differed between Greek and Spanish groups ($t = 2.52$, $p < 0.05$) and also between Greek and Corsican groups ($t = 2.96$, $p > 0.05$). Greek females had the deepest shells. Furthermore, the slope of the SCL/FW regression differed between mainland French and Corsican females ($t = 2.87$, $p > 0.05$) and between mainland French and Spanish ones ($t = 2.20$, $p > 0.05$). In the latter case mainland French individuals had a wider shell. Thus, a deeper or wider shell was detected only in the two groups of smaller females.

Table 1. Allometric equations of the form $y = ax + b$ relating straight carapace length (SCL) (x value) to two selected dimensions of the shell (FW, femoral width and D, depth) (y value). Correlation coefficient = r . All regressions are significant at $p < 0.05$ (\pm confidence limits of slope).

Sites	Sex	SCL = f(FW) slope	r	SCL = f(D) slope	r
Spain	Male				
	Female	1.34 (± 0.12)	0.93	1.20 (± 0.58)	0.60
Mainland France	Male	1.28 (± 0.08)	0.91	1.61 (± 0.15)	0.83
	Female	1.60 (± 0.08)	0.95	1.87 (± 0.24)	0.80
Corsica	Male	1.10 (± 0.14)	0.92	1.40 (± 0.29)	0.82
	Female	1.28 (± 0.07)	0.95	1.26 (± 0.15)	0.83
Greece	Male	1.35 (± 0.06)	0.95	1.66 (± 0.22)	0.80
	Female	1.37 (± 0.09)	0.98	2.34 (± 0.25)	0.95

Table 2. Allometric equations of the form $y = ax + b$ relating femoral width (FW) (y value) to pectoral width (PW) (x value) and of the form $y = bx^a$ relating straight carapace length (SCL) (y value) to body mass (M) (x value). For more details see Table 1.

Sites	Sex	FW = f(PW) slope	r	ln SCL = f(ln M) slope	r
Spain	Male	0.79 (± 0.15)	0.91	0.51 (± 0.11)	0.85
	Female	1.12 (± 0.08)	0.96	0.33 (± 0.03)	0.93
Mainland France	Male	1.04 (± 0.06)	0.91	0.33 (± 0.02)	0.91
	Female	1.09 (± 0.07)	0.93	0.40 (± 0.03)	0.94
Corsica	Male			0.34 (± 0.03)	0.95
	Female	1.14 (± 0.07)	0.94	0.34 (± 0.02)	0.96
Greece	Male	1.30 (± 0.06)	0.96	0.37 (± 0.02)	0.97
	Female	1.20 (± 0.07)	0.98	0.39 (± 0.03)	0.98

Variation in the trapezoidal form of the shell (i.e., carapace wider posteriorly than anteriorly) could not be observed in females as no differences were observed among sites in FW/PW allometry (Table 2). The trapezoidal form of males varied among sites, with Greek males having the back of the shell wider than French ones ($t = 1.98$, $p > 0.05$, Fig. 5). No difference was detected between Spanish and mainland French males. Data from the Corsican population did not permit reliable regression, but analysis with logarithmic form was possible ($r = 0.73$). This was the only group to follow an exponential model:

$$\ln(\text{FW}) = 0.85 (\pm 0.24) * \ln(\text{PW}) + 0.82 (\pm 1.11)$$

The last allometric comparison (between body length and body mass) did not reveal any differences among sites for either sex (Table 2).

In conclusion, few morphometric differences were observed among sites. Overall size and trapezoidal shell form seemed to be the major differences observed.

Color and Pattern. — No sexual differences were observed in these two parameters, but great differences

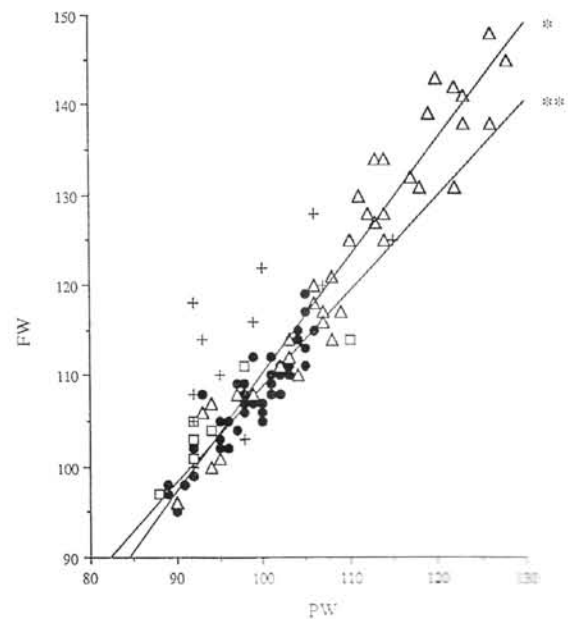


Figure 5. Trapezoidal relationship between femoral and pectoral scute widths (FW and PW, respectively) in males. Spots = mainland France, triangles = Greece, squares = Spain, crosses = Corsica. * = allometric regression of Greek samples, $\text{FW} = 1.04 \text{PW} + 4.78$; ** = allometric regression of mainland French samples, $\text{FW} = 1.30 \text{PW} - 20.18$.

appeared among sites. The distribution of the plastral black pigmentation was similar for Spain and mainland France (Fig. 6). These individuals had the largest pigmentation areas on the plastron with little fragmentation. Corsican animals differed in having less pigmentation. Furthermore, these three western populations were very homogeneous and corresponded to just two or three ventral pattern categories. By contrast, the eastern Greek sample showed wide variation in this parameter. Each type of ventral pattern occurred, and it was the only sample which included pale plastra (number 5, Fig. 3).

Study of the yellow shell color also allowed recognition of geographic variation (Fig. 7). All samples included both a dominant and minor color, usually with a narrow range.

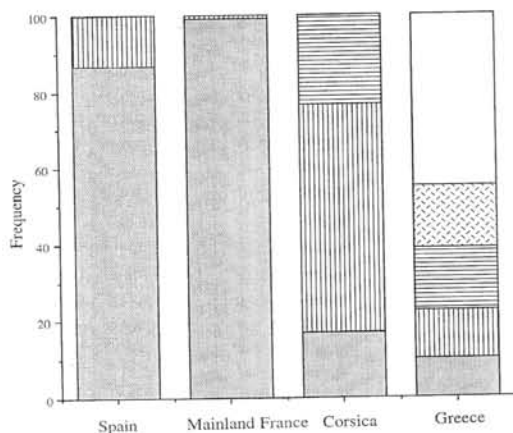


Figure 6. Frequency distribution of black plastral pigmentation patterns (see Fig. 3) in relation to sampling sites. Shading corresponds to ventral pattern 1 (the darkest pattern), vertical lines to 2, horizontal lines to 3, small broken lines to 4, white to 5 (the clearest pattern).

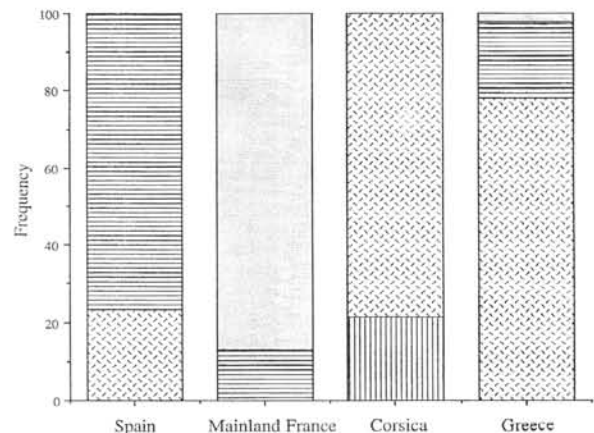


Figure 7. Frequency distribution of yellow shell color tendencies (see Fig. 2) in relation to sampling sites. Vertical lines correspond to greenish yellow, small broken lines to yellow, horizontal lines to ochre yellow, shading to orange.

Greek tortoises were again the only ones to show considerable heterogeneity, with two minor colors. The usual colors of *T. hermanni* are yellow, ochre yellow, and orange. Greenish yellow tortoises were rare and occurred only in the Corsican sample. Moreover, the Corsican and Greek groups had similar primary colors, whereas the mainland French and Spanish tortoises are distinguished by the occurrence of orange and ochre tendencies.

DISCUSSION

The Greek population of the eastern subspecies *T. hermanni boettgeri* can be clearly distinguished from the three western populations of the nominate form by the ratio between femoral and pectoral width of the carapace. Apart from the larger size of the Greek males in this study, our other parameters do not clearly separate the two subspecies. A reason for this may be the high level of variation in the Greek sample. However, the morphometric and color parameters revealed major variation among geographically distant study populations. In particular, the three samples of the nominate form clearly differ from the Greek sample.

Body size differed substantially among populations. For this character it is, however, possible that habitat quality is more important than geographic location. Meek (1989) observed similar body size variation between two Yugoslavian populations of *T. hermanni*. Compared to this study, however, the Greek males grow larger. Their large size and lack of sexual dimorphism may be related to high population density, a male-biased sex ratio (> 2:1), or to differences in mortality rates between sexes, as suspected by Hailey (1990).

Morphologic comparisons revealed only wider or higher shell forms in the two groups of smaller females. We might suppose that an important morphological constraint was the space needed for egg formation. Thus, the evolution of the shape of the shell could directly depend on body size. However, no such morphologic constraint should operate in the variation in the trapezoidal form because it is limited to males, and the individuals with the wider back shell appeared to be the largest ones. We confirmed that males of the eastern population are wider posteriorly, as suggested by Cheylan (1981). We found that only males varied in trapezoidal form and that this also occurred in the western subspecies. Great heterogeneity was found in the Corsican group. If the same were to be confirmed in other Corsican populations, the tortoises from this island would differ from other populations. Cheylan (1992) previously suggested heterogeneity in tortoise morphology and color for this island. The special characters of Corsican tortoises might be explained by the supposed origin of these populations: tortoises on the island may have been introduced on several occasions by humans from the mainland (R. Bour, *pers. comm.*).

Color analyzes have been used previously in studies of geographic variation. For example, skin pigmentation in *Emys orbicularis*, the European pond turtle, combined with other measurements, has distinguished local populations

(Fritz, 1992, 1993). In our case the size and distribution of plastral black pigmentation varied greatly among the four sites. The tendency toward reduction of these black areas in eastern populations, mentioned by Bour (1986) and Cheylan (1981), is substantiated. Moreover, the Greek population is also distinguishable from the others by its great variation in plastral pattern; all patterns were recorded there, whereas the three western populations were highly homogeneous and only a few pattern categories occurred in each.

Testudo hermanni has a fragmented distribution. Local populations show considerable variation in size, body shape, pattern, and color. The trapezoidal form and plastral pigmentation may intergrade clinally from east to west. More populations need to be studied to fully document this variation. Clearly, conservation management should never rely solely on the identity of tortoises as only one of the two recognized subspecies, but must consider the complexity of the local variation of different characters. This study suggests that the trapezoidal form of the shell and pigmentation variation might be useful tools to identify the eastern populations. Once they are more fully understood, these characters may permit the protection of local adaptations during relocation programs of the western subspecies. Available data for the eastern subspecies suggest considerable differences among populations, but these have yet to be studied throughout its range.

Due to the high morphologic variation of *Testudo hermanni*, it is imperative not to use individuals of unknown origin to augment existing wild populations until genetic markers (plasma protein or DNA technology) allow the discrimination of regional and local variation.

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