DIFFERENCES IN THERMOREGULATION BETWEEN *TESTUDO HERMANNI* AND *TESTUDO MARGINATA* AND THEIR ECOLOGICAL SIGNIFICANCE

RONALD E. WILLEMSEN

Monte Cassinostraat 35, 7002 ER Doetinchem, The Netherlands.

(Accepted 30.1.90)

ABSTRACT

The activity patterns and body temperatures of *T. hermanni* and *T. marginta* were studied in the Peloponnese (southern Greece) during May, June, August and October 1984.

T. hermanni

In May the daily activity patterns of *T. hermanni* were unimodal, in June and August they were bimodal. In August during the afternoon the activity increased significantly, in October the activity was very low.

In August basking decreased significantly and mating increased significantly.

During these four months no significant differences in body temperatures were found. In May a maximum body temperature of 35°C was found; in feeding tortoises a maximum temperature of 34°C. After May no temperatures over 32°C were found.

T. marginata

In May and June the activity patterns of *T. marginata* were bimodal with the highest activity during the afternoon. In August an unimodal low activity pattern was found during the afternoon. In October the activity of *T. marginata* was unimodal and shifted towards the middle of the day. Sexual activity was seen in October only.

Body temperatures in all *T. marginata* samples were significantly higher than those in *T. hermanni*. During May a maximum body temperature of 36°C was found in basking tortoises, a maximum of 37°C in feeding tortoises.

The trend towards lower body temperatures in summer was greater in *T. marginata* than in *T. hermanni*. Body temperatures found in feeding tortoises in October equalled those found in May.

Ecological Consequences

In southern Greece the habitat separation between *T. hermanni* and *T. marginata* can be explained by morphological differences and a higher body temperature tolerance in *T. marginata*. Differences in the annual cycle of activities might also be of importance as regards the habitat separation between both species.

INTRODUCTION

Testudo hermanni belongs to the most widespread species of tortoises in Greece, found in almost every habitat and all over the mainland as well as on some islands (Werner, 1938; Willemsen and Hailey, 1989).

The distribution of *T. marginata* was limited to the mainland south of 40° 20′ and to some of the Greek islands (Werner, 1938; Stemmler, 1957; Watson, 1962; Clark, 1963, 1967; Willemsen and Hailey, 1989). *T. hermanni* is limited to certain kinds of habitats in southern Greece; outside these habitats *T. hermanni* is almost completely replaced by *T. marginata* (Willemsen and Hailey, 1989).

Morphologically *T. marginata* is better adapted to heavy terrain and dense vegetation but differences in morphology alone cannot explain the habitat separation between these two species. In northern Greece near the edge of the distribution area of *T. marginata*, *T. hermanni* is found in a high density sympatric with a *T. marginata* population of a low density, whereas in a similar habitat in southern Greece *T. hermanni* have been completely replaced by *T. marginata*.

In northern Greece there is a similar but possibly even more complicated situation with regard to *T. hermanni* and *T. graeca*. At some sites there is a clear habitat separation between *T. hermanni* and *T. graeca* while at other sites *T. hermanni* lives sympatrically with *T. graeca*, different species predominating at different sites. Stubbs (1981) and Wright *et al.* (1988) found that in coastal areas *T. graeca* was more abundant than *T. hermanni* in hotter and drier kinds of vegetation. They also found significantly higher body temperatures in *T. graeca*. Willemsen (unpublished) also found differences in thermoregulation in sympatric living populations of *T. hermanni* and *T. graeca* which could produce ecological separation and which would enable the two species to live sympatrically.

It is possible that differences in thermoregulation are also significant in the habitat separation between *T. hermanni* and *T. marginata* in southern Greece. *T. hermanni* prefers cooler and less dry habitats. Cherchi (1956) gives for normal activity a body temperature which ranges from 16°C to 32°C in *T. hermanni*. They will not voluntarily accept body temperatures over 34°C; juveniles have even lower body temperatures. A number of field studied have also shown that *T. hermanni* will almost never accept body temperatures over 34°C (Meek, 1981, 1984, 1988). In literature no data about body temperatures of *T. marginata* were available.

SITES

Nowhere in Greece were sufficient tortoises of both species found for simultaneous comparison of their body temperatures. The only suitable *T. marginata* population was found near Gytheion, the nearest suitable populations of *T. hermanni* were found near Sparta and Kalamata. These sites are described by Willemsen and Hailey (1989).

METHODS

The activity of each tortoise was recorded, new tortoises were marked and recaptures were remarked with waterproof blue ink on the carapace to avoid wasting time with future recaptures. The use of red ink would have been more practical but there is some evidence that red ink makes juveniles more vulnerable to predators, mostly birds of the *Corvus* group.

All first captures were weighed, measured, sexed and, if possible, age was determinated according to growth lines in the carapace scutes. Of recaptures only activity, weight and body temperatures were noted. The body temperature was measured with a mercury bulb thermometer in the cloaca to the nearest 0.5°C. In this study only *T. hermanni* over 10cm Straight Carapace Length (SCL) were used because the regulation in juveniles might be different (Cherchi, 1956), and the frequency of juveniles was very different in the two *T. hermanni* populations (Willemsen and Hailey, 1989). Unsexable *T. marginata* were not used.

RESULTS

MAY

The daily activity pattern of *T. hermanni* was unimodal from 9.30h to 17.49h, no observations were made from 13.00h to 14.00h (Fig. 1 and Table 1). The activity of *T. marginata* was almost bimodal (Fig. 2 and Table 2). There was little activity between 14.00h and 17.00h.

	Time											
May (Sparta)	0800	0900	1000	1100	1200	1400	1500	1600	1700	1800	1900	2000
Basking		24.8-4.1 19-29 (14)	26.4-4.0 27-32 (15)	30.0-3.7 27-35 (7)	31.0-1.6 28-33 (9)	31.6-1.1 30-33 (6)	30.1-0.0 30-30 (1)					
Feeding					30.0-1.4 29-31 (2)	32.5-0.7 32-33 (2)	31.6-1.1 31-34 (9)	29.2-1.2 31-34 (6)	30.0-0.0 30-30 (1)			
Other		25.0-0.0 25-25 (2)	29.5-2.6 26-32 (4)	31.2-5.2 22-34 (5)	28.3-2.1 26-30 (3)	31.5-1.3 30-33 (4)	29.5-0.7 29-30 (2)	30.0-2.8 28-30 (2)	30.0-0.0 30-30 (3)			
June (Kalamata)												
Basking	25.8-3.4 20-30 (8)	25.2-3.2 20-30 (9)	27.3-3.9 23-31 (4)									
Feeding		29.5-6.3 25-34 (2)	30.1-1.0 29-31 (3)	30.0-0.0 30-30 (1)						34.0-0.0 34-34 (1)	32.0-1.4 31-33 (2)	
Other	27.0-0.0 27-27 (1)	30.0-1.0 29-31 (3)	28.7-3.5 25-32 (3)	31.5-2.1 30-33 (2)								32.0-0.0 32-32 (1)
August (Sparta)												
Basking	24.0-0.0 24-24 (1)	25.0-2.5 22-28 (8)	27.7-2.9 26-31 (3)	30.0-0.0 30-30 (1)							30.0-0.0 30-30 (1)	
Feeding			30.0-0.0 30-30 (1)	32.0-0.0 32-32 (1)					32.0-0.0 32-32 (1)	31.0-0.0 31-31 (1)		
Other		22.5-1.6 21-25 (6)	32.5-0.7 32-33 (2)	32.0-0.0 32-32 (1)					31.0-0.0 31-31 (1)	32.0-1.0 31-33 (3)	28.8-1.6 26-31 (9)	28.7-1.2 28-30 (3)
October (Kalamata)												
Basking				20.0-0.0 20-20 (1)	30.0-0.0 30-30 (1)			29.0-0.0 29-29 (1)				
Feeding				30.0-0.0 30-30 (1)			31.0-0.0 31-31 (1)					
Other								31.7-0.6 31-32 (3)				

TABLE 1: Diural variation of body temperature in *T. hermanni* in different months. Basking, feeding and other activities (includes moving, mating and stationary animals) shown separately. Times are East European summer time. Data are shown as mean –1 S.D., range and sample size.

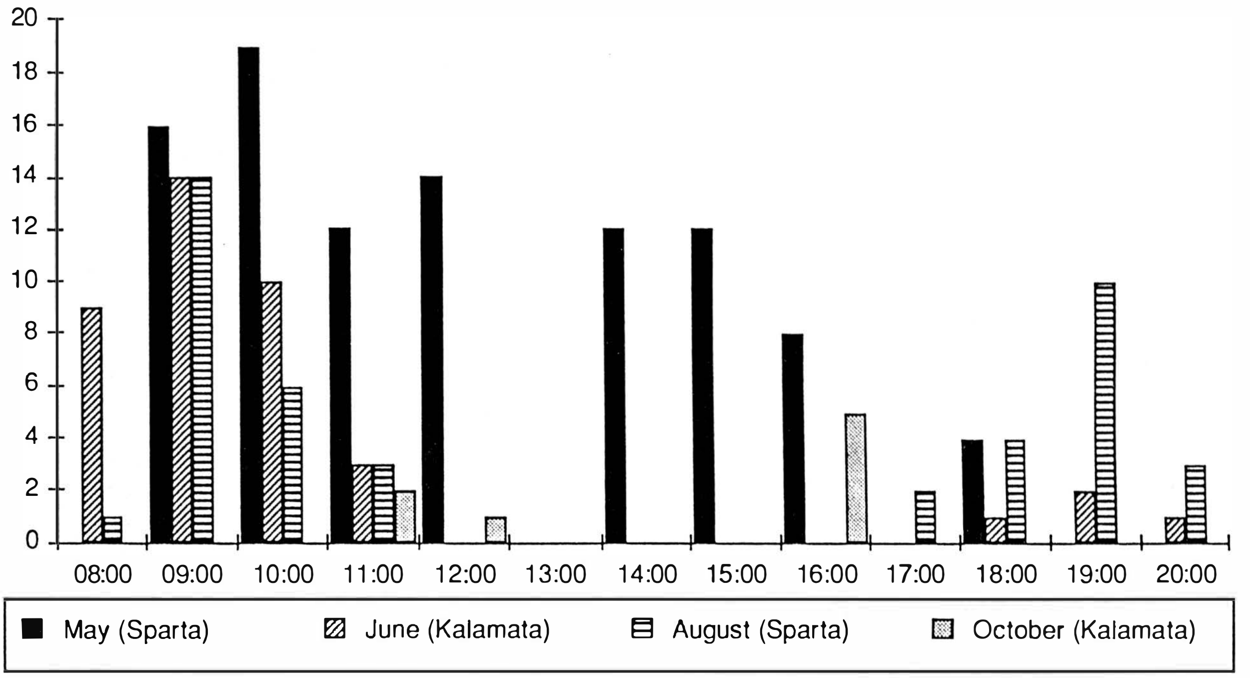

Fig. 1 Activity pattern of *T. hermanni* in the different months at the two sites. Each bar shows the number of tortoises found in 1-hour period. Times are East European summer time.

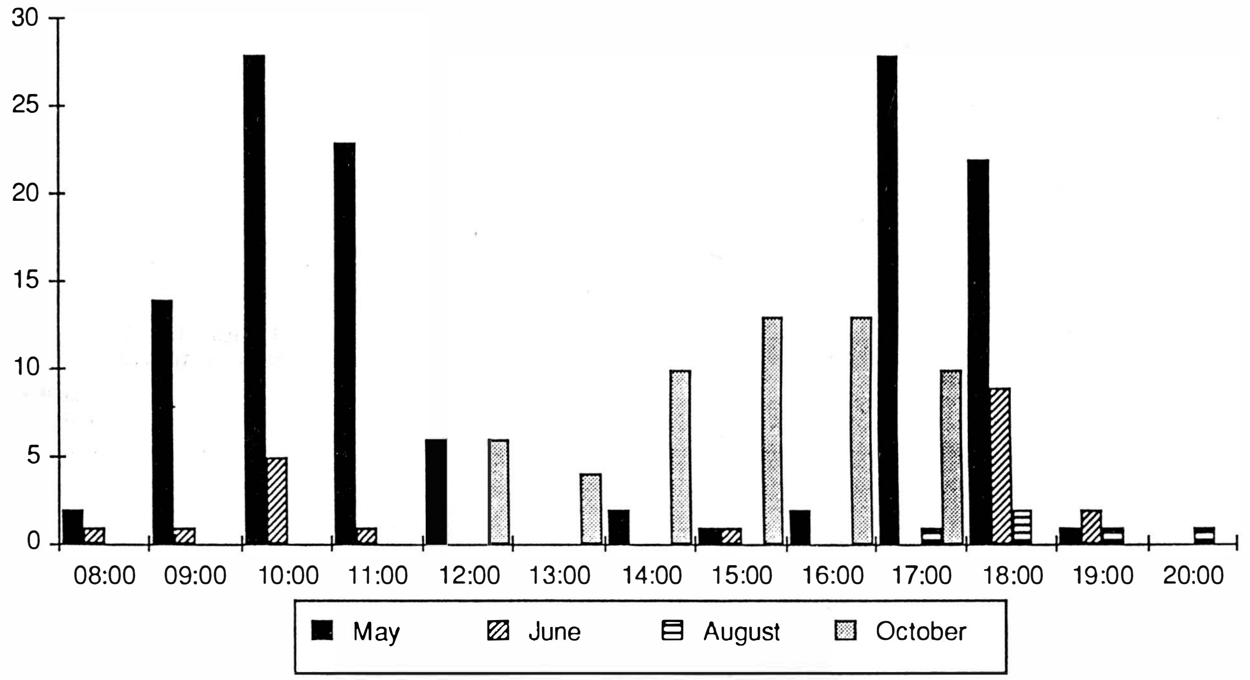

Fig. 2 Activity pattern of *T. marginata* in the different months. Each bar shows the number of tortoises found in 1-hour period. Times are East European summer time.

The first tortoises were seen at 8.56h and the last ones at 19.31h. The morning activity period was similarly important in both species; 63 per cent of *T. hermanni* and 57 per cent of *T. marginata* were found before 13.00h (X^2 = 1.00, p>0.01). However *T. marginata* were active longer in the evening. Only 4 per cent of *T. hermanni* were found after 17.00h compared to 39 per cent of *T. marginata* (X^2 = 37.70, p<0.0001).

Activities

Most tortoises of both species were seen in the morning; 86 per cent of basking *T. hermanni* and 83 per cent of basking *T. marginata* were seen before 13.00h. Basking accounted for a higher proportion of observations of *T. hermanni* (54 per cent) than *T. marginata* (23 per cent) (X^2 = 22.00, p<0.0001). The reverse was found for feeding tortoises which made up 21 per cent of the observations in *T. hermanni*

May	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000
	Time												
Basking	28.0-0 28-28 (1)	28.3-1.9 27-32 (8)	30.4-3.5 22-35 (11)	34.2-0.8 33-35 (5)						35.5-0.8 34-36 (4)	33.00-0.0 33-33 (1)		
Feeding		30.0-2.8 28-32 (2)	31.6-1.7 29-34 (7)	34.1-2.1 30-37 (9)	35.0-1.0 34-36 (3)				35.0-0.0 35-35 (1)	34.2-1.3 32-36 (20)	33.5-1.6 30-36 (18)	32.0-0.0 32-32 (1)	
Other	28.0-0.0 28-28 (1)	28.5-5.1 21-31 (4)	33.3-2.1 30-36 (10)	30.4-3.3 28-35 (9)	34.0-1.7 32-35 (3)		36.5-2.1 35-38 (2)	32.0-0.0 32-32 (1)	30.0-0.0 30-30 (1)	34.5-0.5 34-35 (4)	32.0-1.0 31-33 (3)		
June													
Basking	32.0-0.0 23-23 (1)		26.5-0.7 26-27 (2)								33.0-0.0 33-33 (1)		
Feeding			27.0-0.0 27-27 (1)								32.7-1.2 32-35 (6)	34.0-0.0 34-34 (1)	
Other		34.0-0.0 34-34 (1)	26.0-1.4 25-27 (2)	36.0-0.0 36-36				26.0-0.0 26-26 (1)			33.0-1.4 32-34 (2)	33.00-0.0 33-33 (1)	
August													
Basking												33.00-0.0 33-33 (1)	
Feeding											32.5-2.1 31-34 (2)		
Other										37.0-0.0 37-37 (1)			35-0-0.0 35-35 (1)
October													
Basking							33.5-0.7 33-34 (2)	33.0-0.0 33-33 (1)	30.5-2.1 29-32 (2)				
Feeding					31.0-0.0 31-31 (1)	32.5-0.7 32-33 (2)	33.3-1.0 32-34 (4)	33.5-1.6 32-37 (8)	31.1-1.2 29-33 (8)	29.3-0.6 29-30 (3)			
Other					32.2-1.3 31-34 (5)	32.5-2.1 31-34 (2)	34.0-1.8 32-36 (4)	32.3-1.5 30-33 (4)	31.0-2.0 29-33 (3)	30.0-1.2 28-31 (7)			

TABLE 2: Diurnal variation of body temperature in *T. marginata* in different months. All observations were made at Gytheion. Times are East European summer time. Data are shown as mean −1 S.D., range and sample size.

compared to 47 per cent of *T. marginata* ($X^2 = 17.20$, $p < 0.0001$).

Most (90 per cent) of the feeding *T. hermanni* were found after 13.00h compared to 65 per cent of feeding *T. marginata* ($X^2 = 4.46$, $p < 0.05$).

11 per cent of *T. hermanni* were found inactive, significantly more than the 2 per cent of *T. marginata* ($X^2 = 12.10$, $p < 0.001$). Six *T. hermanni* were involved in sexual activity; only one male *T. marginata* was found attempting to mate with a feeding female.

Thermoregulation

The mean in the body temperature of *T. hermanni* was lower than the temperature of *T. marginata* (Tables 3 and 4; $t = 8.46$, $p < 0.0001$). The body temperatures of *T. marginata* were also significantly higher when basking ($t = 3.88$, $p < 0.0001$), when moving ($t = 2.24$, $p < 0.025$) and when feeding ($t = 6.00$, $p < 0.0001$).

JUNE

The daily pattern of *T. hermanni* was bimodal, in the morning from 8.40h to 11.16h, in the afternoon from 18.58h to 19.52h. (Fig. 1 and Table 1). During the afternoon the activity was low, only 10 per cent of *T. hermanni* were found after 12.00h. The daily activity pattern of *T. marginata* was also bimodal between 8.40h and 11.09h and again between 15.30 and 19.52h (Fig. 2 and Table 2).

During the afternoon *T. marginata* were significantly more active than *T. hermanni* ($X^2 = 17.25$, $p < 0.001$).

Activities

In *T. hermanni* most tortoises were found basking (53 per cent) compared to only 20 per cent in *T. marginata* ($X^2 = 5.71$, $p < 0.05$).

There were no significant differences in the frequency of activities of each species compared to those in May.

Thermoregulation

The mean in the body temperature of *T. hermanni* was lower than the mean in the body temperature of *T. marginata* (Tables 3 and 4; $t = 3.02$, $p < 0.001$). Though the average June body temperature of *T. hermanni* was lower (1.1°C) than the May temperature, the difference was not significant ($t = 1.66$, $p < 0.05$).

	Basking	Moving	Feeding	Mating	Fighting	Stationary	Total
May	27.8-4.3 19-35 (52)	29.5-3.4 22-33 (8)	30.7-1.5 28-34 (20)	27.8-2.8 25-31 (6)		31.0-2.5 29-34 (11)	29.0-3.7 19-35 (97)
June	25.8-3.4 20-31 (21)	30.0-2.2 27-33 (6)	30.8-2.8 25-34 (9)	29.5-3.1 25-32 (4)			27.9-3.1 20-34 (40)
August	26.2-2.9 21-31 (14)	33.0-0.0 33-33 (1)	31.4-1.0 30-32 (4)	30.1-3.4 21-33 (20)	23.0-1.4 22-24 (2)	31.5-0.7 31-32 (2)	28.7-3.6 21-33 (43)
October	26.3-5.5 20-30 (3)	31.0-0.0 31-31 (1)	30.5-0.7 30-31 (2)		32.0-0.0 32-32 (2)		29.4-3.9 20-32 (8)

TABLE 3: Variation of body temperature of *T. hermanni* with activity type in every month. Data are shown as mean, S.D., range and sample size.

	Basking	Moving	Feeding	Mating	Stationary	Total
May	31.3-3.2 22-36 (30)	32.0-2.7 21-38 (34)	33.5-1.9 28-37 (61)	30.0-0.0 30-30 (1)	32.7-4.0 28-35 (3)	32.6-2.7 21-28 (129)
June	27.3-4.3 23-33 (4)	32.2-3.8 26-36 (5)	32.3-2.5 27-35 (8)		28.7-4.7 25-34 (3)	30.7-3.9 23-36 (20)
August	33.00-0.0 33-33 (1)	36.0-1.4 35-37 (2)	32.5-2.1 31-34 (2)			34.0-2.1 31-37 (5)
October	32.2-1.9 29.34 (5)	32.0-1.6 29-35 (15)	32.1-1.9 29-37 (26)	30.9-1.8 28-33 (9)	36.0-0.0 36-36 (1)	31.9-1.9 28-37 (56)

TABLE 4: Variation of body temperature of *T. marginata* with activity type in every month. Data are shown as mean, S. D., range and sample size.

In *T. marginata* however, the mean in the June body temperature was significantly lower than the May body temperature ($t = 2.74$, $p < 0.005$).

Basking tortoises of both species showed significantly lower body temperatures in June (*T. hermanni*: $t = 1.90$, $p < 0.05$; *T. marginata*: $t = 2.27$, $p < 0.025$).

In *T. hermanni* the maximum body temperature found in basking tortoises was 4°C lower than in May, in *T. marginata* 3°C lower than in May (Tables 3 and 4).

In June the body temperature of basking, feeding and moving *T. hermanni* was not significantly different from that one found in *T. marginata* ($t = 0.78$, $p < 0.01$; $t = 1.16$, $p > 0.05$; $t = 1.20$ $p > 0.05$).

AUGUST

The activity of *T. hermanni* was bimodal. In the morning tortoises were found from 8.23h to 11.23h, in the afternoon from 17.32h to 20.07h (Fig. 1 and Table 1).

The activity of *T. marginata* was unimodal and low, only five tortoises were found after 17.00h (Fig. 2 and Table 2). During the afternoon *T. hermanni* were significantly more active than registered in June (44 per cent against 10 per cent; $X^2 = 12.14$, $p < 0.001$).

ACTIVITIES

In August the frequency of basking *T. hermanni* was significantly lower than in May (33 per cent against 54 per cent; $X^2 = 5.32$, $p < 0.025$). Although the frequency of basking *T. hermanni* was almost the same in May and in June (43 and 53 per cent), there was not a significant difference in the frequency of basking *T. hermanni* in June and August ($X^2 = 3.33$, $p > 0.05$). Probably the number of the animals in the samples was too small. In May and August no significant differences were found in the frequency of feeding *T. hermanni* ($X^2 = 2.73$, $p > 0.05$). In August 47 per cent of *T. hermanni* were found in a sexual act, this was significantly more than in June ($X^2 = 31.52$, $p < 0.0001$; $X^2 = 13.56$, $p < 0.001$).

THERMOREGULATION

In May, June and August no significant differences were found in the means of the body temperatures of *T. hermanni* ($T = 0.45$, $p < 0.25$; $t = 1.08$, $p > 0.10$; Table 3). Although the basking *T. hermanni* the maximal body temperature was 4°C lower than in May, there was no significant difference from the mean of May ($t = 1.31$, $p > 0.05$; Table 3). No significant differences in the means of the body temperatures of the other activities were found between *T. hermanni* samples in May, June and August either though no body temperatures over 33°C were found.

In August the mean of the body temperatures of *T. marginata* was significantly higher than the one in June but not significantly higher than in May ($t = 1.81$, $p < 0.05$; $t = 1.15$, $p > 0.010$). The mean of the body temperatures in *T. hermanni* was significantly lower than in *T. marginata* ($t = 3.21$, $p > 0.025$).

OCTOBER

In October the activity of *T. hermanni* was low in southern Greece. Near Sparta only three tortoises were found in two days. The activity was little higher near Kalamata; eight tortoises were found in two days. Tortoises were found from 11.39h to 12.39h and from 16.28h to 16.43h (Fig. 1 and Table 1). The number of animals in the samples was too small to be sure whether the activity pattern was still unimodal or not. The activity of *T. marginata* was high and unimodal. Tortoises were found from 12.30h to 17.32h (Fig. 2 and Table 2).

Activities

The frequency of basking *T. marginata* was 9 per cent, significantly lower than in May; there was no significant difference from June ($X^2 = 5.23$, $p < 0.025$; $X^2 = 1.60$, $p > 0.10$). Except for two fighting males, no sexual activity was seen in *T. hermanni*; in *T. marginata* a high sexual activity was seen (17 per cent; Table 4). In samples from May, June and October almost no differences were found in the frequency of moving *T. marginata* (26, 20 and 27 per cent). The frequency of feeding in *T. marginata* was almost the same as in May: 47 per cent; June 40 per cent and October: 46 per cent).

Thermoregulation

In the means of the body temperatures of *T. hermanni* no significant differences were found in October compared to the samples of May, June and August (May: $t = 0.29$, $p > 0.40$; June: $t = 1.20$, $p > 0.10$; August: $t = 0.50$, $p > 0.025$). The mean of the body temperature in *T. marginata* was significantly lower in October than in May and August ($t = 1.76$, $p < 0.05$; $t = 2.35$, $p < 0.025$) but was significantly higher in June ($t = 1.80$, $p < 0.05$). Although the mean of the body temperature in basking *T. marginata* was higher in May, this difference was not significant ($t = 0.61$, $p < 0.25$) but in October the body temperatures in *T. marginata* were not significantly higher than in June ($t = 2.36$, $p < 0.05$). No differences were found in the body temperature of moving *T. marginata* in the samples of May, June and October (May: 32.0°C; June: 32.2°C and October: 32.0°C). In feeding *T. marginata* the body temperatures were significantly lower than in May ($t = 3.15$, $p < 0.001$), but not significant from June to October ($t = 0.24$, $p > 0.40$). In feeding *T. marginata* the maximum body temperature (37°C) was as high as in May and higher than in June and August. In basking *T. marginata* the maximum body temperature was 34°C and also lower than in May. In October the mean in the body temperature of *T. hermanni* was significant lower than in *T. marginata* ($t = 2.98$, $p < 0.0025$) as well in all other samples.

DISCUSSION

Activity

The activity patterns found during this study are similar to those found in other Greek *T. hermanni* populations. A trend for unimodal activity pattern in spring to a bimodal activity pattern in summer was found between 1975 and 1986 in a great number of Greek *T. hermanni* populations. When an unimodal activity pattern changed into a bimodal one, the activity during the afternoon was always low, exactly as in the pattern found near Kalamata in June. Later in summer the activity was clearly bimodal, sometimes higher in the morning, something in the evening. In autumn the activity was again unimodal but the period of activity was shorter than in spring; daily activity started late and ended early. In southern Yugoslavia the activity of *T. hermanni* was unimodal throughout the year (Meek and Inskeep, 1981; Meek, 1988). In France the daily activity pattern was unimodal, the activity strongly decreased during the hot hours in summer (Cheylan, 1981). In summer in northern Greece the daily activity pattern of *T. hermanni* was bimodal (Stubbs *et al.*, 1981; Wright *et al.*, 1988). In the early dry and hot year 1985 the activity pattern of *T. hermanni* was unimodal already in May (Willemsen unpublished).

During relatively cool, cloudy days in summer the activity pattern of *T. hermanni* can again be unimodal, also in an environment with much shade *T. hermanni* were found still active during the hot hours in summer. It seems the daily activity pattern of *T. hermanni* is determined by air temperature and probably by the intensity of the sun. In the cooler part of its distribution area the activity pattern remains unimodal, in the hotter part the activity is limited to the cooler hours of the day.

The activity of *T. hermanni* is the highest in spring and decreases during summer (Hailey, 1988). This trend was found in all Greek populations although in spring the activity was probably equal, after spring the activity can differ much in the different populations and also from year to year. The activity pattern of *T. hermanni* in a great number of populations over several years will be described in another paper.

The daily activity pattern of *T. marginata* was similar to that of *T. hermanni*, unimodal in spring although in this study the pattern had already become bimodal in May; in April 1983 the activity pattern still was unimodal. After spring the activity pattern became bimodal and was unimodal again in autumn, shifting towards the middle of the day.

However, there were also some differences in the activity pattern of *T. marginata*. Though *T. hermanni* is something almost totally inactive during summer, in general *T. hermanni* can still be found in fair numbers in southern Greece during summer. The low activity in *T. marginata* in August 1984 was not exceptional. Stemmler (1957) could not find any *T. marginata* in summer during his stay in southern Greece but he did find a large number of *T. hermanni* at different sites. Near the border of the distribution area of *T. marginata* in northern Greece, he found several

T. marginata together with *T. hermanni*. Probably *T. marginata* will aestivate more than *T. hermanni*.

Much research on tortoises have been done during the summer months in Greece by many investigators. All authors describe *T. marginata* as a tortoise seldom to be found. Without any doubt all *T. marginata* populations are less dense than the average *T. hermanni* population but the very low densities which have been found in *T. marginata* populations might be caused by sampling at the wrong time.

The high activity in October is not exceptional: Clark (1963) found a high activity in *T. marginata* during autumn but he gives no exact data. Local people found *T. marginata* still active during autumn and even during early winter while *T. hermanni* were only seen during summer. Although *T. hermanni* can again become active on sunny days in winter (Swingland and Stubbs. 1985) it is unlikely that *T. hermanni* would be active in large numbers in southern Greece after the visits in October.

Importance of Activity Patterns

The daily and seasonal activity patterns of tortoises have more than theoretical value, for the number of active tortoises can be used for density calculations (Hailey, 1988). Density calculations are important for conservation purposes, however, without sufficient knowledge on activity patterns errors in these calculations can be disastrous. At this moment only the high activity in spring of *T. hermanni* up to the middle of May, in probably all Greek populations, is a certain fact. Much more detailed knowledge is needed to be sure about the activity pattern after spring. In southern Greece the activity of *T. marginata* is high and probably also takes place in late autumn, but nothing is known about differences between different populations and differences in different years.

Differences in Activities

Differences in basking, moving and inactive *T. hermanni* and *T. marginata* can be easily explained by differences in vegetation of the site near Gytheion. Near Gytheion, except for the animals found in the heath, all tortoises were found on the open patches, for the macchie was inaccessible. This may cause an undersampling of basking and stationary tortoises, and possible an oversampling of feeding tortoises.

The trend of the decreasing number of basking *T. hermanni* in summer was also found by Meek (1988). The relatively large number of basking *T. hermanni* in June could be due to the kind of vegetation as this site had much more shade than Sparta.

In this study no differences in frequency of feeding *T. hermanni* and *T. marginata* were found between the different visits. Meek (1988) found an increasing frequency of feeding *T. hermanni* in summer, but in the present study this was not found.

In France *T. hermanni* was sexually active during its entire active period, but the highest activity was found in April and August (Swingland and Stubbs, 1985). They found the same trend in Greece, but the sexual activity in spring was lower than in France. The results found in 1984 near Kalamata and Sparta match those found in France and in Greece. Meek did not find sexual activity in *T. hermanni* in autumn, but in Greece sexual activity was seen in October (Willemsen), so there could be some differences in behaviour between Greek and Yugoslavian *T. hermanni* populations. Except for one male no sexual activity was seen in *T. marginata* before autumn 1984. Clark (1963) gives a high sexual activity in *T. marginata* in autumn. In Greek *T. marginata* populations no sexual activity was seen after April and before October (Willemsen), so it is likely that the sexual cycle of *T. marginata* differs from that of *T. hermanni*.

Body Temperatures

No significant differences in body temperature of *T. hermanni* were found during four months of research, though it is possible that differences would be significant in larger samples. Cherchi (1956) gives 32°C as maximum body temperature for normal activities and 34°C as maximum voluntary body temperature. In the field basking *T. hermanni* accept body temperatures to 35°C and feeding tortoises to 34°C (Meek, 1988). The body temperature of basking and feeding tortoises is of special interest, for these activities are completely voluntary. Basking tortoises are mostly found close to cover, so that in case of overheating they can go directly into cover. Feeding tortoises are mostly found on open patches, often rather far from the nearest cover, so they have to watch their body temperatures more closely than the basking tortoises. Activity such as moving, mating and especially nesting can not be stopped at once, so in these tortoises the body temperature can easily exceed the maximum voluntary value and sometimes even the critical value.

Near Meteora every year in June, in the nesting season, several mostly old females were found dead on the open patches, which were used as nesting sites. Overheating could be possible cause of death. In moving and stationary tortoises often rather low and rather high temperatures were found, because many of these animals were either at the beginning of their activities and still had a low body temperature, or were at the end of their activities and often had a body temperature over the maximum normal body temperature.

In all studies about thermoregulation of *T. hermanni* the maximum voluntary body temperature remains under 35°C in active tortoises, but the limit which Cherchi gives (32°C) is too low. In the field 34°C is the maximum body temperature for normal activities. Although the mean in SCL in *T. hermanni* populations in Greece and Yugoslavia differs widely (Willemsen and Hailey, 1989), no difference in body temperature tolerance was found in larger and smaller tortoises with a SCL over 10cm (Willemsen).

In June and August there was a trend towards lower body temperatures. Meek (1982, 1988) also found this trend. After May no body temperatures over 31°C were found in basking tortoises. In August the maximum body temperature in feeding *T. hermanni* was 32°C, but in June it was still the same as in May. This relatively high body temperature was probably caused by environmental differences of the site near

Kalamata. It seems *T. hermanni* keep their body temperatures lower in summer than in spring, thus keeping on the safe side in summer. The sample of October was too small to say much about the body temperatures during that month.

In all samples the body temperatures of *T. marginata* was significantly higher than in *T. hermanni*. In basking and in feeding *T. marginata* maximum body temperatures of 36°C and 37°C were found. In contrast to *T. hermanni* the body temperatures of *T. marginata* in feeding tortoises were higher than in basking animals. It is possible that tortoises with a maximum body temperature after basking never left the macchie and so were never found. In *T. marginata* the body temperatures had decreased significantly in June, and the trend towards lower body temperatures was stronger than in *T. hermanni*. Although the mean in the body temperature in *T. marginata* was still higher than in *T. hermanni* in June, the differences in body temperatures of different activities were no longer significantly different. The habitat near Gytheion is much hotter in summer than the relatively cool habitat of Kalamata and also that of Sparta, so in summer *T. marginata* maintains a lower body temperature, to be on the safe side. In August only five *T. marginata* were found during a six day visit, so the activity of *T. marginata* was very low. All tortoises were found during the afternoon. Except in moving tortoises no body temperatures over 34°C were found, so the maximum voluntary body temperature is probably lower than in May.

The unimodal activity during the evening could be explained by the high risk of overheating during the morning hours, when air temperature and heliothermic energy were increasing fast. However, at other cooler sites in southern Greece *T. marginata* was seen in the morning in August, so the unimodal evening activity could be characteristic for the hotter habitats in southern Greece during summer. In October the body temperatures of *T. marginata* were higher than in June but lower than in May and in August. It is possible that if the number of animals in the sample in August had been larger the results would have been the reverse. In October the same maximum body temperature in feeding *T. marginata* were found as in May. The unimodal activity pattern of *T. marginata* found in the middle of the day and the significant lower body temperatures in feeding animals as compared to those in May may indicate that in October overheating was unlikely, so the tortoises could safely use the hottest hours of the day. However, under these circumstances *T. marginata* is still able to reach the same maximum body temperature in feeding tortoises. Pigmentation and shape of *T. marginata* will make it easier to absorb heat, compared to *T. hermanni* of equal size.

The relatively low body temperatures found in *T. hermanni* in October (no body temperature was over 32°C) were possibly caused by the kind of habitat of Kalamata; but we must not rule out the possibility that *T. hermanni* will not be able, under the circumstances of October, to reach the same maximum body temperatures as in May.

In all samples the maximum body temperatures in *T. marginata* were significantly higher than in *T. hermanni*. The maximum voluntary body temperatues of *T. hermanni* tallied with the values which were found in a number of other studies, so the values found in this study can be considered representative of the species *T. hermanni*.

In feeding *T. marginata* the body temperatures were 3°C higher than in *T. hermanni*. In dry and hot habitats this will give an ecological advantage over *T. hermanni*. This partly explains the habitat separation between these two species, but some difficulties remain. If *T. marginata* heats up faster than *T. hermanni*, as suggested by the body temperatures found in October, the ecological advantage of a higher body temperature tolerance in *T. marginata* would be reduced. In this study no lower temperatures than 25°C in feeding *T. hermanni* and no lower than 28°C in feeding *T. marginata* were found.

Cherchi (1956) gives 16°C as the minimum body temperature for normal activity in *T. hermanni*. In spring, especially in northern Greece, the climate is rather cool and wet with a lower heating rate of the sun than in southern Greece. Under these circumstances a lower body temperature minimum in *T. hermanni* could give an ecological advantage over *T. marginata*. In early April 1982 during a period of cool weather only *T. hermanni* were found near Litochoron. On this site *T. marginata* lives sympatrically in low density with *T. hermanni* (Willemsen and Hailey, 1989). In northern Greece the soil vegetation dies in early summer and does not regenerate in autumn, at least not under circumstances which make activities of tortoises still possible, so *T. marginata* will miss its autumnal activity there; sexual activity in autumn could be an indication of importance of an autumnal activity of this species. Thus the climatical circumstances in spring and in autumn could make northern Greece unsuitable for *T. marginata*.

The fact that *T. hermanni* is still active with a lower body temperature could make *T. hermanni* able to complete with *T. marginata* in those kinds of habitats, namely on the border of the distribution area of *T. marginata*, where in southern Greece *T. marginata* has replaced *T. hermanni* completely. In fact *T. hermanni* is found only in relatively wet and cool habitats in southern Greece, often sympatric with a sparse *T. marginata* population, and the reverse is found in dry and hot habitats (Willemsen and Hailey, 1989). This is an indication that the higher body temperature tolerance of *T. marginata* supplies an ecological advantage in those habitats, in spite of a probably faster heating rate. It also seems that aestivation is more common in *T. marginata* than in *T. hermanni* in southern Greece, so if the physiological ability of *T. marginata* to escape the difficult hot summer months by aestivation is greater than in *T. hermanni*, then this will also give *T. marginata* an ecological advantage in hot habitats. Also morphological differences could make *T. marginata* less suitable for habitats in which *T. marginata* lives in southern Greece.

ACKNOWLEDGEMENTS

I thank Dr. Adrian Hailey for his help with the manuscript. I am grateful to Ir. E. W. Tilanus for his computer graphs and to Hanneke Grooters for correcting the text of the manuscript.

REFERENCES

Cherchi, M. A. (1956). Termoregolazione in *Testudo hermanni. Boll. Mus. Inst.* Univ. Genova. **26**, 5-46.

Cheylan, M. (1981). Biologie et Ecologie de la Tortue D'HERMANN, *Testudo hermanni*, GMELIN, 1789. *Mémoires et Traveaux de l'Institut de Montepellier*, No. 13.

Clark, R. J. (1963). On the possibility of an autumnal mating in the tortoise (*Testudo graeca ibera*) *Brit. J. of Herpetology* **3**, 85-86.

Clark, R. J. (1967). Herpetofauna of the islands of the Agro-Saronic Gulf, Greece. *Proceedings of the California Academy of Sciences*. Vol. XXXV, No. 2, 23-36.

Hailey, A. (1988). Length of routine movements in a tortoise. In press.

Hailey, A. (1988). Population ecology and conservation of tortoises: the estimation of density and dynamics of a small population. *Herpetological Journal*, 263-271.

Hailey, A., Wright, J. and Steer, A. (1988). Population ecology and conservation of tortoises: the effects of disturbance. *Herpetological Journal*, 294-301.

Hardin, G. (1960). The competitve exclusion principle. *Science* **131**, 1292-1298.

Lambert, M. R. K. (1981). Temperature, activity and field sighting in the Mediterranean spur-thighed or common garden tortoise *Testudo graeca L. Biol. Cons.* **21**, 39-54.

Meek, R. (1984). Thermoregulatory behaviour in a population of Hermann's tortoise (*Testudo hermanni*) in southern Yugoslavia. *Brit. J. of Herpetology* **6**, 437-445.

Meek, R. (1988). The thermal ecology of Hermann's tortoise (*Testudo hermanni*) in summer and autumn in Yugoslavia. *J. Zool Lond.* **214**.

Meek, R. and Inskeep, R. (1981). Aspects of field biology of a population of Hermann's tortoise (*Testudo hermanni*) in southern Yugoslavia. *Brit. J. of Herpetology* **6**, 159-164.

Stemmler, O. (1957). Schildkröten Griechenlands *Vivaristik* **3**, 159-164.

Stubbs, D., Hailey, A., Tyler, W. and Pulford, E. (1981). *Expedition to Greece* 1980. University of London Natural Society.

Stubbs, D. and Swingland, I. R. (1985). The ecology of a Mediterranean tortoise (*Testudo hermanni*): a declining population.

Thornton, I. (1972). *Darwin's Islands*. A Natural History of the Galapagos. History press Garden City, New York.

Watson, G. E. (1962). Notes on copulation and distribution of Aegean land tortoises. *Copeia* **1962**, 317-321.

Wermuth, H. (1952). *Testudo hermanni robertmertensi* n.subsp. und ihr Vorkommen im Spanien. *Senckenbergiana*, Band 33, Nummer 1/3, Seite 157-164.

Werner, F. (1938). Die Amphibien un Reptilien Griechenlands. *Zoologica* **94**, 1-117.

Willemsen, R. E. and Hailey, A. (1989). Status and conservation of tortoises in Greece. *Herpetological Journal*, 315-330.

Wright, J., Steer, E. and Hailey, A. (1988). Habitat separation in tortoises, and the consequences for activity and thermoregulation. *Can. J. of Zool.*, **66**, 1537-1544.