POPULATION ECOLOGY AND CONSERVATION OF TORTOISES: THE EFFECTS OF DISTURBANCE

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(Accepted 3.12.87)

ABSTRACT

Population characteristics of sympatric *Testudo hermanni* and *T. graeca* were compared at four sites in northern Greece; Alyki, Epanomi, Keramoti and Lagos. These had different habitats and levels of human disturbance. The density of tortoises larger than 10cm was similar at all sites, in the range 7-21ha^{-1}. Population size structures were more variable. The ratio of juveniles to adult females ranged from about 0.1 at the most disturbed site (Lagos) to about 4 in a protected area (Epanomi). This ratio was similar for the two species at any site, even though they occupied different habitats. The main feature of disturbance was thought to be predation of eggs and juveniles by human commensals (rats and domestic animals) rather than habitat degradation.

The sample sex ratio of *T. hermanni* was male-biased at all four sites, with an average of 3.1 males per female. Males had more tick parasites than females, higher body temperatures, and were recaptured twice as frequently. There was an even sex ratio in *T. graeca*, the sexes had similar numbers of ticks and body temperatures, and females were recaptured more frequently. The population sex ratio of *T. hermanni* is known to be male-biased at Alyki. The data on ticks, body temperatures, and recapture frequencies show that sample sex ratios are complicated by sexual differences of activity or microhabitat use. It is suggested that male *T. hermanni* used more open areas than females, within the wood, scrub or heath occupied by this species. *T. graeca* occupied coastal heath at all sites, an open habitat with little spatial variation of cover.

INTRODUCTION

Although tortoises may be found in many habitats in the Mediterranean region, most populations survive at low density. High population densities are often found, however, in coastal areas where farming is unproductive, and which have therefore remained undisturbed. These areas are now under threat from development for tourism (Honegger, 1981). This paper describes the tortoise populations at four coastal sites in north-eastern Greece, which were examined during a study of the habitat separation of *T. hermanni* and *T. graeca* (Wright, Steer and Hailey, submitted). The main reason for the choice of sites was the presence of both tortoise species and a range of habitat types. However, the sites also suffered from different degrees of disturbance, and so made possible a comparative study of the effect of disturbance on tortoise populations.

METHODS

SAMPLING METHODS

Tortoises were studied at the four sites Alyki, Epanomi, Keramoti and Lagos (Fig. 1) in July and August 1985. A large-scale vegetation map of each site was made using landmarks and a measuring line. Five observers were used for 7-10 days at each site, in addition to the vegetation survey. They sampled the area along straight transects so that the whole area was covered roughly uniformly. Distances of sightings perpendicular to the transect were used to calculate population density (Hailey, 1988). Tortoises were handled and individually marked by notching marginal scutes as described by Stubbs, Hailey, Pulford and Tyler (1984), and an independent estimate of population density was obtained using the Jolly mark-recapture method (Begon, 1979). Body temperatures of animals larger than about 10cm were measured rectally with a mercury thermometer.

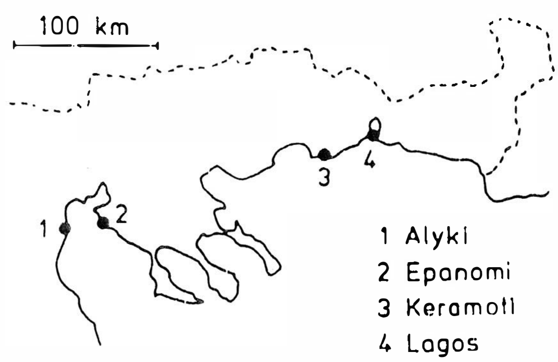

Fig. 1 Location of the four sites in north-eastern Greece.

Tortoises of less than 10cm (*T. hermanni*) or 12cm (*T. graeca*) straight carapace length (SCL) could not be sexed by external characters, and are termed juveniles. The SCL at maturity is considered to be 14cm in males (both species) and 15cm (*T. hermanni*) or 16cm (*T. graeca*) in females; tortoises of intermediate size are termed subadults. The number of tick parasities on exposed areas of skin was counted. This excluded any ticks hidden behind the legs or on the neck, as these parts could not be exposed easily.

Site Descriptions

Brief descriptions of the sites are given below. Maps and details of the vegetation types are given by Stubbs, Swingland, Hailey and Pulford (1985) for Alyki, and by Wright *et al.* (submitted) for Epanomi, Keramoti and Lagos.

Alyki

A strip of heathland separating a shallow lagoon and salt works from the sea. The results reported here were from sector 13, the southern heath; this sector has not been described in previous papers on Alyki, and so a map is provided in Fig. 2. This sector was badly damaged by fire and plough in 1980 (Stubbs, Hailey, Tyler and Pulford, 1981) but the vegetation had largely regenerated by 1985, except for the large shrubs.

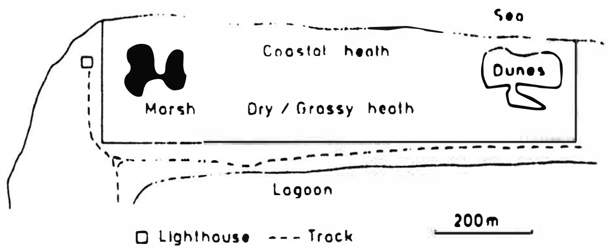

Fig. 2 A map of Alyki sector 13, the southern heath.

Epanomi

A headland of dunes and coastal heath around a lagoon. The study area was next to a holiday village and a large camping ground, 10km south-west of Epanomi town. Three areas were defined (Wright *et al.*, submitted), but few tortoises were found in area 3, which is not considered in this paper:

1. A rectangle of heath vegetation structurally intermediate between dry heath and coastal heath.

2. An area of coastal heath on loose sand and dunes.

Keramoti

The main site was along the coast east from the small town and port; two areas were defined:

1. A strip of dunes and coastal heath behind the beach.

2. A large area with belts of broadleaf woodland in open grazed grassland on sandy soil. The woodland had thick ground vegetation and shrub layers.

Another site (Area 3) is also considered in this paper. This was a small island west of the town, reached by a small bridge, and included coastal heath, scrub and mixed woodland. This was studied as an example of a small tortoise population living at high density in a small well-defined area.

Lagos

The site was on a spit of land between the sea and lake Vistonia, west of the town and port of Lagos. Three areas were defined (Wright *et al.*, submitted) but area 3 is not considered in this paper as few tortoises were found there.

1. A plantation of shore pine with scrub along its coastal and roadside edges. There was little ground vegetation. This area was frequently used for camping and picnics.

2. An area of coastal heath next to the pine wood, including some grazed grassland and a line of dunes along the sea.

Method of Analysis

The method for the estimation of population density (Hailey, 1988) was developed to take account of the low activity of tortoises, by calibrating a standard transect sampling method in areas of known population density. This enabled the proportion of the population which are available for finding (PAF) at the time of sampling to be calculated. At times of peak daily activity in summer, PAF was calculated to be 0.15 and 0.10 in male and female *T. hermanni* of SCL 10cm or more, respectively. This value was based on surveys of three populations of *T. hermanni* in 1981-1983.

The activity of tortoises in Greece during the summer of 1985 was low compared to other years, probably because this was an unusually dry year (M. Lazaridou-Dimitriadis and R. E. Willemsen, pers. comm.). A calibration was made in July and August 1985 in a population of known density (Alyki main heath), simultaneously with the surveys of the other sites. The results of 256 sightings of *T. hermanni* enabled calculation of PAF as:

Morning: males, 0.040 females, 0.047
Evening: males, 0.048 females, 0.024

There was thus less difference between the sexes in 1985, as well as lower activity generally, than in 1981-1983. In this paper sightings of males and females were pooled, and sighting frequency was averaged over morning and evening activity periods. This gave a single density estimate for all individuals larger than 10cm, using the average value PAF = 0.04. In the absence of specific data, this value was also used for *T. graeca*.

Statistical tests follow Sokal and Rohlf (1981); results in tables are shown as NS = $P>0.05$, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$.

RESULTS

Population Density

Sighting frequency, effective transect width and the calculated population densities of tortoises larger than 10cm are shown in Table 1, together with estimates from mark-recapture. It was not possible to use the transect method in the strips of dense woodland of Keramoti area 2. Recapture frequencies were too low to give accurate estimates from mark-recapture, as shown by the large standard errors. Indeed, the population sizes estimated by mark-recapture were lower than the number of individuals marked in six of

Site/area		(ha)	Species	W (m)	N	F ($No.h^{-1}$)	Density ($No.ha^{-1}$)	Individuals marked	Jolly No. (and S.E.)
Alyki	13	12	*T.h.*	4.4	201	2.0	19	162	260 (235)
Epanomi	1	18	*T.h.*	4.8	36	1.2	10	32	15 (12)
	1	18	*T.g.*	6.5	63	2.6	16	61	53 (50)
	2*	10	*T.g.*	4.9	29	1.5	19	28	0 (0)
Keramoti	1	19	*T.g.*	8.1	68	1.8	9	44	16 (15)
	3	4	*T.g.*	4.8	43	2.4	21	30	14 (6)
Lagos	1	6	*T.h.*	4.1	78	1.0	10	63	39 (33)
	2	6	*T.g.*	7.3	93	1.3	7	67	84 (74)

TABLE 1: Sighting characteristics and density estimates for *T. hermanni* and *T. graeca* larger than 10cm. The effective transect width W (based on N sightings) and mean sighting frequency (F) at peak activity times are defined by Hailey (1988); density is calculated using equation (2) in that paper, using PAF = 0.04. The number of individuals marked, and the Jolly mark-recapture estimate (with S.E.) is also shown. * Walking speed $2km.h^{-1}$, otherwise $3km.h^{-1}$.

the eight populations. In the other two populations, the estimated population size was equivalent to a density similar to that calculated from transect sampling (Table 1). The inadequacy of short-term mark-recapture studies for estimating tortoise population density has been noted previously (Hailey, 1988), and will not be discussed further.

Population Structure

This paper uses the sample structure of individuals (that is, excluding recaptures) as an estimate of the population strucuture. It should be noted that this underestimates the proportion of smaller tortoises, which are harder to find (see sighting profiles in Hailey, 1988). The bias against small animals decreases as the sample approaches a complete census. Sample structure provides a useful comparison between sites which are sampled at a similar intensity, as shown by the ratio of sightings to individuals marked (Table 2).

Only five *T. graeca* were found at Alyki during the survey of sector 13 in 1985. We therefore include data on population structure collected over the whole Alyki area between 1980 and 1986, using the size of each tortoise when last captured. The number of individual juveniles and adult males and females marked at each site is shown in Table 3a.

Sex ratio

The sex ratio is described as the number of adult males per adult female. This ratio differed significantly from 1:1 in *T. hermanni* at all four sites, with a mean of 3.1 males per female (Table 3b). There was also significant variation of the sex ratio between sites. In contrast the overall ratio was 1.1 males per female in *T. graeca*, not significantly different from 1:1, and there were no significant differences between sites.

Size structure

The size frequency distributions of individuals are shown in Figs. 3 (*T. hermanni*) and 4 (*T. graeca*). Juveniles have been divided evenly between the sexes. There were large differences in size structure between the four sites, with many small individuals at Epanomi, and few at Lagos. The trend was similar for both species.

We use the ratio of juveniles: adult females as a summary statistic of the size structure of tortoise

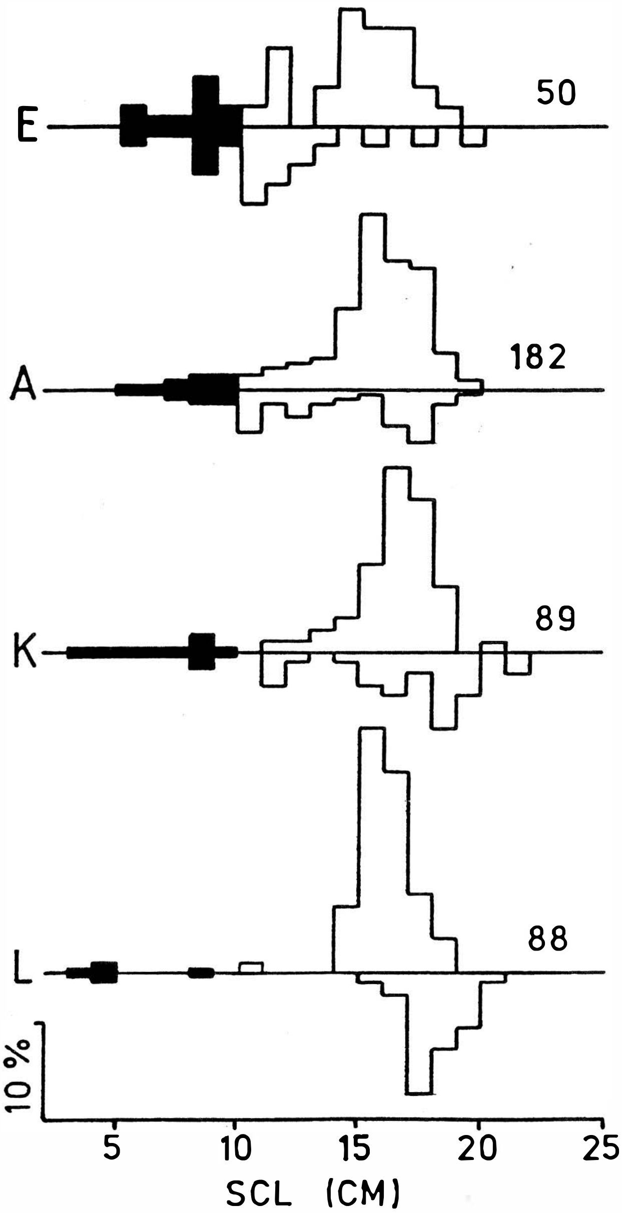

Fig. 3 Size frequency histograms of *T. hermanni* at Epanomi (E), Alyki (A), Keramoti (K) and Lagos (L), excluding recaptures. Males are shown above the line, females below; juveniles less than 10cm are divided evenly between the two sides of the histogram (shaded). Percentages are of the total number of individuals, which is also shown.

Site	Recaptures	All adults Individuals	Ratio	Recaptures	Adult male *T. hermanni* Individuals	Ratio
Alyki	32	126	0.25	28	104	0.27
Epanomi	14	53	0.26	6	19	0.32
Keramoti	47	144	0.33	17	49	0.35
Lagos	46	173	0.27	18	56	0.32
G test		1.15 NS			0.58 NS	

TABLE 2: The ratio of recaptures to individuals marked of all adult tortoises, and of adult male *T. hermanni*, to show that sampling intensity was similar at the four sites.

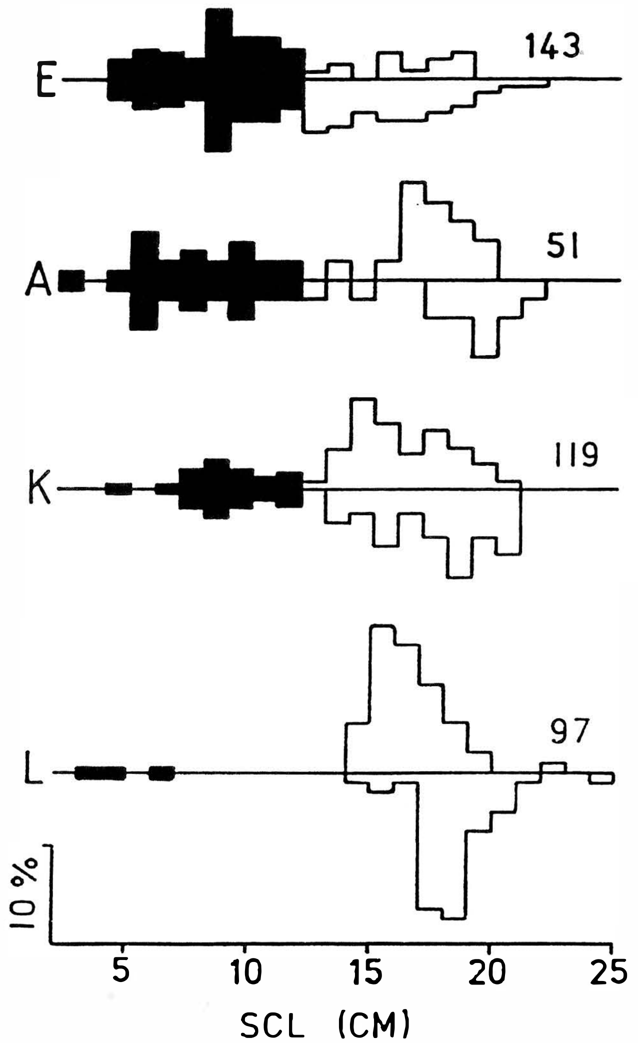

Fig. 4 Size frequency histograms of *T. graeca*. Explanation as in Fig. 3, except that juveniles are less than 12cm.

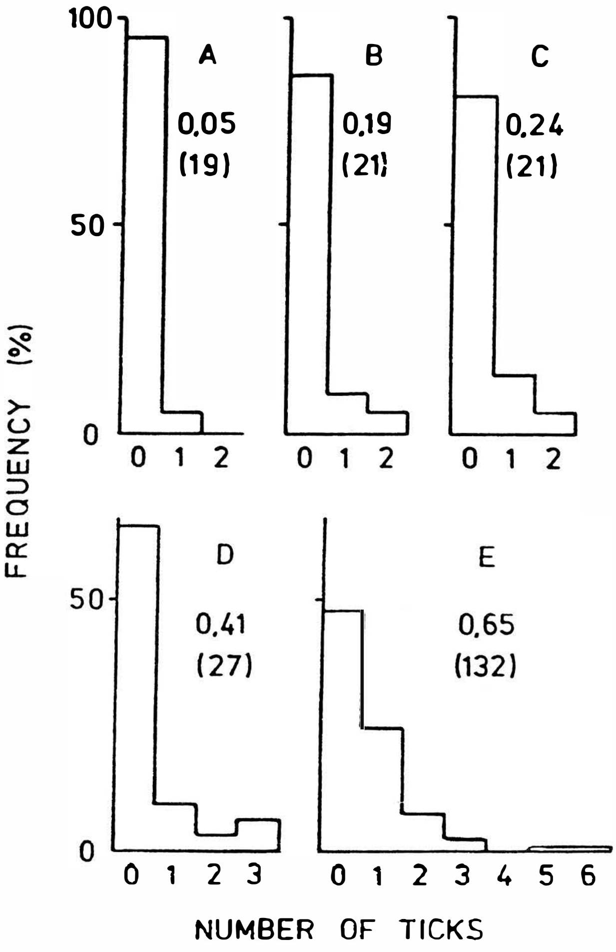

Fig. 5 Frequency histograms of numbers of ticks per tortoise in *T. hermanni* at Alyki. (a) juveniles, (b) subadult females, (c) subadult males, (d) adult females, (e) adult males. The mean and sample size are shown.

populations, for use in conservation. This excludes males for two reasons. First, the sex ratio varies considerably between sites and in different species (above). Second, tortoises are promiscuous (Swingland and Stubbs, 1985), so a population's reproductive potential is not directly related to the number of males.

Values of this ratio are shown in Table 3c. There were large and significant differences between the sites, ranging from about 0.1 at Lagos to about 4 at Epanomi. A similar trend was shown by the two species; ratios did not differ significantly between them at any of the four sites.

Tick Infections

The ticks infecting *T. hermanni* at Alyki in 1979 were identified as *Hyalomma aegyptium* (Stubbs, Espin and Mather, 1979), which is a common parasite of tortoises (Reichenbach-Klinke and Elkan, 1965; Frank, 1981). Ticks on tortoises at Alyki in subsequent years, and at other sites, were apparently the same, but have not been reliably identified.

Juvenile and subadult tortoises had fewer ticks than adults in each species and at each site. The data for *T. hermanni* at Alyki are shown in Fig. 5 as an example; similar patterns were shown in other samples where the number of small tortoises handled was sufficiently

	T. hermanni			*T. graeca*		
Site	Males	Females	Juveniles	Males	Females	Juveniles
Alyki	104	22	17	15	11	22
Epanomi	19	3	11	12	19	83
Keramoti	49	22	9	39	34	26
Lagos	56	26	3	49	42	3

(a) Sample sizes. Data for *T. graeca* at Alyki include captures 1980-1986.

Site	Males/Females	X^2	Males/Females	X^2
Alyki	4.7	53.4 ***	1.4	0.61 NS
Epanomi	6.3	11.6 ***	0.63	1.58 NS
Keramoti	2.2	10.3 **	1.1	0.34 NS
Lagos	2.1	11.0 ***	1.2	0.54 NS
G test	8.76*		2.69 NS	
Pooled	3.1	79.8 ***	1.1	0.37 NS

(b) Ratio of adult males per adult female at each site, and at all sites pooled. The X^2 tests are against an expected 1:1 ratio; the G test is of variation of the ratio between sites.

Site	Juveniles/Females	Juveniles/Females	G
Alyki	0.77	2.0	3.80 NS
Epanomi	3.7	4.4	0.06 NS
Keramoti	0.41	0.76	1.77 NS
Lagos	0.15	0.07	0.29 NS
G test	21.6***	84.1***	

(c) Ratio of juveniles per adult female at each site. G tests comparing the two species at each site, and the four sites for each species.

TABLE 3: Population structure in terms of sex ratio and ratio of juveniles to adult females.

Site	Alyki	Keramoti	Lagos	Epanomi
T. hermanni	0.61 (159)	0.67 (92)	1.44 (81)	2.00 (29)
T. graeca	2.64 (31)*	2.40 (141)	2.12 (109)	3.46 (46)

(a) All adult tortoises.

Male	0.65 (132)	0.76 (67)	1.69 (55)	2.04 (24)
Female	0.41 (27)	0.44 (25)	0.92 (26)	1.80 (5)
Male/Female	1.58	1.73	1.84	1.13

(b) Sexual differences in *T. hermanni*.

Male	2.53 (15)	2.59 (66)	2.06 (49)	3.80 (15)
Female	2.75 (16)	2.23 (75)	2.17 (60)	3.29 (31)
Male/Female	0.92	1.16	0.95	1.15

(c) Sexual differences in *T. graeca*.

TABLE 4: Mean infection levels with the tick *Hyalomma aegyptium* at the four sites. Values are the mean number of ticks per adult tortoise (with number of tortoises), including recaptures but excluding tortoises with numerous juvenile ticks (see Fig. 6). *Results from July or August 1980-1986.

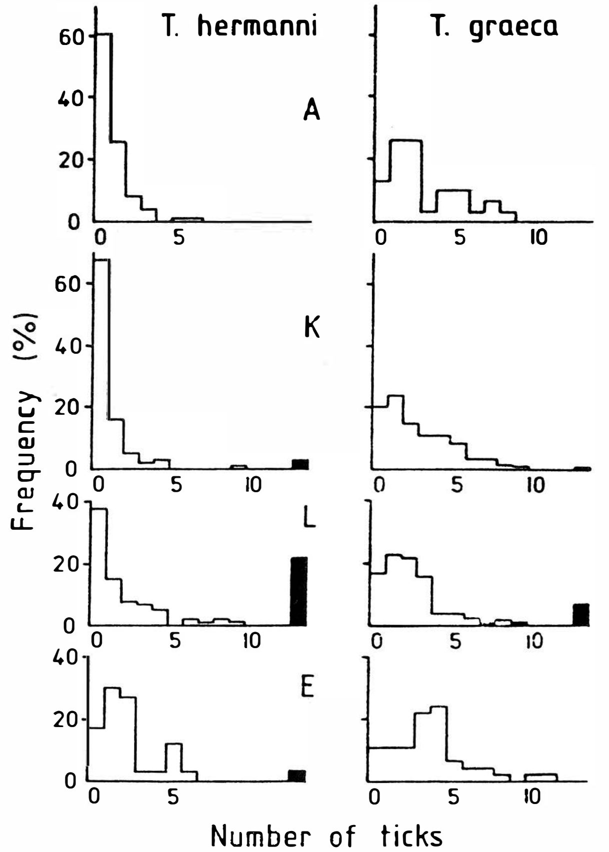

Fig. 6 Frequency histograms of ticks per tortoise at Alyki (A), Keramoti (K), Lagos (L) and Epanomi (E). Adult tortoises only, sexes pooled. The shaded bars show tortoises with 15-60 juvenile ticks. Means and sample sizes in Table 4.

large. The subsequent analysis considers ticks on adult males and females only.

Mean infection levels on *T. graeca* varied from 2.1 to 3.5 at the four sites. *Testudo hermanni* had fewer ticks, and there was more variation between sites, with means from 0.6 to 2.0 (Fig. 6). Adult male *T. hermanni* had more ticks than females, whereas male and female *T. graeca* had similar infection levels (Table 4).

	T. hermanni	*T. graeca*
Male	29.0 ±3.2 (284)	30.3 ±2.9 (116)
Female	28.0 ±3.1 (81)	30.8 ±3.1 (143)
t test	2.53*	1.45 NS

(a) Mean body temperature ±S.D. (with sample size).

	T. hermanni		*T. graeca*	
Male	69 : 228	0.30	19 : 100	0.19
Female	11 : 73	0.15	40 : 95	0.42
G test	4.36*		6.70**	

(b) Number of recaptures : individuals, and ratio.

TABLE 5: Sexual differences of (a) body temperature and (b) recapture frequency in adult *T. hermanni* and *T. graeca*, all sites pooled. t and G tests are between the sexes. Keramoti area 3 included in (a) but not in (b).

Body Temperature and Activity

Activity periods and body temperatures of *T. hermanni* and *T. graeca* at the four sites have been compared by Wright *et al.* (submitted) in relation to habitat use. That paper pooled all measured body temperatures, that is from all tortoises larger than about 10cm, irrespective of sex. Sexual differences of body temperature are analysed here, in relation to interspecific differences in sex ratio and tick infection. Adult male *T. hermanni* had significantly higher body temperatures than adult females (Table 5), by an average of 1.0°C. There was an opposite trend in *T. graeca*, females having body temperatures about 0.5°C higher, but this was not significant.

There were significant differences between the probability of recapture of males and females in both species (Table 5). Male *T. hermanni* were recaptured twice as frequently as females, while exactly the opposite was found in *T. graeca*.

Habitat Disturbance

There was no evidence of recent catastrophic events at any of the sites. There was presumably some disturbance when the plantation of shore pine was initiated at Lagos. This was thought to be about 30 years ago, from the size of the trees. All of the sites were currently liable to some degree of chronic disturbance.

There was little direct disturbance at Epanomi, where camping was restricted to a fenced area; most of the site was a protected area. Alyki was also undisturbed, because of its isolation: this area is recognised as being of national interest, but is without effective protection. There was some beach activity and fishing at both Epanomi and Alyki, but vehicles kept to definite tracks. Camping at Keramoti was less regulated, and there was more use by vehicles as the area was close to the town. The site at Lagos was also close to the town, and used intensively for unofficial camping and for day trips: there were abundant traces of human activity (litter, faeces).

The use of the sites by grazing animals varied seasonally. For example at Alyki sheep used the heath from October to May, and were moved to farms several km away for the summer. Epanomi was also visited at different times, and sheep were seen in winter and spring, but not in summer. Sheep were seen in summer at Keramoti and at Lagos.

The Island Population

The island (area 3) at Keramoti had a range of habitat types similar to those found in other areas at that site. Body temperaures were therefore pooled with those in areas 1 and 2, and will not be considered separately. Population density of *T. graeca* larger than 10cm in the 4ha island was estimated as 21ha^{-1}, the highest of any area (Table 1). In total, 33 *T. graeca* were marked in area 3, comprising 8 juveniles, 5 sub-adults, 10 adult females, and 10 adult males. The sex ratio (1:1) and juvenile to female ratio (0.8) were thus similar to those of *T. graeca* in areas 1 and 2 (Table 3). Three adult *T. hermanni* were also found.

DISCUSSION

Sampling and Size Structure

Juveniles are often under represented in studies of tortoises (e.g. Lambert, 1982; Meek and Inskeep, 1981; Meek, 1985). This pattern has implications for dynamics and conservation, if it reflects the true population structure rather than the difficulty of finding juveniles (Lambert, 1981). For example, Stubbs and Swingland (1985) found fewer juvenile *T. hermanni* in woodland in France than in heathland in Greece, but could not rule out the possibility that juveniles were simply harder to find in woodland.

The present study comparing two species in several habitat types at four sites is therefore interesting in two respects:

1. *Testudo graeca* occupied similar coastal heath habitat at all four sites (Wright *et al.*, submitted). The substantial variation of size structure between sites therefore reflects differences in their true population structures.

2. The size structures of the two species were similar at each site, even though *T. hermanni* occupied habitats ranging from grassy heath to pine and broadleaved woods. This suggests that habitat type has a rather small effect on the difficulty of finding juveniles, and that the population size structures of the two species are determined by similar factors.

Effects of Disturbance

The four sites were found to have densities of tortoises larger than 10cm of 7 to 21ha^{-1}. These coastal sites thus support dense populations compared to inland thorn scrub habitat, where sightings are often an order of magnitude less frequent (Lambert, 1981; personal observations). However, adults of long-lived species may persist for several years after recruitment has ended (e.g. Berry, 1976; Beebee, 1979). In addition, large, old female *Testudo* may have reduced reproductive potential (Hailey and Loumbourdis, 1988). The population density of adults is therefore not sufficient information to assess the need for active conservation measures.

The ratio of juveniles to adult females must also be considered. This varied widely between the sites, and was probably related to disturbance. Juvenile tortoises and nests are vulnerable to predation by human commensals such as rats, cats and dogs, which are more abundant near towns. The site at Lagos was the nearest to a town, followed by Keramoti; Epanomi and Alyki were relatively isolated.

Conservation Techniques

This section discusses ecological techniques for conserving tortoise populations, rather than general policies for tortoise and habitat conservation.

The scarcity of juveniles at Lagos was similar to that in woodland in France (Stubbs and Swingland, 1985), but the causes were probably different. The problem in France was deterioration of the habitat; open areas used for nesting were becoming overgrown following the decline of traditional agricultural practices. Nests were then concentrated in a few remaining open areas, where they were vulnerable to natural egg predators such as beech marten and badgers (Stubbs and Swingland, 1985). It is undesirable to control such natural predators, and so indirect conservation measures must be used, such as:

1. Habitat modification, to prevent encroachment on open areas (e.g. Corbett and Tamarind, 1979).

2. Removal of eggs and hatching in captivity, dispersing the juveniles to avoid concentrations of predators (Devaux, Pouvreau and Stubbs, 1986).

The problem of human commensals at sites such as Lagos needs different solutions. It would be possible to control these directly, by fencing out cats and dogs and trapping rats. A more economical measure would be the removal of eggs and releasing juveniles, as in France. The juveniles should, however, be kept in captivity for a few years before release so that they are large enough to resist predators, rather than simply dispersing them to avoid concentrations of predators.

Sex Ratio, Activity and Tick Infections

Sample sex ratios of adult *T. hermanni* were biased towards males at all four sites. Was this because males were more abundant than females, or because they were more available for finding? These explanations are not exclusive, and both are known to contribute to the male bias at Alyki (Hailey, 1988). The main difference between the behaviour of male and female tortoises is that males must search for mates. This behaviour could increase the availability for finding of males in two ways; 1. Males are more active. 2. Males frequent places where tortoises are more obvious, such as open microhabitat.

The even ratio in *T. graeca* suggests that males are not more active than females in this species. This conclusion should apply to *T. hermanni*, as active searching for mates is similar in the two species, although the details of courtship behaviour differ. We therefore favour hypothesis 2: male *T. hermanni* are more available for finding than females because they frequent more open areas. This would not affect the sex ratio of *T. graeca*, as this species occupied open coastal heathland where there was little variation of cover. Sighting profiles of male and female *T. hermanni* are similar (Hailey, 1988), because tortoises moving in cover are rarely found, and so do not skew the profile towards short distances from the transect. Male *T. hermanni* had higher body temperatures than females, consistent with their use of more open areas.

Infection of tortoises by ticks is from unattached ticks in the environment, rather than between tortoises, and will be related to the behaviour of both ticks and tortoises. The sexes had similar infection levels in *T. graeca*, consistent with similar activity levels within a uniform habitat. *Testudo graeca* had more ticks than *T. hermanni*, suggesting that transmission was greater in open habitats. This could be explained by the observed tendency for free infective ticks to climb. Ticks would be concentrated into the few plants in open areas, which would bring them into contact with feeding tortoises, increasing the chance of infection. Male *T. hermanni* had more ticks than females, consistent with the suggested use of more open microhabitat.

ACKNOWLEDGEMENTS

Fieldwork was supported by expedition grants from the British Ecological Society, World Society for the Preservation of Animals, Condor Conservation, Sir Philip Reckitt Educational Trust, University of East Anglia Expeditions Committee, University College of North Wales Students' Union Exploration Club, Miss Hilda Hawkins and other personal sponsors. Anna Dubiel, Karen Barnett, Brian Moulden, Lesley Dean and Jeanette Lunt helped collect data, and A. Barnett, M. Perry, B. Antipas, R. Oxley, E. Pulford and D. Stubbs gave advice and logistic support. A.H. was supported by a European Science Exchange Program fellowship from the Royal Society and the National Hellenic Research Foundation, made possible by the kind provision of facilities by Prof. M. E. Kattoulas and Dr. N. S. Loumbourdis. We are also grateful to Dr. I. R. Swingland for support from the Ecology Research group, University of Kent, and to V. Goutner (site locations) and Dr. M. R. K. Lambert, R. Meek, and R. E. Willemsen (discussion).

REFERENCES

Beebee, T. J. C. (1979). Population interactions between the toads *Bufo bufo* (Linnaeus) and *Bufo calamita* (Laurenti): some theoretical considerations. *British Journal of Herpetology* **6**, 1-5.

Begon, M. (1979). *Investigating animal abundance: capture - recapture for biologists.* London: Edward Arnold.

Berry, K. H. (1976). A comparison of size classes and sex ratios in four populations of the desert tortoise. *Proceedings of the 1976 symposium*, 38-50. San Diego: The Desert Tortoise Council.

Corbett, K. F. and Tamarind, D. L. (1979). Conservation of the sand lizard, *Lacerta agilis*, by habitat management. *British Journal of Herpetology* **5**, 799-823.

Devaux, B., Pouvreau, J.-P., and Stubbs, D. (1986). *Programme de sauvegarde de la tortue d'Hermann.* Station d'Observation et de Protection des Tortues des Maures (SOPTOM).

Frank, W. (1981). Ectoparasites. In *Diseases of the reptilia*, Cooper, J. E. and Jackson, O. F. (Eds), Vol. 1, p.359-383. London: Academic Press.

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

Hailey, A. and Loumbourdis, N. S. (1988). Egg size and shape, clutch dynamics, and reproductive effort in European tortoises. *Canadian Journal of Zoology*. In press.

Honegger, R. E. (1981). *Threatened amphibians and reptiles in Europe.* Supplementary volume of the *Handbuch der reptilien und amphibien Europas.* Wiesbaden: Akademische Verlag.

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

Lambert, M. R. K. (1982). Studies on the growth, structure and abundance of the Mediterranean spur-thighed tortoise, *Testudo graeca* in field populations. *Journal of Zoology, London* **196**, 165-189.

Lambert, M. R. K. (1984). Threats to Mediterranean (West Palaearctic) tortoises and their effects on wild populations: an overview. *Amphibia-Reptilia* **5**, 5-15.

Meek, R. (1985). Aspects of the ecology of *Testudo hermanni* in southern Yugoslavia. *British Journal of Herpetology* **6**, 437-445.

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

Reichenbach-Klinke, H. and Elkan, E. (1965). *The principal diseases of lower vertebrates.* London: Academic Press (Reprinted T.F.H. Publications, Hong Kong).

Stubbs, D., Espin, P. and Mather, R. (1979). *Report on expedition to Greece 1979.* University of London Natural History Society.

Stubbs, D., Hailey, A., Pulford, E. and Tyler, W. (1984). Population ecology of European tortoises: review of field techniques. *Amphibia-Reptilia* **5**, 57-68.

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

Stubbs, D. and Swingland, I. R. (1985). The ecology of a Mediterranean tortoise (*Testudo hermanni*): a declining population. *Canadian Journal of Zoology* **63**, 169-180.

Stubbs, D., Swingland, I. R., Hailey, A. and Pulford, E. (1985). The ecology of the Mediterranean tortoise *Testudo hermanni* in northern Greece (the effects of a catastrophe on population structure and density). *Biological conservation* **31**, 125-152.

Swingland, I. R. and Stubbs, D. (1985). The ecology of a Mediterranean tortoise (*Testudo hermanni*): reproduction. *Journal of Zoology, London (A)* **205**, 595-610.

Wright, J., Steer, E. and Hailey, A. (MS). Habitat separation in tortoises, and the consequences for activity and thermoregulation.