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POPULATION ECOLOGY AND CONSERVATION OF TORTOISES: THE ESTIMATION OF DENSITY, AND DYNAMICS OF A SMALL POPULATION

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ABSTRACT

Part 1: Line transect methods were used in three areas with known densities of *Testudo hermanni*. This enabled calculation of the proportion of the population available for finding (PAF); that is, excluding tortoises in refuges or in thick cover. At times of peak daily activity PAF varied between about 0.1 and 0.3, and was greater in spring than in summer. Males had higher PAF than females on summer evenings, the main courtship period, and PAF of males was greater in a population with a male-biased sex ratio. Transect sampling is useful for estimating the density of tortoise populations, provided that the low PAF is taken into account. Values of effective transect width are given for a variety of habitat types.

Part 2: A small population of *T. graeca* at Alyki was studied between 1980-1986; its size was estimated at about 25 adults, with an even sex ratio. Immature animals were recruited into the adult population, which was stable or increasing during this period. Adult size and juvenile growth rate were similar to other coastal populations of *T. graeca* in the region. The implications for the conservation of endangered tortoises are discussed.

INTRODUCTION

The threat to Mediterranean tortoise populations from collection for the pet trade (Lambert, 1969, 1979, 1981a) has now ended. The problem of habitat loss is, however, still present (Lambert, 1984; Cheylan, 1984). Basic information on tortoise populations is needed to evaluate this threat (Honegger, 1981; Groombridge, 1982). This paper considers two aspects of the population ecology of tortoises which have special relevance to conservation.

PART 1: ESTIMATING THE POPULATION DENSITY OF TORTOISES

INTRODUCTION

At present there is no tested method for the rapid estimation of the population density of Mediterranean tortoises. Short term mark-recapture studies may give misleading results. For example after a short study, Stubbs, Espin and Mather (1979) calculated that there were about 400 Testudo hermanni in an area of heathland; a later estimate from several man-months of study in the same area was over 3,000 tortoises (pre-fire estimate of Stubbs, Swingland, Hailey and Pulford, 1985). Sighting frequency gives a relative measure of abundance, if weather, time of day and season are taken into account (Lambert, 1981b), but does not given an absolute value for population density. It is sensitive to minor features of the habitat, such as the noisiness of leaf litter (Hailey, Pulford and Stubbs, 1984) and type of tortoise activity (Lambert, 1981b), and so may produce misleading comparisons between sites.

Line transect methods enable population density to be calculated from sighting frequency (Burnham, Anderson and Laake, 1980). They depend, however, on the animals being available for sighting, and tortoises are known to be inactive for much of the time (Auffenberg and Iverson, 1979). The first part of this paper calibrates the effect of low activity, by applying line transect methods to three areas where population density of *T. hermanni* is known from long-term markrecapture studies.

METHODS

All line transect methods are of the form

D = N / 2.L.W. (1)

where D is population density, N animals are seen along a transect of length L, and W is a measure of one half of the effective width of the strip sampled (Seber, 1981). This relation may be expressed in terms of sighting frequency (F) by replacing N/L by F/S, where S is walking speed. Low activity is taken account of by including a term for the proportion of the population which is available for finding at the time of sampling (PAF), so that

$$D = F / 2.S.W.PAF$$
(2)

Tortoises in refuges (usually shallow scrapes under vegetation, termed pallets), or stationary in dense cover, are seldom seen during transect sampling (see Hailey *et al.*, 1984), and are therefore considered to be unavailable for finding.

Two methods of calculating the effective width are used here; these differ in the way in which the curve of numbers found against distance from the transect (the sighting profile) is described:

(a) If the sighting profile shows exponential decrease, that is a concave shape, then

$$W = \overline{x}$$

where \overline{x} is the mean distance of sightings perpendicular to the transect (Caughley, 1977).

(b) Using the flexible power curve method of Eberhardt (1968),

$W = 2.\overline{x}.k(k+2) / (k+1)^2$

where k describes the shape of the sighting profile, and is estimated by regression (Caughley, 1977), Concave, linear, and convex sighting profiles give k less than 1, exactly 1, and greater than 1, respectively.

These methods were used in three areas where population density was known from long-term mark recapture studies: the Massif des Maures, France (Stubbs and Swingland, 1985), and two separate populations at Alyki, Greece (Stubbs et al., 1985). Sampling was by slow walking along irregular transects, passing around shrubs and areas of dense cover. Initially this was done throughout the day, to identify the periods of peak activity, but was then restricted to peak periods to measure maximum sighting frequency. This work was carried out in August 1981 and April 1982 (France) and in July-August 1982 and April-May 1983 (Greece). Time spent handling tortoises was excluded from calculations of sighting frequency. The distance of each sighting perpendicular to the transect was paced out, and the paces were calibrated against a 30m line for each observer. Sighting profiles were also constructed from data collected during mark-recapture studies throughout 1981-1983.

There were three main vegetation types at Alyki. Coastal heath: open loose sand and dunes, with a sparse cover of herbs. Dry heath: firm sandy soil with scattered shrubs, herbs and grasses. Juncus marsh: rushes, asphodels and dense grass, in damp areas. Most work was done in two separate areas of dry heath; a 55 ha part of the main heath, and the 7 ha salt works heath. These areas and vegetation types are described in more detail by Stubbs, Hailey, Tyler and Pulford (1981) and Stubbs et al., (1985). The habitat of the Massif des Maures was mostly dense evergreen oak forest, with some maquis at higher altitudes. Apart from a few cultivated clearings used by adults during the May-June nesting season (Swingland and Stubbs, 1985), the forest was a closed canopy with dense undergrowth and a thick noisy leaf litter.

It was not possible to measure the distance of sightings perpendicular to the transect in the forest. Searching was modified to a walk-stop-listen pattern, as the noise of walking interfered with finding tortoises, most of which were located by sound. This type of sampling has been described by Emlen (1971). As there was no real transect, distances of sightings perpendicular to it (PD) could not be found. However, the straight distance (SD) between the observer and each tortoise was measured. The two distance measures are related by

$PD = SD.Sin \Theta$

where Θ is the angle between the sight line and the transect. If angles around the observer are random, as when animals are detected by sound, then on average

PD = SD.0.64

(0.64 is the mean Sin Θ for all angles between 0 and 180°). Sighting profiles in forest were therefore constructed using 0.64.SD. This adjustment is

Vegetation type	x (m)	k	W (m)	N	% by sound
Evergreen forest	5.1	1.28	8.2	2110	84
Maquis	4.9	2.32	8.9	105	81
Juncus marsh	3.0	0.47	3.2	234	35
Dry heath	4.2	0.96	6.2	610	18
Coastal heath	6.7	1.06	10.2	123	12

TABLE 1: Descriptive statistics of sighting profiles of *T*: *hermanni* according to vegetation type. All tortoises larger than 10cm straight carapace length, except those in pallets. The sample size (N) and the percentage of the sample detected by sound are also shown.

unsuitable for more open areas where most animals are found by sight, where the mean sighting angle is usually about 33° (Burnham *et al.*, 1981).

RESULTS

EFFECTIVE WIDTH

Sighting profiles for juveniles (less than 10cm straight carapace length) were narrower than those of larger tortoises (Fig. 1). Juveniles were therefore excluded from further analysis; tortoises longer than 10cm are subadults or adults. There were only slight



Fig. 1 Sighting profiles of adult and subadult *T. hermanni* in different vegetation types, and of juveniles (n = 110) in dry heath. Sample sizes and descriptive statistics for the vegetation types are given in Table 1.

differences between sighting profiles for spring and summer, or between males and females (Fig. 2). The data for different seasons and for the sexes were therefore pooled.

Sighting profiles differed between the vegetation types (Fig. 1). The effective width of the strip sampled was greatest in evergreen forest and maquis, where tortoises could be heard over long distances, and in coastal heath, where they could be seen easily (Table 1). Effective widths calculated by method (b) were greater than mean distances from the transect (method a). This difference was greatest in evergreen forest and maquis, where sighting profiles were convex, with k greater than 1. Sighting profiles were approximately linear in dry heath and coastal heath, with k about 1. Only in Juncus marsh was the exponential model a good fit.



Fig. 2 Sighting profiles of *T. hermanni* in evergreen forest in the Massif des Maures: variation with sex and season. •-females, summer; \leftarrow females, spring; O-males, summer; Λ -males, spring.

SIGHTING FREQUENCY AND PAF

There were morning and evening peaks of sighting frequency in both areas of dry heath in Greece, in both spring and summer; the peaks were closer together and there was some midday activity in spring. The mean sighting frequency during the peak periods is shown in Table 2. Walking speed was 3km.h⁻¹ on the main heath, and 2.5km.h⁻¹ on the smaller salt works heath. In France, activity was at a uniform level between 10-17h local time in late summer (late August and early September), with a mean sighting frequency of 2.6 males.h⁻¹ and 1.3 females.h⁻¹. In spring, peak sighting frequency was found between 12-15h; 4.3 males.h⁻¹. and 3.6 females.h⁻¹. Walking speed was 2.0km.h⁻¹.

	Main Heath		Salt Wo	rks Heath	eath	
	Males	Females	Males	Females		
Spring 08-12h	13	4.6	7.2	7.6		
17-19h	24	9.9	—			
Summer 08-11 h	9.2	2.3	5.6	4.1		
18-21h	17	2.3	11	5.4		

TABLE 2: Sighting frequency (No.h⁻¹) of *T. hermanni* in two populations at Alyki: means for peak activity periods (local times shown) in spring 1983 and summer 1982. All tortoises larger than 10cm SCL, except those in pallets. There was no data for the salt works heath during spring afternoons.

Population density of subadult and adult *T. hermanni* in the 55ha of the main heath covered by sighting frequency observations, and in the salt works heath, were estimated from Stubbs *et al.* (1985) as:

Main heath18 males8.4 females ha⁻¹Salt works heath20 males 19 females ha⁻¹

The average density of adults and subadults over the 35ha Massif des Maures study area was about 10ha⁻¹ (Stubbs and Swingland, 1985). Sighting frequency observations were made in the most intensively studied 9ha of the study area, where all resident tortoises had been marked; they also exclude the nesting season (when non-residents migrate into this area). The density of resident adults and subadults was therefore used; 5.2 males and 4.4 females ha⁻¹.

The proportion of the population which was available for finding at the time of peak activity is shown in Table 3. This was calculated from equation (2), using the effective width for evergreen forest and dry heath (Table 1), and the values for walking speed, population density and peak sighting frequency above. It is striking that even during peak periods, only a minority of the population was available for finding. Even the highest sighting frequency recorded, 30 males and 8 females h⁻¹ (early evening in spring on the main heath) corresponds to availability of only 49% of males and 27% of females.

DISCUSSION

PROPORTION AVAILABLE FOR FINDING

Bury and Luckenbach (1977) and Morgan and Bourn (1981) have indicated that census methods (that

is, grids or transects) are better than mark-recapture for estimating the population density of tortoises. These studies used animals which can be found even when inactive; *Gopherus* in burrows in the desert, and giant tortoises under the scarce shade trees, respectively. This paper shows how transect methods can be extended for use on the small Mediterranean tortoises in scrub habitats.

General discussions of line transect sampling assume that all animals in an area are available for finding, that is PAF = 1.0 (Caughley, 1978; Seber, 1981). Using this value would result in a five or ten fold underestimate of population density of *T. hermanni*. The effect of non-availability has probably been neglected because transect methods were developed for birds and large mammals, which are rarely inactive during peak activity periods. Reptiles, however, spend only a small part of their time active (Huey, 1982).

Line transect methods are a suitable method for rapid estimation of tortoise population density if this low activity is taken into account. The values of PAF in Table 3 may be used as a rough adjustment for future surveys. I suggest general values for PAF of:

Summer; 0.15 for males and 0.1 for females Spring; 0.25 for both sexes.

Effective width W is best calculated from sighting profiles using method (b) above, although the values in Table 1 could be used for areas of these habitats with very low density where sample sizes were low.

In the only previous correction for activity on survey methods for Mediterranean tortoises, Lambert (1981b) suggested that about 60% of animals in an area would

	Main Heath		Salt Works Heath		Massif des Maures	
	Males	Females	Males	Females	Males	Females
Population sex ratio	2.1:1		1.0:1		1.2:1	
Spring AM	0.19	0.15	0.12	0.13	_	_
Midday					0.25	0.25
PM	0.36	0.32		_	-	
Summer AM	0.14	0.074	0.090	0.070	_	_
Midday			_		0.15	0.090
PM	0.25	0.074	0.18	0.092		_

TABLE 3: The proportion of T. hermanni available for finding (PAF) at peak activity periods in three populations of known density. Calculated from equation (2) in the text. All tortoises larger than 10cm SCL; the population sex ratios from mark-recapture studies are also shown.

be found by normal, non-intensive searching during the optimum activity period. I obtain a different result from his data, as follows. On average, a captive female *T. graeca* spent 12% of the daily active period actually moving. Two thirds of field sightings were moving, so that the total sample was 1.5 times the number of moving animals. By analogy with the captive female, the moving animals would be 12% of these present in the area sampled. Therefore only 18% of the tortoises in an area would be found, similar to values of PAF reported here.

DIFFERENCES BETWEEN SEXES

Availability for finding of males and of females was similar in spring, in all three populations. This is a period when there is little courtship (at least in these populations; Swingland and Stubbs, 1985), most activity being basking and feeding. Males were, however, more available for finding than females in summer, especially in the evening which is the main time of courtship (Hailey *et al.*, 1984). Both sexes were more available for finding in spring than in summer, in all three populations.

The relationship between tortoise activity and availability for finding will be considered in detail elsewhere. The low availability for finding in summer is known to be due to low activity, from a study using thread-trailing (Hailey, in preparation). Summer activity is probably limited by the increased time needed to process dry food (Coe, Bourn and Swingland, 1979). Mediterranean tortoises are apparently completely inactive in summer in very dry areas (Raxworthy, Rice, Smith and Claudius, 1984).

In summer, PAF of females was similar in the three populations. However, males were more available for finding on the main heath, where the population sex ratio was biased with more than two males per female (Stubbs *et al.*, 1985). The best comparison is with the saltworks heath, which had similar habitat, adult population density, and PAF of females to the main heath; the only differences were the population sex ratio and the PAF of males. The simplest hypothesis is that males were more active on the main heath because of greater competition for females: this will be examined elsewhere.

PART 2: DYNAMICS OF A SMALL POPULATION

INTRODUCTION

Five of the 39 living species of tortoise are now endangered (Anonymous, 1986). One species, *Geochelone yniphora*, is one of the 12 most threatened animals in the world (Hoogmoed, 1985), with a total population in the wild and in captivity of only 100-400 individuals (Curl, Scoones, Guy and Rakotoarisoa, 1985). In addition to the causes of their present status, small populations have the problems of locating mates and of inbreeding; they are also difficult to study. The ecology of any small natural population of tortoises is therefore of interest as a model for the chronically endangered species. This section concerns a very small population of *T. graeca* at Alyki, information about which has been collected over seven years during study of a large population of *T. hermanni*.

METHODS

The same methods, and a common marking scheme, were used for both species (Stubbs *et al.*, 1984, 1985). Sampling was carried out in summer 1980 and 1982 and in spring 1983, and between April 1984 and November 1986. Sector 9 was examined most frequently in 1986 to obtain more information on the population on *T. graeca*. The size at sexual maturity in *T. graeca* from northern Greece is not known precisely. In this paper, males of 14cm and females of 16cm straight carapace length are considered to be adults.

RESULTS

DISTRIBUTION AT ALYKI

Testudo graeca at Alyki were largely restricted to the coastal heath in sectors 8 and 9 (Fig. 3a), in contrast to *T. hermanni* which was found all over the site (Stubbs et al., 1985). Within the coastal heath area, *T. graeca* was more common in the central, exposed part, while *T. hermanni* was more of ten found in peripheral areas with greater plant cover (Fig. 3b). The role of habitat use in niche separation of *T. graeca* and *T. hermanni*, and its consequences, are discussed by Wright, Steer and Hailey (MS). These authors also consider the distribution of *T. graeca* in Greece, and the possible origins of the Alyki population.



Fig. 3 (a) Distribution of *T. graeca* over the Alyki heath. The shaded area shows the main area occupied by this species, \bullet show all sightings of individuals outside this area between 1980-1986. The lighthouse (\Box) marks the border between the main heath and the southern heath to the south. (b) An enlarged map of sectors 8, 9 and 12, showing details of vegetation and sightings of individual *T. graeca* (\blacklozenge) and *T. hermanni* (\bullet) in July-October 1986. Within the coastal heath, both species avoided the dunes (1); *T. hermanni* was prevalent in peripheral areas with *Artemisia* (2) or herbs (4), and *T. graeca* was prevalent in the central exposed part (3). *T. hermanni* was also found in sector 12, especially the areas of dry heath.

There was a possibility that the few *T. graeca* found on the main heath represented the edge of a larger population centred in the southern heath. A survey in the summer of 1985 (Wright, Steer and Hailey, MS) therefore concentrated in the southern heath. In total, 365 individual tortoises were handled on the southern heath between 1980-1986: only eight of these were *T. graeca*. The southern heath *T. graeca* were all small, length range 58-122mm. This is the size at which the related *T. hermanni* are thought to disperse, the adults holding stable home ranges (Stubbs and Swingland, 1985). It is therefore assumed that the *T. graeca* in sectors 8 and 9 were the main population, with a few dispersing juveniles reaching the southern heath.

POPULATION SIZE

The population of adult *T. graeca* was estimated from analysis of recaptures to be at most 14 males and 12 females (Table 4). In total, 15 adult males and 11 adult females were handled, most of them in several years (Fig. 4); 13 males and 9 females were known to be alive in 1986. The population therefore comprised about 25 adults, with an approximately even sex ratio.

	1980	1982	1983	1984	1985	1986
(a) Jolly-Seber	estimates of	adult p	oopula	tion si	ze.	
Males		8	7	14*	9	
Females		6	6	!!*	12*	
(b) Numbers of and number of	new immatu these recruite	ure tor ed to a	toises idults	marke by 198	ed eact 6.	n year,
Marked	5	3	3	4	10	7
Recruited	4	2	1	0	0	

TABLE 4: Size of and recruitment to the adult population ofT. graeca at Alyki, in the years 1980-1986.

* rounded up, otherwise integer results.



Fig. 4 Captures of individual adult *T. graeca* at Alyki in different years; (a) males (b) females. Tortoises were numbered using the scheme of Stubbs *et al.* (1984). Some tortoises were immature when first captured and were recruited into the adult population; capture when immature is shown as 0.

POPULATION DYNAMICS

Minimum survival rates of adults can be calculated from the data in Fig. 4. Eight males were handled in 1982, of which at least six were alive in 1986, equivalent to annual survival of 0.93 (= 0.75 ^{1/}/₄). The



Fig. 5 (a) Relation between number of growth rings and body size of *T. graeca* at Alyki; all tortoises with 8 or fewer rings, including recaptures in different years. The regression line from Table 5 is also shown. (b) Growth curves for *T. graeca* (_____) and *T. hermanni* (_____) at Alyki, from the curves of growth rate on length in Fig. 6. The two curves for each species are for females (above) and males. Growth of juveniles is the average of the growth ring — length regressions in Table 5.

Site	Species	а	b	SEb	N	SCL ₆
Alyki	T: h.*	38	10.9	1.14	50	103
	<i>T.h.</i>	37	10.0	2.37	38	97
	T.g.**	30	11.8	1.07	23	101
Epanomi	<i>T</i> `. <i>h</i> .	21	12.9	2.61	21	98
	<i>T</i> .g.	32	11.3	0.95	99	100
Keramoti	<i>T.h.</i>	26	11.5	2.75	11	95
	T.g.	32	10.9	1.76	35	97

TABLE 5: Statistics of the regressions of straight capapace length (SCL, in mm) on number of growth rings. All tortoises with eight or less rings, including recaptures. a is the SCL at age 0 and b is the growth rate in mm.year⁻¹, with standard error. SCL₆ is the estimated length at age six. Dataare from animals handled during summer 1985, except: * random sample of those handled in 1984; ** all those handled 1980-1986.

corresponding figures for females are; six handled 1982, four recaptured 1986, giving minimum annual survival of 0.90.

Thirty-two immature *T. graeca* were handled in total. Some of these were recruited into the adult population during the study. Of the 11 immature *T. graeca* first marked before 1984, seven were recaptured and of adult size by 1986 (Table 4b).

Growth

Growth rings in scutes are unreliable indicators of age in adult tortoises (Castanet and Cheylan, 1979; Stubbs *et al.*, 1985), and so only those of tortoises with eight or less rings were considered. These are compared to data for *T. hermanni* at Alyki, and for *T. graeca* and *T. hermanni* examined by Wright *et al.* (MS) at several sites in summer 1985. There was a linear relationship between straight carapace length and growth ring number in all the populations studied; data for *T. graeca* at Alyki are shown in Fig. 5a. Regression parameters for these populations are shown in Table 5. These all predict hatchling length of about 30mm, and growth to about 10cm after six years. The 95% confidence limits of all slopes overlap the mean of 11mm.year⁻¹.

Observed growth of *T. graeca* between captures in alternate years is shown in Fig. 6. The pattern of growth in tortoises, and the relation between observed growth and growth rings, will be considered in detail elsewhere. It is of interest here to compare growth of *T. graeca* and *T. hermanni* at Alyki, as both of these have been measured over two years. Data for *T. hermanni* were for exactly two years, from summer 1980 to summer 1982, and are from Fig. 6 of Stubbs et al. (1985).

Growth rates at 10cm were similar in the two species. In males, the curve for *T. graeca* was shifted to the right, so that they grew at the same rate but maintained growth at larger sizes. In females, *T. graeca* grew faster as well as for longer. The average curves of growth rate on length are converted to curves of size on age in Fig. 5b: growth between hatching and 6 years is from the average of the growth ring equations from Table 5. Fig. 5b emphasises that male *T. hermanni* stop growing before male *T. graeca* and female *T. hermanni*, and that female *T. graeca* grow at an even faster rate.



Fig. 6 Growth in length after two years against initial length of *T. graeca* at Alyki, with curve fitted by eye (______); (a) males, (b) females. Juveniles are included in both parts. Curves for growth of *T. hermanni* after two years (_____) were fitted by eye to the data in Fig. 6 of Stubbs *et al.* (1985).

DISCUSSION

The population of *T. graeca* at Alyki consisted of about 25 adults, occupying an area of 15 ha. Despite this small size and low density, the population showed no decline over a seven year period; indeed Table 4 shows an increasing trend. The vigour of the population can also be considered at the level of individual tortoises. Adult *T. graeca* were of similar size to, or larger than, those at other sites in northern Greece (Wright *et al.*, MS); they were not stunted. Juveniles grew at similar rates to those at other sites (Table 5). Small populations of tortoises may therefore be ecologically viable.

The question of genetic viability in the long term is more difficult to judge; the average loss of variation due to inbreeding can be calculated, but not the effect of this on ecological vigour. Theoretically, a population of 25 animals would lose half of its present degree of heterozygosity in about 33 generations (Fig. 33.2 of Strickberger, 1976); over 500 years for Mediterranean tortoises (generation time is longer than the age at sexual maturity). The problem of inbreeding should therefore not cause immediate concern in tortoise conservation. For example, it may be better to protect several small populations in situ, rather than pool them in a single reserve, with the possible problems of relocation (Berry, 1986).

A small population of animals sympatric with a large population of a closely related species has an additionalproblem. Individuals of the rare species will encounter the common species much more frequently than they will encounter conspecifies. This may result in the breakdown of reproductive isolation (Tinsley, 1981). The reproductive potential of the rare species would then be lowered by infertile eggs or hybrids. Courtship of T. graeca at Alyki has only been observed seven times, and one of these was with a female T. hermanni. Hybridisation in Testudo has been observed in capivity (review in Kirsche, 1984); the impact on wild populations awaits further study, although tortoises with apparent hybrid characteristics have been found in the wild (Sofianidou, personal communication, and personal observations).

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