THE GIANT TORTOISE POPULATION OF ALDABRA (CRYPTODIRA: TESTUDINIDAE)

PART 1: PRELIMINARY RESULTS

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ABSTRACT

The preliminary results of a study of the endemic giant tortoise population of Aldabra Atoll in the Indian Ocean (*Geochelone gigantea* Schweigger) are briefly described. Their number would appear to have increased dramatically since the turn of the century to their present level of some 141 000 individuals. Crude estimates of mortality and reproductive rates are also given.

INTRODUCTION

Until the advent of man, giant tortoise populations existed on many islands of the western Indian Ocean, including the Seychelles and Mauritius. They also occurred on the Galapagos Archipelago in the Pacific. As a result of man's activity many of the Galapagos races are now on the verge of extinction and some have already died out (MacFarland *et al.* 1974), while in the Indian Ocean wild populations of giant tortoises have become extinct everywhere except on the atoll of Aldabra.

The atoll lies ten degrees south of the equator at the northern entrance to the Moçambique Channel, some 640 km east of Tanzania and 420 km north-west of Madagascar. Four major islands formed from raised coral limestone bound a central lagoon; the overall dimensions are 35 by 12 km with a total land surface area, excluding mangroves, of 138 km^2 (Figure 1). The atoll possesses limited natural resources of commercial importance and many areas are virtually inaccessible because of dense vegetation and treacherous terrain. As a result Aldabra has remained relatively unspoilt and, until recently, little known.

The ecology and behaviour of the Aldabran giant tortoise *Geochelone* (*Testudo*) *gigantea* Schweigger, which is the major terrestrial herbivore, have been described by Gaymer (1968), Grubb (1971) and Frazier (1972). Since the establishment of the Royal Society Aldabra Research Station a long term project has been initiated to study the dynamics of the tortoise population. The aims of the first phase of the project, on which I worked in 1973 and 1974, were: (*a*) to conduct a large scale marking programme; (*b*) to carry out an extensive census of the population; and (*c*) to perform an initial study of tortoise reproduction; the results of which would form the basis for future work on the population's recruitment, growth, movement and energetics. This paper summarizes the preliminary findings, details of which will be presented elsewhere.

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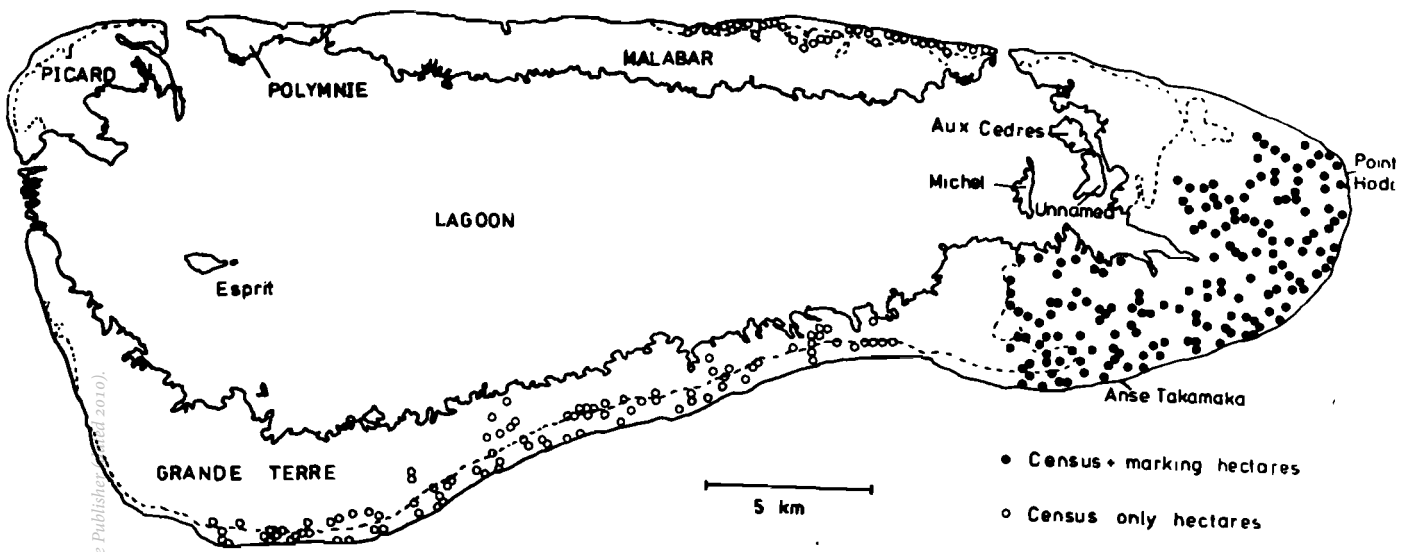

FIGURE 1
Aldabra Atoll, Indian Ocean, showing the distribution of hectare sampling sites. Dashed line indicates extent of dense *Pemphis* scrub.

METHODS

Marking

In principle the method of marking giant tortoises employed was that described by Gaymer (1973). A shallow depression was created in, but not through, the keratinous scute of the carapace, into which a sequentially numbered titanium disc 19 mm in diameter and 1 mm in depth was implanted and bonded to the scute with an epoxy resin. In practice a number of time-saving modifications were adopted, including immobilizing the tortoise by inserting it into a sling suspended from a heavy duty balance mounted on a light steel tripod and using a portable generator to power an electric drill which was used to cut the depression in the scute.

To provide baseline data for subsequent recapture work eight morphometric measurements, including weight, were made on each animal at the time of marking, and where possible sex and growth-ring counts were recorded. Abnormalities and scute damage were also noted and condition was determined by the presence or absence of fresh white growth-rings around the boundary of each scute.

Sampling

Previous work and a preliminary survey, carried out before the census/marking operations began, indicated that giant tortoises were most abundant on Grande Terre, particularly in the south-eastern region of that island but also in a relatively narrow zone along the south coast. The work initially concentrated on these areas but subsequently all the major islands were surveyed. The sampling procedure used was inevitably a compromise between various theoretical considerations and the limitations imposed by environmental conditions. A series of random stratified hectares based on the Aldabra grid reference system were determined from random number tables and located on aerial photographs. Five hectares were sampled in each square kilometre (Figure 1). In most cases, hectares could be accurately located in the field by using various geomorphological and vegetational features. Their boundaries were then marked out using a 400 m line and compass, and all tortoises found within were examined. Marking was carried out in those hectares shown as solid circles in Figure 1. The open circles indicate census sites where animals were examined and measured but not marked.

Wherever the remains of dead tortoises were found within hectares their position, size, sex and degree of breakdown were also recorded.

Post-mortems

Twenty-nine female tortoises from various parts of Grande Terre and of differing size were collected. They were initially weighed and measured and then decapitated (the fastest and most humane method of killing). Subsequently a power saw was used to cut through the sides of the plastron which was then removed to gain access to the body cavity. Detailed examinations were made and many samples preserved, but particular emphasis was placed on the reproductive organs. Their mass and dimensions were recorded and all ova greater than 5 mm in diameter were counted and measured.

RESULTS

Marking

During 1969 and 1970 field trials of the marking method were carried out by Gaymer and 700 tortoises were marked. Recaptures of some of these animals in the years following indicated an acceptably low disc-loss rate of about 0,5 per cent per annum. During 1972 and 1974 a further 6 200 tortoises were marked; of these, 4 260 were marked in random hectares in the eastern region of Grande Terre.

Distribution

Tortoises are found on all the major islands of the atoll except Polymnie. A few tortoises also occur on some of the larger lagoon islands. Table 1 shows the tortoise distribution broken down by island and the estimated number of tortoises that occurs on each. However, on those islands where tortoises do occur their distribution is uneven. Over half the land area of Aldabra, from the lagoon mangroves to the coastal zone, is covered with an almost impenetrable tangle of dense scrub vegetation composed largely of *Pemphis acidula* Forst. growing on deeply pitted and eroded coral limestone rock. Little soil is present and virtually no ground vegetation occurs on this terrain and few if any tortoises were found in hectares examined in *Pemphis* scrub.

The population estimates for Grande Terre and Ile Malabar are derived from the mean tortoise densities obtained in 260 and 32 hectares respectively. On the other islands it was not possible to use this method because of the limited areas involved and/or the small number of tortoises present. The figures were arrived at after extensive exploration. The total size of the Aldabran giant tortoise population is estimated to be 141 000 animals. Ninety-seven per cent of the population occurs in the largest of the islands – Grande Terre – and the vast majority of these in the eastern region. Here the underlying geomorphological structure is very different from other parts of the atoll and a distinctive vegetational community complex of woodland, mixed scrub and extensive open areas of grass, sedge and bare rock exists.

Table 2 shows the mean densities associated with each habitat type, from which it can be seen that the highest densities occur in the relatively open areas of low vegetation and bare ground. In these habitats the various grasses and herbs on which tortoises feed are most abundant. The higher tortoise densities that occur in relatively open areas are also shown in Figure 2, where the mean density is plotted against the estimated proportion of available shade. Notice that where no shade is available tortoise densities are comparatively low.

Mortalities

No large predators occur on Aldabra and as a result only the smallest tortoises are susceptible to predation. Although predation was never witnessed, tortoises of various sizes were occasionally found with amputated or clawless limbs and damaged carapaces. It is believed that some of these deformities at least may have been the result of unsuccessful attacks by the coconut crab (*Birgus latro* L.) or the black rat (*Rattus rattus* L.) or the sacred ibis (*Threskiornis aethiopica abbotti* (Ridgeway)), when the tortoises were young. It is unfortunately not possible to assess the losses due to predation at this stage, as their remains are likely to be removed or completely destroyed. However the remains of larger animals that die from other causes do persist in the

TABLE 1

Distribution and abundance of giant tortoises on Aldabra

(a) estimated from densities in adjacent ha, (b) estimated after extensive search

Island	*Area km²*	*Tortoise density/ha*			*Number of tortoises*	*% of total population*
		Mean	*S.E.*	*Range*		
Grande Terre						
Eastern census	32,35	27,3	±2,34	0–217	88 316	62,6
South Coast census	9,75	20,2	±2,29	0– 96	19 666	13,9
Other suitable	10,85	20(a)			21 700	15,4
Pemphis areas	46,82	1,6	±0,63	0– 8	7 768	5,5
Ile Malabar						
Census	3,2	7,0	±0,67	0– 16	2 249	1,6
Pemphis areas	24,8	0			0	
Ile Picard						
Non-*Pemphis* areas	2,5	5(b)			1 250	0,9
Pemphis areas	5,0	0			0	
Ile Polymnie						
Whole area	1,9				0	
Lesser Islands						
Ile Michel	0,3				ca. 10(b)	
Ile au Cedre	0,4				ca. 50(b)	
Unnamed island	0,2				ca. 10(b)	
Ile Esprit	0,1				0	
					141 019	

TABLE 2

Giant tortoise densities with habitat

Predominant habitat type	*Mean tortoise density/ha*	*Standard error*	*Number of samples*
woodland	18,0	± 5,3	13
scrub	18,1	± 1,9	72
low scrub	19,1	± 4,9	22
tall herb	18,2	± 2,3	6
low vegetation > 50 per cent ground cover	62,3	± 7,6	11
low vegetation < 50 per cent ground cover	41,9	± 6,5	44

field, sometimes for considerable periods. During 1973/74 32 tortoises with known dates of death were monitored for up to 18 months in order to determine their rate of decomposition. Relatively small tortoises have incompletely ossified carapaces and as a result their skeletons disintegrate within a few months. Carapaces of larger animals are well ossified and probably remain intact for more than two years.

The mean mortality density in the eastern region of Grande Terre was 1,2/ha ± 0,3 (range 0–9/ha). The live tortoise population in that area was estimated to be about 100 000. If it is assumed that the remains of an average-sized tortoise persist in the field for approximately two years then it can be calculated that the crude mortality rate is in the order of 2–3 per cent per annum.

Reproduction

External secondary sexual characteristics were apparent in individuals above 50 cm straight length and have been described by Grubb (1971) and Bourn and Coe (in preparation). Males have larger tails and a deeper plastron depression than females. It was not possible to distinguish the sex of smaller animals on external features. The sex ratio of those tortoises large enough to be sexed was approximately 1 : 1, although considerable variation was found from hectare to hectare. Mating commenced at the beginning of the wet season in November or December,

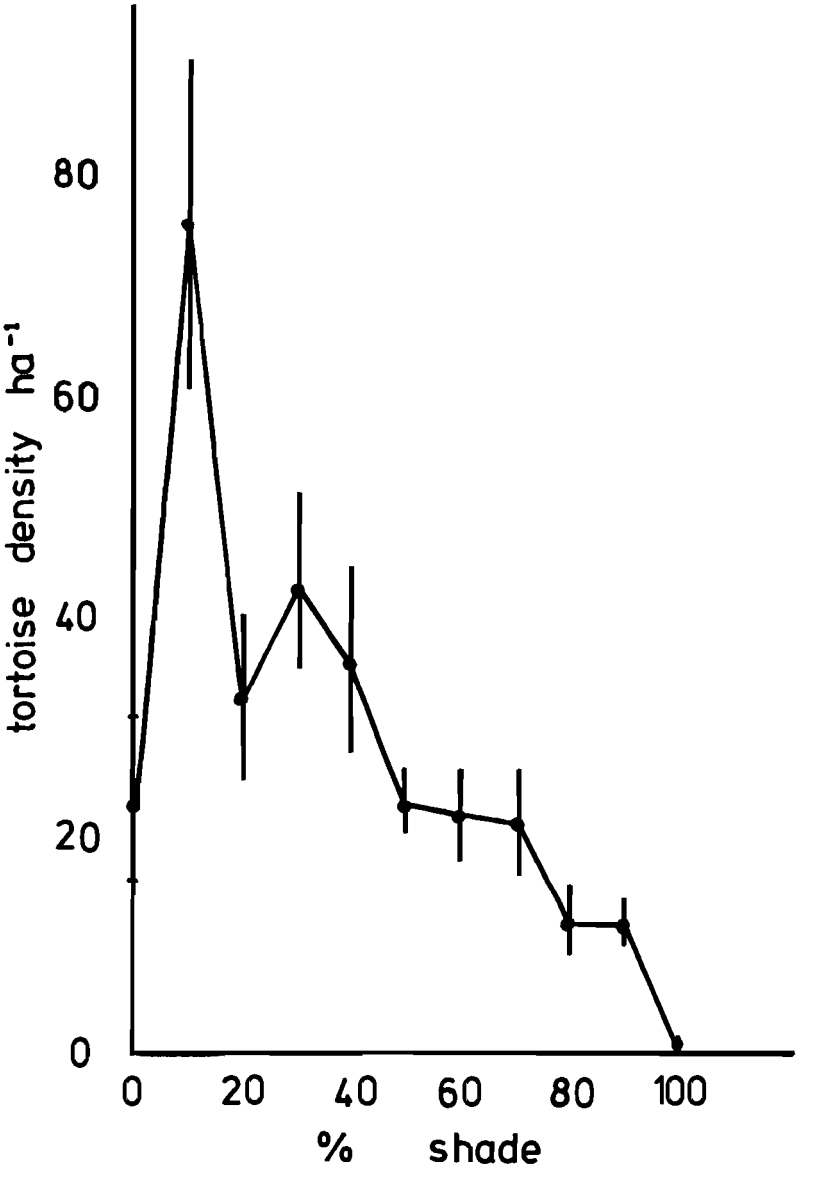

FIGURE 2
Mean tortoise density in sample hectares against percentage shade cover available. The vertical lines represent ±1 standard error of each mean.

gradually increased in frequency to peak in April at the end of the dry season, and subsequently declined as the dry season advanced. Nesting occurred in June, July and August and recent hatchlings were first seen at the onset of the next wet season. The post-mortem examinations showed that females reached sexual maturity at about 55 cm straight length. The size of ova and weights of ovaries in mature females were lowest at the end of the dry season but during the rains and the months immediately following there was a progressive increase in the size of a small number of follicles, and ovary mass increased correspondingly until June when shelled eggs were first found in the oviducts.

About half of the mature females that were examined during the nesting period contained shelled eggs. Of these the mean number of eggs produced was 10,8/female with a range of between 9–15/female. The census showed that 22 per cent of the 100 000 tortoises in eastern Grande Terre were large enough to be considered mature females, i.e. 22 000. If half of these laid about 10 eggs each then the total egg-producing potential of the population in that part of Aldabra was approximately 110 000 eggs per annum.

DISCUSSION AND CONCLUSIONS

Many of the early accounts of European exploration and colonization of the islands of the western Indian Ocean comment on the number of tortoises found, the ease with which they could be caught and the quality of their meat. Rothschild (1915) presented evidence to suggest that at the beginning of the eighteenth century tortoises were abundant on Mauritius, Réunion, Rodrigues and Seychelles but that their number had declined as a result of extensive slaughter by sailors and colonists. By 1840 wild tortoise populations had disappeared from all islands of the Indian Ocean except Aldabra, where perhaps because of the size of the atoll and its inhospitable environment giant tortoises survived. Stoddart (1971), in reviewing the limited information available, concluded that considerable numbers of tortoises had also been collected and removed from Aldabra and that the population had probably come close to extinction by the end of the nineteenth century. Various other estimates of the population size have been made since 1950; 80 000 by Palombelli (1954) (quoted by Gaymer 1968), 33 000 by Gaymer (1968) and 100 000 by Grubb (1971); but it is believed that the figure of 141 000 presented in this paper, derived from random hectare counts carried out in almost all the areas in which tortoises occur, is the most accurate. The number of tortoises seems therefore to have increased dramatically during the past 75 years.

A population obviously cannot expand indefinitely in a limited environment; it is therefore appropriate to pose a number of questions: Is the tortoise population still expanding, or has it reached a state of equilibrium, or is it declining? What are the natural constraints on the population? What are the effects of such high tortoise densities on the vegetation? How does increased competition affect the tortoise population itself? We hope eventually to be able to provide quantitative answers to such questions but at this stage in the study only general observations are possible.

Over much of the atoll the limestone rock, from which Aldabra is formed, is exposed and has been weathered to produce a deeply pitted, jagged terrain, interspersed with pockets of soil

or sand on which a variety of plants commonly eaten by tortoises grow. Despite their apparent ungainliness tortoises are remarkably manoeuverable animals, able to negotiate extremely rough terrain. However, losses do occur when tortoises become inextricably wedged in the rocks, fall into holes or overturn and are unable to right themselves; of 650 mortalities examined it was evident that at least 19 per cent of them had been so trapped.

During the hottest period of the day tortoises are inactive and shelter in the shade of trees or small bushes. In most areas of the atoll shade cover is readily available, but in the eastern region, particularly in the coastal zone some 2 500 m in width, stretching from Point Hodoul to Anse Takamaka there are very few shade trees and bleached carapace remains are common. Seventy per cent of those mortalities, not physically trapped, were found to be in unshaded positions in the open. It is believed that one of the most important causes of death in the tortoise population is due to over-exposure and the resultant heat stress of animals unable to find suitable shade cover during the heat of the day. Deaths from this cause probably occur most commonly in the wet, hot, summer months between November and March. During prolonged periods of rain and overcast skies tortoises remain in the open and do not seek shade cover. After two or three days they may have wandered considerable distances from their original shade trees into areas where shade is absent, and may die of exposure to intense solar radiation and resultant heat stress.

There is considerable circumstantial evidence (Merton *et al.* 1976; Hnatiuk *et al.* 1976) to suggest that the general activity of the large number of giant tortoises in the south-east of Grande Terre is having a profound effect on the vegetation. One of the most obvious changes taking place is the reduction in the amount of shade cover, which is so important to tortoise survival. At what stage shade availability will become limiting on the population as a whole is a matter for speculation but in certain areas where the remains of former shade trees occur many recent tortoise mortalities can now be seen.

Another factor which is probably acting as a constraint on the tortoise population is the availability of food. Some preliminary observations indicate that the daily food consumption of individual tortoises in eastern Grande Terre is very low: 27–88 gm dry mass per day, although the amount is almost certainly dependent on habitat, density, season and size of the tortoise. Comparisons of the sizes of animals of the same age on Ile Malabar and Grande Terre, and recapture analysis from both areas show that the growth rates of the Malabar tortoises are considerably higher than those of Grande Terre animals. This is presumably a reflection on the densities of tortoises in both areas and differing degrees of competition. What effect this differential growth rate may have on the age or size of maturity has yet to be determined but Swingland (pers. comm.) has found that Malabar females produce more eggs of a larger size than females on Grande Terre, which would appear to indicate a biologically fitter population. Why then are there so few tortoises on Ile Malabar? A possible explanation that Swingland is investigating is that suitable nesting grounds with adequate depths of soil are much more restricted on Ile Malabar than on Grande Terre, and that therefore there may be greater nest site competition between Malabar females. Alternatively nest and hatchling predation may be higher on Ile Malabar.

It has been estimated that the annual potential egg production in the eastern region of Grande Terre is about 110 000. However analysis of the population structure indicates that this

figure is far in excess of the number of tortoises surviving to one year. Considerable losses must therefore occur, but so far the factors controlling the number of eggs laid, the number that hatch and the survival of the hatchlings, have yet to be elucidated.

The second phase of the Giant Tortoise Project, concentrating on a detailed reproductive study and a recapture programme, is now in progress. When that work is complete we hope to be able to say more about the factors influencing this unique reptilian species.

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