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THE SIZE, STRUCTURE AND DISTRIBUTION OF THE GIANT TORTOISE POPULATION OF ALDABRA

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(*Communicated by T. S. Westoll, F.R.S. – Received* 9 *August* 1976)

[Plate 1]

CONTENTS

The results of a two year field study of the endemic giant tortoise population (*Geochelone gigantea*) on the western Indian Ocean atoll of Aldabra are described. The work entailed an extensive sample census from which the size of the population was estimated to be 150000 individuals. A large scale marking programme was also carried out. 6882 tortoises (4.6% of the total population) have now been individually marked and measured. Tortoises are unevenly distributed over the atoll with local densities ranging from 0 to 217 per hectare. Various environmental factors are considered in relation to their distribution. A method of age estimation, based on growth ring counts, is described and the characteristics of populations in high and low density areas are compared. Analysis of preliminary recapture information shows that the majority of tortoises are relatively sedentary in their habits, although some are capable of long distance movements; and that individual growth rate is density dependent. The remains of 643 natural tortoise mortalities were examined. Life tables of survivorship and mortality were calculated for the tortoise population in the south-east of the atoll. Crude estimates of mortality and recruitment indicate that the tortoise population in that area is on the decline. Tortoise biomass estimates are far in excess of those for other natural tropical ecosystems with similar rainfall. The vegetation in the southeast is being greatly modified by tortoise activity and there is every indication that the tortoise population there exceeds 'the stable carrying capacity'.

Introduction

The western Indian Ocean atoll of Aldabra lies 10° south of the equator, 640 km east of Tanzania and 420 km northwest of Madagascar (figure 1); because of its isolation and limited natural resources it has remained relatively unspoilt and until recently little scientific research work had been carried out there. During the past decade, as a result of proposed military development now in abeyance, the atoll has been the subject of public concern and considerable scientific interest (Westoll & Stoddard 1971).

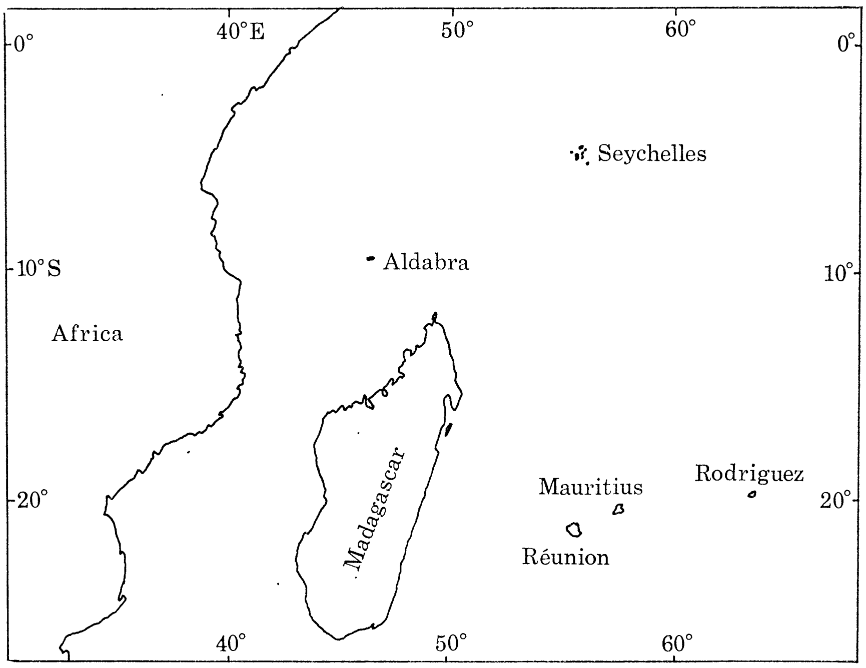


Figure 1. Map of the western Indian Ocean, showing the location of Aldabra Atoll in relation to other islands mentioned in the text.

Four major islands, formed from coral limestone raised some 8 m above sea level, surround a central lagoon. The overall dimensions of the atoll are 35 km by 12 km and the total land surface area, excluding mangrove forests, is 138 km² (figure 2). The distribution of the vegetation and habitat types, described by Fosberg (1971), Renvoize (1971), Grubb (1971) and Hnatiuk (1976), is closely related to the geomorphology of the atoll which has been described by Stoddart, Taylor, Fosberg & Farrow (1971) and Braithwaite, Taylor & Kennedy (1973). More than half of the atoll, from the lagoon mangroves to a narrow coastal zone, is covered by a dense almost impenetrable scrub vegetation; however, in the southeast a much more open grassland, mixed scrub and woodland community exists and along the south and east coasts a relatively open coastal vegetation of low scrub and grassland occurs. The climate has been described by Farrow (1971). There are two distinct seasons: from November to April the light and variable winds of the northwest monsoon bring rain, and temperatures are high, while from

May until October the prevailing southeast trade winds blow with lower rainfall and temperatures. Over the last eight years mean annual rainfall has been 1056 mm (Stoddart, D. R., personal communication); the fluctuations in daily mean maximum and minimum temperatures (22.2–31.2 °C) are greater than the seasonal range of mean monthly temperatures (24.9–28.4 °C); and during the hotter months black bulb thermometer readings often exceed 70 °C (Stoddart & Mole 1976).

It is in this environment that a population of giant tortoises, *Geochelone* (*Testudo*) *gigantea* Schweigger, survives. Early records show that the Indian Ocean giant tortoise used to occur on many of the islands in the western Indian Ocean, including the Seychelles, Mauritius, Reunion, Rodrigues and Aldabra. However, tortoises were widely used for food and trade and by the beginning of the twentieth century wild populations had become extinct everywhere except Aldabra (Rothschild 1915), where their numbers had been drastically reduced (Stoddart 1971). Small semi-domesticated stocks now exist on the Seychelles and Mauritius, but because of the large scale shipment of tortoises around the region their taxonomy is confused and their exact origin uncertain.

The only other population of giant tortoises in the world today are races of *Geochelone elephantopus* (Halan) occurring on islands of the Galapagos Archipelago in the Pacific Ocean. They too were nearly exterminated and MacFarland, Villa & Toro (1974) have estimated the total population to be about 10000. Past estimates of the size of the Aldabran giant tortoise population have been based on brief visits, dubious mark/recapture analysis, limited survey, and/or guesswork. The results have varied considerably: 80000 by Palombelli (1954), 33000 by Gaymer (1968) and 100000 by Grubb (1971). Whatever the figure, they are the major terrestrial herbivore on Aldabra and as has been shown by Grubb (1971), Merton, Bourn & Hnatiuk (1976) and Hnatiuk, Woodell & Bourn (1976) they have a considerable impact on the vegetation. Their ecology and behaviour have been described by Gaymer (1968), Grubb (1971) and Frazier (1972). The work described here was carried out between December 1972 and September 1974; the primary objective was to conduct a wide ranging census and marking programme in order to provide baseline data for a long term study of tortoise population dynamics and energetics.

Methods

(*a*) *Census*

From the results of a preliminary survey of the atoll and from the observations of previous workers (Gaymer 1968; Grubb 1971; Frazier 1972) it was concluded that giant tortoises were most common on Grande Terre, particularly in the southeastern region but also in a zone up to 1 km, in width along the south coast of that island. The census and marking operations initially concentrated on these areas although all of the atoll's major islands were surveyed during the period of investigation.

An approximate 5% census was conducted using a stratified random sample of hectares, based on the Aldabran grid reference system. Five two-figure random numbers were obtained from tables (Kendall & Babington-Smith 1939) for each square kilometre. The first figure of the pair gave the easting and the second the northing in multiples of 100 m. The exact location was then pinpointed on a photomosaic map of the atoll, using a grid overlay, and subsequently transferred to larger scale individual aerial photographs. Where only part of a square kilometre was occupied by land, proportionately fewer sites were selected. In the field the hectares could usually be located without difficulty, using various geomorphological and vegetational features. Only in very dense uniform vegetation did uncertainty of position arise, but this did not affect the randomization procedure.

While every attempt was made to locate each hectare as accurately as possible, distortions in the reference grid, the uncorrected photomosaic map and individual aerial photographs meant that in general an overall accuracy of no more than ± 200 m was possible.

Once the hectare had been located on the ground a perimeter line 400 m in length was laid out using compass bearings. The area was then thoroughly searched by three people. Where marking was to take place all tortoises found were collected together at a central point and immobilized; where tortoises were not to be permanently marked they were individually examined and measured where they were found. Tortoises found on the boundary were collected only along two sides and ignored on the other two. Animals moving into the area after initial collection were also ignored. Collection usually took about three quarters of an hour, but in a few hectares where densities were exceptionally high, two separate half hectare samples were made.

Each marking hectare in the southeast was marked in the field for future reference and 20 hectares in the Cinq Cases area were recounted six months after initial examination. The remains of all dead tortoises which had not completely disintegrated were examined, measured and placed at the site marker.

Figure 2 shows the location of the census sites on Aldabra. The solid circles represent marking and census hectares, the open circles represent census hectares where no marking was carried out. The dashed line indicates the extent of very dense inland scrub composed mainly of *Pemphis acidula* Forst. It can be seen that both Ile Picard and Ile Malabar are largely covered with this scrub. In an attempt to establish how far tortoises were able to penetrate this habitat, three transects were cut on Ile Malabar from the ocean coastline through to the lagoon mangroves. No tortoises or signs of their presence, in the form of dung or skeletal remains, were found. Sampling of populations on these two islands was therefore confined to the relatively narrow coastal strip of more open vegetation. On Ile Malabar sample hectares were sited approximately every 250 m within this strip. On Ile Picard the very low tortoise densities encountered precluded the possibility of using the hectare sampling method, and instead the areas of more open vegetation were extensively searched.

(*b*) *Marking*

In the past, attempts to identify tortoises have included colour coding (Gaymer 1968; Grubb 1971), individual paint numbering (Frazier 1972), scute carving and notching (Viteri 1975). Paint has the disadvantage that it is worn away with time, carving is tedious, notching, although permanant, damages the carapace bone and is difficult to interpret. Gaymer (1973) devised a method of drilling a shallow depression in, but not through, the carapace scute and implanting a serially numbered titanium disk, bonding it to the surface with an epoxy resin. In principle this was the method employed, although in practice some time saving modifications were adopted. A portable generator was used as the power source for an electric drill with a specially machined mount and drill bit that ensured adequate purchase, accurate drilling of the depression and minimal damage to the underlying carapace bone (plate 1, *a*–*d*).

A tortoise to be marked was immobilized by suspending it in a sling hung from a balance mounted on a portable tripod. The drill and bit were positioned over a suitably flat surface of

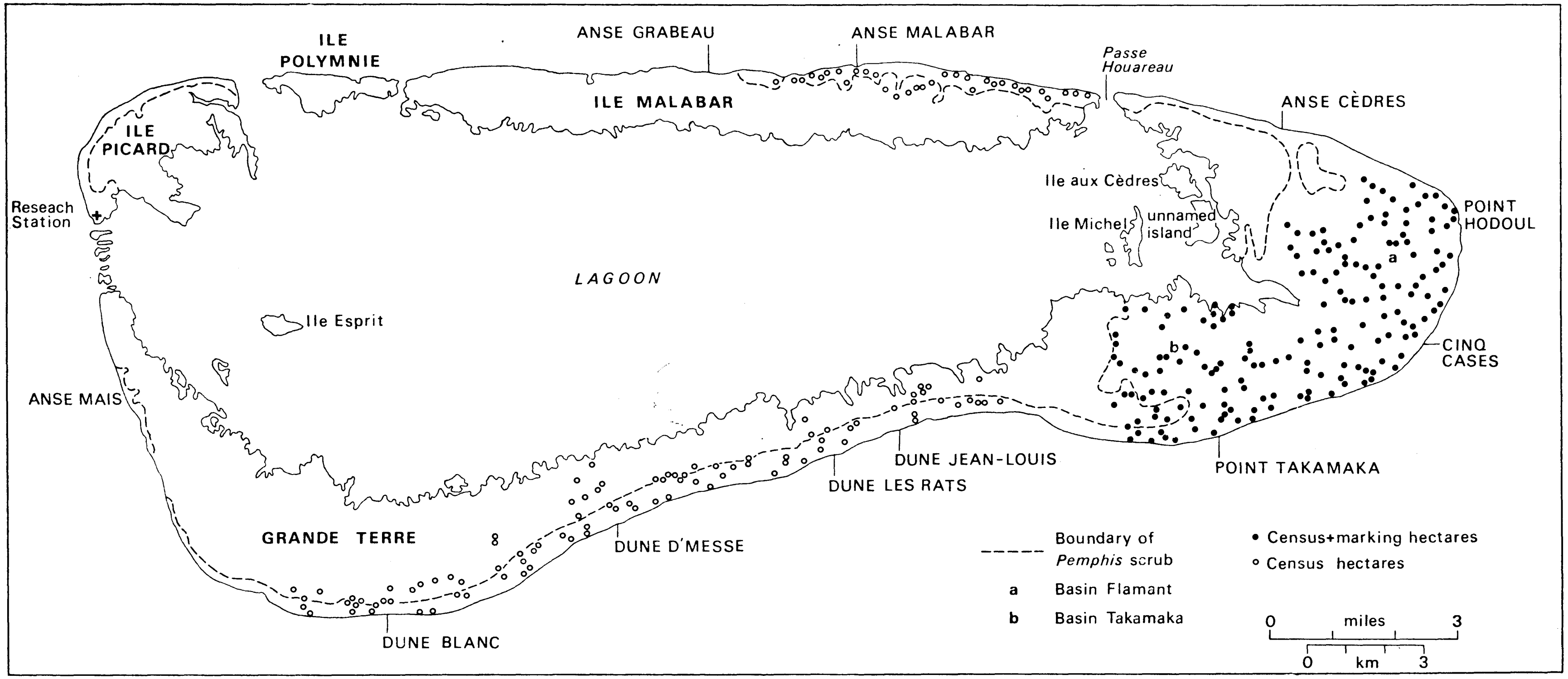


FIGURE 2. Map of Aldabra Atoll, showing location of giant tortoise census and marking hectares, and the place names mentioned in the text. The vegetation in the area bounded by the dashed line and the ocean shore is composed largely of relatively open mixed scrub/grassland and was considered to be most suitable for tortoises The vegetation on the lagoon side of the dashed line is composed mainly of dense *Pemphis* scrub in which few tortoises were found. a = Basin Flamant; b = Basin Takamaka.

the fourth central scute and drilling commenced. As considerable force was required to create the depression, an assistant was required to hold the tortoise steady. Once a depression of 1–2 mm had been made it was filled with freshly mixed epoxy resin and a cleaned titanium disk was eased into position so that a rim of epoxy resin was extruded around its edge. Strips of self adhesive tape were then applied so that as much as possible of exposed surface of the disk was covered without obscuring the number and so that the disk-epoxy surface lay flush with the surrounding scute. The tortoise was then measured, examined and subsequently released, allowing the epoxy resin to harden, a process which took about 6 h, after the animal had been released.

Gaymer (1973) mass marked a total of 700 tortoises at Anse Cedre, Anse Mais, Basin Takamaka, Dune d'Messe, Dune les Rats and Passe Houareau in 1969 and 1970. He placed the disks slightly below the boss and along the midline of the fourth central scute because this scute was considered to receive least abrasion. As disk loss was a possibility it was important to be able to distinguish animals marked at different times, so it was decided to position code the placing of subsequent disks. In the period January to July 1973 disks were placed to the right of the midline of the fourth central scute; and during the period November 1973 to September 1974 disks were placed to the left.

In addition to tortoises marked in the hectares in the southeast of the atoll in 1973/4, other tortoises were marked *en masse* in the vicinity of Anse Mais, Dune d'Messe, Dune Jean Louis, Passe Houareau and Anse Malabar.

(c) *Data collection*

Habitat descriptions for each hectare were recorded, including the predominant types of vegetation and limestone rock formation, the presence or absence of freshwater pools, the occurrence of major plant species, and the amount of shade cover available to tortoises. The grid reference, the time of day, and rainfall in the preceding 24 h were also recorded. The classification of vegetation and rock types was based on that described by Peake (1972) using the area covered as the criterion for dominance. Six habitat types were defined in terms of their height: 'woodland' greater than 4.5 m; 'scrub' between 2 and 4.5 m; 'low scrub' and 'tall herb' between 0.15 and 2 m, distinguished by the woody nature of low scrub; 'low vegetation' which was below 0.15 m; and bare ground. Four geomorphological types were defined: 'granular substrate'; 'platin', limestone rock with little surface; 'pave', limestone rock with a relief less than 0.5 m; and 'champignon', extremely rough and jagged limestone with a surface relief of several meters (Stoddart 1971).

For each tortoise marked, the mass, the curved length from nuchal to supracaudal scutes, the curved width from the junction of the lateral and marginal scutes on one side, over the boss of third central to the junction of the lateral and marginals on the other side, the curved width of the third central scute, the straight length from nuchal to supracaudal scutes, the straight width over the boss of the third central scute, the height from the plastron to the top of the third central scute boss, and the maximum depression of the plastron cavity, were measured. For further morphological descriptions see figures and texts on p. 344 of Gaymer (1968) and p. 330 of Grubb (1971). In addition where possible the number of scute growth rings were counted, the occurrence of any abnormalities and the condition of the animals as indicated by the presence or absence of white growth rings around the scute margins, were noted.

Observations of recaptured animals were usually restricted to their disk number, the grid reference location, the curved width of the third central scute, and weight, except for the

100 individuals whose dimensions were all remeasured within 48 h of marking in order to assess the accuracy of measuring. Marked tortoises found within new hectares were remeasured but not remarked.

The original record cards are held at the Royal Society Aldabra Research Station and a copy of these is deposited with the Royal Society Aldabra Data Unit at the British Museum (Natural History), while the computer cards and a computer magnetic tape of the data are lodged with the Animal Ecology Research Group, Zoology Department, Oxford University.

Table 1 summarizes the tortoise work during 1973/74. In all, 292 hectares were examined: in addition to the 700 animals marked by Gaymer a further 6182 tortoises were marked with disks making a total of 6882; 1804 unmarked tortoises were measured; 1029 marked animals were recaptured and 643 natural mortalities were observed.

Table 1. Summary of tortoise work 1973/74

number of hectares		
southeast Grande Terre census and marking		168
south coast Grande Terre census		92
Ile Malabar census		32
	total	**292**
number of tortoises marked		
marking trials, Anse Mais		50
marked releases, Ile Picard		52
mass marking:		
Dune d'Messe		700
Dune Jean Louis		950
Anse Malabar		101
Passe Houareau		67
hectare marking Grande Terre		4262
by Gaymer 1969/70		700
	total	**6882**
number of unmarked tortoises examined		
south coast census		1455
Ile Malabar census		189
southeast Grande Terre (too small to mark)		160
	total	**1804**
number of recaptures		
Gaymer's		220
Bourn's:		
Immediate		110
mass recaptures:		
Dune d'Messe		64
Dune Jean Louis		129
Anse Mais		28
hectare recounts Cinq Cases		138
traverses of southeast Grande Terre		221
south coast census		54
Ile Malabar census		20
miscellaneous		55
	total	**1029**
number of natural mortalities		
census hectares:		
southeast Grande Terre		168
south coast Grande Terre		61
Ile Malabar		9
miscellaneous		405
	total	**643**

Results

(a) Distribution

Tortoises were found on all the major islands of the atoll except Ile Polymnie. A few of the larger lagoon islands also had small tortoise populations, e.g. Ile Michel, Ile aux Cedres and an unnamed island to the south of Ile aux Cedres although none occurred on Ile Esprit.

On the islands occupied by tortoises they were not evenly distributed. The Ile Malabar and Ile Picard populations were restricted to the comparatively open mixed scrub of a relatively narrow coastal belt on the ocean sides of the islands. This vegetation type is coincident with and and probably dependent on the underlying rock structure of 'Aldabra limestone' (Braithwaite *et al.* 1973). Here the terrain is generally less pitted with some accumulations of soil in which various grass, sedge and herb species commonly eaten by tortoises (Grubb 1971; Frazier 1972) are found. The boundary between the mixed scrub and the very dense scrub dominated by *Pemphis acidula* further inland is usually quite distinct. The underlying rock inland is 'Takamaka limestone'. It is at a slightly lower elevation, is much more deeply pitted and eroded, has very little soil, and few forms of low vegetation occur. After prolonged searches within this habitat no tortoises were found either on Ile Malabar or Ile Picard.

Some areas of Ile Polymnie would appear to be suitable for tortoises but no signs of their presence were discovered, except for the long-dead remains of a single specimen. The only explanation that can be offered is that any population that formerly existed there must have been small and that it was probably eliminated by man.

The situation on Grande Terre was different from that on the other islands in that comparatively large areas of the southeast are formed from 'Aldabra limestone', and soil, while not abundant, is more plentiful than elsewhere; a greater variety of plant species occur, including many low forms which were heavily grazed by tortoises; and semipermanent freshwater pools are relatively common. Tortoises were abundant in this area. They were also common along much of the south coast where a narrow strip of grassland with occasional patches of low scrub is a characteristic feature of the perched coral sand beaches. Immediately inland from this there is a zone of relatively open mixed scrub with some soil pockets and areas of low vegetation with underlying 'Aldabra limestone'. This zone is generally wider than that found on Ile Picard and Ile Malabar, although it gradually becomes narrower towards the southwest. Large numbers of tortoises were also found in these two habitats. Still further inland dense *Pemphis* scrub occurs on deeply pitted 'Takamaka limestone'. Searches in this habitat on Grande Terre showed that some tortoises occurred although their density was very low.

Mangrove forests fringe the lagoon shores of all the major islands of the atoll. They are most extensive in the southeast of the lagoon where large stands of *Avicennia marina* (Forsk.) grow on regularly inundated mud flats and form an open woodland habitat. Low densities of tortoises frequented these areas in the southeast and were occasionally seen afloat on a high tide. It is possible that animals floating in this manner could have been washed into the lagoon and so might have colonized some of the lagoon islands, although human introduction is a more likely possibility.

A visual display of the tortoise distribution in the southeast of the atoll was generated from the total number of animals found in each hectare by a Calcomp General Purpose Contouring Programme, in the form of isodensity lines, figure 3. It was not possible to generate similar maps for other parts of the atoll because of the relatively narrow and irregular shapes of the habitats suitable for tortoises. The contours in figure 3 are set at density values of 10 tortoises per hectare and were computed by comparing the density of any one census site with its immediate 20 neighbours and determining the density gradient between them. The thicker contours represent densities of 50 tortoises per hectare, from which it can be seen that the highest concentrations occurred inland from Cinq Cases and Anse Takamaka. The dashed line indicates the approximate extent of the mangrove woodland and tidally inundated mud flats, where densities were low.

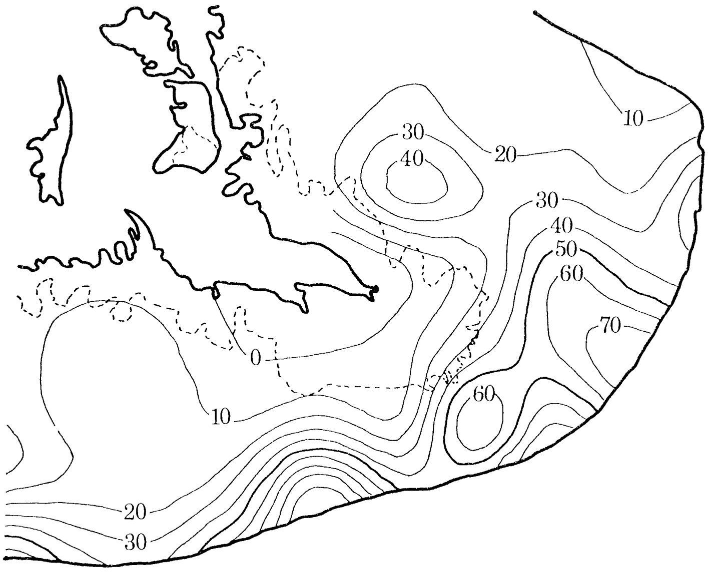


FIGURE 3. Tortoise density contour map, showing their distribution in the eastern region of Aldabra, where the bulk of the population occurs. The map was generated by a Calcomp General Purpose Contouring Programme from tortoise counts in sample hectares throughout the region. The contour intervals are at 10 tortoises per hectare. The dashed line indicates the boundary between the lagoon mangroves/mudflats and dry land. Highest densities occur in the extreme southeast.

(*b*) *Population size*

Coe (1974), reporting on the progress of ongoing field work, gave a provisional estimate of the Aldabran tortoise population size as 'nearly 200000' which has been quoted by Rodhouse *et al.* (1975). Preliminary analysis of more extensive fieldwork yielded a figure of 141019 (Bourn 1976); however, subsequent more refined analysis, which is described here, estimates the total giant tortoise population on Aldabra to be around 150000 (see table 2).

Estimates of the number of tortoises in various regions of Aldabra were derived largely from counts in sample hectares. In the southeast of Grande Terre 168 hectares were randomly stratified on the Aldabran 1 km grid at 5 ha km^{-2}. For each square kilometre the estimated number of tortoises and the standard error of the estimate were determined on the basis of a 5% sample. The estimated number of tortoises within the whole census area was obtained by summation of estimates for each individual square kilometre and 95% confidence limits calculated using an equation derived by Satterthwaite (1946). (See also Morgan & Bourn 1977.)

In the south coast census the 92 sample hectares were also randomly distributed at 5 ha km^{-2} but because of the 'linear' nature of the habitat the degree of stratification was open to question. As a result a mean density figure was calculated from all census hectares and multiplied by the area sampled to give the estimated population size. The uncertainty over stratification does not affect the population size estimate but means that the confidence limits are greater than they otherwise might have been.

The number of tortoises in unsampled suitable habitats on Grande Terre was estimated by multiplying the area they occupied (determined from maps and aerial photographs) by the mean density obtained for adjacent sampled hectares. The number of tortoises in unsampled *Pemphis* hectares was derived in a similar manner except that the mean tortoise density figure used was that found in 14 *Pemphis* hectares which were sampled.

TABLE 2. TORTOISE POPULATION ON ALDABRA

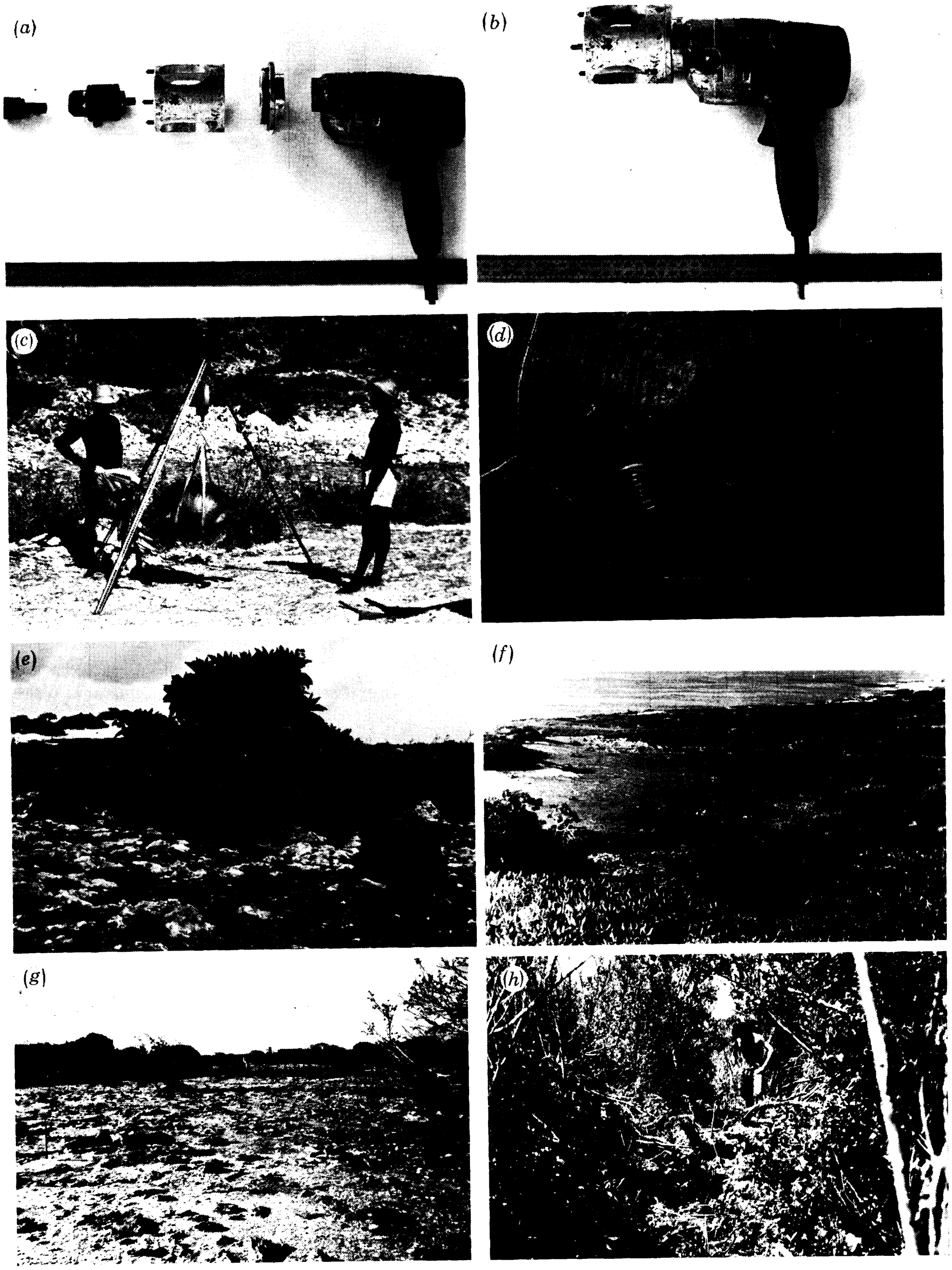
island	Area/ha	tortoise density/ha mean s.e.	d.f.	no. of tortoises	95% confidence limits	% of total population
Grande Terre						
eastern census area	3360	26.95 ± 1.79	19	90560	77994–103126	60.2
south coast census area	1840	20.17 ± 2.29	74	30891	23770–38192	20.5
other suitable areas	960	20†		19200	14200–24200§	12.8
other *Pemphis* areas	3817	1.64 ± 0.63	13	6260	346–12174	4.2
Ile Malabar						
census area	320	7.03 ± 0.67	31	2250	1812–2688	1.5
Pemphis areas	2476	0		0		
Ile Picard						
Non *Pemphis* areas	247	5‡		1235	735–1735 §	
Pemphis areas	500	0		0		
Ile Polymnie						
whole area	189	0		0		
lesser islands						
Ile Michel	33			10		
Ile aux Cedres	43			50		
unnamed island	22			10		
Ile Esprit	10	0		0		
			total	**150466**	**134026–166907**	

† Estimated from densities in adjacent sampled hectares.
‡ Estimated after extensive search.
§ Imputed values.

On Ile Malabar, transects cut through the dense *Pemphis* scrub inland showed that tortoises did not penetrate into it and as a result the sample census was restricted to the narrow coastal belt of suitable habitat. This habitat was of very limited extent and sample hectares were located approximately every 250 m over its entire length. The size of the Malabar tortoise population was estimated from the mean density for all 32 hectares examined and the total area of suitable habitat.

The size of the tortoise populations on Ile Picard and the lesser islands of the atoll was determined after extensive searches had been carried out. These estimates were the most uncertain of all, but unquestionably tortoises occurred at extremely low densities compared with the Grande Terre and Ile Malabar populations. As the populations on Ile Picard and the lesser islands were estimated to be less than 1% of the total population the uncertainty over their exact size is considered to be of little importance.

To obtain confidence limits for total population estimates of 150466 it was necessary to impute



(*a*), (*b*) Exploded and assembled electric power drill and attachments used for tortoise marking. (*c*) Portable tripod and balance used for immobilizing tortoises so that they could be marked and measured. (*d*) Close-up of dorsal scutes of a giant tortoise, showing implanted disk (01641) in the fourth central scute. Although the central area of the scute is beginning to show signs of abrasion, approximately eighteen growth rings can be counted. This is considered to represent the animal's age. Note the white margins of each scute, which denote recent growth. (*e*) Tortoises seeking shelter from the midday sun in the shade of a *Tournfortia argentia* bush on the south coast of Grande Terre near Dune Jean Louis. (*f*)–(*h*) Contrast of three typical habitats on Aldabra. (*f*) A view of the grasslands and low scrub along the south coast of Grande Terre. Over 70 tortoises can be seen. (*g*) The extensive open areas of the southeast of Grande Terre with well cropped 'tortoise turf' on shallow soil and underlying limestone protruding. Note the dead standing trees in the left background. (*h*) Extremely dense *Pemphis acidula* 'jungle' inland on Ile Malabar. The photograph was taken looking down a transect cut with great difficulty through this vegetation type.

(*Facing p.* 149)

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the 95 % confidence limits for the number of tortoises in 'other suitable areas' of Grande Terre (say 5000) and the 'non-*Pemphis*' areas of Ile Picard (say 500). The 95 % confidence limits for the total population estimate are given by the square root of the sum of squares of the individual 95 % limits, and were calculated to be 134026 and 166907. Although these figures cannot be regarded as exact they do indicate the order of magnitude of the confidence limits and hence the overall precision of the total population estimate.

Over 97 % of Aldabran giant tortoises occur on Grande Terre and 62.6 % in the southeast of that island, where the mean density was 2695 km^{-2}, with local concentrations of up to 217 ha^{-1}. Along the south coast the mean density was 2017 $k^{-}m^{2}$. On Ile Malabar the mean density was a quarter of that in the southeast, at 703 $k^{-}m^{2}$, with a very much smaller area of suitable habitat, making a total estimated population of 2250 tortoises. Ile Picard had an even lower estimated density and population size. There were no tortoises on Ile Polymnie. The number of tortoises on all the lagoon islands was considered to be less than 100. In view of the fact that some very small animals may have been overlooked during the census these figures must be regarded as minimum estimates.

The results described in this section are based on a random sample census of the tortoise population. An independent estimate of population size can of course be obtained from mark-recapture analysis. This is discussed in a later section ((*e*) (iv)) and Morgan & Bourn (1977) compare the two methods of estimation in detail.

(*c*) *Tortoise distribution with habitat* (plate 1, *e–h*)

The bulk of the tortoise population occurs in the southeast of Grande Terre and its geographical distribution has been given in a contour map (figure 3). Having determined the geographical distribution of tortoises it is important to attempt to account for the observed distribution in terms of habitats occupied. The southeast was sampled on a random basis and as a result mean tortoise densities can be calculated for each habitat type. Table 3 shows the mean densities, the standard errors of the means and the number of samples for the various habitat parameters considered. Analyses of variance for each of the groupings showed that density varied significantly ($p < 0.001$) with habitat type and shade availability. No significant differences were found with geomorphological type, the presence or absence of fresh-water pools, the occurrence of rainfall in the previous 24 h, or the time of sampling. Neither were significant differences found between seasons for 20 hectares first examined in April 1973 at the end of the wet season and recounted six months later at the end of the dry season.

Highest densities occurred where the habitat vegetation type was either low vegetation or bare ground and there there was little, but at least some, shade. Tortoises are primarily grazers feeding largely on grasses, herbs and sedges, e.g. 'tortoise turf' (Grubb 1971; Merton *et al.* 1976) and *Sporobilis virginicus* L. (Hnatiuk *et al.* 1976), which are two of the major components of low vegetation. In the bare ground habitats there are large expanses of exposed rock, but there are also small soil pockets in which a variety of plant species commonly eaten by tortoises occur. The densities in low vegetation and bare ground habitats, although significantly different from the other habitat types, were not significantly different from each other. High tortoise concentrations occur in habitats where favoured food plants are plentiful. 'Tortoise turf' is a complex of at least 21 species, more than half of which are 'dwarfed', in that, when transplanted sods and seeds are grown under well watered conditions and in the absence of grazing, 11 of the species persisted in their diminutive growth form. It has been suggested by Grubb

(1971) and Merton *et al.* (1976) that this form of growth is the result of selection through intense tortoise grazing pressure.

Tortoises, being poikilothermic animals, must avoid intense solar radiation and it has been shown by Gaymer (1968), Grubb (1971) and Frazier (1972) that they show a marked bimodal diurnal activity pattern, feeding in the early morning and later afternoon and seeking shelter under shade trees from mid-morning to mid-afternoon. The observed variation in tortoise densities with the amount of available shade may be explained both in terms of thermoregulation and nutritional requirements. Where shade was abundant, tortoise food in the form of low vegetation was sparse and few tortoises were encountered. As the amount of shade cover decreased the amount of low vegetation increased, and tortoises became more

Table 3. Tortoise densities broken down by habitat in S.E. Grande Terre

	mean density / ha	standard deviation of mean	sample size
habitat type			
woodland	18.0	19.0	13
scrub	18.1	16.5	72
low scrub	17.1	23.1	22
tall herb	18.2	5.7	6
low vegetation	62.3	25.2	11
bare ground	41.9	43.2	44
shade available (% cover)			
0	23.1	19.7	7
10	75.6	52.8	13
20	32.3	24.7	10
30	42.9	35.3	20
40	35.6	30.2	14
50	22.9	12.6	17
60	22.0	18.5	21
70	21.1	22.9	23
80	12.1	12.5	16
90	12.2	8.7	19
100	0.6	1.8	8
geomorphology			
granular substrate	28.9	29.1	54
platin	26.3	22.2	24
pavé	33.0	28.7	87
champignon	27.5	41.5	52
freshwater pools			
present	28.1	24.3	98
absent	26.2	57.3	70
rainfall			
+ve	27.1	28.3	101
−ve	27.7	33.4	67
time			
a.m.	29.7	32.5	109
p.m.	24.1	25.7	56
season			
original	41.9	31.1	20
reexamined	37.2	29.6	20

abundant, until a maximum density was reached at about 10% shade cover. Where even less shade was available, despite the fact that food plants were present, fewer tortoises were found presumably because they were unable to find protection from the midday sun.

(d) *Population structure*

The size of any animal population is determined by factors inherent within the population and on environmental conditions. Some of these tend to increase the number of individuals while others tend to reduce them. Of prime importance in understanding the dynamics of an animal population is an accurate assessment of its structure, that is to say the ratios of males to females, immature to mature individuals, and the proportion of animals of different age or size classes. The methods for determining the structure of a population are variable and are dependent, on the species being considered. The accuracy of interpreting the information available is often based on a number of assumptions which may be difficult to substantiate. Before discussing in detail the structure of the Aldabran giant tortoise population it is therefore necessary to consider some of the characteristics and peculiarities of giant tortoises themselves. The data used were obtained from each animal encountered during random hectare censuses of the tortoise populations on Ile Malabar and in the southeast of Grande Terre, and is considered to be representative of those populations as a whole.

Table 4. Sex ratio of two tortoise populations

	unsexed (immature)	males	females	total
southeast Grande Terre	2074 (47.5%)	1038 (23.8%)	1258 (28.8%)	4370
		sex ratio	1 : 1.2	
Ile Malabar	90 (23.0%)	138 (35.2%)	164 (41.8%)	392
		sex ratio	1 : 1.2	

(i) *Sex determination*

The absence of external genitalia makes the sex of an individual tortoise difficult to determine and except for size and the amount of wear, the carapace of one animal looks very similar to any other. During the course of the study a number of characteristics were distinguished. Adult males have larger, thinner tails and more concave plastrons than females; females have larger claws on their hind feet, have a more domed appearance and generally do not grow as large as males. Validation of these characteristics was possible from post-mortem examinations of a number of individuals and numerous observations of mating attempts. Nevertheless the characteristics are very much a matter of degree and were only of use for animals larger than 0.65 m curved length (0.50 m straight length; 190 mm curved width of third dorsal scute). It was not possible to sex individuals below that size. Cloacal examination proved to be difficult and unreliable because in young animals the penis and clitoris were very similar in structure.

The post-mortem examinations of Grande Terre tortoises (Bourn 1977) showed that sexual maturity was reached at about 0.70 m curved length (0.55 m straight length; 210 mm curved width of third dorsal scute) which corresponded to the size at which secondary sexual characteristics became evident. Unsexed animals were therefore likely to be immature. However it was easier to identify positively a small female than a small male and as a result small males were probably more often included in the unsexed category and thus underestimated. Of the 4370 tortoises examined during the census of the southeast of Grande Terre, 2074 (47.5 %) were too small to sex and the ratio of males to females was 1:1.2. The sex ratio of the 392 individuals examined on Ile Malabar was the same, although the proportion of animals that could be sexed was lower – 23 % (see table 4). The divergence of the ratio from unity is thought to be the result of the failure to identify small males, previously mentioned.

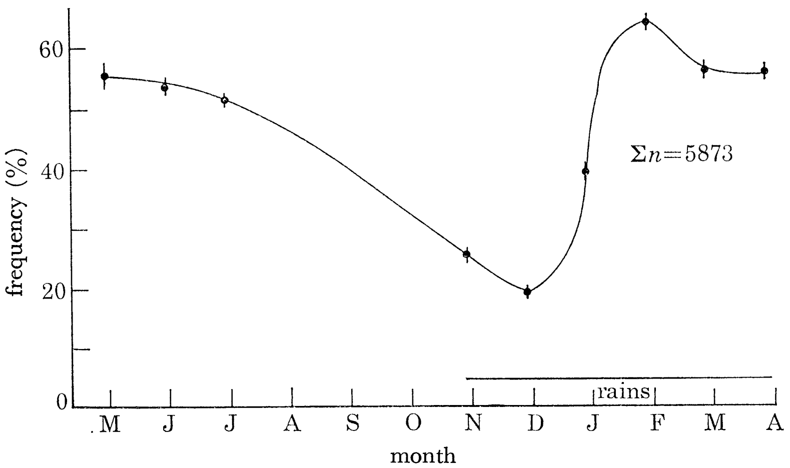

FIGURE 4. The proportion of tortoises examined each month in which fresh white growth rings were evident (±1 s.e.). The rings reflect the periodic nature of tortoise growth. Only those months in which more than one hundred observations were made are shown; in total 5873 tortoises were examined.

(ii) *Growth and ageing*

The tortoise carapace consists of an external surface layer of contiguous scutes made of a horny, keratinous material, with an underlying layer of bone. The degree of ossification increases with age and size. Scutes are present on hatching and at that stage have a distinctive stippled surface, which in older individuals is known as the areolar region. As growth takes place concentric rings of keratin are laid down around the periphery of each scute. During periods of active growth a thin white growth ring is apparent around the scute margins where the new material is laid down. The scutes of relatively small animals have a markedly corrugated surface, although with increasing size and continual natural wear the corrugations are lost and the scutes become smooth.

The climate of Aldabra is seasonal (Farrow 1971), with the months from November to April being wet and hot, while from May to October it is relatively dry and cool. During and immediately after the rains there is a green flush of vegetation; as a result, the quantity and quality of tortoise food, and in turn their condition and growth rate, can be expected to fluctuate seasonally. Indeed the proportion of animals with white growth rings is highest during and immediately after the wet season (see figure 4), which suggests that growth is discontinuous. However, although Aldabra's climate is seasonal, the pattern of rainfall is not always regular. Records since 1968 (Stoddart & Mole, 1976) show that some years may have two or three rainfall peaks during one wet season, which could give rise to a number of subannual rings. After close examination and detailed analysis of growth ring measurements on two hundred small tortoises (less than 30 cm straight length) it was possible to distinguish subannual from annual rings, on the basis of the thickness and the intensity of growth layers forming the rings.

Comparison of the number of subannual rings with the rainfall pattern of the presumed year in which growth took place showed that in years with polymodal rainfall patterns 64 % had subannual rings, whereas in unimodal years only 24 % had discernible subannual rings. The meteorological data on which these figures are based were collected some 30 km from where the tortoises were found. Despite this and probable local variation in rainfall pattern the figures seem to suggest that tortoise growth rings are clearly related to rainfall and that with distinct wet and dry seasons the major growth rings are formed annually. Further evidence to support this was obtained from a number of animals, re-examined one year after having been marked, which showed an additional growth ring, and also from growth ring counts of plaster casts made each year since 1940 on captive animals (Cairncross, B. L., personal communication).

The total annual rainfall is extremely variable: for the period 1968–75 the mean was 1056 mm,

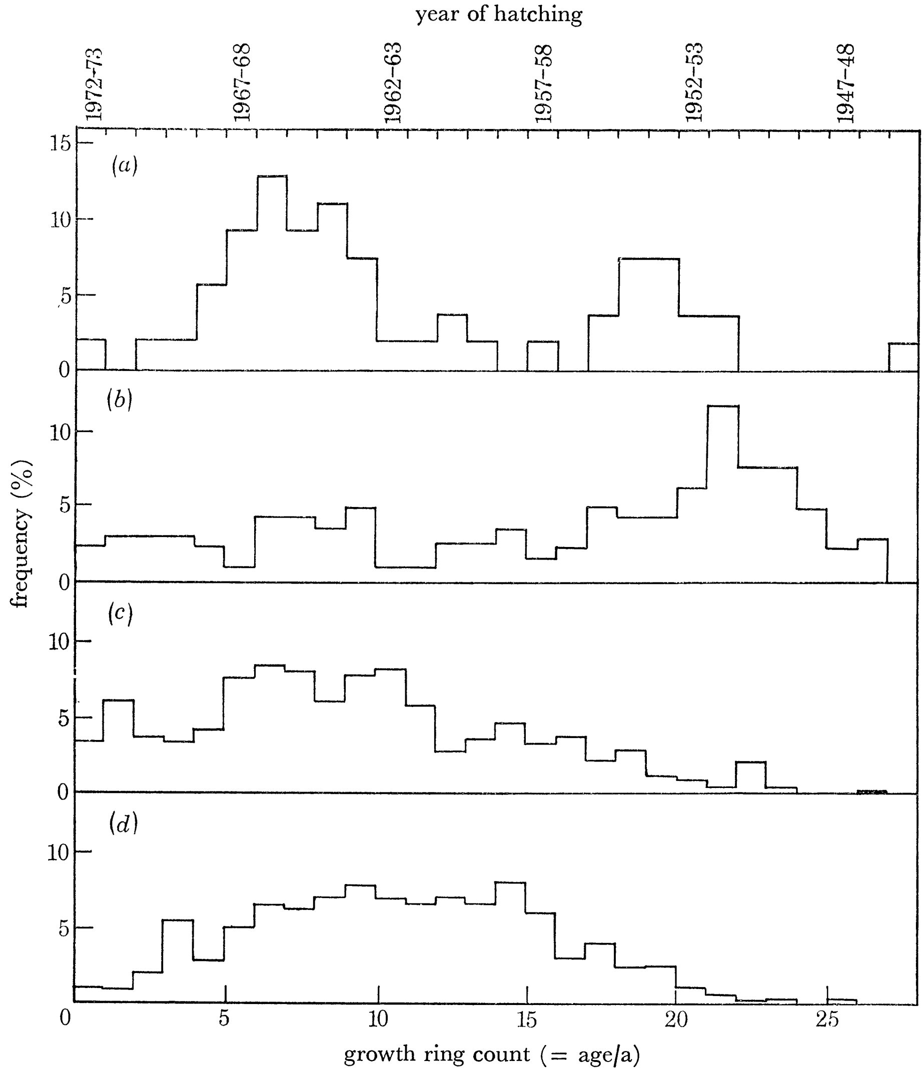

FIGURE 5. Histograms to show the age structure of those segments of four tortoise populations from which growth ring counts were possible. On Ile Picard (*a*) the growth rings of 55 tortoises could be counted (71.4 % of those sampled), on Ile Malabar (*b*) the growth rings of 274 could be counted (68.0 % of those sampled, on the south coast of Grande Terre (*c*) the growth rings of 450 tortoises could be counted (30.1 % of those sampled), and in the southeast of Grande Terre (*d*) the growth rings of 756 tortoises could be counted (17.1 % of those sampled). The presumed year of hatching is given on the top axis.

with a range between 547 and 1487 mm. As a result tortoise growth is likely to vary from year to year and it is possible that in some years little or no growth takes place. In spite of the difficulties described it is still believed that growth ring counts are the best available indicator of tortoise age. Natural abrasive processes gradually wear away growth rings and eventually the scute surface becomes smooth. The ageing technique is therefore only applicable to relatively young tortoises although the maximum number that could be counted varied with individual and locality. Figure 5 shows the age structure of those members of the tortoise populations on Ile Picard, Ile Malabar and two areas of Grande Terre whose growth rings could be counted in this way. The percentage frequencies are based on sample sizes of 55, 274, 450 and 756 respectively. The structures of the Ile Malabar and Ile Picard populations where tortoise densities are low are dissimilar from each other and from the two samples from Grande Terre where densities were considerably higher. The Picard population has two frequency peaks, with animals between 5 and 10 years old (hatching 1963–9); and 18 and 20 years old (hatching 1953–5); the Malabar population has one peak with animals 20–24 years old (hatching 1949–53). The Grande Terre populations are basically similar, with broad bands of higher frequency with animals between 5 and 12 years old (hatching 1961–9) on the south coast and between 5 and 16 years old (hatching 1957–69) in the southeast. All populations, however, have the common feature that tortoises with less than five growth rings appear to represent a relatively low proportion of the ageable population. Some young tortoises, by virtue of their small size, were probably overlooked during the census and thus their frequency underestimated. It is therefore difficult to determine whether or not their low frequency is due to undersampling or to reduced recruitment. Comparison of the two Grande Terre populations does indicate however that the relative frequency of tortoises with less than five growth rings in the southeast is approximately half that on the south coast (20.4 % as opposed to 11.6 %). The habitats in the two areas are not identical: the southeast is generally much more open and small tortoises should have been easier to find there. The lower frequencies of young animals in the southeast may therefore genuinely reflect reduced recruitment.

With increasing age and size tortoises are less likely to be overlooked but the degree of scute wear also increases and counting growth rings becomes more difficult. The apparent decline in frequency of older animals in the two Grande Terre populations is almost certainly due to an inability to assess the number of growth rings of an increasing proportion of each age class. The amount of abrasion is probably in part dependent on tortoise density, and as a result the apparent decline in frequency does not occur on Ile Picard and Ile Malabar until animals are appreciably older.

(iii) *Size index*

It is not possible to age a large proportion of the tortoise population because most individuals have smooth scutes and growth rings cannot be counted. In order therefore to classify the tortoise population an alternative measure must be used. Eight basic measurements were made on each tortoise examined, although during subsequent analysis the curved width of the third dorsal scute was found to be the most useful index of size. It was the most accurately measured parameter (± 1 mm in 97 out of 100 tortoises remeasured within 48 h), convenient to use in the field and involved least disturbance of individuals. During growth analysis of recaptured animals, which is presented in a later section, tortoises were found to grow very slowly and in order to detect changes in size the most accurately measured parameter was required.

If the curved width of the third dorsal scute is to be used as an index of tortoise size it is important to know what relationship it bears to other tortoise measurements. Seven other tortoise measurements were taken during the census – curved length, curved width, straight length, straight width, height, weight and maximum plastron depression for animals in the southeast of Grande Terre. Mean values of each parameter were computed for 25 mm increments of the third dorsal scute. In the first instance regression equations were calculated for males and females separately; significant differences ($p = < 0.001$) were found for curved length,

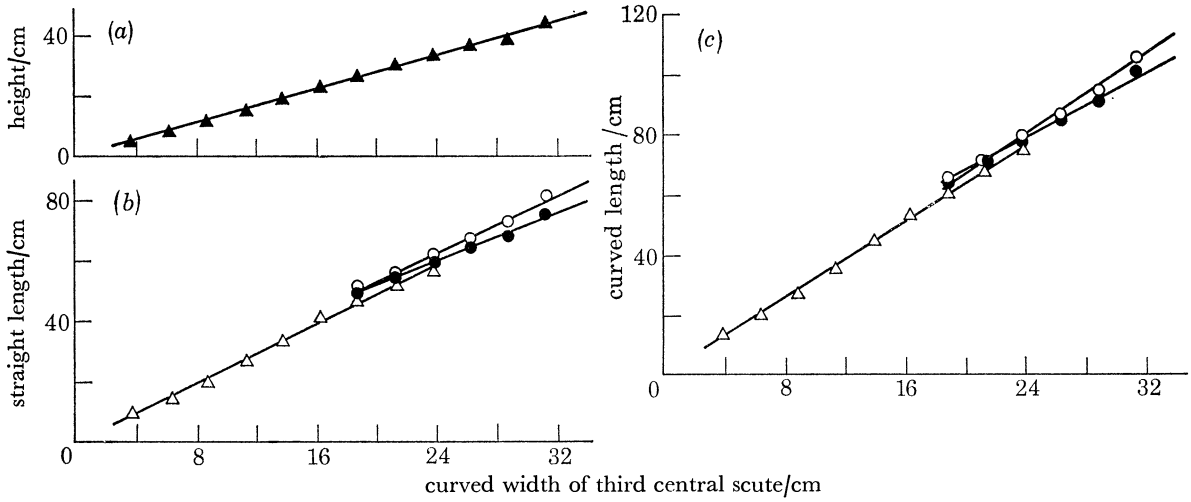

FIGURE 6. Variation of height (a), straight length (b) and curved length (c) with the curved width of the third central scute, for male (○), female (●) and unsexed tortoises (△) in the southeast of Grande Terre. No significant differences were found between the sexes for height. Mean values of each parameter were computed for 25 mm increments in curved width of third central scute.

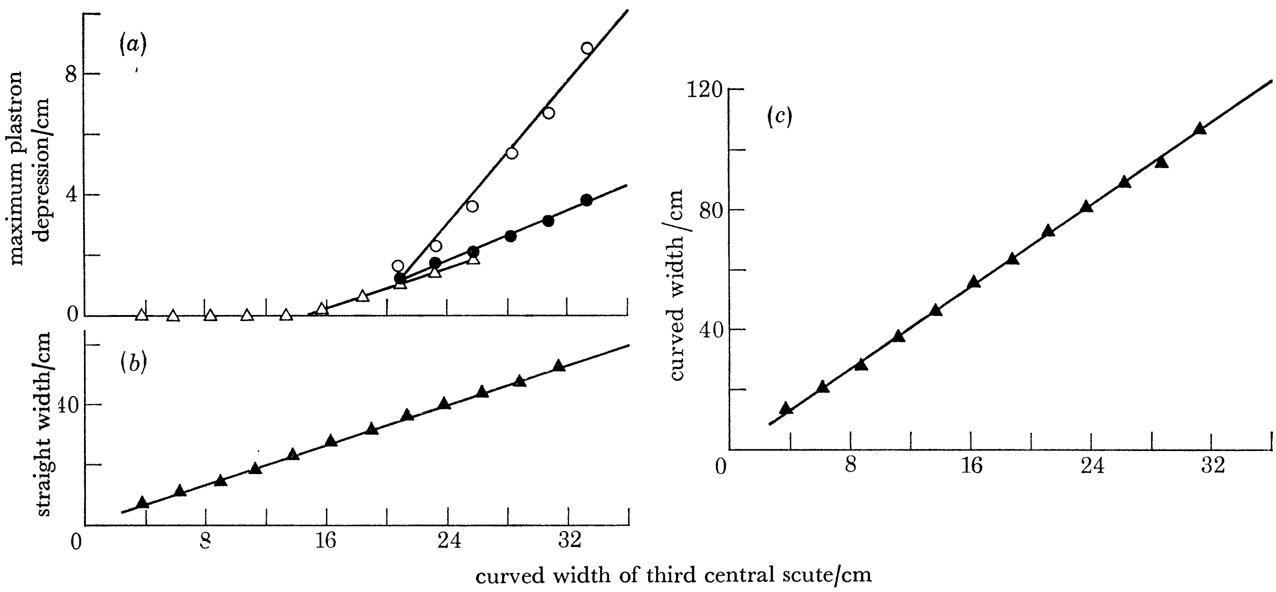

FIGURE 7. Variation of maximum plastron depression (a), straight width (b) and curved width (c) with the curved width of the third central scute, for male (○), female (●) and unsexed tortoises (△) in the southeast of Grande Terre. No significant differences between the sexes were found for curved width or straight width. Mean values for each parameter were computed for 25 mm increments in curved width of third central scute.

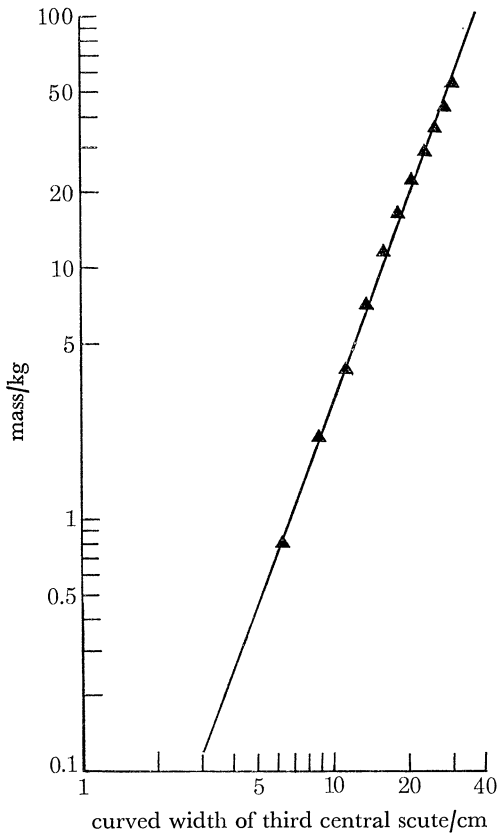

Figure 8. The relation between tortoise mass and curved width of third central scute in the southeast of Grande Terre. No significant differences were found between the sexes. Mean mass was computed for 25 mm increments in curved width of third central scute.

Table 5. Slopes, intercepts and correlation coefficients for various tortoise measurements against the curved width of the third dorsal scute, for tortoises in the southeast of Grande Terre

parameter	sex	slope	intercept	correlation coefficient	n
curved length	male	3.33205	−0.192917	0.998	1036
	female	2.65598	14.1677	0.999	1255
	unsexed	3.14601	0.473984	0.999	2070
straight length	male	2.35539	5.81422	0.995	737
	female	1.92114	13.7255	0.998	958
	unsexed	2.442	−0.188431	0.998	1567
height	all	1.37762	−0.543854	0.999	3258
curved width	all	3.39343	−0.863052	0.999	1642
straight width	all	1.66879	0.519104	0.999	4370
mass (log/log)	all	2.61151	−2.14988	0.999	4342
maximum plastron depression	male	0.587429	−9.98173	0.989	1028
	female	0.202285	−2.65058	0.996	1255
	unsexed	—	—	—	—

n = sample size.

straight length and maximum plastron depression. Where there were no significant differences a new regression was calculated for the combined values of male, female and unsexed tortoises.

The regression lines for the relationships between the curved width of the third dorsal scute and the other measured parameters are shown in figures 6, 7 and 8. The slopes measured are given in table 5. High correlations were obtained for normal plots of third scute against all parameters, except weight, which, however, when transformed to the base ten logarithm scale, also gave a high correlation. No significant differences were found when the regression lines calculated for the Malabar population were compared with those of the Grande Terre population, although Malabar tortoises grew to a larger size.

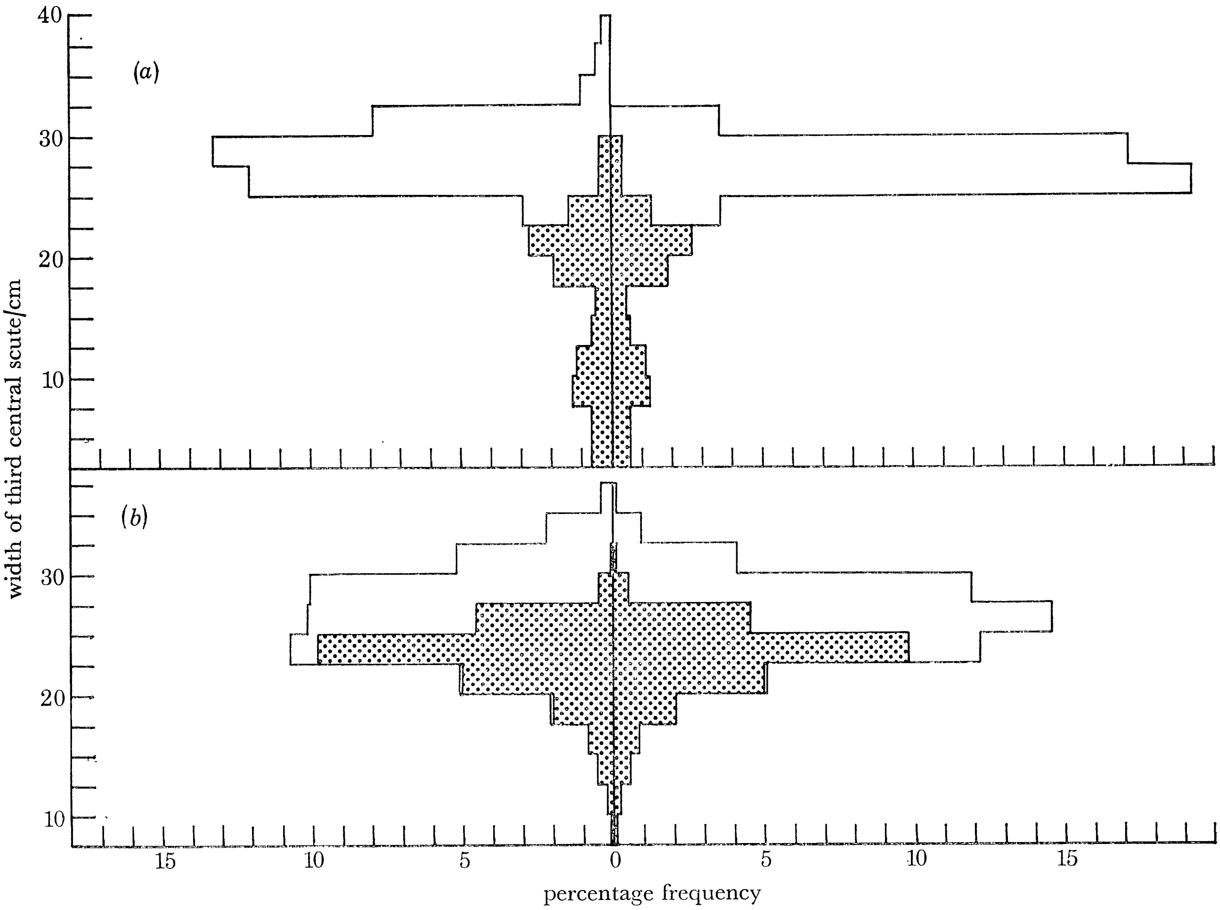

FIGURE 9. The size structure of the tortoise populations on Ile Malabar (*a*) and in the southeast of Grande Terre (*b*). The population pyramids show the percentage frequency of each size class based on 25 mm increments in the width of the third central scute; males to the left, females to the right with unexsexed individuals (stippled) divided equally between the sexes. 392 tortoises were sampled in the Malabar population and 4370 tortoises were sampled in the southeast Grande Terre population.

(iv) *Size structure*

Using the 25 mm increments of the third dorsal scute width as the basis for subdividing the tortoises sampled in the census of Ile Malabar and Grande Terre, 'population pyramids' were constructed to show the size structure of the two populations (figure 9). The horizontal axis represents the percentage of each size class, with males to the left and females to the right of the

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vertical axis which represents the width of the third dorsal scute. The overall sex ratio was taken to be approximately 1:1 and unsexed individuals divided equally between males and females.

The shape of the 'pyramid' is indicative of a declining population, in which the pre-reproductive size classes form a relatively small proportion. Young tortoises, with a third scute width of less than 50 mm, represent a very small proportion of the Grand Terre population (0.2 %) as compared with the Ile Malabar population in which the proportion is six times as great (1.3 %). The Ile Malabar tortoises were generally larger than those on Grande Terre with 72.8 % of the Malabar population having a third scute measurement between 250 mm and 325 mm, whereas 69.5 % of the southeast Grande Terre population had a third scute measurement between 175 and 250 mm. Females on both islands were generally smaller than males.

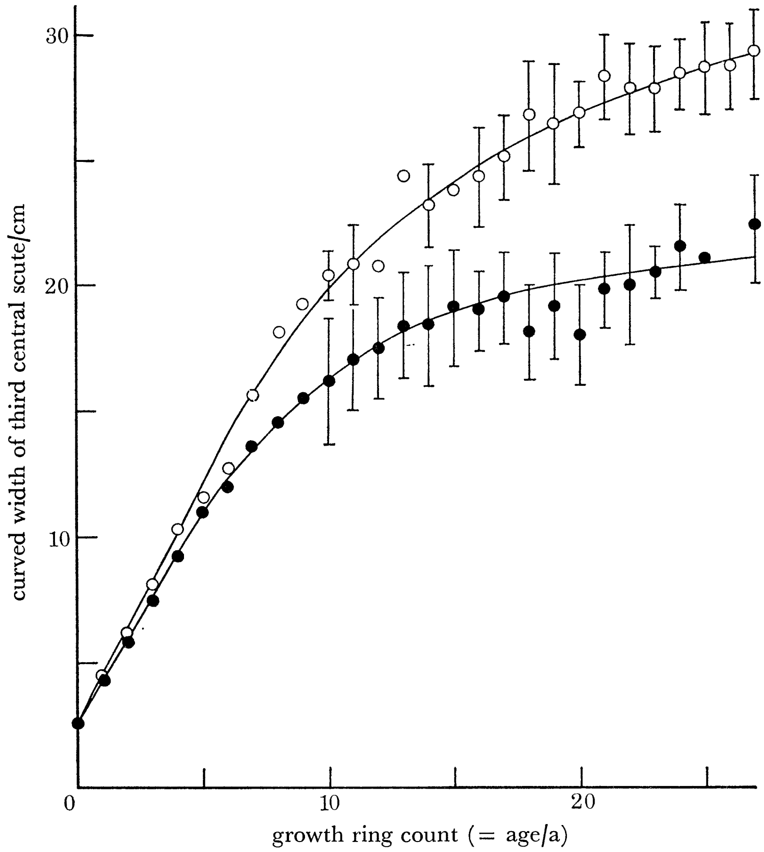

Figure 10. The relation between growth ring counts, which were considered to be equivalent to age, and the mean curved width of the third central scute for 738 tortoises in the southeast of Grande Terre (●) and 274 tortoises on Ile Malabar (○). Vertical lines represent ±1 standard deviation; for the sake of clarity standard deviations are not shown for tortoises less than 10 years old. In older animals, where no standard deviation is given, fewer than five animals were sampled.

(v) *Age prediction*

The relation between the width of the third dorsal scute and the number of growth rings, which were assumed to be equivalent to the age of an animal has been demonstrated by Grubb (1971). The more extensive data described here confirm the relation and make a predictive growth model possible. Figure 10 compares the changes in the mean width of the third dorsal scute with increasing age claws between 0 and 27 for the two populations. The upper curve, reflecting more rapid growth, is for tortoises on Ile Malabar where mean tortoise densities were low (7 tortoises per hectare) and the lower curve is for tortoises in the southeast of Grande Terre, where tortoise densities were considerably higher (27 tortoises per hectare). From the first year of growth the mean curved width of the third dorsal scute of Malabar tortoises was consistently and increasingly greater than that of southeastern tortoises, although over the first 10 years the standard deviation of the means did overlap.

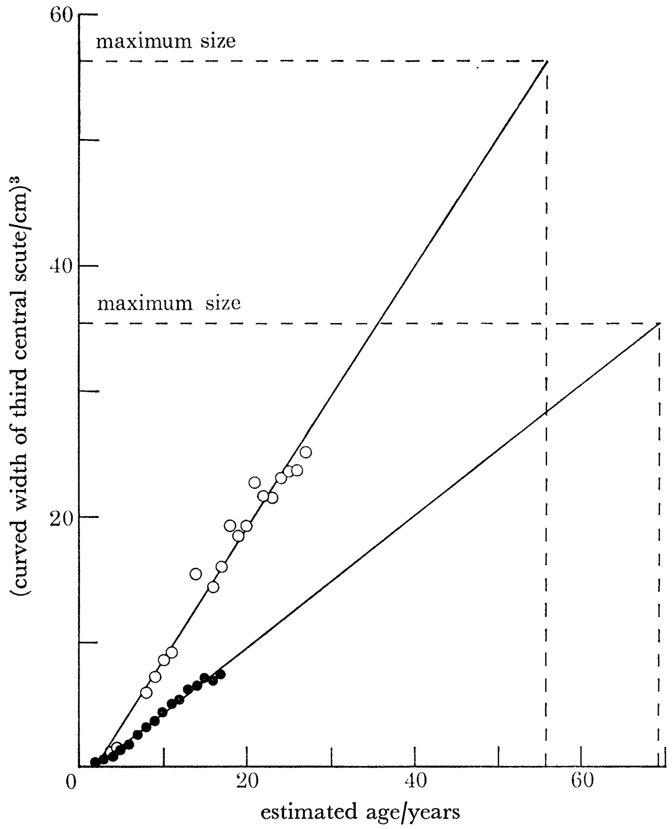

FIGURE 11. The relation between age (as determined by growth ring counts) and the cubed width of the third central scute. For the 274 Ile Malabar tortoises (○) the regression equation was $y = 1063.59x - 2269.13$; $r = 0.990$. For the 647 Grande Terre tortoises (●) the regression equation was $y = 524.28x - 1105.07$; $r = 0.994$. If this relation holds for larger animals whose growth rings could not be counted, then their age may be estimated by extrapolation. The largest animal on Ile Malabar, with a third dorsal scute measurement of 38.3 cm, would have been about 55 years old, while in the southeast of Grande Terre the largest animal, with a third scute measurement of 32.8 cm, would have been about 70 years old.

The greater fluctuations around the ideal growth curve for the Ile Malabar population was thought to be a function of the smaller sample sizes involved in determining the mean for each class. The growth curve for the southeastern population was reasonably smooth up to 17 growth rings but subsequently became more erratic, although the trend was still upwards. This was thought to be a compound effect of (*a*) smaller sample sizes of older age classes as growth rings were increasingly more difficult to count as increments became smaller, and (*b*) growth ring counts becoming increasingly inaccurate as the result of abrasion of early growth rings in the centre of the scute. Ile Malabar tortoises generally had more easily recognizable growth rings, partly because at lower densities they were subject to less abrasion than Grande Terre tortoises.

Nevertheless it proved extremely difficult to count reliably more than 27 growth rings on any Aldabran tortoise in the field. Even in captivity, where abrasion is presumably less than in the wild it was not possible to count the growth rings of giant tortoises known to be between 37 and 40 years old.

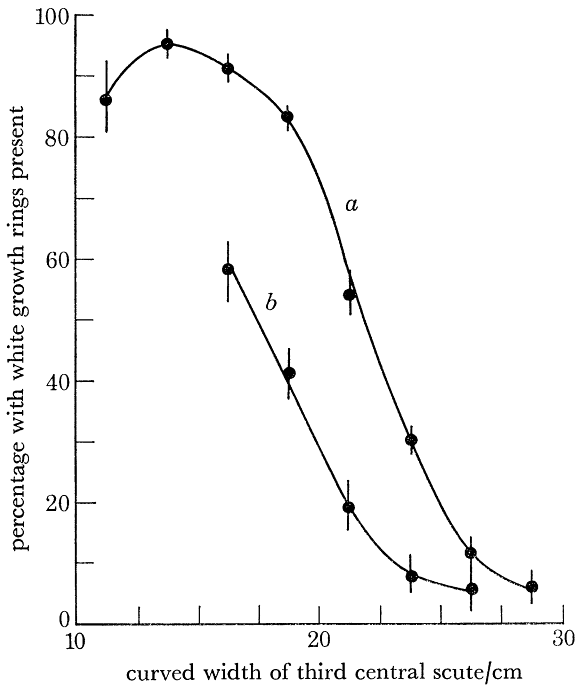

FIGURE 12. The proportions of different sized tortoises with fresh white growth rings evident around their scute margins, at the end of the wet season (*a*) (March, April and May) and at the end of the dry season (*b*) (September, October and November). 2233 tortoises were examined in the wet season sample and 548 in the dry season sample. The vertical lines represent ±1 standard error.

By transforming the data a highly correlated linear relation between the cube of the curved width of the third dorsal scute and age was obtained (figure 11). Growth ring counts greater than 17 for Grande Terre animals were considered to be unreliable and have been excluded, whereas growth ring counts up to 27 for Ile Malabar tortoises were thought to be more accurate and have been included. Regression analysis of the two sets of data provide the growth equations for the two populations with their slopes representing the growth rates. The growth rate of Malabar tortoises was approximately twice that of tortoises in the southeast. If it is assumed that (*a*) tortoises continue to grow throughout their life span, as is indicated by the presence of fresh white growth rings in some of the largest specimens examined, and (*b*) that the rate of growth remains constant, then the regression lines or equations may be extrapolated beyond the maximum age that can reliably be determined and used as a predictive growth model for the population as a whole. Figure 11 shows these extrapolations for both populations and indicates that on the basis of the model the largest Malabar tortoise found might have been 55 years old and that of Grande Terre about 70.

In contrast to most mammals and some reptiles, it is generally accepted that chelonians, crocodiles and snakes are capable of growth throughout their lives. The validity of the predictive growth model for the Aldabran tortoise population hinges on this assumption. Bellairs (1969) has suggested that this capacity for continual growth is due to a different pattern of skeletal development and ossification. In the post-natal life of most mammals, secondary centres of ossification develop in the epiphyses of long bones. When these spread and unite with the diaphyses at maturity, no further growth is possible. Haines (1969) stated that in chelonians, crocodiles and snakes the epiphyses remain cartilaginous throughout life and even aged individuals retain the capacity for further growth. There is some circumstantial evidence to support this contention for Aldabran tortoises. Figure 12 shows the proportion of each size class with discernible fresh white growth rings during two periods of the census in the southeast: during March–April–May, at the end of the wet season; and during September–October–November, at the end of the dry season. Clearly a higher proportion of all size classes were actively growing at the end of the rains and immediately afterwards. Figure 12 also shows that the proportion of individuals with white growth rings appears to decline with increasing size, which could be interpreted as indicating that larger animals tend to stop growing. However the predicted and observed growth of very large animals was only 1–2 mm each year. Growth of this order is much less likely to be manifest as obvious white growth rings and as a result growth may well continue undetected.

(vi) *Age structure*

Using the growth model which relates age linearly with the cube of the width of the third dorsal scute it is possible to estimate the age of all animals whose growth rings could not be counted:

$$\text{age} = ((\text{width of third dorsal scute})^3 + \text{intercept})/\text{slope}.$$

Age was computed for all Malabar and southeastern Grande Terre tortoises, using the appropriate values for the slope and intercept. The proportions of animals falling within five year increments were calculated and the results plotted in the form of 'population pyramids' similar to those previously used to describe the size structure of the Malabar and Grande Terre populations, the difference being that the vertical axis was divided into five year increments. Again unsexed animals were divided equally between males and females (figure 13).

Despite the fact that tortoises on Ile Malabar are larger than those on Grande Terre it appeared from the estimated population age structure that they were probably younger, the age range for Malabar being 0–55 years while that of the southeastern population of Grande Terre was 0–70 years. This may be accounted for by the more rapid growth rate of Malabar tortoises. The population structures indicated that on Ile Malabar the oldest tortoises encountered hatched in the period 1919–24 while in the southeast they hatched between 1904 and 1909.

During the eighteenth and nineteenth centuries there had been considerable trade in giant tortoises around the western Indian Ocean and by the beginning of the twentieth century most island populations had become extinct except on Aldabra where, according to the evidence available, very few tortoises remained (Wharton, 1879; Fairfield, Griffith & Abbott 1893; Abbott 1893; Voeltzkow 1897; Fryer 1910; Rothschild 1915). Concern had been shown over the future of the Aldabran giant tortoise population as early as 1874 (Stoddart 1971) but not until the tenancy of 1900–4 was any provision made in the lease of the atoll for their protection. No information has been found on how effective this protection was, although under the terms of the 1955 lease no more than 50 tortoises could be exported each year. Until 1971, when the Royal Society obtained the lease, some tortoises undoubtedly were killed on the atoll for food.

It is not possible to assess what effect this had on the tortoise populations on each island but it was probably most marked on Ile Picard where the permanent settlement was established and where numerous tortoise remains bearing unmistakable signs of unnatural death have been found. Elsewhere on the atoll the killing of tortoises was probably restricted to the vicinity of the various temporary encampments. Animals exported from the atoll, some destined for zoological gardens around the world, were probably selected primarily for their large size and their accessibility in relation to suitable loading beaches, although some small individuals were almost certainly taken for customary reasons on the Seychelles and because of the ease with which they could be transported and hidden.

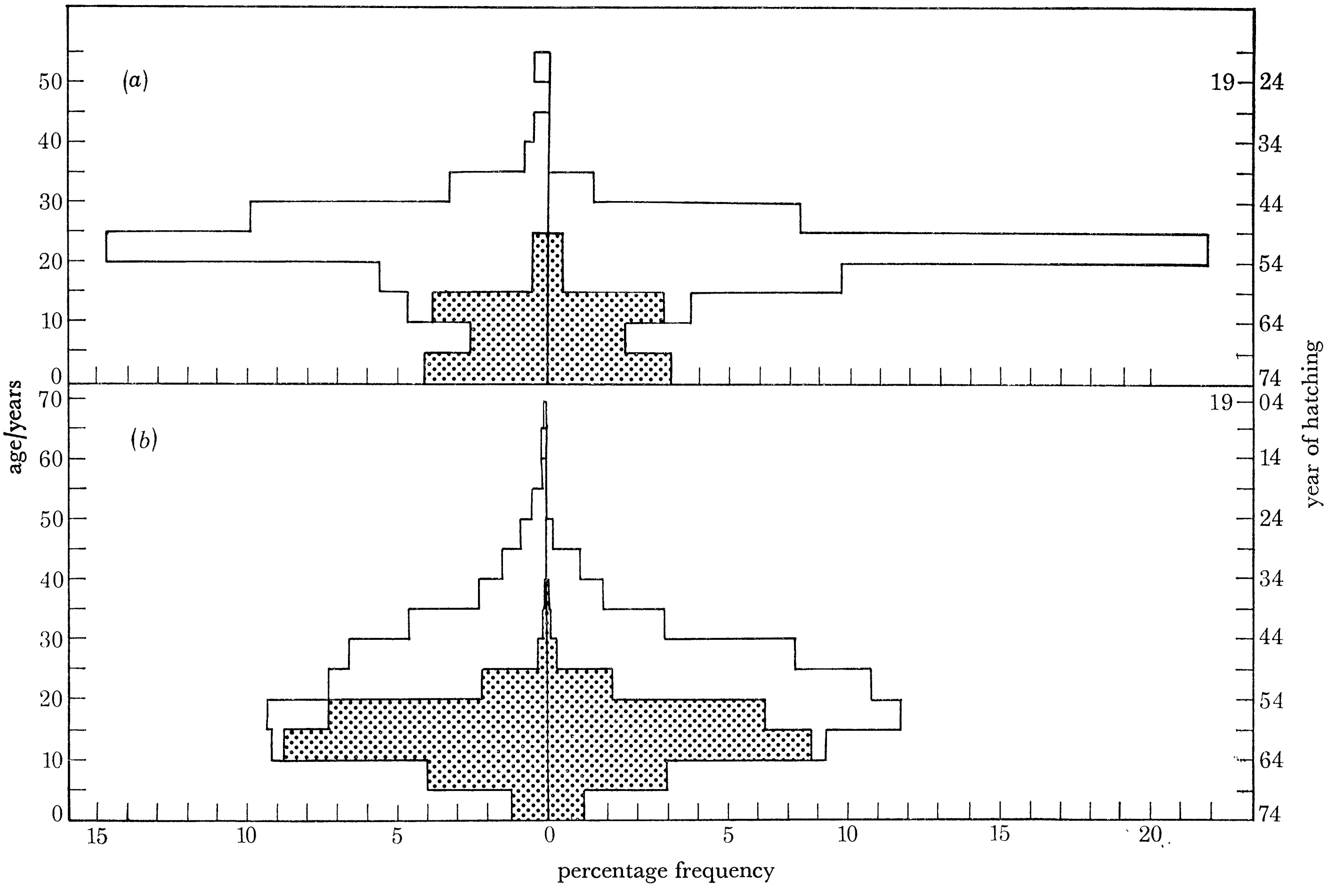

FIGURE 13. Estimated age structure of tortoise population in Ile Malabar (*a*) and in the southeast of Grande Terre (*b*). The population pyramids show the percentage frequency of five year incremental age classes; males to the left, females to the right with unsexed individuals (stippled) divided equally between the sexes. The presumed year of hatching is shown on the right axis. 392 Malabar tortoises were sampled and 4370 in the southeast of Grande Terre.

Interpretation of the age structure of the populations was therefore complicated by a number of factors. The populations have in all probability expanded dramatically in the last 70 years and in certain areas large and small tortoises have probably been removed from the population. The effects of human interference have probably been most marked on the relatively small populations on Ile Malabar and Ile Picard. The Picard population was once exterminated and subsequently reintroductions were made (Abbott 1938; Dupont 1907). Recently the Malabar population has probably been severely affected as it contains the largest individuals.

The age structure of the southeastern tortoise population was more symmetrical than that of the Malabar population, with an increasing proportion of each age class from 1904 until 1959. If the population had been stable during this period the increasing proportion might be accounted for by a steady loss of older animals from the population due to natural causes, but because of the probable expansion of the population the increased proportions must be the net result of increased recruitment as well as mortality losses. Since 1959 the size of each age class was found to be smaller than the previous one, which is indicative of reduced annual recruitment in the past 15 years. From the proportion of the population in the youngest age class and the total number of individuals in the population a crude estimate of mean annual recruitment for the period 1969–74 could be calculated. In the southeast of Grande Terre this figure was 4.8 per 1000, while for the Ile Malabar population the figure was 16.8 per 1000. These figures are certainly underestimates as they fail to take into account mortality of very young tortoises, which may be considerable, and possible under-sampling of very small individuals that could have been missed during the census.

The age structure of the Malabar population was much more irregular. From 1919 to 1954 the rate of increase in the proportion of each age class was greater than on Grande Terre; 37 % of the Malabar population was between 20 and 25 years old while on Grande Terre that age class represented only 18 % of the population; subsequent age classes declined in proportion except for the youngest which made up 8.2 % of the Malabar population – three times the proportion on Grande Terre; the proportion of immature animals was half that present in the Grande Terre population; and on the basis of the age at which sexes could be distinguished the onset of sexual maturity occurred earlier on Ile Malabar.

The largest single age class of Malabar tortoises, representing 37 % of the island's population hatched in the period 1949–54. It is probably no coincidence that between April 1948 and February 1955 the lease of Aldabra lay vacant and presumably the atoll remained uninhabited (Stoddart 1971). During that period the tortoise population would have been unmolested and young tortoises could not have been removed. One can only speculate on the possibility that many of the animals that produced these age classes may have been removed from the population under the terms of commercial lease of the atoll that was taken up again in 1955, and that the increased proportion of tortoises 0–5 years old is due to the recent onset of maturity in individuals that hatched between 1949–54. If this is the case then the Ile Malabar population may well be on the point of increasing dramatically in size. However, the habitats on Ile Malabar and in the south-east of Grande Terre are very different and one of the limiting factors for the Malabar population may be the availability of suitable nesting sites. A typical tortoise nest is about 25 cm in depth (Bourn 1976) and areas of Ile Malabar with that depth of soil are relatively uncommon. It is also of interest to note that between 1917 and 1932, the period in which the age classes of the southeastern population began to increase in size, there is also no record of an Aldabran lease being held (Stoddard 1971).

(*e*) *Recapture analysis*

Although the primary objective of the first phase of the tortoise project was to provide the baseline data for a detailed recapture programme in subsequent phases of the project, some initial recapture work was carried out. Recapture information was obtained when bulk marking areas were revisited; previously marked animals were found in new census hectares and during a series of random traverses conducted in the southeast of the atoll.

(i) *Observed growth*

The pattern of tortoise growth is episodic and dependent on seasonal climatic variation and concomitant factors related to food availability; because of this, individuals recaptured within eleven months of marking were excluded from analysis and for the remainder an annual rate of increase in curved width of the third central scute was computed. This parameter was used because it was the most accurately measured and growth changes were found to be relatively small. For each size class the mean growth rates and their standard deviations were calculated for all the animals recaptured in selected areas. The sample sizes were too small to segregate into males and females. When plotted logarithmically, size class and mean growth rate were found to have an approximately linear negative relation (figure 14). That is to say, the larger the animal the smaller the annual increase in the curved width of the third central scute.

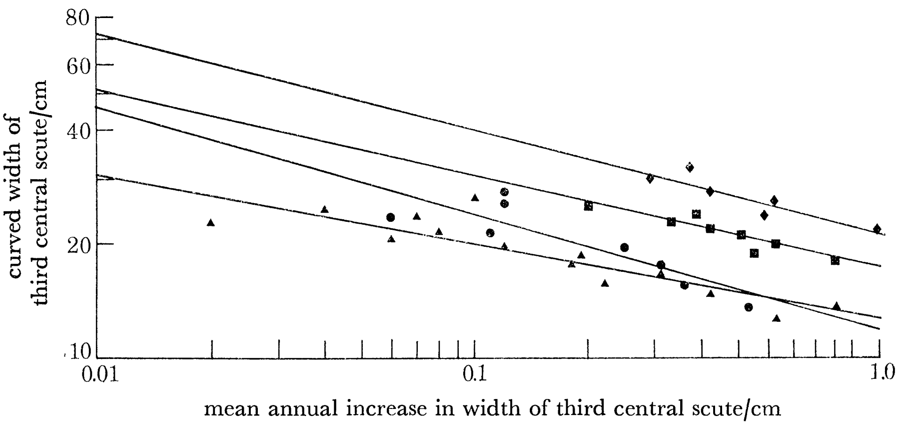

FIGURE 14. Differential growth rates of tortoises recaptured in four regions of Aldabra. The mean increase in width of the third central scute was calculated for various size groups of recaptured tortoises that had been marked in each region approximately one year previously. The logarithm of mean growth was then plotted against size, and regression equations calculated: Ile Malabar (◆) $y = 1.353–0.262x$; $n = 47$;$r = -0.91$. Anse Mais (■) $y = 1.292–0.123x$; $n = 102$; $r = -0.84$. South coast (●) $y = 1.119–0.254x$; $n = -297$; $r = -0.83$. Southeast (▲) $y = 1.127–0.185x$; $n = 185$; $r = -0.88$.

However the growth rates of tortoises in different parts of Aldabra were not the same, as indicated by the slopes and intercepts of the growth regression lines for the different areas considered. Ile Malabar tortoises had a faster growth rate than tortoises on Grande Terre which confirms the conclusion drawn from the relationship between the number of growth rings (age) and the width of the third dorsal scute (figure 10). Of the areas of Grande Terre considered, tortoises grew more quickly at Anse Mais than along the south coast and more slowly in the southeast.

The census showed that Ile Malabar tortoise density was 7/ha, that for the south coast of Grande Terre was 20/ha and that for the southeast of Grande Terre was 27/ha. The density of tortoises around Anse Mais is not known precisely but is intermediate between that of Ile Malabar and the south coast. It seems clear therefore that individual growth is closely related to tortoise density. The observed growth rates also confirm the differential growth deduced from growth ring counts and third central scute measurements of tortoises on Ile Malabar and in the southeast of Grande Terre (figure 10). Recapture of 10 animals 16 months after they had been taken from Dune Jean Louis on the south coast and released on Ile Picard, where tortoise density was much lower, showed substantially faster growth than Dune Jean Louis tortoises during the same period. While the habitats of the areas considered are not identical and food availability and quality may of course differ, there seems to be considerable circumstantial evidence to suggest that tortoise growth rate is density dependent.

Table 6. Long distance records of tortoise movement

disk number	marked at	recaptured at	straight line distance (km)	months elapsed
00009	Passe Houareau	Anse Malabar	5.7	47
00009	Passe Houareau	Anse Grabeau	7.7	60
00100	Anse Mais	Dune Blanc	9.4	54
00294	Dune d'Messe	Takamaka Lagoon	15.4	46
01563	Dune Jean Louis	Basin Takamaka	7.2	14
01574	Dune Jean Louis	nr. Basin Takamaka	7.6	4
01660	Dune Jean Louis	nr. Point Hodoul	15.2	12
01879	Dune Jean Louis	Anse Mais	25.5	14
05507	nr. Basin Flamant	east side of Passe Houareau	6.9	7

(ii) *Movement*

Tortoises were found to be capable of moving surprisingly long distances in relatively short periods of time and appeared able to range throughout areas of suitable habitat on Ile Malabar and on Grande Terre (see table 6). However, analysis of all recapture records showed that long distance movements were exceptional. The straight line distance moved from the point of marking to the point of recapture was computed using the grid reference figures and simple trigonometry. The distances thus calculated must of course be considered as minimum estimates. The movement of tortoises recaptured on return to bulk marking areas would obviously be biased in favour of more sedentary animals; analysis was therefore restricted to tortoises recaptured during a series of random traverses of the southeast, conducted after the marking programme had been concluded. All tortoises encountered along predetermined but random routes were counted and those with disks reexamined.

A total of 3701 tortoises were recorded including 221 recaptures. Of the recaptured animals, 147 had been marked between 11 and 14 months previously. The frequency distribution of total distance moved in a straight line by these individuals that had been in the field for about a year was strongly skewed towards zero with 56 % being recaptured less than 500 m from their site of marking and only 8 % having moved more than 2000 m.

Morgan (1975) examined the proportion of marked to unmarked tortoises encountered along the traverses and the number of 'runs' of unmarked animals between successive recaptures and found that the distribution of marked tortoises within the population did not differ significantly from that expected if they were locally uniformly mixed.

One may therefore conclude that most tortoises within the population in the southeast of the atoll are relatively sedentary, ranging less than 500 m in a year, but that a small porportion are capable of travelling much greater distances.

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(iii) *Disk losses*

During 1970–2, 143 tortoises marked by Gaymer were resighted, of which three had lost their disks. A similar disk loss rate, of about 0.5 % per annum, was found during the random traverses of the southeast (1/221 recaptures, after about a year in the field). It should be remembered that although having lost a disk a tortoise could not be individually identified, it was still possible to recognize it as a marked animal by the remaining epoxy resin or the drilled depression in the scute.

FIGURE 15. Contour map of tortoise mortality density, showing the distribution of tortoise skeletal remains in the eastern region of Aldabra, where the bulk of the live tortoise population occurs. The map was generated by a Calcomp General Purpose Contouring Programme from tortoise mortality counts in sample hectares throughout the region. The contour intervals are at one mortality per hectare. The dashed line indicates the boundary between the lagoon mangroves/mudflats and dry land. The highest mortality density occurred in the extreme southeast.

(iv) *Estimation of population size in the southeast of Aldabra*

Morgan & Bourn (1977) have examined the recapture data collected in the random traverses of the southeast of the atoll. On the assumptions that (*a*) marked tortoises were uniformly mixed within the population in the areas surrounding the original marking hectares, and (*b*) that losses from the population due to mortality and emigration were of the order of 3 % per annum, using a modified version of the 'Petersen estimate' of population size a figure of 69186 was obtained, with 95 % confidence limits of 61206 and 78193. This estimate was for the south-eastern census area alone, and refers to those tortoises large enough to bear a disk. If an allowance is made for those tortoises which were too small to be marked (8.7 %) then the corrected mark/recapture estimate of population size is 75779. This estimate is 14781 fewer than that derived from the direct sample census, although the 95 % confidence limits do just overlap. Morgan & Bourn (1977) consider the reliability of the two estimates and conclude that the census estimate is probably the more accurate.

(*f*) *Mortality*

The terrestrial ecosystem of Aldabra is remarkable for the absence of large predators, a fact accentuated by the failure of giant tortoises to withdraw their heads when asleep. However, potential tortoise predators are present and include coconut crabs (*Birgus latro* L.), pied crows (*Corvus albus* (Müller)), sacred ibises (*Threskiornis aethioica abbottii* (Ridgeway)), flightless rails (*Dryolimnas cuvieri* (Pucheran)) and introduced rats (*Rattus rattus* L.) and cats (*Felis catus* L.). These creatures would only be able to prey on smaller tortoises, and individuals above 30 cm curved length would be large enough to escape attack. The remains of larger animals, dying from other causes, persist in the field for considerable periods and during the census details of their number, size, degree of breakdown and position were recorded. Their distribution is shown in the contour map of the southeast of the atoll (figure 15), produced by the Calcomp General Purpose Contour Programme described previously. Contour increments were set at one mortality/hectare. Comparison with figure 4 shows that areas of highest mortality approximately coincide with those of highest live density.

Of the 547 mortalities which were examined in the southeast, including those found in census hectares, 17 % had died because they had become inextricably trapped in deeply pitted terrain, wedged under tree roots or had overturned and been unable to right themselves. Of the remainder, three quarters had died in open, unshaded positions, about half of which were more than 50 m from the nearest available shade. The cause of the majority of their deaths was considered to be heat stress due to an inability to find suitable shade cover during the hottest part of the day. Deaths from this cause were witnessed during the summer months and were probably most common then. Disease, malnutrition and senescence are other causes of death, but at the present time it is not possible to assess their importance.

The mean density of tortoise mortalities in the southeastern census area was 1.2/ha, with a standard error of 0.3 and a range of between 0 and 9/ha. The remains of 31 tortoises with known dates of death were monitored for up to 18 months in order to determine the rate of breakdown. Considerable variation was found, but in general terms the skeletal remains of larger animals broke down more slowly than those of smaller individuals, presumably because of a higher degree of carapace ossification; and the remains in sheltered positions broke down more rapidly than those in exposed positions probably because they were more susceptible to damage by other tortoises seeking shade and also subject to prolonged scavenging by coconut crabs. Tortoises with a curved length less than 70 cm had usually reached what was regarded as the final stage of breakdown, with collapsed carapace and crumbling bones, after about 200 days; larger animals took much longer and it is probable that their remains persisted for 2–3 years (Bourn & Coe 1978).

It is considered reasonable to assume that the average persistence of the remains of animals with a curved length greater than 60 cm is about two years and it follows from the mean mortality and live density figures that the annual mortality rate for animals larger than 60 cm curved length is about 29/1000. Insufficient marked mortalities were encountered during the limited recapture work, but it is hoped that during the follow-up programme sufficient numbers of dead marked tortoises will be found to provide an independent assessment of mortality rate. It is not possible to estimate losses from the population of tortoises smaller than this, in particular those small enough to be subject to predation, although it is suspected that these may be considerable.

The mean mortality density on Ile Malabar was 0.28/ha, representing an annual mortality rate very similar to that in the southeast of 27/1000 for tortoises with a curved length over 60 cm; however, these figures are based on a very small sample since only 15 mortalities were found. The age of those mortalities in the southeast whose third scute width could be measured was estimated using the age/size class model for the southeastern tortoise population, previously described, and the age frequency distribution plotted (figure 16). From these data, a life-table

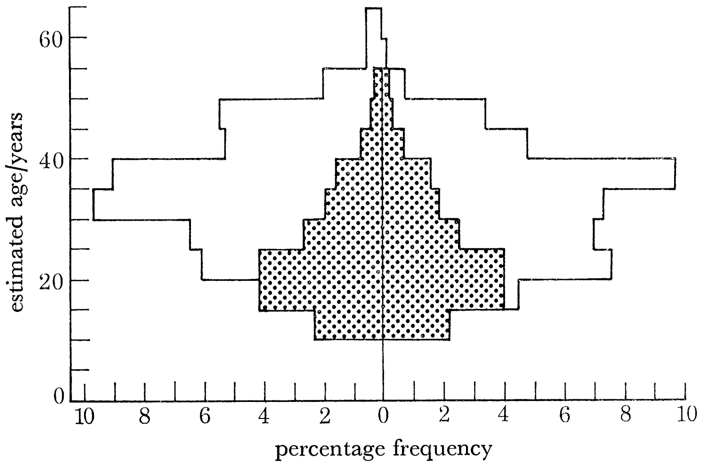

Figure 16. Estimated age structure of tortoise mortalities found in the southeast of Grande Terre. The mortality pyramid shows the percentage frequency of five year incremental age classes; males to the left, females to the right with unsexed individuals equally divided between the sexes.

Table 7. Survivorship and mortality rate of southeastern tortoises from mortality data and survival estimated from live census data

	mortality data			live census data	
estimated age years (x)	number dying in age interval out of 1000 deaths (dx)	number surviving at beginning of age interval (lx)	mortality rate/1000 alive at beginning of age interval (1000 dx/lx)	number alive in each age interval (n)	number surviving at beginning of each age interval ($l'x$)
15–19	91	1000	91	918	1000
20–24	144	909	158	792	863
25–29	144	765	188	646	704
30–34	180	621	290	372	406
35–39	200	441	454	179	195
40–44	106	241	440	116	126
45–49	94	135	696	49	53
50–54	28	41	683	25	27
55–59	8	13	615	6	7
60–64	5	5	1000	8	7

of mortality rates and survival for each five year age class greater than 15 years old was determined (after Deevey 1947; Giles 1971) and shown in Table 7. Mortality rates for younger animals could not be reliably determined because their remains were much less persistent. For comparison this table also shows survivorships calculated from the age structure of the living tortoise population in the southeast. This latter calculation assumed that the decreasing number of tortoises with increasing age class above 15 years old was a reflection of mortality, rather than increased recruitment prior to 1959. The two survivorship curves are plotted in figure 17, from which it appears that survivorship as determined from mortality data is slightly greater than that determined from the live population structure. However, it should be noted that the mortality data used did not take into account differential rates of breakdown of tortoise remains. As has been mentioned the remains of young tortoises probably break down more quickly than older ones, and as a result the mortality rates of younger tortoises are probably slightly underestimated, while those for older animals are slightly overestimated. This in effect means that the survivorship curve determined from mortality data is biased to the right and should in fact lie even closer to the survivorship curve determined from the population age structure.

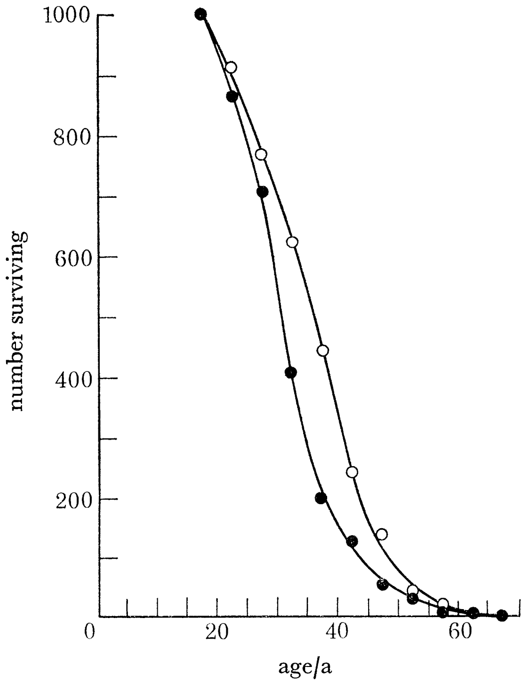

FIGURE 17. Two survivorship curves for the tortoise population in the southeast of Grande Terre. The curve with open circles is derived from mortality data while the curve with closed circles is derived from the structure of the live tortoise population. See text and table 7 for explanation.

(g) *Reproduction*

Frazier (1972) and Bourn (1977) have described various aspects of the reproductive cycle of the Aldabran giant tortoise. In summary, mating commenced soon after the onset of the rains, increased in frequency to peak in April, at the end of the wet season, and subsequently declined as the dry season advanced. Nesting activity seemed to be restricted to the coolest months of the year: June, July and August; and hatchlings were first seen at the beginning of the following wet season. A series of post-mortems were carried out throughout the study period on Grande Terre tortoises. In total, 29 females and 9 males of differing size were examined. Females became reproductively mature at 0.55 m straight length (equivalent 25–30 years of age) and males when they were slightly larger. Size frequency distributions of ova showed that no large ova were present in females examined at the end of the dry season, during the wet season and the months immediately following there appeared to be a progressive increase in size of a small number of ova in each mature ovary examined, and maximum size was reached in June/July when structures homologous to *corpora lutea* appeared in some ovaries and shelled eggs were first found in the oviducts. Taking into consideration the number of large ripe ova, the number of *corpora lutea* and the number of shelled eggs found in mature females during the nesting period it was possible to estimate the total number of eggs that might have been produced by individual females. Five out of eight mature females contained shelled eggs or were considered likely to produce eggs. The mean number was 10.8 eggs/female with a range of between 9 and 15.

22 % of the Grande Terre tortoise population were large enough to be considered reproductively mature females. If half of these produced 10.8 eggs each, then the total egg producing potential of the Grande Terre population is in the order of 175000 eggs per annum. Swingland (personal communication) has found that the onset of sexual maturity occurs at a younger age in the Ile Malabar populations and that the number of eggs produced by each female is con-considerably higher than on Grande Terre. However because of the much smaller number of Malabar tortoises their total egg production must be much lower.

(*h*) *Abnormalities*

39% of all animals examined in the southeastern census showed some form of carapace damage and in 3 % of these, this was extensive. The most common deformity (51 %) was the presence of split or cracking scutes, usually in the hind region and involving the fifth central and fourth left and right lateral scutes. It is suggested that this damage occurs when individuals slip backwards while traversing rocky irregular terrain and so put carapace bone and scutes under considerable strain.

19 % of the animals had supernumerary scutes elsewhere on the carapace, some of which, by their regularity, suggested abnormal embryonic development. 2 % had large pits in their carapace, sometimes up to 4 cm in depth, which were almost certainly incurred as a result of falls. A very small number of individuals were found with virtually all of their scutes missing or peeling off and replaced by scar tissue. Grubb (1971) has suggested that this may have been the result of disease; however, an alternative suggestion is that the damage may have been caused by fire, which in the past has affected limited areas of Aldabra.

1 % of all tortoises examined in the southeast had amputated limbs or missing claws. It is suggested that these deformities may have been inflicted when young by coconut crabs or rats; certainly rats are known to attack young tortoises in the Galapagos (MacFarland *et al.* 1974) and captive one year old tortoises on Aldabra.

Discussion and conclusions

There is little doubt that by the end of the nineteenth century, as a result of collection and killing by man (Rothschild 1915), the tortoise population of Aldabra was extremely small. Wharton (1879) stated that 'the reptiles are now very scarce' and that a party of his sailors were only able to find one specimen 'after much trouble and search'. In 1892 Spurs, the lessee living on the atoll, who had reintroduced tortoises to Ile Picard from the 'principal section' (Grande Terre?) is reported to have claimed that there 'were more than 1000 tortoises' all told on the atoll (Riseley-Griffith 1892). However, Abbott (1893) after a stay of four months, considered this to be a 'considerable overestimate'. Voeltzkow (1895) found only three tortoises during a four day search in the southeast of the atoll, and six others near Dune d'Messe on the south coast. The diary of Bergne's visit in 1901 (Stoddart 1971) contains no reference to tortoises. Roberts (1905) after four months' stay said that most tortoises were found on Grande Terre but that he did not see many. Fryer's 1908 diary of his six month sojourn on Aldabra makes little mention of tortoises in areas where they are now common (Stoddart 1971). Nicoll (1908) claimed that tortoises were restricted to the northern side of the atoll. Fryer (1911) said that the tortoise 'still occurs in fair numbers on the extreme east of the Main Island (Grande Terre) and is scattered in small numbers in the rest of the atoll. It is also found on Malabar and Picard islands but is stated to have been introduced...only two were found on Malabar, both young specimens...'. Dupont (1929) reported that he saw 'very many tortoises all over the place' and that tortoises had 'selected the Cinq Cases area for their breeding ground almost to the exclusion of other parts of the atoll'. Dupont's visit was made in the height of the nesting season (July/August 1929) and strongly implies that the population had increased considerably since the turn of the century, that large numbers of nesting females were found in the southeast, and that the population was still expanding.

The current size of the Aldabran giant tortoise population is estimated to be 150466 individuals. With such a large number of tortoises occupying such a small area of land one is inevitably led to ask the questions: 'Is the population still increasing in size?' and 'What effect are they having on their habitat?' The uneven distribution of tortoises on the various islands of the atoll at mean densities varying from 0 to 27 animals per hectare provides a natural opportunity to compare populations at different densities, although it should be borne in mind that there are certain important differences between islands, largely based on underlying geomorphology.

Crude estimates of mean annual recruitment in the period 1969–74 give figures of 16.8/1000 for the Malabar population and only 4.8/1000 for the population in the southeast of Grande Terre. However these figures are certainly under-estimates because they do not take into account mortality or any bias due to undersampling of very young tortoises. Nevertheless they indicate that the recruitment rate in the Malabar population is considerably higher than that in the southeast population. This is supported by Swingland's belief (personal communication) that Malabar females reach maturity at a younger age and produce more eggs than females in the southeast.

The mortality rate could only be estimated for animals above 60 cm curved length. In the southeast of the atoll it was 29/1000, while on Ile Malabar, based on a very small sample, it was about 27/1000. With crude mortality etsimates exceeding those of recruitment the size of both populations would appear to be decreasing. However life table calculations showed that age-specific mortality rates generally increased with advancing age/size. It is probable therefore that mortality rates of tortoises smaller than 60 cm curved length were considerably less than those for larger animals although losses from the population of very small tortoises which are subject to predation might be high. The overall mortality rate of the southeastern population is therefore likely to be less than 29/1000. Even allowing for an overall mortality of half that found (14.5/1000) and a real recruitment rate of twice that estimated (9.6/1000) it would still appear that the southeastern population is decreasing in size. Making the same allowances for the Malabar population the overall mortality rate would be 13.5/1000 and real recruitment rate would be 33.6/1000: under these conditions the number of Malabar tortoises would increase.

However, this is a matter of conjecture and before the dynamics of the populations can be understood more accurate information on reproductive potential, nesting and hatching success, annual recruitment and differential mortality rates is required.

Tortoises are poikilothermic, and as such they must find shelter from direct solar radiation during the hottest part of the day and it is not uncommon to see 100 or more individuals under a single shade tree. The underlying soils, which are generally very shallow everywhere, are greatly disturbed by their presence and erosion takes place. The trunks and exposed root systems are damaged by the abrasion of tortoise carapaces and plastrons. Many trees have been killed as a result. Tortoise feeding and abrasion have also severely restricted the natural regeneration of many shrub and tree species. In effect mixed scrub and woodland are being replaced by extensive open areas of grassland and bare rock, and the amount of shade available to tortoises is being reduced (Merton *et al.* 1976; Hnatiuk *et al.* 1976). Primary production figures for the various vegetation types have yet to be evaluated but the census showed that high tortoise densities were associated with these open areas and most of the low forms of vegetation occurring were very heavily grazed. It is probable, therefore, that grasslands provide more food for tortoises than other habitats. However, the absence of shade is believed to be an important cause of death, and mortality density was found to be highest in open areas. While habitat changes may increase the amount of tortoise food available and so indirectly encourage population growth, the reduction in shade cover may have the opposite effect by increasing natural mortality.

Large concentrations of a few other reptilian species still do occur in other parts of the world, for instance the marine iguana, *Amblyrhynchus cristatus* Bell, on the Galapagos Archipelago (Eibl-Eibesfeldt 1960), various species of sea turtle, *Chelonia mydas* L., on Europa Island (Hughes 1974) and Kemp's ridley *Lepidochelys kempi* in Mexico (Hildebrand 1963), and the Nile crocodile *Crocodylus niloticus* Laurenti in Lake Rudolf, Kenya (Graham 1968). However, these species are basically aquatic with individuals often ranging over wide areas and aggregations usually only occurring during temporary periods ashore for breeding or basking in the sun.

Except for a few feral goats on Aldabra (thought to number less than 1000 in total), giant tortoises are the only large terrestrial herbivore found on the atoll. As far as we are aware, no other extant reptilian population occupies such a dominant rôle in any terrestrial ecosystem. The mean mass of individuals sampled in the southeastern census was 21.65 kg (s.e. $\pm$ 0.15) from which a tortoise biomass figure of 58352 kg km^{-2} was derived. The only comparable figure for a reptilian population which we have been able to find is for the Nile crocodile in Lake Rudolf, where Graham (1968) calculated that in certain favoured areas crocodile biomass was between 3500–15000 kg km^{-2}.

However a considerable body of information is available for the large mammalian herbivore communities of Africa which has been reviewed by Coe, Cumming & Phillipson (1976). They concluded that for areas of Africa with annual rainfall up to about 700 mm there was a linear relation between the logarithm of mean annual rainfall and the logarithm of large herbivore biomass. They suggest that this relation may be a reflection of a natural balance between rainfall, primary production and stable carrying capacity and that areas with large herbivore biomasses significantly higher than the norm for a given rainfall cannot be maintained for long periods without overgrazing and habitat degradation.

Aldabra's mean annual rainfall for the past eight years (1056 mm) is admittedly higher than the range Coe *et al.* (1976) specified in their conclusion, although they did consider higher

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rainfall areas. By extrapolating their regression line a predicted biomass value of 10000 kg km^{-2} is obtained for areas with Aldabra's rainfall. This is about one sixth of that actually found in the southeast of the atoll. If allowance is made for the fact that only part of the Aldabran terrestrial ecosystem is being considered and tortoise biomass is recalculated for the atoll as a whole, a figure of 21168 kg km^{-2} is obtained (mean mass 19.42 kg (s.e. $\pm$ 0.14), total population 150396, total area 138 km^2). This figure is still more than twice as high as that predicted but lies close to that calculated for the Rwenzori National Park (biomass 19928 kg km^2, rainfall 1010 mm). Coe *et al.* (1976) rejected this point from their calculations on the basis that the rich volcanic and alluvial soils of the Rwenzoris were likely to support higher primary production than more typical areas of Africa with less fertile soils. Aldabran soils are guano based (Piggott 1968) and primary production and herbivore biomass on the atoll may therefore be higher than that predicted from rainfall figures. On the other hand it is arguable that the tortoise induced habitat modification in the southeast and the apparent decline of the tortoise population in that area indicate that the present tortoise biomass is well in excess of the atoll's stable carrying capacity. It follows from this that the tortoise population in the southeast will continue to decline, although at what rate is uncertain. It may well be that the lower metabolic rate of the reptilian body and the ability of the tortoise to withstand long periods with little or no food and water will mean that, given normal climatic conditions, the decline will be gradual, but consecutive years of low rainfall will place the population under greater stress and lead to mass mortalities.

The increase in the size of the tortoise population at the beginning of this century, followed by an apparent decline in recent years suggests a cyclical pattern of rise and fall. We are unable to confirm or deny this possibility. All that we can say is that the present overpopulation is almost certainly a direct result of man's interference during the nineteenth century. If after decimation the population began to expand very rapidly the animals, although large in number, would be small in size and would find an abundant food supply. However with low mortality and rapid growth the population would eventually exceed habitat carrying capacity, leading to the present situation in the southeast of Aldabra. Population stabilizing mechanisms which might have operated under completely natural conditions may well therefore have been overriden by the effects of human interference.

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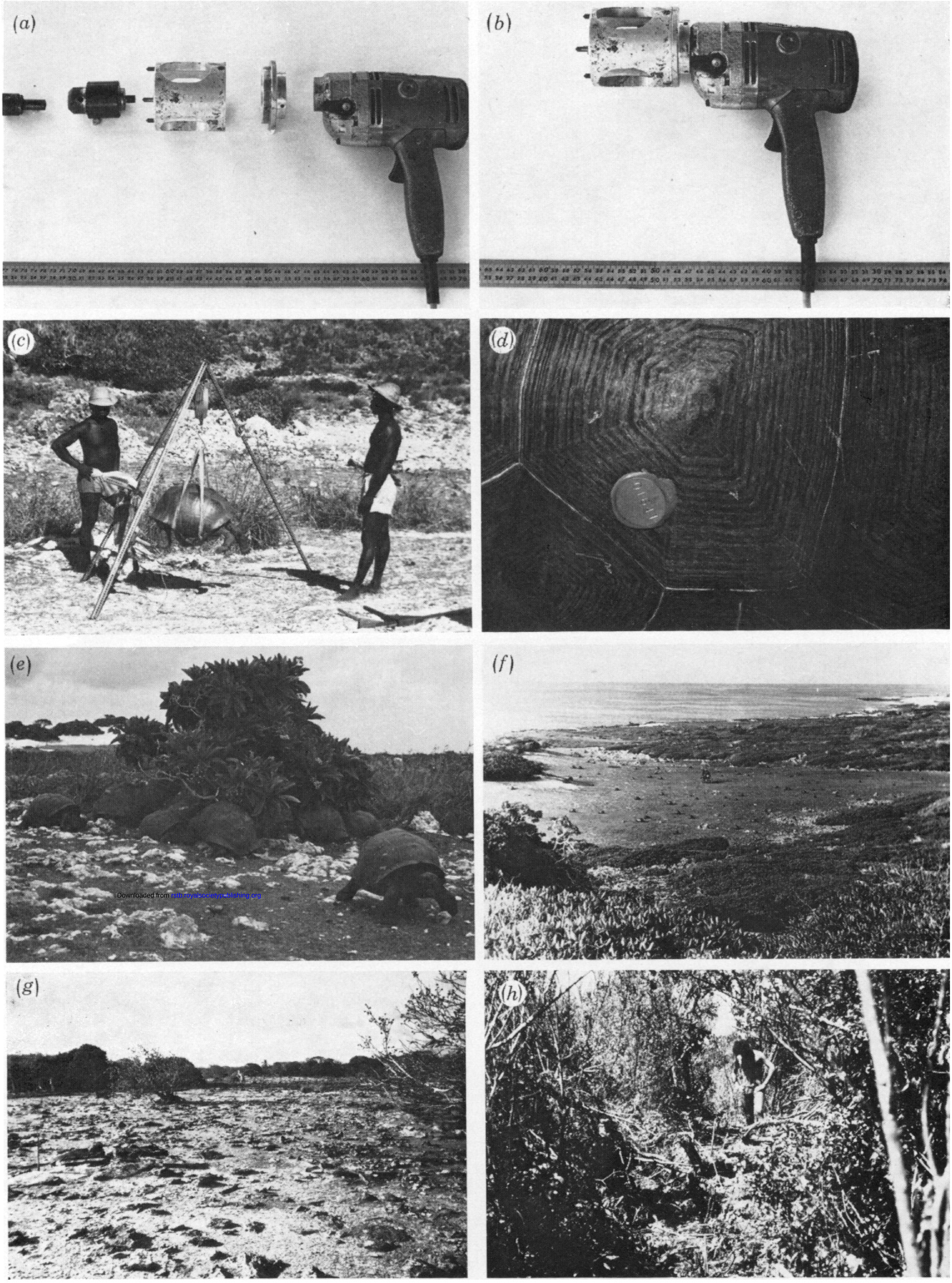

), (*b*) Exploded and assembled electric power drill and attachments used for tortoise marking. (*c*) Portable tripod and balance used for immobilizing tortoises so that they could be marked and measured. (*d*) Close-up of dorsal scutes of a giant tortoise, showing implanted disk (01641) in the fourth central scute. Although the central area of the scute is beginning to show signs of abrasion, approximately eighteen growth rings can be counted. This is considered to represent the animal's age. Note the white margins of each scute, which denote recent growth. (*e*) Tortoises seeking shelter from the midday sun in the shade of a *Tournfortia argentia* bush on the south coast of Grande Terre near Dune Jean Louis. (*f*)–(*h*) Contrast of three typical habitats on Aldabra. (*f*) A view of the grasslands and low scrub along the south coast of Grande Terre. Over 70 tortoises can be seen. (*g*) The extensive open areas of the southeast of Grande Terre with well cropped 'tortoise turf' on shallow soil and underlying limestone protruding. Note the dead standing trees in the left background. (*h*) Extremely dense *Pemphis acidula* 'jungle' inland on Ile Malabar. The photograph was taken looking down a transect cut with great difficulty through this vegetation type.