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BEHAVIOURAL AND ECOLOGICAL OBSERVATIONS ON GIANT TORTOISES ON ALDABRA ATOLL

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Thesis submitted for the Degree of Doctor of Philosophy at the University of Oxford

Merton College,
Oxford.

Michaelmas Term,
1971.

pour torti numero

quatre vingt dix neuf

" ... the master was an old Turtle - we used to call him Tortoise -"

"Why did you call him Tortoise, if he wasn't one?" Alice asked.

"We called him Tortoise because he taught us," said the Mock Turtle angrily. "Really you are very dull!"

Lewis Carroll

PREFACE

This is a story about tortoises, giant tortoises that can grow to over 500 pounds, tortoises that live at a density of nearly one in every fifty square metres. Nowadays these creatures are restricted to remote tropical islands, but their fate is not at all certain. In the last hundred years huge populations have been completely exterminated from numerous islands. Consequently, my approach was to spend as much time as possible with the tortoises and let them teach me what they could. As a result, my observations were made with an open mind without trying to prove or disprove any hypotheses. My efforts in the field then, were in gathering, not analysing, data. There are obvious drawbacks with such a technique, (for example, much of the data is still mouldering in field notebooks), but I feel that it is the lesser of two evils, for data on species restricted to remote islands are not easily gathered - especially if the animals disappear from the face of the earth.

My plans for the analysis of these data were overly ambitious and I had hoped to include more intensive analysis of certain topics, especially activity and temperature regulation. I had also hoped to include more extensive accounts of the animals' biology. Part Four is much shorter than I had originally planned; sections on nesting and breeding seasons and comparative breeding biology were drafted but not included. Part Five was to have dealt with population data and studies of home range and movement, but this section was left out entirely due to lack of both time and space.

Although this grandiose plan may sound as if a great deal is known about giant tortoises, this is not at all the case. Even the most superficial account of their natural history is incomplete; for example, I have seen but six successful matings and a mere five completed nests. Hence, I have spread my work rather widely hoping to make a broad foundation for more intensive work in the future.

The layout of the present study is composed of four major parts. The first is a description of Aldabra atoll, especially as

it relates to the giant tortoises. A great deal of this section was based on the results of a discussion meeting published in Philosophical Transactions of the Royal Society of London, B., Volume 260, number 836, March 1971. I have also drawn from my own experiences on the atoll which are restricted mainly to the south coast.

The second part consists largely of topics on the general biology of the species so that the reader may get some idea of what tortoises are all about. Part Three, dealing with activity and thermoregulation, is the most rigorously treated section. Part Four discusses mating behaviour in some detail. I have also tried to show how tortoise mating fits in with generalized concepts of courtship and mating, and although I have mentioned many of the contemporary theories in which there are a multitude of intervening variables and hypothetical constructs, my attempt has been to underplay these immeasurable entities. This study is zoological not theological.

One assumption which I have made, from the first to the last page, although this is the only place where I will state it explicitly as such, is that the tortoises are adapted to the environment in which they live. The way they are and the things they do have arisen by natural selection.

ACKNOWLEDGEMENTS

Field work in 1968 was done while on the Royal Society Expedition to Aldabra Atoll, and the following two years I was supported by a Natural Environment Research Council grant. I am grateful to both these organisations for their assistance, and also to fellow expedition members. I owe a great debt to my Seychellois field assistants, Harry Charles, George Marie, Wilem Francois, 'Te-Te', and Maurice Lablache.

I am grateful to Dr. M. J. Coe and Professor N. Tinbergen, F.R.S. for their help and encouragement; and to Professor J.W.S. Pringle, F.R.S. for allowing me to work in the Department of Zoology. Dr. N. Arnold, Brian Cogan, Tony Hutson and Dr. J. Taylor, all of the British Museum (Natural History), have provided information and answers to many questions.

Dr. C. R. Dawkins, Dr. F. C. Marriot and Raymond O'Conner advised in analysis. Bernard Dod has kept me from solecism, and Lee Machlis and Kathy Oates also made helpful comments on the M.S.

The photographs were taken by John Haywood and Lary Shaffer, and the printing and mounting was done by David Lees, Tim Halliday, Beth and Lary Shaffer. David Lees, Beth and Lary Shaffer and Jamie Smith drew a large number of diagrams for me. Dr. M. MacRoberts made the sonogram.

I have likewise been fortunate in having typing assistance from Mrs. C. Lawless, Mrs. P. Searle and David Dawson. Theresa Mahon has generously helped in running off the stencils. Paul Handford and David Lees have helped greatly with xeroxing. Kathy Oates, Linda Partridge, Graham Bell, David Dawson, Paul Handford, Raymond O'Connor and Luke Schifferli have helped in collation. Dr. S. Neill drew the cartoon.

I owe a great debt to my friends and colleagues.

"A faithful friend is a secure shelter;
whoever finds one has found a treasure.
A faithful friend is beyond price;
his worth is more than money can buy."

Ecclesiasticus

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ABSTRACT

This study is the result of twenty months' field work on Aldabra. Aldabra is a raised limestone atoll, with the highest point of land 18 m above sea level. In the main, it is covered with low dense scrub, and has little fresh-water; the terrain is very broken and treacherous. There is distinct seasonality in climate. The southern summer, November to April, is hot, cloudy, and rainy, while the other six months are dry and clear but cool. The most noticable change during the seasons is in the wind. It is light and variable in summer but a steady thirteen knots in winter. Aldabra, although not the ideal tropical paradise, supports the largest population of giant tortoises anywhere in the world today; 100 000 animals may occur on the atoll. These are the last representatives of a population that once occurred over many islands of the western Indian Ocean. The closest relative is a species, now extinct, from Madagascar.

The animals grow to large size, although none reach the 500 pound mark recorded in the earlier part of this century. General topics of morphology, that relate to the rest of the study, are discussed.

The locomotory gaits are described: tortoises have a gait which apparently does not occur in other animals. Rate of locomotion is related to air temperature. Records of long distance movements are also mentioned; a giant tortoise can probably cover a kilometre a day.

Feeding is dealt with in some detail. Grazing movements are described. Biting at grass occurs in long uninterupted sequences, and biting rate is related to the animal's temperature. Rate of food intake cannot be measured directly but it is evidently quite slow. Tortoises show selection for both species and components of plants. Seasonal changes in feeding habits seem to be related

to seasonal availability of preferred food items. For some reason, dead leaves are highly preferred. Yet, tortoises eat a great variety of objects and pilot tests show that supplementing food increases rate of growth and/or breeding. The general impression is that the tortoises are over-eating their food supply and are food limited.

Several feeding strategies are evident. The tortoises show distinct selection for some plant foods. They also show strong tendencies to feed in the same area day after day, and this has a marked effect on the vegetation. Apparently the animals are maintaining grass in a state of high production by constant cropping and are also providing themselves with a supply of dead or wilting leaves by continually breaking branches.

Drinking is a behaviour not often seen, for drinking water is rarely available. Water is sucked up through the nares, the anterior of the head having a proboscis-like structure. This is a very efficient means of taking in water quickly.

Defecation is always preceded by a defecation posture, with the posterior elevated. Time and rate of defecation are related to activity. It may take over a month for an inactive animal to pass solid objects. Urination is rarely seen; its occurrence indicates that the animal is being disturbed. The voiding of fluid may serve to offset the attack of a predator, as well as to increase heat loss in times of heat stress.

The pattern of diurnal activity is very distinctive. Tortoises are active only during the hours of daylight, but they avoid activity during the midday, when they sleep. Habitat selection is also closely tied to activity: animals are in the open during the early and late parts of the day and in the shade at midday. This applies to tortoises on grassland plains as well as in mixed scrub.

Feeding and sleeping are the main activities, the latter occupying somewhat more of the tortoises' time. About five hours a day are spent active. The transition from feeding to sleeping, or vice versa involves activities such as moving or lying awake but inactive. The general pattern of diurnal activity breaks down on rainy days when the animals are active for more of the day, spending less time sleeping.

Tortoises evidently do not have either high or efficient rates of assimilation, but the amount of time they spend feeding is comparatively little, thus illustrating the advantages in being poikilotherms.

Activity is restricted to within daylight hours, probably because the animals' visual abilities are poor at night.

The biphasic activity cycle is a means by which the animals can avoid the midday heat. Variation in daily activity is related to variation in the daily temperature regime. Detailed temperature records on individual tortoises show that the animals heat and cool with environmental temperatures. However, there is a lag of considerable magnitude. It may take ten hours for the animal's temperature to catch up with the environment and there may be a differential of 5 degrees between the two. Heat exchange in the giant tortoise is passive.

The selection of a micro-habitat is closely related to its thermal characteristics. At midday the animals move from the hot exposed areas to cool shaded areas. If the animal does not select a sufficiently cool micro-habitat at midday it will experience continued heating even though it is in the shade. This is most probably due to reradiation from the environment.

Besides changing micro-habitats, the tortoises have a number of other means of thermoregulation. Digging into the soil puts the animal in contact with a cool substrate. Bathing also has thermoregularory implications. One interesting finding is that tortoises face away from the sun. More face away the hotter the air temperature. This exposes less vascularised area to the sun and probably retards heating considerably. The opposite response, facing towards the sun, is less frequent. The thermal problems of Aldabran tortoises seem to be involved mainly with dissipating heat rather than acquiring it.

There are also obvious seasonal changes in activity. During winter the animals are active at midday but for less time per day. Also in the winter, most of the animals are in the scrub and the grassland plains are essentially vacated. The annual migration to and from the plains coincides with the availability of Sporobolus. The reduced activity during the winter is possibly a means of conserving energy when environmental conditions are inhospitable. The tortoises appear to be almost in a state of "suspended animation" again illustrating the advantage in being a poikilotherm.

Mating behaviour can be described in five phases, according to the behaviour of the male: approach, mounting, groan and thrust, coition, and dismount. Males do not always mount females, and the great majority of matings are unsuccessful due to the female's failure to cooperate. Consequently, most of the male's behaviour functions to break down the female's resistance, and finally to stimulate her to expose her cloaca. The behaviour of mating tortoises can be explained by contemporary concepts of its causation. These explanations may be useful as a frame of reference, but further than that they are misleading, for they involve variables which cannot be measured.

The mating technique of the male may be perfected with experience, but as yet the evidence for this is slight. The evolution of tortoise mating behaviour is discussed mainly to bring to light the many questions that still exist. Because there are few comparative studies it is difficult to do more than this.

Cursory observations on sleeping tortoises showed that they hold their breath, often for as long as fifteen minutes. This is contrary to conventional ideas about breathing rhythms in these animals and I have discussed this point in considerable detail in Appendix II.

PART ONE

ALDABRA ATOLL

Chapter 1

THE ATOLL

Geography

Aldabra atoll (9° 19' to 9° 26' S by 46° 12' to 46° 31' E) lies at the northern end of the Mozambique Channel, 640 km east of the African mainland and 420 km north-west of Madagascar (Figure 1). It is the largest of four atolls in the "Aldabra Group" which includes Cosmoledo, Assumption, and Astove (Figure 2). Aldabra is 34 km east-west by 14·5 km north-south, covering a total area of 365 sq. km. The land ring is composed of four major islands: South, Middle, Polymnie, and Picard, which surround a large lagoon. The respective area of these islands is: 110, 26·4, 1·8, and 9·3 sq. km, and the total terrestrial area, including many small islets is only 155 sq. km. Between each of the four major islands are channels which vary from five to twenty-five m deep and from twenty to 750 m wide (Stoddart et al. 1971) (Figure 3).

Recent maps and charts of Aldabra include: Admiralty charts numbers 718 and 2899; Directorate of Overseas Surveys map "Aldabra" (two sheets); and Piggott 1963 (Sheet number three). The origin of Aldabran place names has been discussed by Stoddart (1971 c).

Geology and Geomorphology

Aldabra, together with its sister island Assumption, rises as an isolated double-peaked mountain from a sea floor over 4,000 m deep (Figure 2). Dredging, seismic, and other studies indicate that the islands are truly oceanic - that is, they have never been connected to any mainland, but are of volcanic origin. In common with other islands in the Aldabra Group, but unlike most islands in the western Indian Ocean, Aldabra is a raised limestone atoll. The highest point of land is Dune Jean Louis, a sand dune on the south

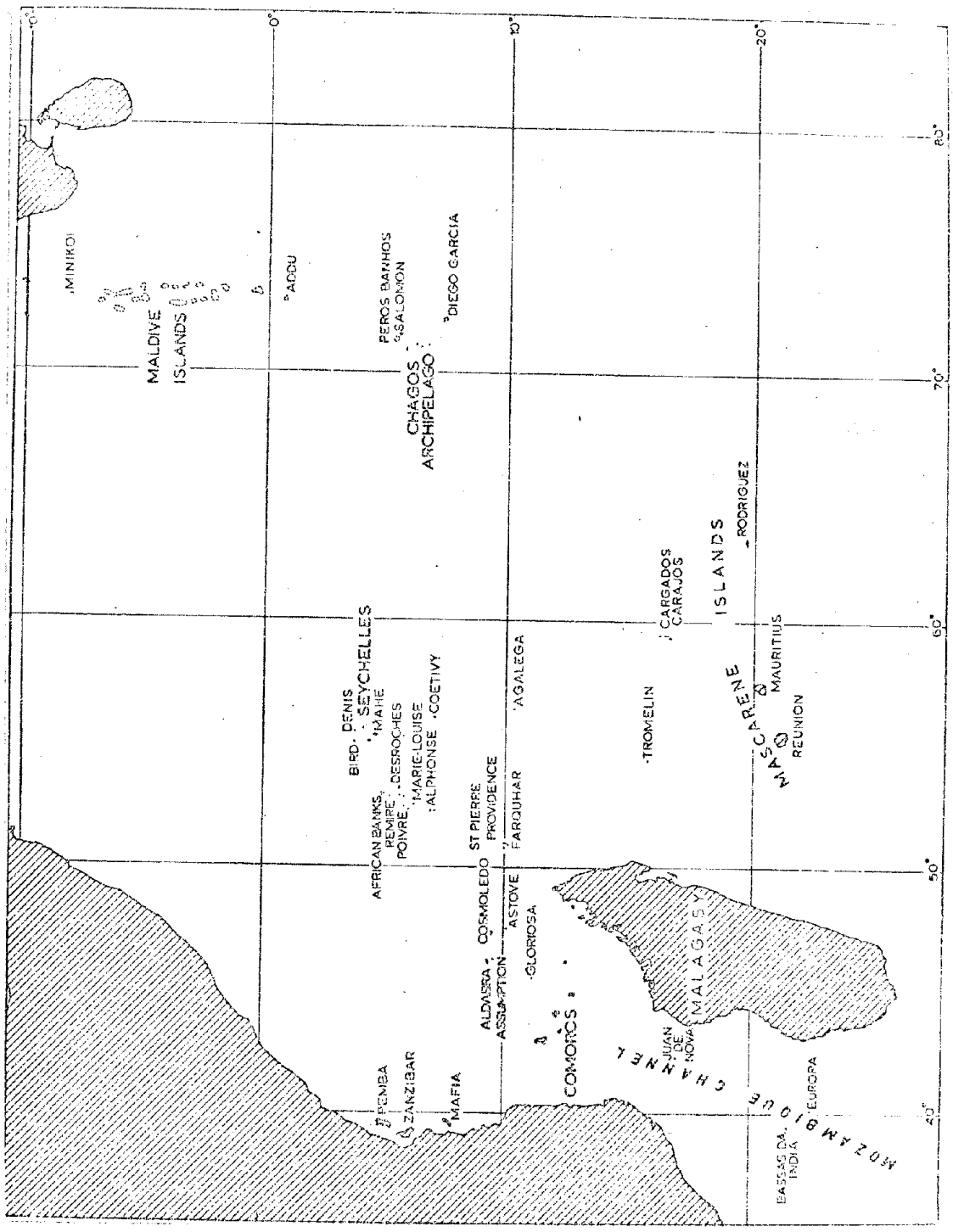


Figure 1. The western Indian Ocean, showing the location of Aldabra between "Malagasy" (i.e. Madagascar) and Africa.
(From Stoddart 1971a, p. 6.)

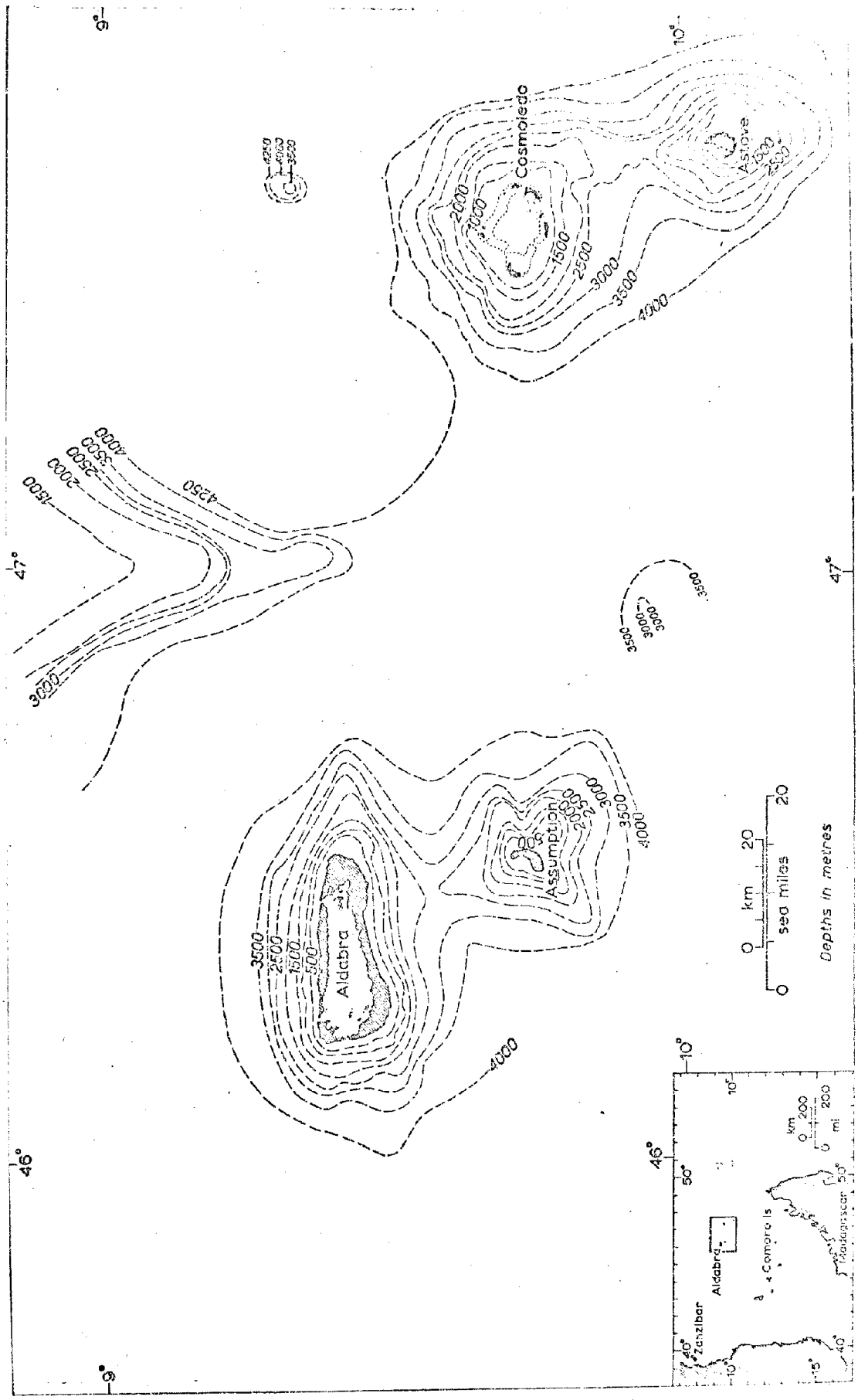


Figure 2. The Aldabra Group of atolls: Aldabra, Assumption, Cosmoledo and Astove. Bathymetric lines drawn in. (From Stoddart 1971a, p. 7.)

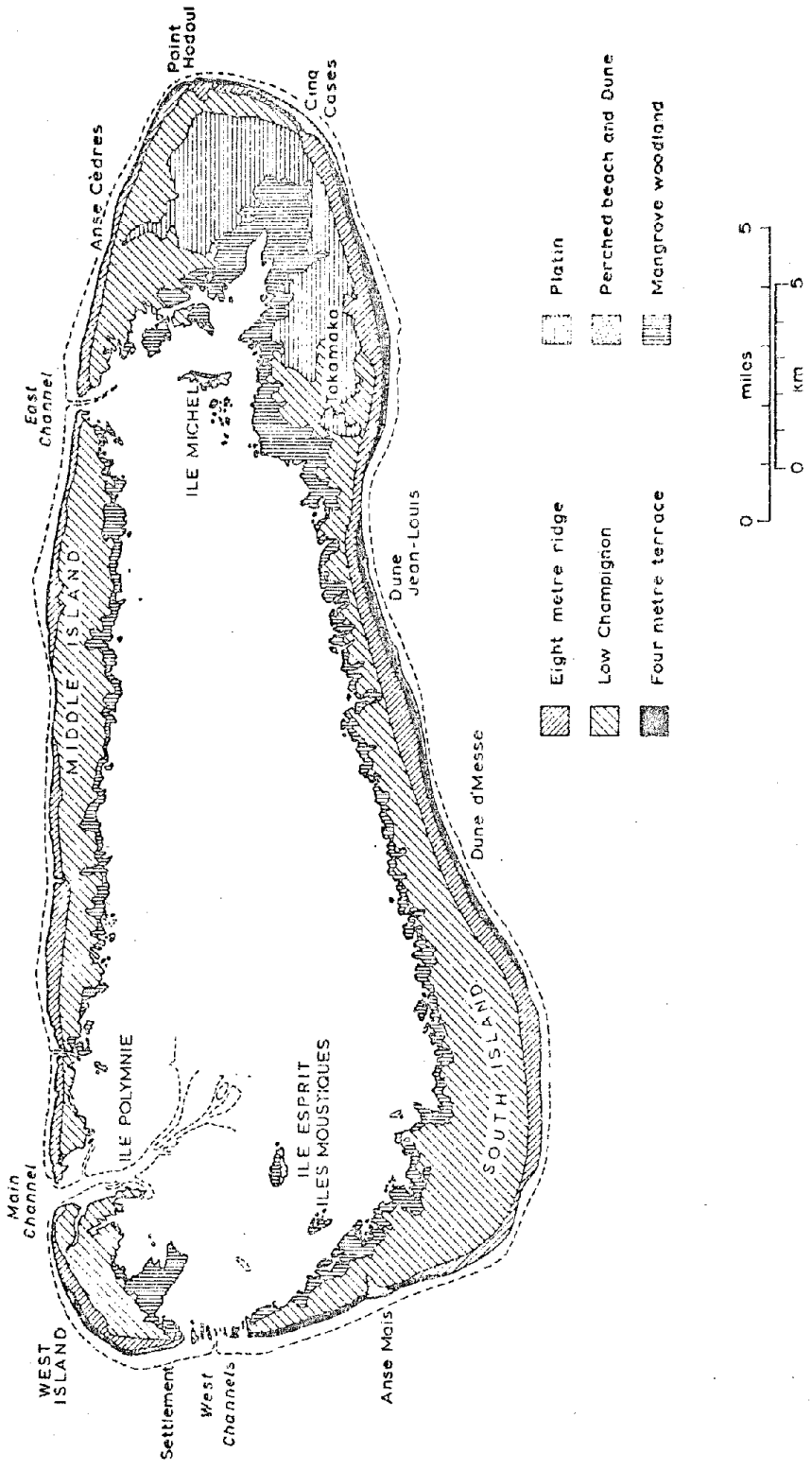


Figure 3. Aldabra topography, showing distribution of major surface types of limestone. Pavé is on the "Eight metre ridge", and smoothed champignon is on the "Four metre terrace" mainly in the southeast. (From Stoddart et al. 1971, p. 38.)

coast which rises to 18 m above sea level. However, the highest intact limestone, on Ile Esprit, is only 8·5 m above sea level. Two elevated limestone terraces, cut by erosion at different geological times, have been described. One is raised 4 m above the sea and the other, 8 m (Stoddart et al. 1971), but the geological history of the atoll is quite complex. Braithwaite and Taylor (in preparation) have identified ten different horizons, corresponding to either depositional or erosional events; and the stratigraphic relationships of the marine and terrestrial layers (Figure 4) indicate that the land has been inundated by the sea at least twice. Thus, there are three distinct terrestrial periods, and tortoise fossils occur in the earliest and latest of these. The latest layer gives a Uranium/Thorium series date of 125 000 B.P., corresponding to the last major interglacial. No date is available for the earliest terrestrial layer, but it is thought to correspond to the penultimate interglacial, about 300 000 B.P. Thus, tortoises probably colonized Aldabra on two separate occasions, and since the deposition of the newer limestone in the last interglacial there has always been some land area above sea level. In fact, during the last glacial the atoll probably stood as a steep-sided, flat-topped island 100 m above the sea (Braithwaite and Taylor, in preparation).

Three major surface types of limestone can be described; they are platin, pavé, and champignon. Platin is most restricted in distribution (Figure 3), occurring almost exclusively in the southeast of the atoll. In its most extreme form platin is nearly without surface relief, forming vast areas of flat pavement (Figure 5). At certain localities the surface is covered with huge flat slabs which may be several metres across and up to a decimetre thick. Solution pans are shallow and often filled with sediment that is level with the surrounding rock. However, large pools with steep, undercut sides are not uncommon; and they commonly contain fresh-

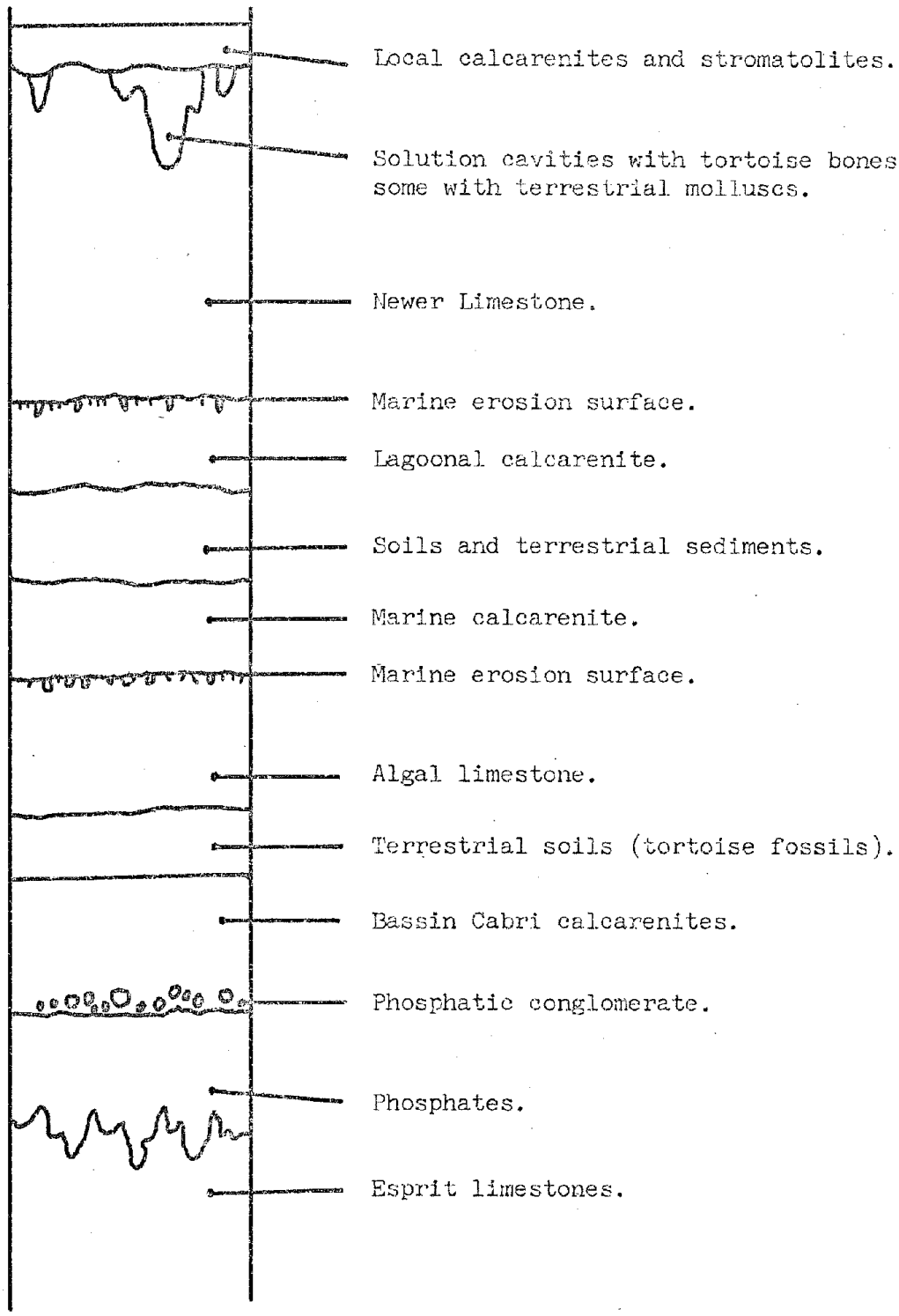
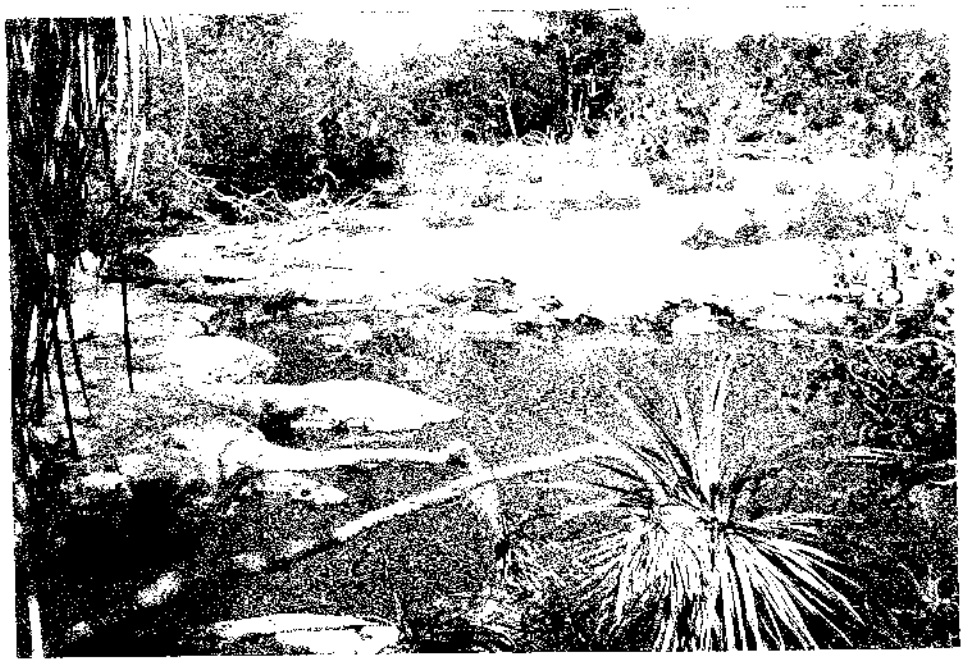
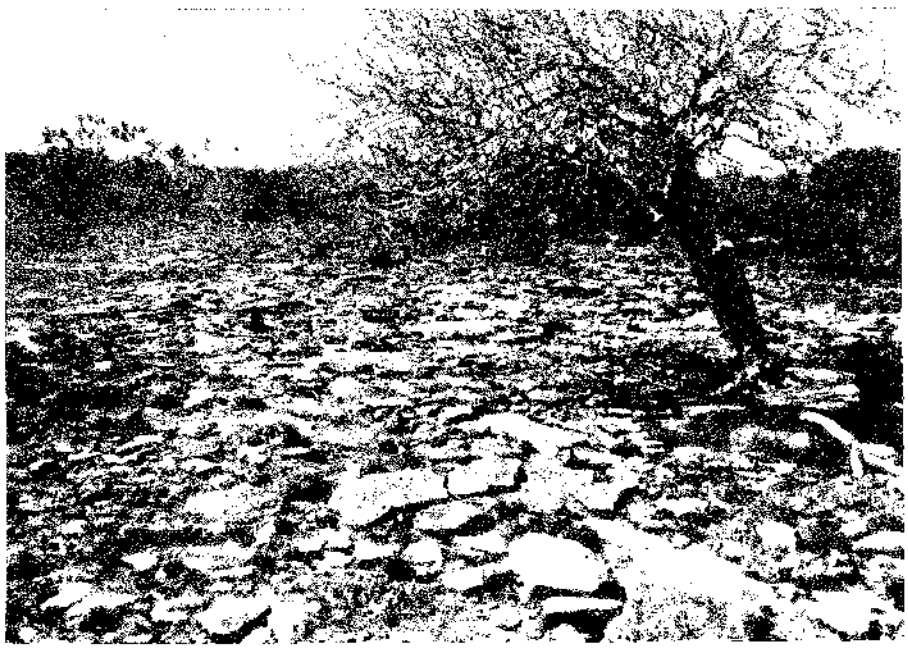


Figure 4. Stratigraphy of Aldabra Limestone. Not to scale.

(From Braithwaite and Taylor - in preparation)



A



B

Figure 5. Platin.

A. A glade south of Anse Cèdres, showing very smooth limestone.

B. Large slabs of limestone on the surface, also south of Anse Cèdres. (From Stoddart et al. 1971 Fig. 2a)

water, and sediment, to say nothing of scores of bathing tortoises. Pinnacles and residuals occur, some standing over a metre high, but on the whole they are rare. There are good indications that erosive forces from the lagoon have reduced the area of platin considerably, leaving highly dissected champignon in its place (Fryer 1911; Stoddart et al. 1971).

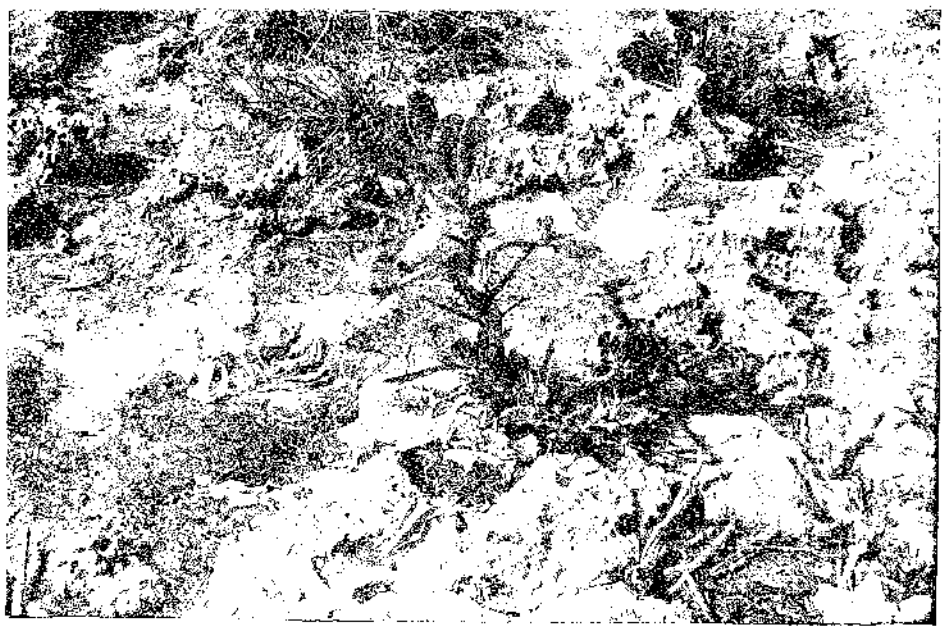
Pavé, although contributing little to the terrestrial area of Aldabra, is fairly widespread for it occurs on the 8 m ridge which runs round most of the atoll (Figure 3). Pavé is like platin in that both surfaces are smooth, but pavé has much more surface relief; frequently it has a hummocky appearance (Figure 6). Although large pools are rare, the surface is dimpled and broken with a multitude of solution pans. In common with the platin, these pans are often filled with fine organic particles or other sediment. Pinnacles less than a metre high are common (Stoddart et al. 1971).

Champignon is the most wide spread of all the surface types, for it covers nearly four-fifths of the land area (Figure 3). ("Champignon" is the local Seychellois name for karst topography, common to so many Pacific islands.) It shows a great amount of surface relief, being intricately dissected with extensive honeycombing and frequent deep, vertical-walled pits (Figure 7). The vertical distance from the bottom of one of these pits to the top of a pinnacle or prominence can be as much as four metres. Small, but sharp-toothed pinnacles jut out from the surface in countless numbers, and the terrain resembles broken glass set in cement. This highly dissected champignon supports a dense monotonous scrub of Pemphis acidula Forst., Mysteroxylon aethiopicum (Thunb.) Leosn., and Sideroxylon inerme L. (Stoddart et al. 1971).

In some areas the champignon surface is eroded and the sharp quality of the pinnacles is reduced. Compared with pavé or platin this terrain has complex surface relief, but it is relatively smooth



A

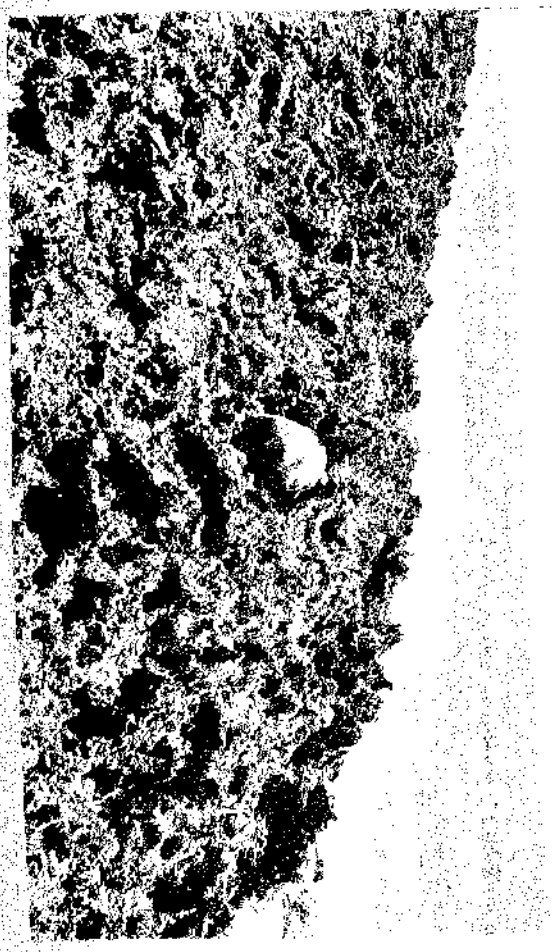


B

Figure 6. Pavé, Dune Jean Louis.
Showing relatively smooth terrain and open mixed scrub.

A. Tortoise drinking from temporary pool of rain-water.

B. Scaevola bush damaged by tortoise browsing.



B.



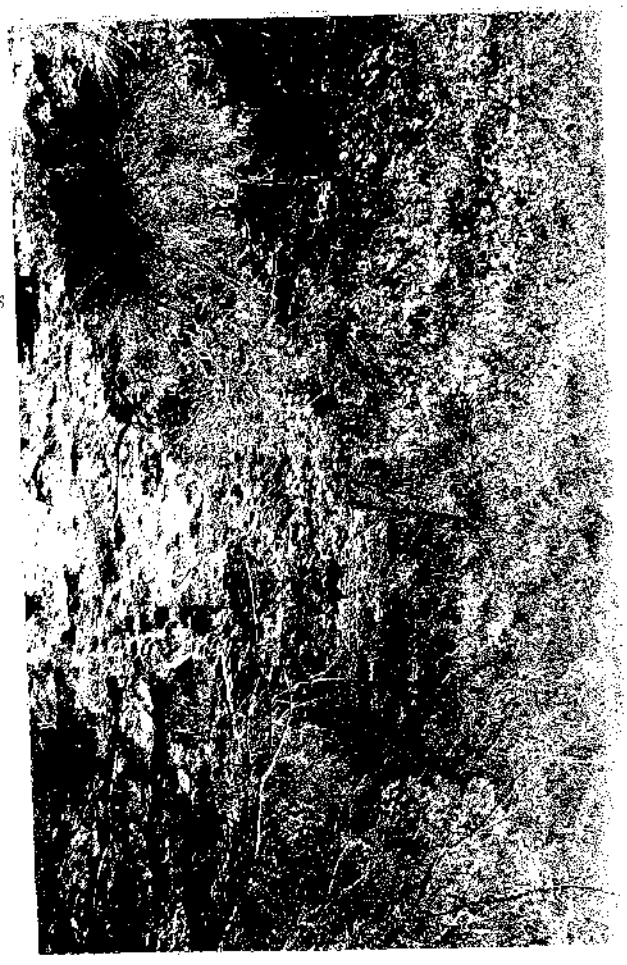
A.

Figure 7. Champignon

A. Tidal basin showing deeply dissected limestone, and dense but low Pemphis scrub (Basin Cabre).

B. Intricately dissected champignon on coastal cliffs (North of Takamaka).

C. Transition of pavé and mixed scrub into champignon and dense Pemphis (Dune Jean Louis).



C.

in comparison with most areas of extensively dissected champignon (Figure 8). Smooth champignon supports a varied flora of herbs and shrubs which are most common in and around pits and depressions. Tortoises occur in high densities on this type of terrain, and Fosberg has even suggested that they may be an important cause of erosion in that countless numbers of the animals have been scraping and bumping their hard shells along the ground for thousands of years (Stoddart et al. 1971).

Much of the limestone is covered with sand, especially along the south and east coasts. Here, the south-easterly tradewinds have blown the sand up over the coastal cliffs forming perched, or storm, beaches that are nearly continuous from the east point to the south-west point of the atoll. These beaches have developed narrow grass-land plains that are covered predominantly by Sporobolus virginicus (L.), although sedges, herbs, and other grasses also occur (Figure 9). Along the northern and western coasts there are occasional sand beaches but no extensive coastal plains.

Piggott (1968, p. 51) refers to the dune sand as Farquhar Series soil, and the coarser sand on some lagoon shores he classes as Shioya Series. Organic soil is almost entirely restricted to pockets in the platin and pavé, and is never very deep or extensive; Piggott calls this Desnoeufs Series soil.

Standing fresh-water occurs almost exclusively in the south-east of the atoll where there are a large number of fresh-water pools (Figure 10). Apparently fresh-water in this area forms a lens floating on top of the sea-water (see McKenzie 1971), for there are also permanent wells in the platin (McKenzie 1971). The pavé has almost no pools that hold fresh-water the year round, but there is no deficiency of solution pans and depressions that catch rain-water, although the puddles are small and temporary. Even the champignon provides a certain amount of standing water after hard



A



B

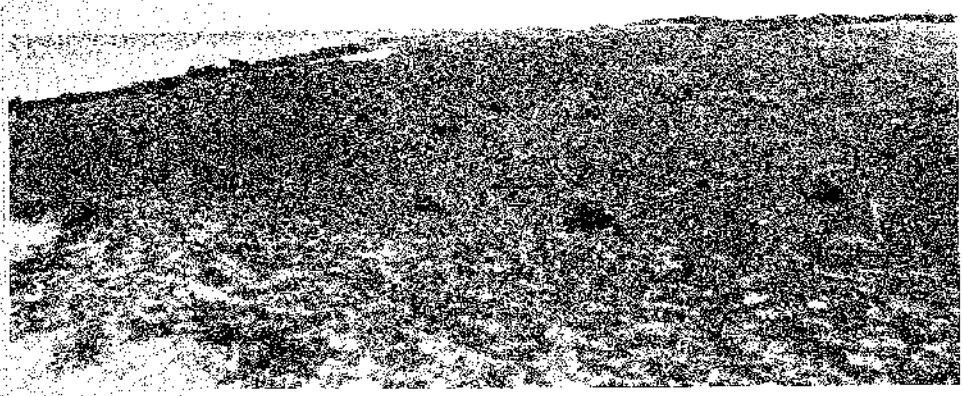
Figure 8. Smooth champignon.

A. North of Grand Trimeau (by Dune d'Messe).

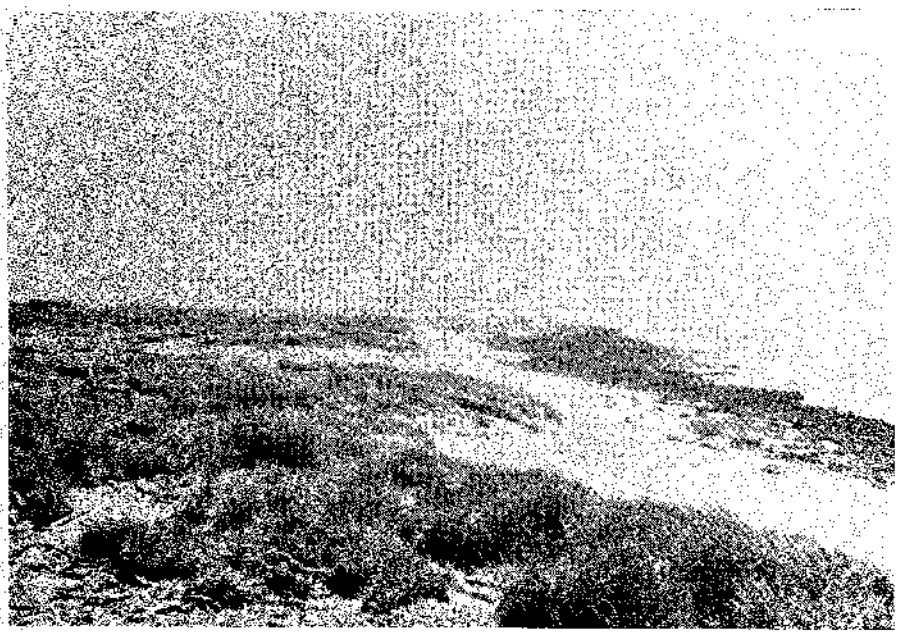
B. Near Dune d'Messe.

Showing broken terrain but smooth surface, also plants restricted to pits and depressions.

(From Stoddart et al. 1971, Figs. 21 & 22.)



A

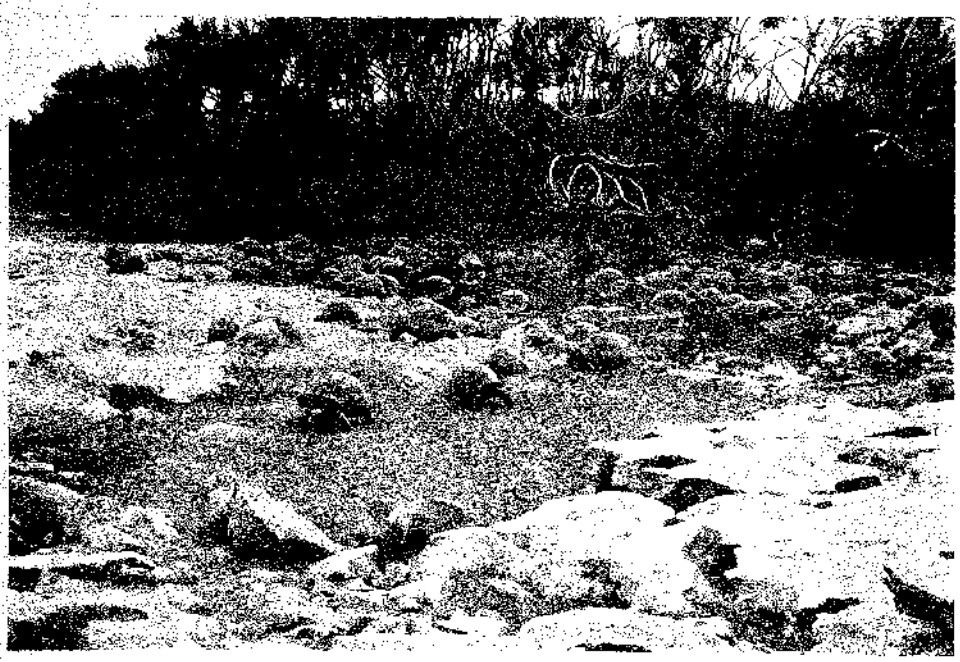


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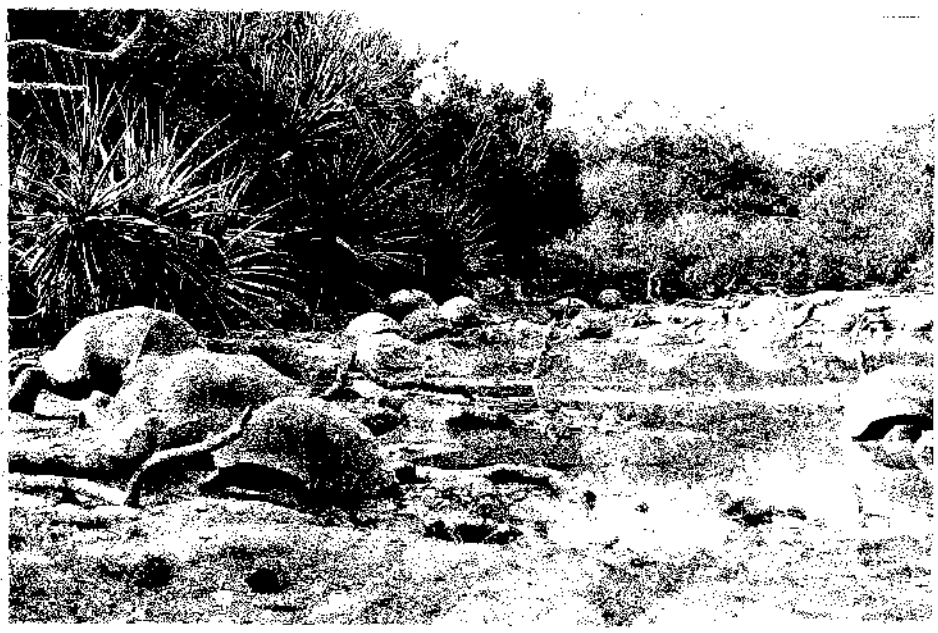
Figure 9. Grassland plains.

A. North of Cinq Cases, Sporobolus plain.

B. East of Takamaka, Sclerodactylon on perched beach.
(From Stoddart et al. 1971, Fig. 33.)



A



B

Figure 10. Fresh-water pool west of Cinq Cases with Pandanus grove and tortoises.

A. Looking west.

B. Looking north.

rains, but these puddles are small and transient because catchment areas are small and run-off and evaporation are very rapid.

Climate

The first time comprehensive meteorological records were made on Aldabra was during the Royal Society Expedition in 1967 and 1968; Farrow (1971) has examined these data. He argues that although some authors class Aldabra as within the Savannah Belt, its climate is more characteristic of the boundary of this zone. Instead of having more wet than dry months per year, the wet and dry seasons are nearly equal in length.

Recordings from the main meteorological station. Annual rainfall varies from 350 to 1200 mm, with an average of 760·1 mm. This is far less than values predicted by world atlases (Times Atlas 1967) and indicates that Aldabra is in the most arid sector of the Western Indian Ocean (Farrow 1971; Stoddart 1971 d). Rainfall is greatest during the monsoon, from November to April, and there is so little precipitation during the other half of the year that the effect of winter rains on the atoll is probably negligible (Farrow 1971, p. 81). The annual rainfall pattern is bimodal, for average daily and average monthly precipitation is greatest at the beginning and end of the monsoon (Figure 11). This double peaked pattern, while characteristic of some continental areas, is atypical of oceanic islands which usually have a single peak in annual rainfall. The diurnal occurrence of precipitation follows certain patterns; early morning rains are frequent in the summer whereas late afternoon rains commonly fall in the winter (Figure 12). Throughout the year midday rains are infrequent (Farrow 1971; Stoddart 1971 d). Measures of atmospheric pressure, wind speed and direction (taken at 0900 local time, 0600 GMT) show distinct seasonality. Pressure

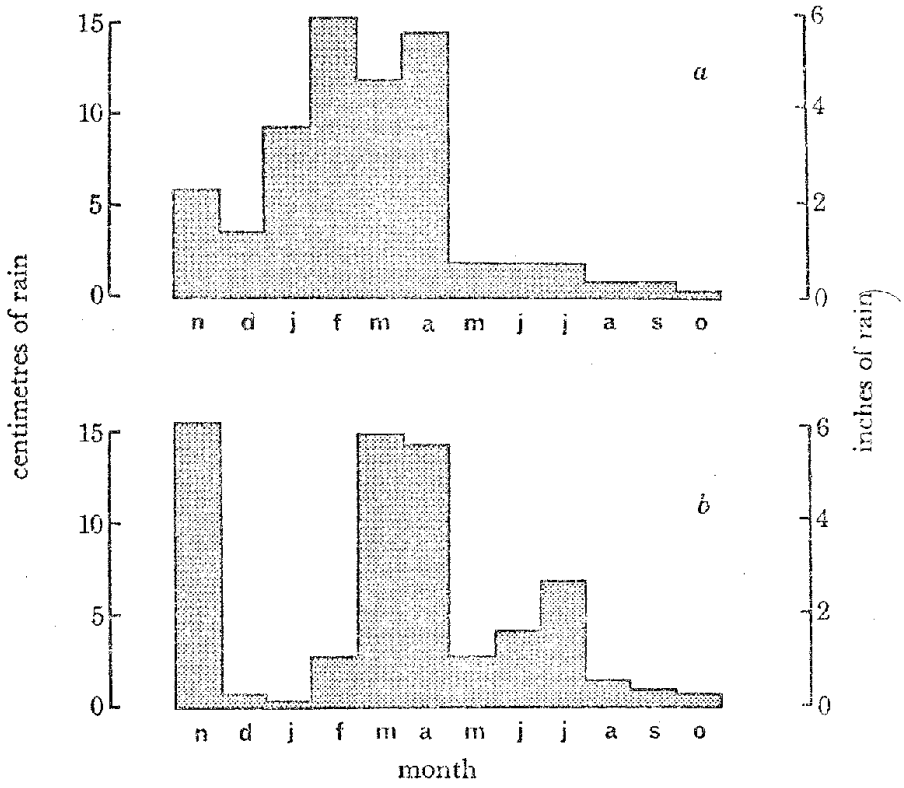


Figure 11. Monthly rainfall at Aldabra.

a. 1967/1968 - from Settlement. Data from 5 inch rain-gauge.

b. 7 year average from East African Meteorological Department.

(From Farrow 1971, p. 80.)

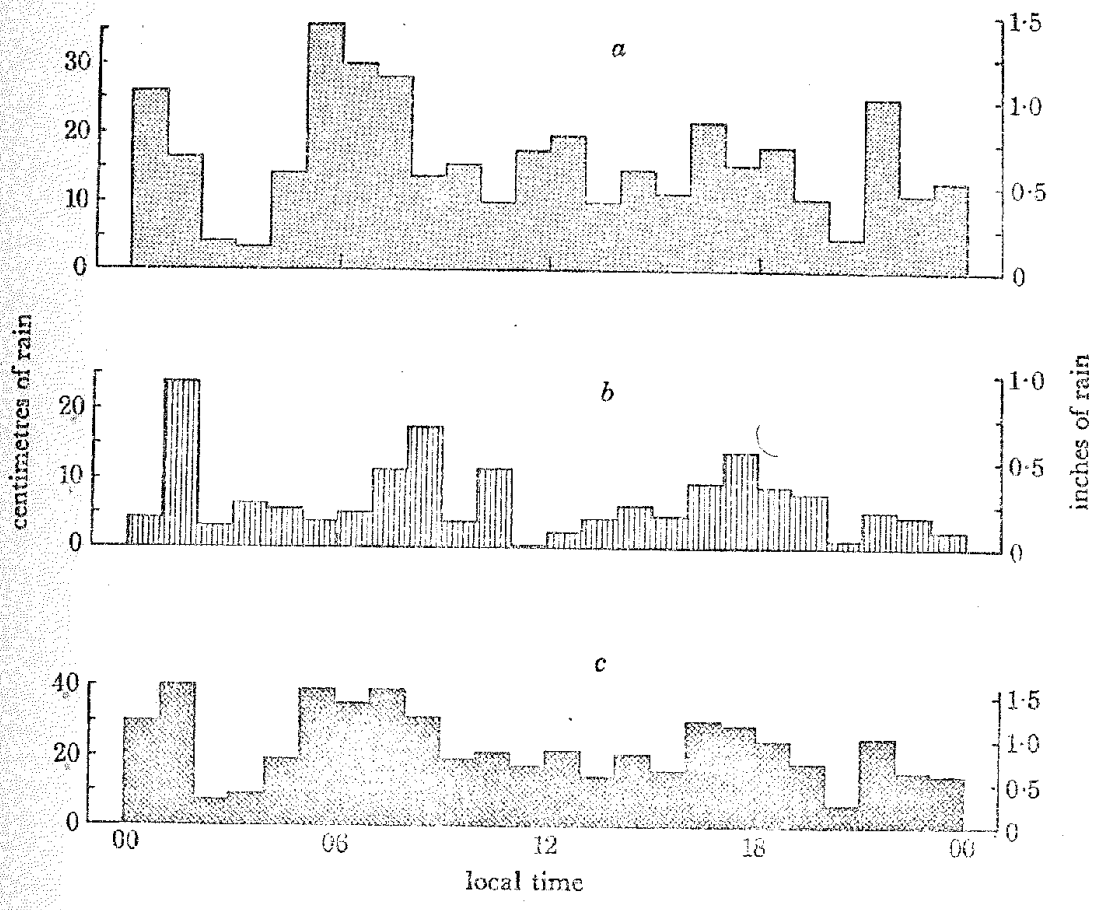


Figure 12. Diurnal variation in rainfall at Settlement.
a. Monsoon (November 1967 to April 1968); b. trades (May to October 1968); c. whole year. Data from Dines tilting syphon rain-gauge charts.
(From Farrow 1971, p. 89.)

is highest (up to 1016·7 m/bar) from about May to October, and during these months the trade wind blows almost constantly from the south-east at about 7 m / sec. This is the southern winter or "trades". During the other six months of the year, November to April, the atmospheric pressure is at its lowest (1010·2 m/bar) (Figure 13). The winds are calm and variable, and often from the north-west (Figure 14). This is the southern summer or "monsoon" (Farrow 1971).

Air shade temperature shows considerable seasonal fluctuation as well. Average monthly maxima reach 32°C in the summer and 27·5°C in the winter, while average monthly minima vary from 25·6°C in summer to 21·9°C in winter. The greatest shade maximum, 36·3°C, was recorded in January, 1968; and the lowest minimum, 19·5°C in June, 1968. Diurnal range in temperature averages 6·5°C, but may be as much as 10·9°C. There is a much greater range in diurnal temperatures during summer than in winter (Figure 15). Maximum temperatures usually occur at midday, while minima occur at dawn (Farrow 1971).

Seasonal trends in amount of sunshine and cloud cover can also be shown (Figure 16). There is more cloud, hence less sunlight, in the summer. By Farrow's (1971) calculations there were 3·8 to 6·0 hours of sunshine per day from November to April, and 4·8 to 7·4 hours per day occurred during the winter from May to October.

Farrow (1971) presents little data on relative humidity. It seems to be a fairly constant 93% at night and 70% in late afternoon. The lowest record was 50% in late September/early October.

Local climatic variation. In 1968 it became obvious that the recordings from the meteorological station at Picard were not necessarily representative of the climate of the whole atoll. Data from East Channel (in the north-east) (Farrow 1971) clearly show that the sheltered position of the Picard station grossly underestimates wind speed. Maximum temperatures at Picard were 3°C

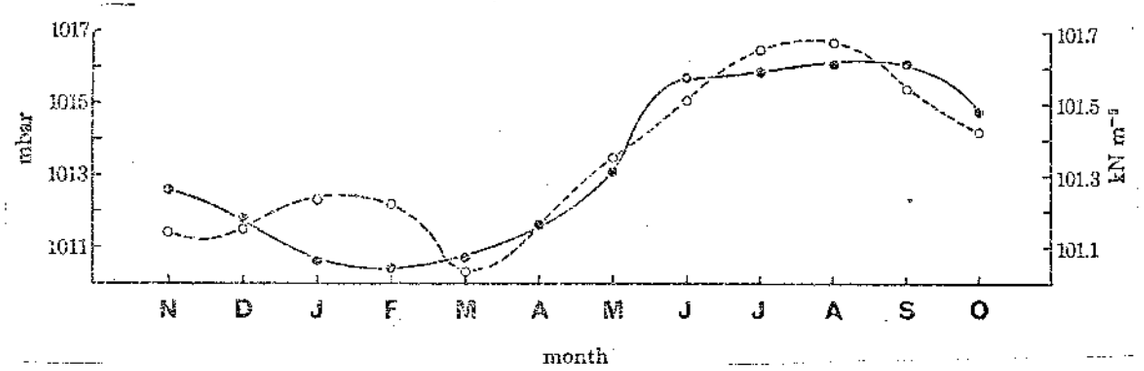


Figure 13. Mean monthly atmospheric pressure over Aldabra. o--o data from Settlement 1967/1968; •—• 20-year average from "Environmental Atlas for the Western Indian Ocean and Gulf of Aden. (Anonymous 1969). (From Farrow 1971, p. 70.)

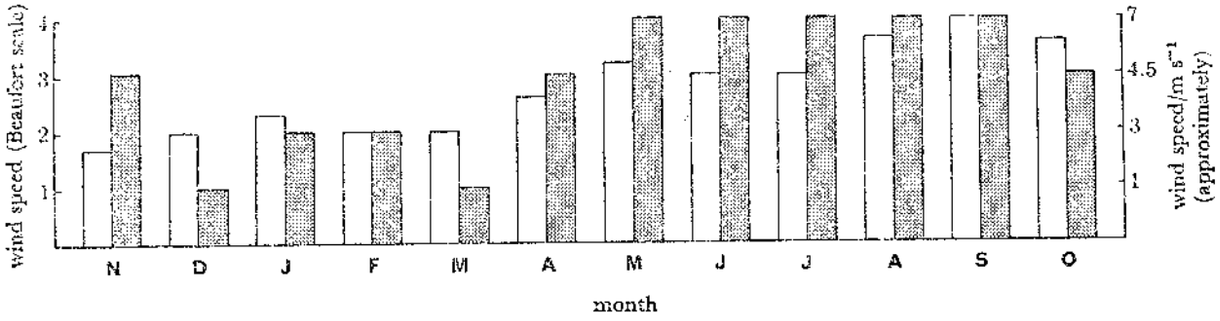


Figure 14. Mean monthly wind speed: at Settlement 1967/1968 - unshaded, and 20-year average from world atlas - shaded.

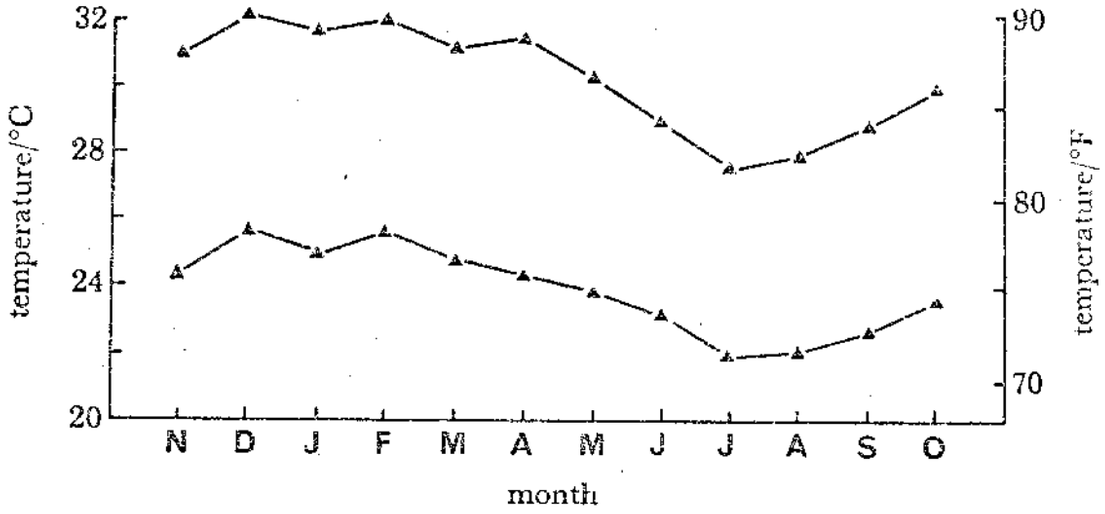


Figure 15. Mean monthly maximum and minimum air temperatures at Settlement 1967/1968.
(From Farrow 1971, p. 74.)

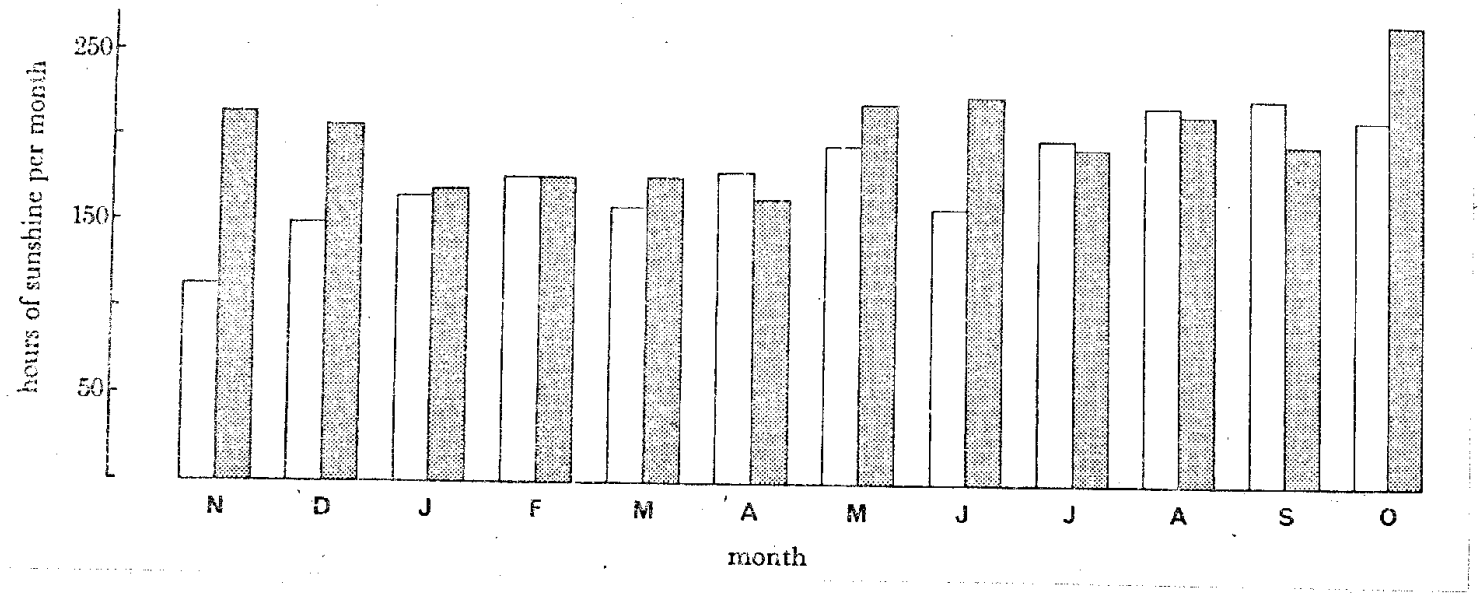


Figure 16. Calculated mean monthly sunshine totals: 1967/1968 - unshaded; 20-year average from world atlas - shaded.
(From Farrow 1971, p. 77.)

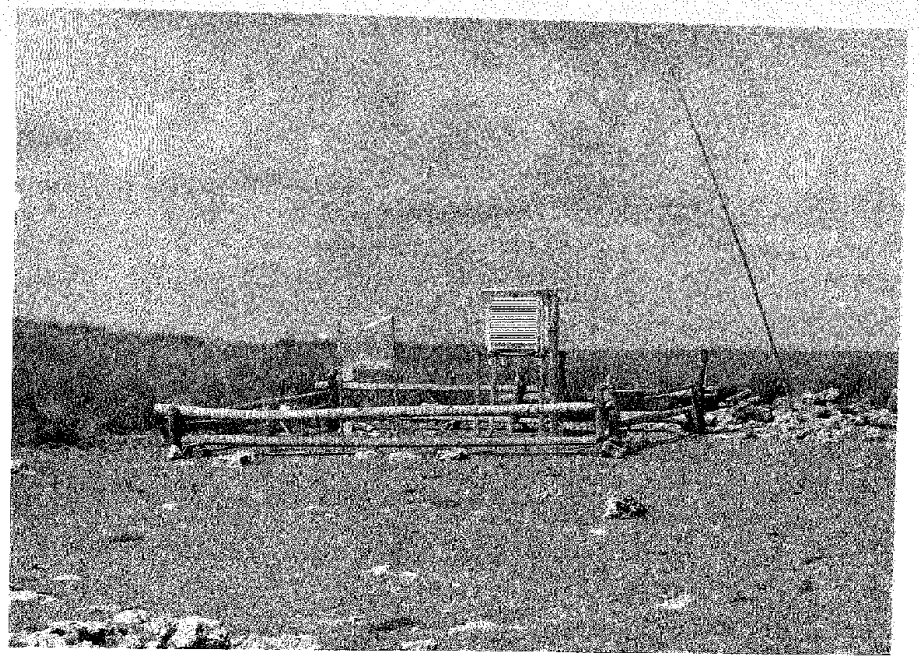


Figure 17. The meteorological station at Dune Jean Louis, viewed from the North.

higher and minima slightly lower than at East Channel. There was also a strong indication in September/October 1968 that rainfall was more common in the east of the atoll. The atoll's effect on climate is conspicuous during the trades when cloud banks line up along the south, north, and north-east coasts (Farrow 1971, p. 85; personal observation).

Because of this variation in local climate I decided to record meteorological data at my study area on the south coast at Dune Jean Louis. A stout bamboo fence was built around a 2 x 3 m plot of grass at the south-east corner of a large grassland plain, 60 m from the sea. The fence was necessary to protect the meteorological equipment from tortoises (Figure 17). Inside the fence a small Stevenson screen was erected with its base one m above the ground. It housed a wet and dry bulb and maximum and minimum thermometers. Also inside the fence were placed a five inch rain gauge, a black bulb thermometer, a 30 cm soil thermometer, and a "hand held" anemometer fixed to a post. Because the soil within the enclosure was shallow the 60 cm and 90 cm soil thermometers were buried in the Dune Jean Louis beach, about 2 m inland from the crest. Temperature, wind, and rain records, estimates of cloud cover in eighths ("oktas"), and observations on general weather conditions were made at 0900 local time (0600 GMT). Appendix I gives dates when I was at the Dune Jean Louis camp.

It must be emphasized that the results from meteorological observations at Dune Jean Louis are representative of that locality for the period June 1969 to June 1970. It is clear that there is a great amount of annual variation in the weather at Aldabra, but I have not examined the 1969/70 records from the main meteorological station. Hence, differences between the 1967/68 Picard data and the 1969/70 Dune Jean Louis data must be interpreted with caution, for they may be due to year and/or locality effects.

Rainfall at Dune Jean Louis shows a distinct summer peak, with the greatest monthly rainfall (265·6 mm) occurring in March. Unlike the Picard data there is no suggestion of bimodality in annual precipitation (Figure 18). The lowest rainfall period occurred during August, September, and October which is consistent with Picard (Figure 11). August was the driest month with only 7·5 mm of rain. Total rainfall during the 12 month period was 1013·7 mm, high in comparison with other years at the main station (Farrow 1971, p. 79), and considerably above the mean annual rainfall figure of 760·1 mm given by Stoddart (1971 d, p. 8).

Wind speed is highest during the winter, averaging 14·5 knots in August and dropping to four knots in March (Figure 19). Both the marked decline in March and the general seasonal pattern are consistent with previous observations from Picard (Figure 14) (Farrow 1971, pp. 71, 73).

Average monthly air temperatures from the Stevenson screen are shown in Figure 20. Maxima vary from 31·2°C in January and March to 26·1°C in August, winter values being much lower than summer values. The greatest shade maximum was 33·1°C, probably from March when I was away from camp. The overall seasonal pattern is similar to Picard but maximum temperatures are one or two degrees lower at Dune Jean Louis. Monthly minima vary from 25·9°C in January to 22·5°C in September, again, winter values are lower than summer values. The lowest minimum was 20·1°C in September. These temperatures, along with the seasonal pattern, are comparable with those from Picard. Diurnal range in temperature varies from 5·7°C in summer to 3·7°C in winter, considerably less fluctuation than recorded at Picard. The seasonal pattern of greatest diurnal variation in summer is similar to the main station. There appears to be a sudden change between winter and summer temperatures at Dune Jean Louis, while at Picard the transition is more gradual (Figure 15).

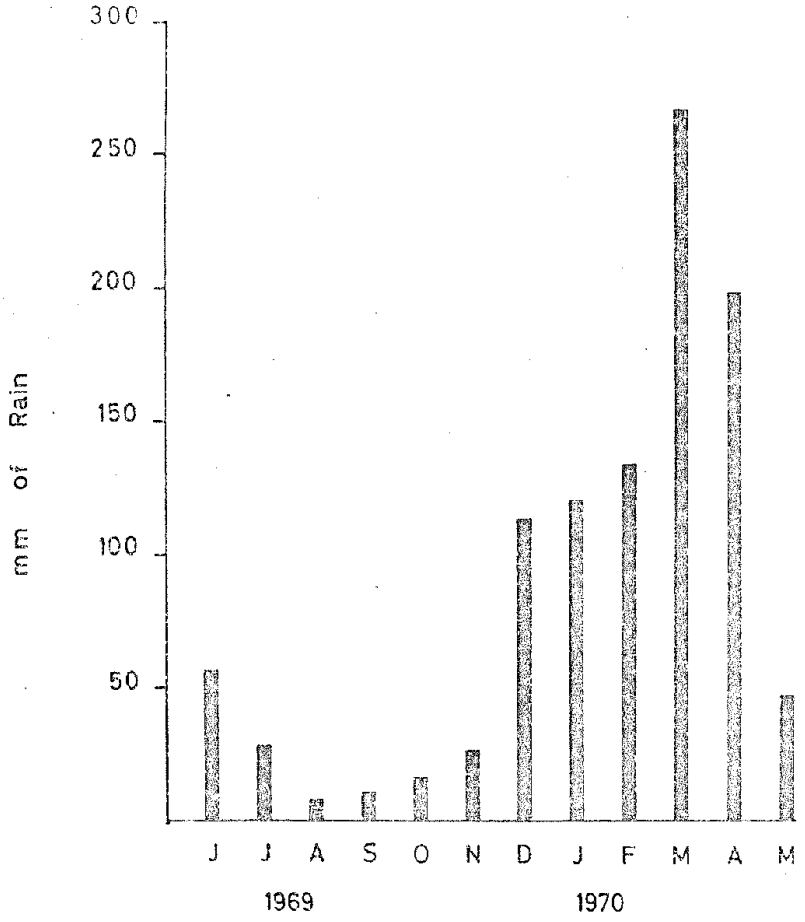


Figure 18. Total monthly rainfall from June 1969 to May 1970 at Dune Jean Louis, Aldabra (in mm). Collected in a 5 inch rain-gauge.

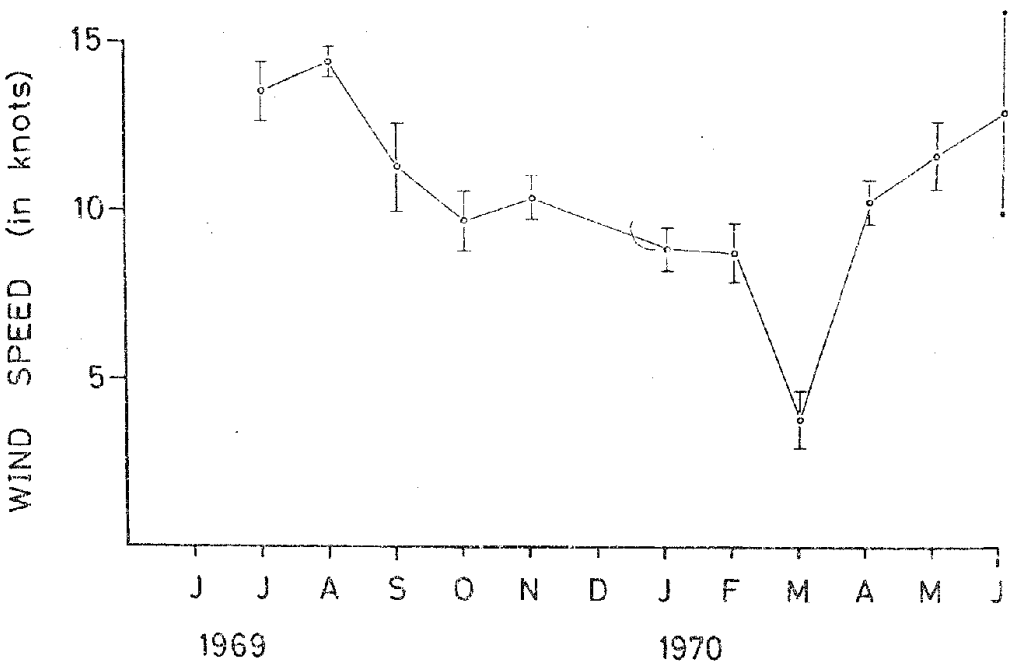


Figure 19. Mean monthly wind speed (± 1 standard error) in knots, recorded Dune Jean Louis, 0900 hours (= 0600 GMT), with a hand-held anemometer. ● = individual reading.

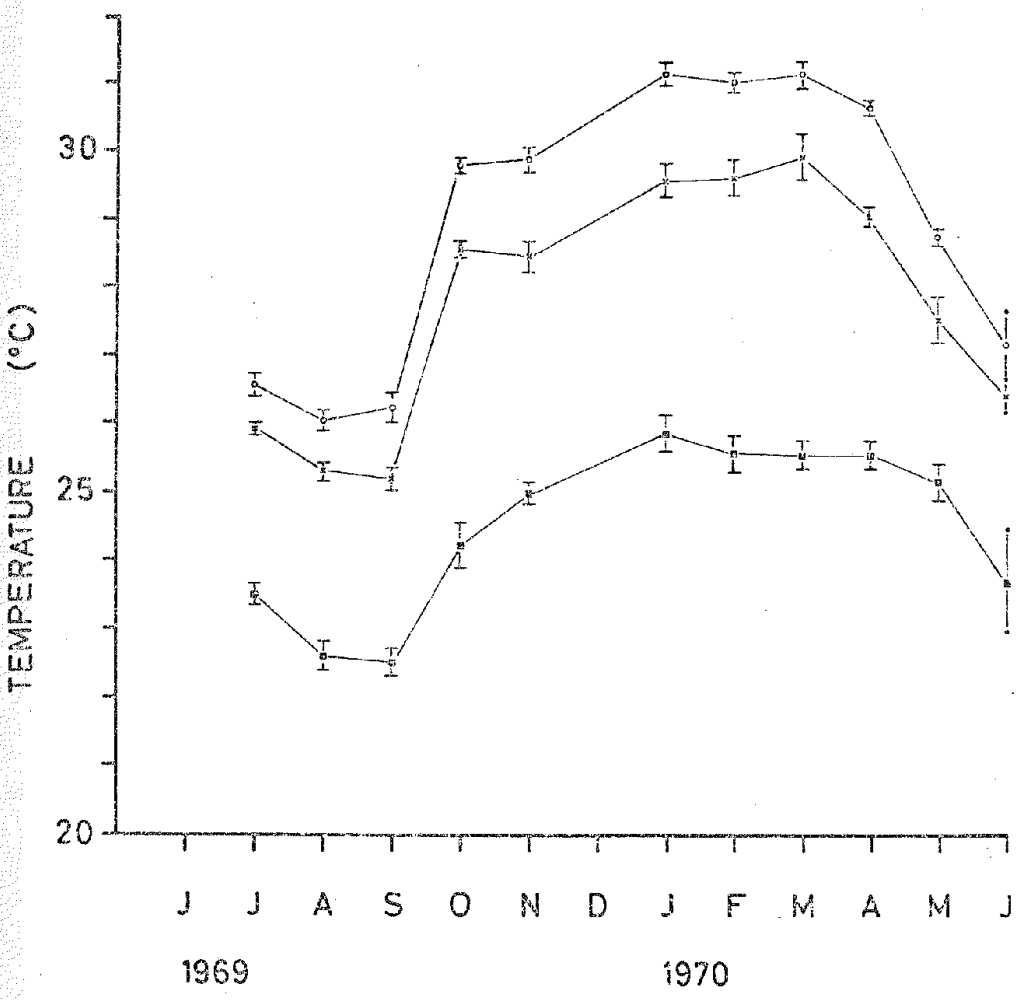


Figure 20. Mean monthly air temperatures (± 1 standard error). Recorded at 0900 hours (= 0600 GMT) Dune Jean Louis. o = maximum; closed square (■) = minimum; x = dry bulb; ● = individual reading.

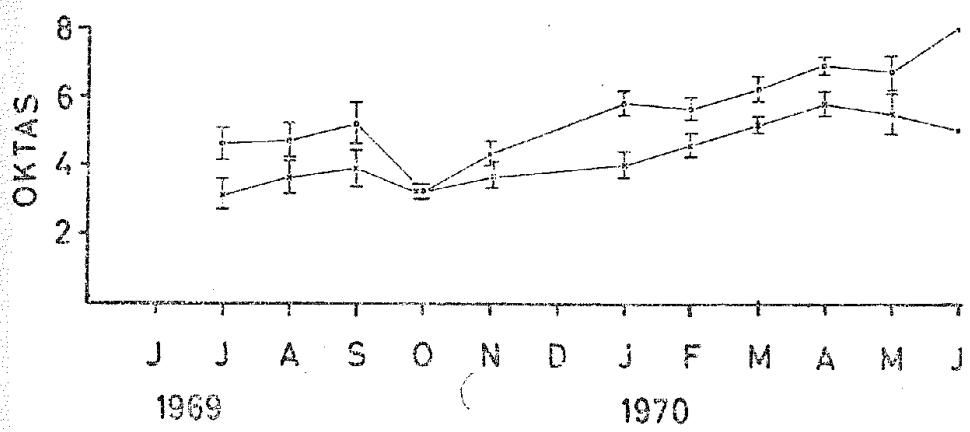


Figure 21. Mean monthly cloud cover (± 1 standard error). Recorded at 0900 hours (= 0600 GMT) Dune Jean Louis. o = total cloud; x = low cloud only; ● = individual reading; "Oktas" = eights of the sky.

There is no clear seasonal pattern in mean monthly cloud cover, either in total amount of cloud or in low cloud alone (Figure 21). Instead, there is a strong tendency for increase in cloud cover during the period of observation. However, the marked decline in the October value is consistent with the Picard data (Figure 16). Farrow (1971, p. 77) used the following conversion from cloud cover to sunshine hours: $S = T\ (8-C)/8$, where "S" is the number of sunshine hours per day, "T" is the number of hours from sunrise to sunset and "C" is the amount of cloud cover in "oktas" or eighths of the sky. On this basis there was a steady decrease in sunshine from 6·3 hours per day in October 1969 to 1·9 hours per day in January 1970, quite different from the main station.

Monthly means in black bulb temperatures rise to a peak of 64·5°C in January from the low value of 59°C in August (Figure 22). There is an obvious seasonal pattern with summer months high and winter months low, and the transition from summer to winter is very rapid. Variation in black bulb temperatures is greatest in summer, with the standard error of the February mean at about 1·6°C. Standard error of the July and August means is a low of 0·3°C.

Black bulb temperature minus shade maximum temperature can be used as a measure of solar radiation. These values range from 34·6°C to 31·3°C and, as one would expect from the data on cloud cover, there is no clear seasonal pattern (Figure 23). Instead, there is a trend for decreasing values during the period of observation. The marked peak in solar radiation in September 1969 precedes the peak in daily sunshine that occurred in October. This is not unlike the findings at Picard where August, September, and October were the sunniest months of the 1967/68 observation period. The variation in solar radiation values is greatest in summer months. The standard error of the February mean was 1·6°C, while

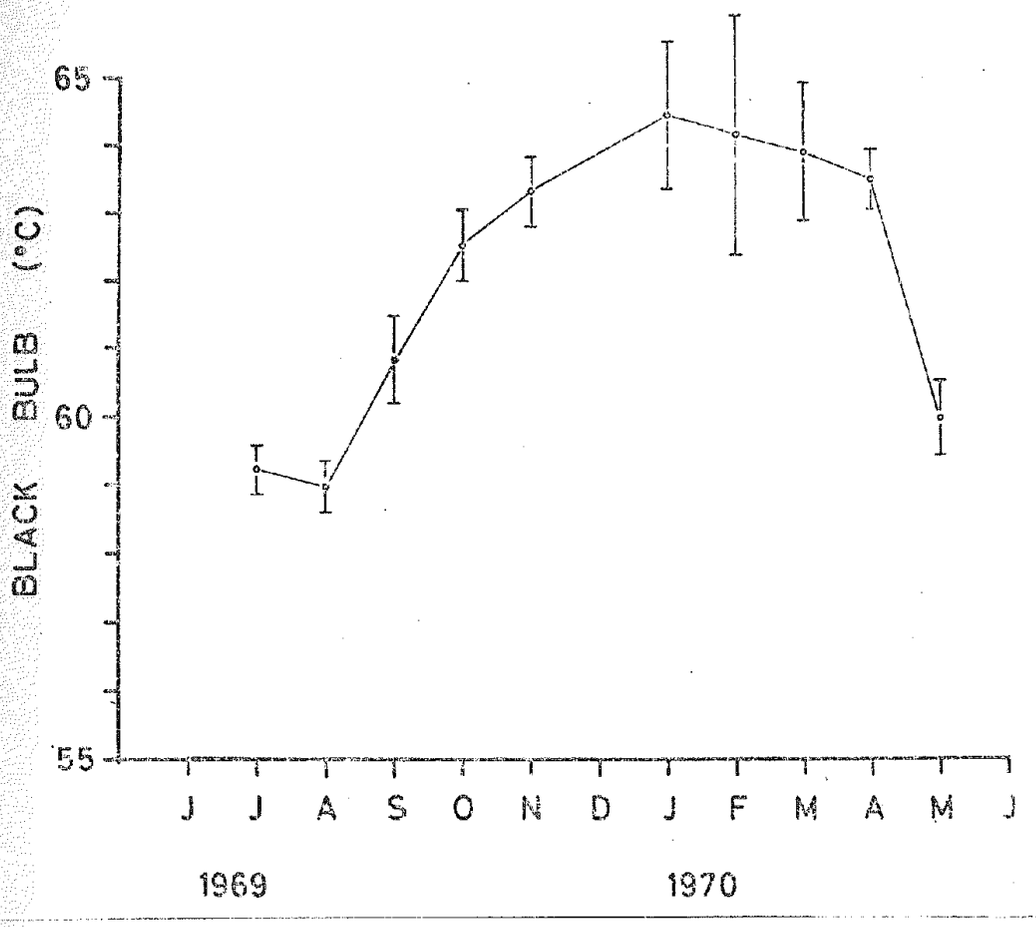


Figure 22. Mean monthly black bulb reading (± 1 standard error) Recorded at 0900 hours (= 0600 GMT) Dune Jean Louis.

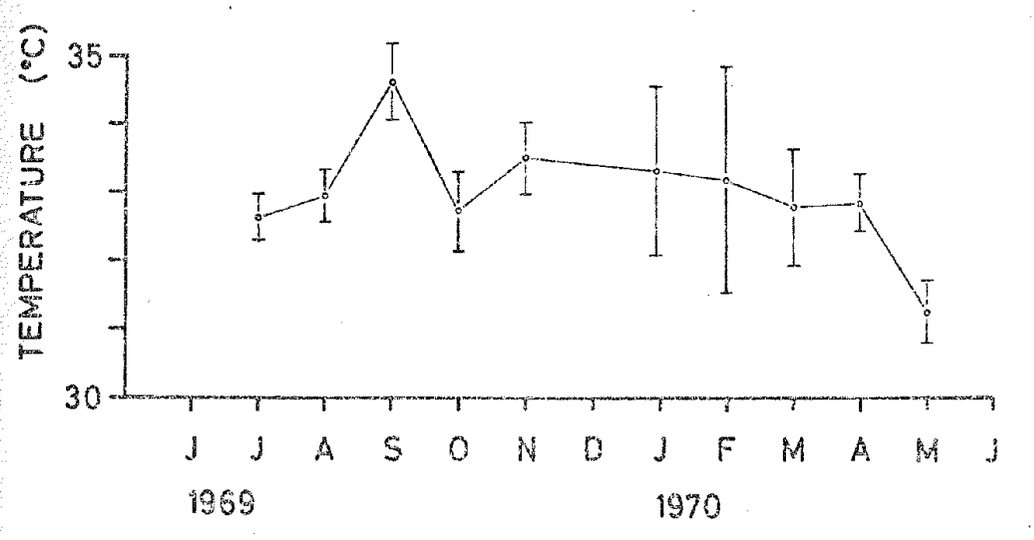


Figure 23. Mean monthly difference between black bulb and maximum thermometers (± 1 standard error). Recorded at Dune Jean Louis.

the standard error of the June mean was 0·3°C. This pattern is obviously related to the large amount of variation in black bulb temperatures that occurred during the summer (Figure 22). Variation in monthly maximum temperatures is fairly constant, although there is a tendency for dry bulb temperatures to be slightly more variable in the summer.

Soil temperatures (Figure 24) show a seasonal pattern, rising quickly to a peak in summer and gradually declining during the winter. The 30 cm thermometer rises from 28·5°C in winter to a peak at 31°C in November. It gradually declines back to 28·9°C in June 1970. Rain affects the 30 cm thermometer quite suddenly; within several hours of a hard rain it may drop several tenths of a degree. Soil temperatures at 30 cm show more variation in summer than in winter. Standard error of the March mean is 2°C, while the same measure of variation is less than 0·5°C in winter months.

Soil temperature at 60 cm rises from 26·6°C in October to a peak of 29°C in March and then declines (Figure 24). Daily variation in temperature at this depth is very small, although a hard rain can depress the mercury 0·1°C within a day. The 90 cm thermometer shows the same trend as seen in the 60 cm. Although the October low is 26·3°C the March peak is 29°C, similar to the 60 cm reading. Temperatures at 90 cm are lower than those at 60 cm until March when there is an inversion and then soil at 90 cm is warmer than that at 60 cm. Once the soil at 90 cm obtains the summer heat, it gives it up very slowly. There is little variation in daily soil temperature at 90 cm, but a very hard rain may have a slight cooling effect within a day or two of its falling.

Table 1 summarizes the meteorological observations made at Dune Jean Louis in 1969 and 1970. Monsoon months are characterized by: heavy rainfall, low wind, high air temperatures, great range in diurnal temperature, high black bulb readings, great variation in black bulb readings, great variation in solar radiation index (i.e.

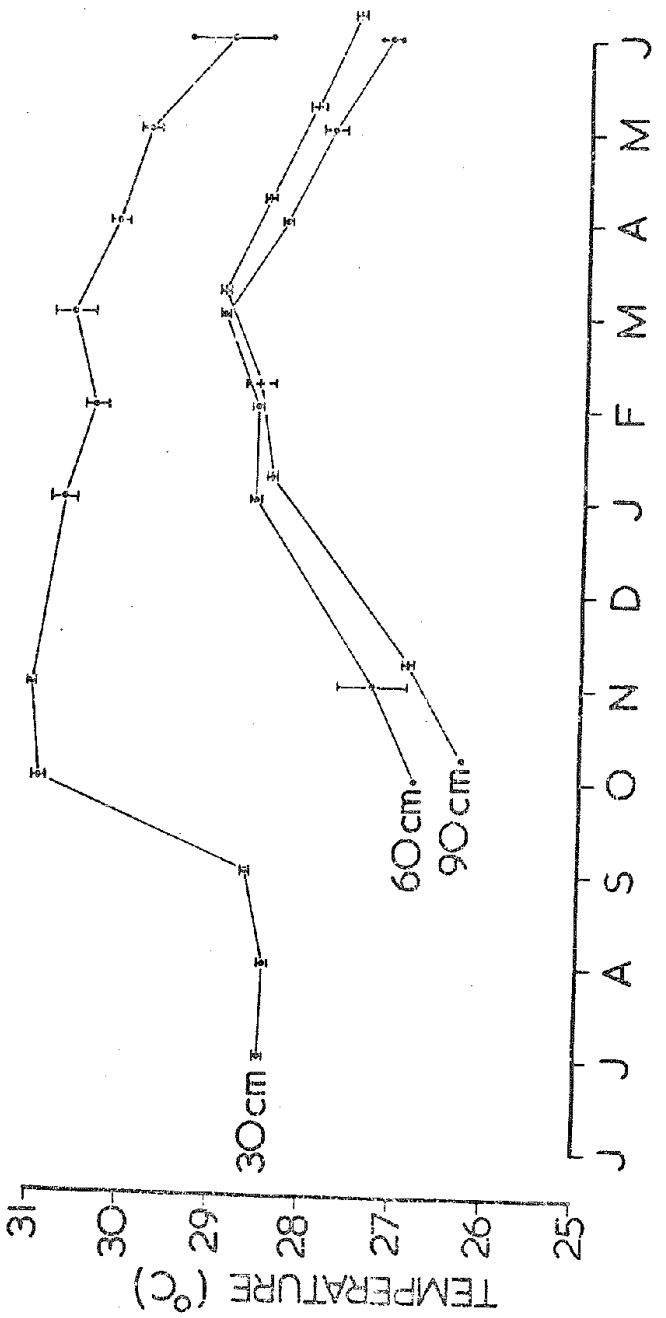


Figure 24. Soil temperatures at Dune Jean Louis recorded at 0900 hours (0600 GMT). Mean ± 1 standard error.
• = individual observation

TABLE 1. Summary of meteorological data from 1969/70 at Dune Jean Louis

Month	Rain	Wind	Max.	Min.	Max. - Min.	Total cloud	Sun	Black bulb Mean	Black bulb (two St.Er.)	Black bulb-Max. Mean	Black bulb-Max. (two St.Er.)	30cm Soil Mean	30cm Soil (two St.Er.)	60cm Soil	90cm Soil
MONSOON															
Nov.	-	o	o	+	o	o	o	+	o	o	o	*+*	-	-	-
Dec.	+														
Jan.	+	-	+	+	+	o	o	+	+	o	+	+	+	+	+
Feb.	+	-	+	+	+	o	o	+	+	o	+	+	+	+	+
March	*+*	*-*	+	+	+	o	o	+	+	o	+	+	+	+	+
April	*+*	o	+	+	+	o	o	+	-	o	o	+	+	+	+
TRADES															
May	-	o	o	+	-	o	o	-	o	-	o	o	+	-	+
June	-	+	o	-	-	o	o	-		o	o	-		-	-
July	-	+	-	-	-	o	o	-	-	o	-	-	-		
Aug.	*-*	+	-	-	-	o	o	-	-	o	-	-	-		
Sept.	*-*	o	-	-	-	o	o	o	o	+	o	-	-		
Oct.	*-*	-	o	o	+	*-*	*+*	o	o	o	o	*+*	-	-	-
Symbols used	*-* < 20	*-* < 5	- ≤ 27	- ≤ 24	- ≤ 5	*-* < 4	*+* > 6	- < 60	- < 1	- < 32	- < ·75	- ≤ 29	< 2	- ≤ 28	- ≤ 28
	- < 100	- < 10	+ > 30	+ > 25	+ > 5			+ > 63	+ > 2	+ > 34	+ > 1·5	+ > 30	+ > 2	+ > 28	+ > 28
	+ > 100	+ > 12										*+*=31			
	+ > 200														
Units	mm	knots	°C	°C	°C	Oktas	hr./day	°C	°C	°C	°C	°C	°C	°C	°C

o = reading does not fall above or below "+" or "-".

black bulb - maximum), high soil temperatures, and great variation in soil temperatures. The other six months are characterized by: low rain, high wind, low air temperature, small range in diurnal air temperatures, low black bulb readings, low variation in black bulb readings and solar radiation index, low soil temperatures, and little variation in soil temperatures.

Certain months are exceptional. March and April, at the end of the monsoon, are the wettest and calmest. The driest and sunniest period is at the end of the trades, October especially. Soil temperatures peak just before rainfall becomes intense, evidently because of upward heat flow from surface evaporation. High rains are also probably involved in causing variation in black bulb and soil temperature readings.

Flora and Vegetation

Botanical studies at Aldabra are in their infancy, for a complete checklist is still wanting. Just over 200 species of flowering plants have been recorded from the atoll, and nearly 10% are endemic. The angiosperm flora is composed of a variety of herbs, grasses, sedges, and shrubs, but includes only a few large trees. Floral affinities with various geographical areas are discussed by Renvoize (1971), and Fosberg (1971) has made a preliminary analysis of the vegetation. He lists sixty-three vegetation types based on the I.B.P. - Fosberg scheme. Most of these types are very localized, and he estimates that only twenty-three occur in areas large enough to be mapped on available 1: 25 000 (i.e. 1 cm = 250 m) maps. About 75% of Fosberg's vegetation types are important to tortoises, but such types as submerged sublittoral meadows, mangrove forests, and various dense scrub forests are seldom, if ever, visited by the reptiles.

Major Terrestrial Habitats

For the present purpose it is useful to divide the terrestrial area into seven major habitats. These are based on limestone surface type and associated vegetation. Figure 25 illustrates the distribution of these habitats.

Casuarina woods. Woods of Casuarina equisetifolia (L.) are restricted in distribution, occurring mainly around the passes at East Channel, Main Channel, and at the settlement by West Channels. At most, the woods are a kilometre long and several hundred metres wide. The trees grow on smoothed champignon that is often covered by a layer of sand, which in turn is covered with a layer of litter. The litter of Casuarina needles is so thick that there is usually little ground vegetation and thus little food for tortoises (Figure 26). Except for the woods on the western side of East Channel, the chelonians seldom occur in this habitat, and when they do it is mainly to utilize the shade.

Mangrove forests. The mangrove forests are confined to the sheltered shores of the lagoon. They form nearly a complete ring on the interior of the atoll, varying in width from a few hundred metres wide to two km in the north-west and the south-east. Four species of tree are common and three additional species are restricted to a few localities. The limestone is heavily dissected and often covered by tides. Movement through the forests is both difficult and dangerous, and there is little for a tortoise to eat (Figure 27). Not surprisingly, they are almost never found in this habitat.

In the south-east of the atoll the mangrove forest gives way to a mangrove swamp composed mainly of small Avicennia trees. There is a large amount of open, unvegetated ground and wide meandering creeks are common. A great abundance of tortoises occurs in this particular mangrove habitat (Figure 27) (Grubb 1971 a, p. 352).

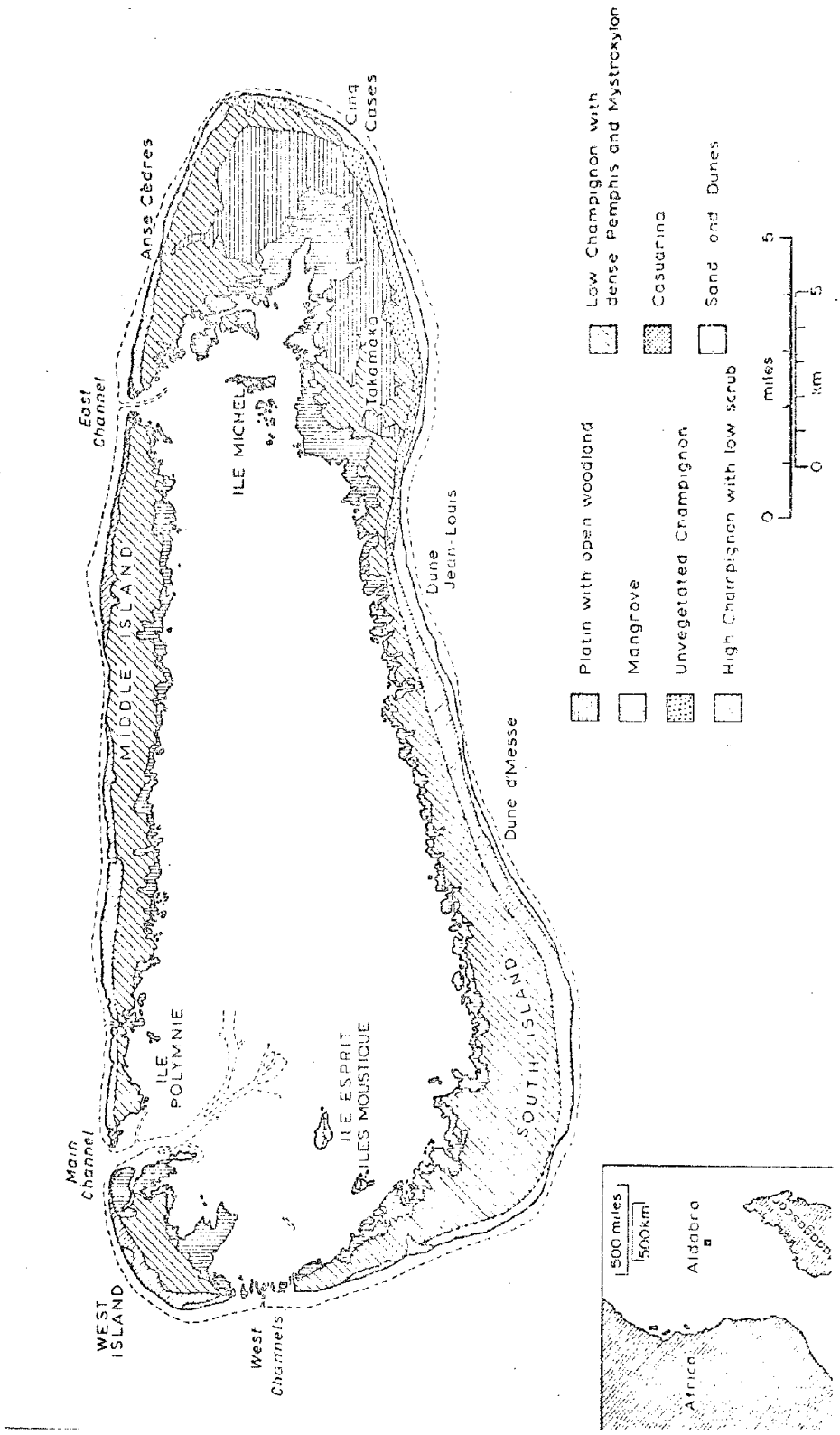


Figure 25. Distribution of major terrestrial habitats at Aldabra.
("Unvegetated champignon" = smoothed champignon; "high champignon with low scrub" = pavé and mixed scrub.)
(From Stoddart 1971a, p. 18.)

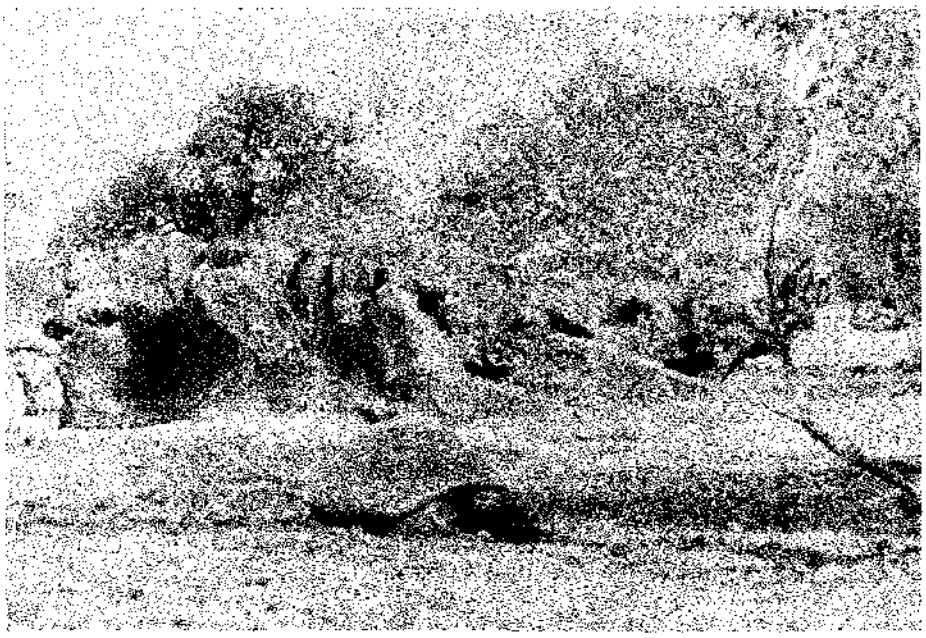


Figure 26. Casuarina woods at Anse Cèdres, showing the lack of ground vegetation.
(From Stoddart 1971 b, Fig. 12.)



Figure 21: Mangroves

1. Dense prop roots and [illegible]
2. Open [illegible]
3. Zone with [illegible]



B.



C.

MacNae (1971) has made a preliminary survey of the mangroves.

Champignon and dense Pemphis. Three quarters of the land area of Aldabra is heavily dissected, low level champignon. This habitat occurs inland from the mangrove forests and is up to three km wide in the south-west of the atoll. It is covered with a dense scrub forest of Pemphis acidula, Mysteroxylon aethiopicum, and Sideroxylon inerme (Figure 7). The dominance of these three species, especially the Pemphis, is such that the scrub looks homogeneous when in fact it is quite heterogeneous. Although the canopy is complete, it is low (one to two metres high) and does not provide dense shade. Ground cover is uncommon except where the three dominants give way to small, mixed species stands. In these isolated areas the number of species may be quite high, and the vegetation provides deep shade. Usually herbs or sedges, and possibly some leaf litter, are present as well. On the whole, movement through the dense Pemphis and over the heavily dissected champignon is tedious work; Fryer (1911) has described this in some detail, calling this habitat an "obstacle to exploration". Certainly it is an obstacle to tortoises, for they almost never occur on it.

Smooth champignon. Smooth champignon is at a higher elevation than the heavily dissected limestone. It occurs along the east and south-east coasts in a narrow strip several hundred metres wide, where the south-east trade winds have their full effect. In reference to this habitat Stoddart (1971 a, p. 18) uses the term "unvegetated champignon". From a distance it does look barren of plants, but in actuality it supports quite a variety (Figure 8). There are many small herbs, but because of heavy cropping by tortoises they are inconspicuous and only able to flourish in depressions and crevices where the animals cannot reach. Fully exposed shrubs are scarce, hence shade is rare in this habitat. Yet, shrubs and small trees

are common in the pits that frequently perforate the smooth champignon. The leaves and branches of these shrubs are strictly limited to the centre of the pit, and as soon as they extend within a foot or so of the edge they are promptly taken by tortoises. The animals occur in this habitat in large numbers, except at midday when they move elsewhere for shade.

Pavé and mixed scrub. Pavé forms a narrow strip along the north, south, and west coasts, seaward of the low champignon and dense Pemphis. The low champignon is a metre or more below the level of the pavé, which Stoddart (1971 a, p. 18) refers to as "high champignon". At most the zone of pavé is one km wide, usually it is less. Along the north and west coasts the pavé is adjacent to sea cliffs, but along the south coast its seaward edge is delimited by sand dunes and perched beaches. In the south, the scrub is low and stunted, usually one metre high, and very rarely above two (Figure 6). Because these bushes occur in clumps, the canopy is discontinuous, but deep shade is not uncommon in this habitat. The usual vegetational formation for most of the south coast pavé is rows of shrubs running north-west to south-east in line with the trade winds. Although the rows are generally only one plant wide, and no more than a metre across, they are extremely dense and nearly impenetrable except where natural breaks in the vegetation occur. These "wind rows" of vegetation form countless alleys across the pavé in which movement is relatively easy, for there are essentially only herbs and sedges between the rows. The mixed scrub and pavé in the Dune Jean Louis area, to be described later, depart from this general pattern in that there are few wind rows and the vegetation is open.

Mixed scrub and pavé along the north coast is also without conspicuous wind rows, but it has clumps of shrubs interspersed with small glades, creating a mosaic pattern. There are many large

depressions in which soil collects and supports isolated stands of trees up to three or four metres high. These trees provide deep shade below which is a ground cover of grasses and sedges.

West coast mixed scrub is most often growing on sand which is on top of pavé. There tend to be dense shrubs at the seaward and lagoonward edges of the zone, with long narrow glades in the middle. Small grassland pastures are common in the opening. However, much of this area has been interfered with for coconut plantations.

Pavé is the tortoise habitat along the north and east coasts, and it is heavily populated by the animals along the south coast.

Coastal plains. The south and east seaward coasts are exposed to tremendous winds and waves during the south-easterly trades. These forces transport sand to the shore and carry it over sea cliffs that may be up to three metres high. Such "perched beaches" often support narrow, but extensive grassland plains (Figure 9). Sporobolus virginicus (L.) is the dominant grass over much of the area, and it is usually kept cropped to less than three cm high by large herds of tortoises that graze these plains. Sclerodactylon macrostachyum (Benth.) Camus occurs in swards adjacent to the Sporobolus. The Sclerodactylon grows to nearly fifty cm high, and the transition from the high to the low species is extremely sudden. It is not clear whether one is replacing the other. Stoddart (1968) suggested that Sclerodactylon was invading the Sporobolus, but the situation appears to be static, as Grubb (1971 a, p. 353) has also commented.

Sedges often occur between the Sporobolus plain and the mixed scrub. Cyperus ligularus (L.), with fruiting bodies nearly fifty cm high, grows in dense homogeneous swards, while smaller sedges Fimbristylis spp. occur in discrete clumps or cushions. The Sporobolus grassland appears homogeneous, but a variety of prostrate herbs are found in association with the grass. Where the plains give way to bare, wind-blown sand or the pit left by a nesting sea

turtle, Euphorbia prostrata Ait. and Launaea sp. are usually found in the absence of grass. Euphorbia particularly seems successful in colonizing bare sand. Its distribution, however, is not limited to the colonization of wind-blown areas. The western slope of Dune le Rat, on the south coast, has a reddish cast with the high density of this rubiginous species.

Platin and open woodland. Several features of this habitat stand out as unique. The terrain is smooth and pavement-like. Fresh-water pools are frequent and they are commonly flanked by groves of screw pine, Pandanus sp. (Figure 5). Mixed species woods, with trees three to four metres high, occur in a mosaic with glades and clumps of low mixed scrub. Swards of grass and sedge are common in the glades, although there may also be bare limestone. The woods afford dense shade and, relative to the rest of Aldabra, there is abundant organic soil and litter under the trees. Despite the mosaic quality of the habitat it is incredibly easy to lose one's way for there are few terrestrial bearings (except for the roar of the sea) that a visitor to the area can use for orientation.

Of the different habitats on Aldabra, platin supports the greatest variety of indigenous plants. This habitat supports the largest population of giant tortoises anywhere in the world. It is estimated that over 98,000 tortoises occur on the 30 sq. km of platin (Grubb 1971, p. 366). Concentrated at a density of 23 animals per hectare, the giant tortoise is one of the most ubiquitous features of this habitat.

The Study Area

The majority of the work was carried out from a semi-permanent camp at Dune Jean Louis, on the south coast (see the time schedule in Appendix I), and most of the observations were made from the

grass plain on the east side of the dune, "East plain" (Figure 28). Numerous observations were also made on neighbouring plains, bordering areas of shade trees, and areas of mixed scrub lagoonward from the dune (i.e. north).

East plain is over 300 m long and about 50 m wide, and like the adjacent dune and beach area it lies in a north-west to south-east orientation. It is three to five m above sea level and nearly flat, although there is a slight depression in the centre. After very heavy rains temporary puddles collect, but within a few hours they evaporate or soak away, and there is usually no water on the plain. At several places, especially at the south-eastern end of the plain, pinnacles of rock protrude up to one m through from the sand.

The plain consists primarily of a short turf, Sporobolus virginicus, which never grows to more than about two cm high. Herbaceous prostrates (Sida parvifolia DC., Launaea sp., Euphorbia prostrata, and Phyllanthus sp.) are dispersed among the grass. Phyllanthus tends to occur around rocks while Launaea and Euphorbia occur on more exposed and disturbed sand - often being the first to colonize. A few scattered clumps of the long spiky grass, Sclerodactylon macrostachyum, also occur on the plain, and elevated above the plains proper, growing on the rock pinnacles, are occasional isolated herbs and small grasses.

Sharp changes in the vegetation occur at the edges of the Sporobolus grassland. A dense sward of Sclerodactylon macrostachyum is in the south-east between the plain and the sea. Growing nearly half a metre high, it forms a very distinct border to the short grass plain. Along the northern edge of east plain are shrubs and small trees which vary from 0·5 to 2 m in height; in order of decreasing abundance they include: Scaevola taccada (Gaertn.) Roxb., Colubrina asiatica (L.) Brong., Tournefortia argentea L.f.,

Figure 28. The study area.

A. Aerial view. Dune Jean Louis in centre (Indian Ocean along the right), mixed scrub in conspicuous 'wind rows', but very open at Dune Jean Louis. The photograph represents an east to west distance of nearly 1 km.

B. View from the top of Dune Jean Louis looking E.S.E. across the eastern Sporobolus plain.



A



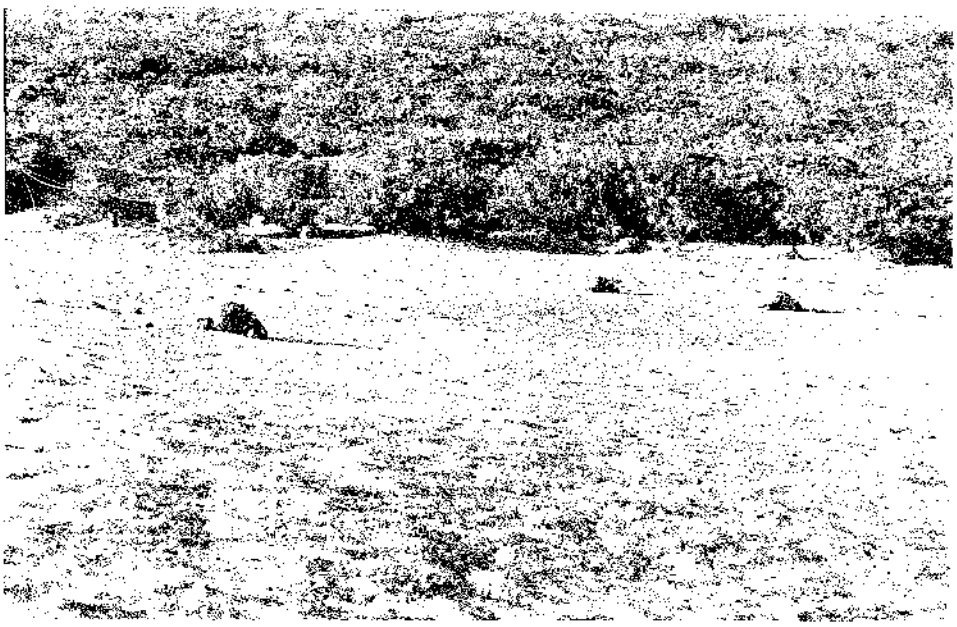
B

and Pemphis acidula. The Scaevola, in particular, forms a zone that separates the grassland from the inland mixed scrub. At the north-east there are few shrubs and it is mostly Cyperus that delimits the plain. To the west the grass changes suddenly into bare sand and dune (Figure 29).

On the dune itself, and behind it in the lee of the south-east trade winds, are large trees: Tournefortia argentea, Guettarda speciosa L., Thespesia populnea (L.) Sol. ex Cornea., and Ficus thonningii Bl. Some of the large Guettarda have canopies seven m high and fifteen m in diameter.

A ridge runs along most of the south coast about 300 m inland, and associated with it is a thin but very dense zone of Pemphis acidula and other shrubs. Farther inland is a heterogeneous assemblage of shrubs, small trees, herbs, and grass; this is the "mixed scrub" and pavé. The majority of shrubs in the south coast mixed scrub fall into conspicuous wind rows which align south-east to north-west with the trade winds.

The mixed scrub at Dune Jean Louis, however, departs from this general pattern. There is no dense zone of Pemphis behind the dune, and the inland vegetation does not fall into conspicuous wind rows but is open except in a few isolated places (Figure 30). In addition there is an unusually high density of the candelabra tree, Euphorbia abbottii Baker (Figure30), which is most dramatically illustrated at the transition from monsoon to trades. During the summer the scrub is green, but as soon as the south-easterly trades begin to blow the overall colour becomes red almost overnight and then some days later, brown. This is not due to a general transformation in the mixed scrub, for most of the shrubs on Aldabra are evergreen. Instead, the colour change is due entirely to changes in the candelabra tree, for as soon as the winds begin, its leaves turn red very quickly and then a few days later they drop, exposing the brown



A



B

Figure 29. Dune Jean Louis.

A. The east plain with distinct border of Scaevola.

B. The dune with Tournefortia trees.

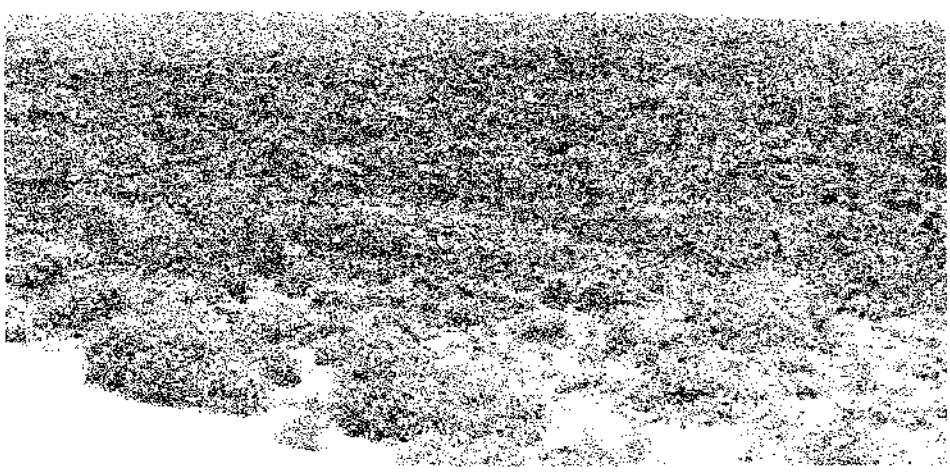


Figure 30. View north-east from Dune Jean Louis showing open mixed scrub. Euphorbia trees are conspicuous with their straight vertical trunks and small canopies.

branches and trunk. Euphorbia trees in the lee of the wind or in pits do not undergo this change but stay green.

The mixed scrub area is up to one km wide in certain areas, but at Dune Jean Louis it is never more than half a km wide. At its inland border the mixed scrub suddenly changes to dense Pemphis acidula, Mysteroxylon aethiopicum, Sideroxylon inerme, and other woody shrubs. Accompanying the vegetational change is a drop in the level of the terrain along with a dramatic increase in roughness and degree of dissection. At the edge of the lagoon the dense Pemphis changes over to low mangrove forests, but tortoises do not occur in either the dense Pemphis or the mangrove forest.

Fauna

Being an isolated, oceanic, low-lying atoll, Aldabra has an impoverished fauna. Peake(1971) has shown however, that the number of species of several taxa fits general predictions in regard to terrestrial area and degree of isolation. He also discusses faunal affinities between Aldabra and other zoogeographic regions. A general review of the various taxa present is in Stoddart and Wright (1967), and Stoddart (1971 a) summarizes past work on various taxa. The most recent work on various groups is as follows: insects (Legrand 1965; Cogan, Hutson, and Shaffer 1971); entomostraca (McKenzie 1971); land crabs (Grubb 1971 b); land mollusca(Wright 1971, and Peake1971); land birds (Benson and Penny 1971; Penny and Diamond 1971); sea and shore birds (Diamond 1971; Penny 1971); bats (Hill 1971), and introduced mammals (Stoddart 1971 b). Recent tortoise studies are by Honegger (1967), Gaymer (1968), and Grubb (1971 a). Studies on marine fauna are: littoral (Taylor 1971); sublittoral and benthic (Price 1971; Stoddart and Yonge 1971), and sea turtles (Frazier 1971).

In brief, the terrestrial fauna of Aldabra is as follows:

Indigenous mammals are limited to three species of bats. Introduced mammals include goats (which may compete for food with the tortoises), and rats, cats and dogs (which may prey on small tortoises), but these interactions have yet to be shown. There are twenty species of land birds, eleven species of breeding sea birds, and over a dozen species of migrant waders. The white-throated rail (Dryolimnas cuvieri (Pucheran)) and the cattle egret (Bubulcus ibis (L.)) both follow tortoises and catch insects disturbed by the reptiles. Beside the giant tortoises, the Testudine fauna includes green sea turtles (Chelonia mydas L.) and hawksbills (Eretmochelys imbricata L.) which nest on the beaches of Aldabra, occasionally digging up tortoise pastures in the process. The remainder of the herpetofauna consists of a skink (Cryptablepharus (=Ablepharus) boutonii (Desjardin)) and two geckos (Phelsuma abbotti Stejneger and Hemidactylus mercatorius Gray). The lizards are often seen crawling over the tortoises, and seem to use them as a source of both heat and food.

The invertebrate fauna includes eleven species of land crabs, some of which are directly important to the tortoises. Birgus latro L., the "coconut" or "robber" crab, is the largest and may prey on young tortoises. Cardisoma carnifex (Herbst.), the second largest, feeds alongside tortoises on the platin and burrows under them on the coastal plains. The three species of hermit crabs in order of decreasing size and increasing abundance are: Coenobita clypeatus Latreille, C. perlatus Milne-Edwards, and C. rugosus H. Milne-Edwards; these all feed on tortoise dung. There is an inland ghost crab, Ocypode cordimana Desmarst which burrows into the Sporobolus plains, often causing erosion. The number of insect species is thought to exceed 1,000 and several species of Diptera have direct relevance to the tortoises. Aedes fryeri (Theobald) - a mosquito, and Neavella albipectus (Bigot) - a horse fly, both suck tortoise blood. Hecamede lacteipennis Lamb. and Chlorichaeta tuberculosa

Becker - shore flies, and at least three species of Leptocdra - dung flies, feed on tortoise dung.

Influence of Man

Aldabra Atoll is presently part of the British Indian Ocean Territory ("B.I.O.T."). Since the late 1800's it has been leased for commercial exploitation - mangrove cutting, fishing, turtling, and exporting tortoises. Perhaps two dozen tortoises a year have been consumed on the atoll in recent times, and an additional fifty per year are allowed to be exported. However, there is little means of enforcing the export quota; and in addition, there is no quota on animals shipped to Seychelles, even though they may later be exported from the colony. These tortoises are usually sold by weight to animal dealers or zoos; hence, there is a demand for large animals. Populations where tortoises are often collected, e.g. Anse Mais and Anse Malabar, have a paucity of large males, apparently for this reason.

Yet, man's interference with the tortoise population over the last hundred years is probably much less than it was during the 17th, 18th, and early 19th centuries. Rothschild (1915, p. 424) cites many records of large numbers of tortoises being shipped from the atoll. For example, in 1847 two ships alone carried off 1,200 animals. By these accounts it is clear that the tortoise population on Aldabra was immense. However, by the late 19th century it was difficult to find the animals; in 1878 a ship's crew took three days to find one tortoise (Stoddart 1971 b, p. 621). This fits the same sequence of events from other parts of the world where man's persistent removal of large numbers of these animals has led to extinction or gross depletion of many races. Both the Galapagos (Townsend 1925, Perry 1970) and the western Indian Ocean races have been affected (Günther 1877; Rothschild 1915; Stoddart 1971 b).

PART TWO

GENERAL BIOLOGY

OF

THE GIANT TORTOISE

Chapters 2 to 9

TAXONOMY, SYSTEMATICS AND DISTRIBUTION

Subclass	Anapsida
Order	Testudinata (= Chelonia)
Suborder	Cryptodira
Family	Testudinidae
Subfamily	Testudininae

Giant land tortoises of this subfamily are known from all major land areas except Australia and have an excellent fossil history throughout the Cenozoic (Hay 1908; Romer 1956; Williams 1950 a, 1952; Auffenberg 1963).

The generic name of the giant tortoises is in dispute. Most old world workers use Linnaeus' name "Testudo" to include the giant as well as many other smaller species of land-living chelonians. New world workers usually follow Williams (in Loveridge and Williams 1957, p. 220) and refer to the giant tortoises as "Geochelone". This taxon, which some authors feel is an artificial fragmentation of Testudo, also includes a number of species smaller than 20 cm long. Representatives of Williams' Geochelone are known, in recent times, from: South-east Asia, India, and Ceylon - seven species (Williams 1952; Wermuth and Mertens 1961); Madagascar - two species (and several extinct in recent times) (Boulenger 1894; Rothschild 1915; Blanc 1971); The Mascarene Islands - numerous species, which became extinct in historical times, but the taxonomy of this group is in need of revision so it is not possible to say just how many species actually existed (Günther 1877; Gadow 1894; Rothschild 1915; Blanc 1971); Seychelles and Aldabra Islands - one species (Günther 1877; Rothschild 1915; Williams 1952; Wermuth and Mertens 1961); The African mainland - two species (Loveridge and Williams 1957); South America and the West Indies - (Auffenberg

1971; Williams 1950 a); Galapagos Archipelago - one species and fifteen races (Günther 1877; Van Denburgh 1914; Garman 1917; Rothschild 1915). See also Boulenger (1889), Williams (1952), Wermuth and Mertens (1961), and Pritchard (1967) for a more comprehensive discussion of the taxonomy.

The Aldabran tortoise, along with recent Madagascan forms and fossil forms from Africa and Madagascar, was first placed in the subgenus "Asterochelys" (Williams 1952), but because of certain skull characters it was later considered distinct from the African species and was removed to "Aldabrachelys" together with recent Madagascan species (Loveridge and Williams 1957). However, Auffenberg's (1966) examination of carpal bones raises some questions as to the phylogenetic position of this subgenus. The specific name for the Aldabran Giant Tortoise is "gigantea" after Schweigger (1812). Synonyms for this species are:

Testudo daudinii		Duméril and Bibron (1835)
Testudo elephantina		Duméril and Bibron (1835)
Testudo hololissa		Günther (1877, p. 39)
Testudo ponderosa	(?)	Günther (1877, p. 35)
Aldabrachelys gigantea		Stoddart (1968, p. 478).

Several allopatric races have been described, but these are also considered conspecific:

Testudo gigantea	Schweigger (1812)	"Brasil"/Mahé, Seychelles
Testudo gouffei	Rothschild (1906)	Seychelles or Farquhar
Testudo sumerei	Sauzier (1892 ?)	Seychelles.

See Günther (1877), Rothschild (1915), Wermuth and Mertens (1961), and Blanc (1971) for more details in this synonomy.

It is a moot point whether or not the populations isolated on different islands at Aldabra should be given subspecific status as done by Wermuth and Mertens (1961) and Blanc (1971); certainly there is no reason at present for maintaining differences in

specific rank between these isolated populations on Aldabra (Gaymer 1968). Rothschild (1915) claimed that giant tortoises were native on most of the islands in the western Indian Ocean (Figure 31), but it is not possible to verify all the localities that he lists. Honegger (1967) found large reptilian eggs (presumably of tortoise) on Assumption, and I have collected fossil tortoise bones from both Aldabra and Astove (see also Grubb 1971 b, p. 364). Several Seychellois claim that they have seen large fossil bones on Cosmoledo, Assumption, and St. Pierre, and there are historical records of tortoises from the Granitic Seychelles (Rothschild 1915; Honegger 1967; Stoddart 1971 b). Stoddart's claim (1971 b, p. 620, Fig. 16) that Geochelone gigantea occurred in the Mascarenes is in error; the Mascarene tortoises form a species group distinct from those on Aldabra (Günther 1877; Rothschild 1915) and are placed in a distinct subgenus, Cylindraspis (Williams 1952).

Figure 31. Distribution of Geochelone in the region of the Western Indian Ocean.

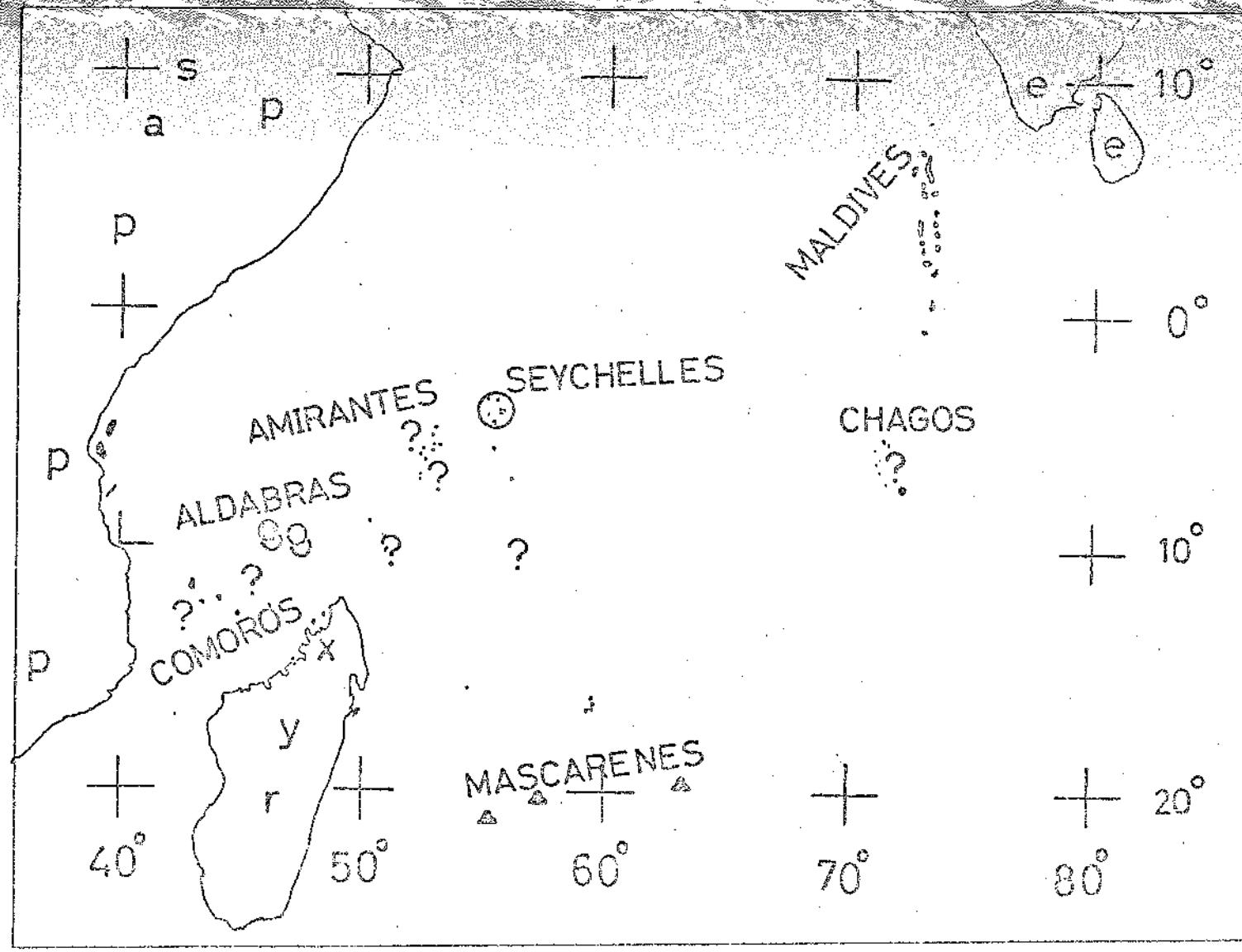
● = G. gigantea

? = Historical record of G. gigantea but no, or doubtful, specimens exist. (Based on Rothschild 1915.)

o = G. sp. unidentified fossils

▲ = G. (Cylindraspis) spp.
a = † G. ammon
e = G. elegans
p = G. pardalis
r = G. radiata
s = G. sulcata
x = † G. grandidieri
y = G. yniphora

(Based on Williams 1952; Loveridge and Williams 1957.)



MORPHOLOGY AND ANATOMY

External Appearance

Size. The most noted feature of giant tortoises is their size. Geochelone (= Testudo (= Colossochelys)) atlas (Falconer and Cautley) from the lower Pliocene of the Silwalik Hills in India was up to eight feet long (Swinton 1965, p. 54). The largest Aldabran giant tortoise in recent times was recorded by Rothschild (1928, p. 660) as 560 lbs (254·5 kg) and 66 inches (167·6 cm) long over the curve of the shell. There are no tortoises even approaching this size on Aldabra today. The largest animal I have seen was a male at Anse Malabar on Middle Island whose carapace measured over the curve was 133 cm long. This is far above the mean size of animals on Aldabra nowadays (Honegger 1967; pp. 25, 26; Gaymer 1968, p. 347; Grubb 1971 a, p. 343) but Honegger has recorded a male 138 cm long at the same locality. Average adult size varies from place to place on Aldabra; it ranges between 0·5 and 1 m long.

Five newly hatched tortoises had weights of: 36, 37, 37, 39, and 39·5 g. The carapace of the 39 g animal was 52·5 mm long. The other animals were not completely "unfolded" when they hatched and were still somewhat spherical.

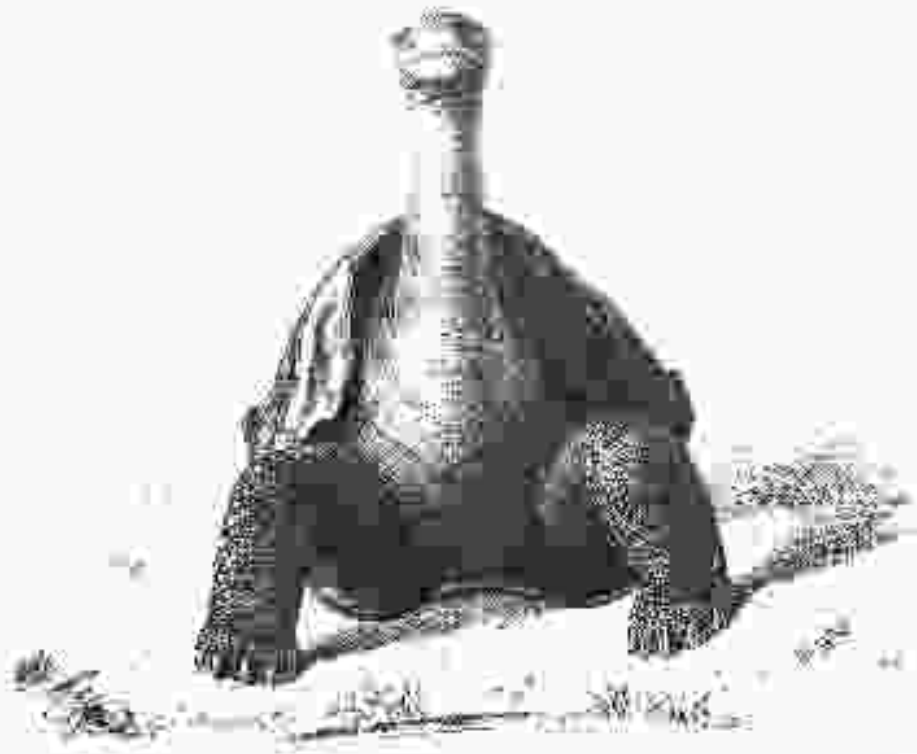
Shape. The shell of a giant tortoise is rather like a dome, but could be more exactly described as half an elipsoid rotated about its major axis. Rothschild (1915) and Grubb (1971 a) have made detailed measurements of various shell paramenters; and I made similar measurements on two hundred immatures, but these data will not be presented here. Some animals tend to be elongate while others are nearly round in shape. Often this difference is related to sex, males being elongate, females being round and

highly domed. In some individuals the edge of the shell turns up, while in others it turns down. The most dramatic variant in shape is the so called "saddle-backed" form; it has the anterior of the shell very open, high in front, and compressed at the sides (Figure 32). Many of the Galapagos races are of this type (Günther 1877; Darwin 1900; Van Denburgh 1914; Rothschild 1915; Garman 1917; Wermuth and Mertens 1961). A saddle-backed form was described from Rodriguez; and Testudo daudinii, thought to have come from Aldabra's Middle Island, appeared much like a saddle-back from the description and plate of it (Günther 1877). However, this specimen is not like any tortoise now on the atoll, for they are all dome-shaped.

These different variations in shape have been given taxonomic significance in the past (Rothschild 1915) but excluding the saddle-backed condition, there is considerable variation within the Aldabra population and many of Rothschild's key characters seem to be of little use. One important distinguishing feature between the supposed South and Middle Island races was the presence of conspicuous striations on the shells of the latter. In fact these striations are produced by growth and are probably more related to environmental than genetic conditions. Ontogenetic changes in shape may also occur (Grubb 1971 a).

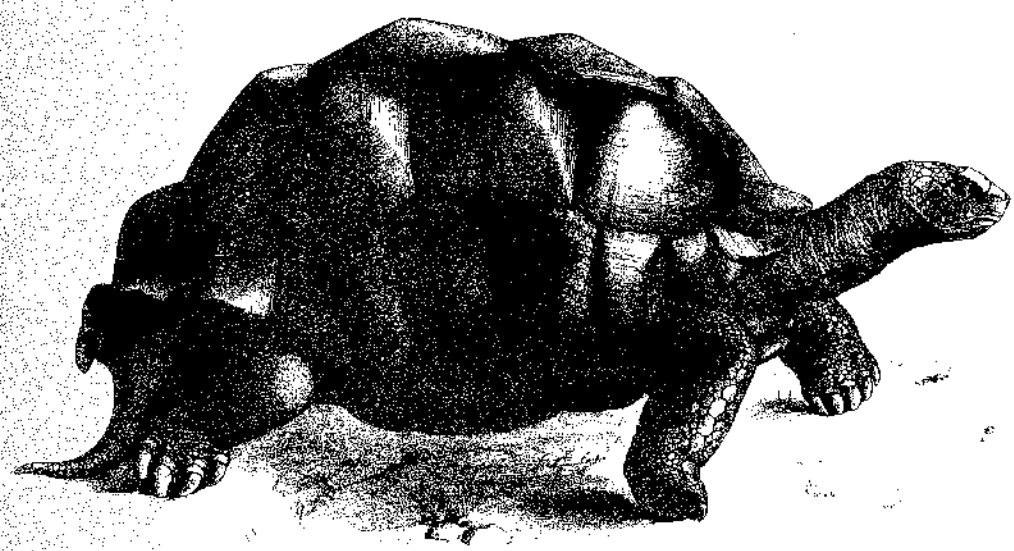
Colouration. On the whole, Aldabran tortoises are mat-black in colour, but when wet they appear jet-black. Immatures tend to be a deeper black than adults, especially large or senile individuals. In some localities, Dune d'Messe for example, a large proportion of animals have a red cast to the shell. Heller (1903, p. 59) reports a similar phenomenon on Duncan Island in the Galapagos, but he attributes this to the red soil found there.

Hatchlings of the Aldabran species are yellow, and after several weeks they gradually become jet-black. There appears to be a large





C.



D.

Figure 12. Shell shapes of giant tortoises.

A. Front view of Geochelone elephantopus (= Testudo abingdonii), adult male from Abingdon Island, Galapagos.

B. Side view of the same showing elevated anterior and lateral compression of shell with large amount of soft parts in the anterior exposed.

C. G. gigantea (= Testudo daudinii), adult male from Aldabra showing unusually strong 'saddle-backed' tendencies for this species.

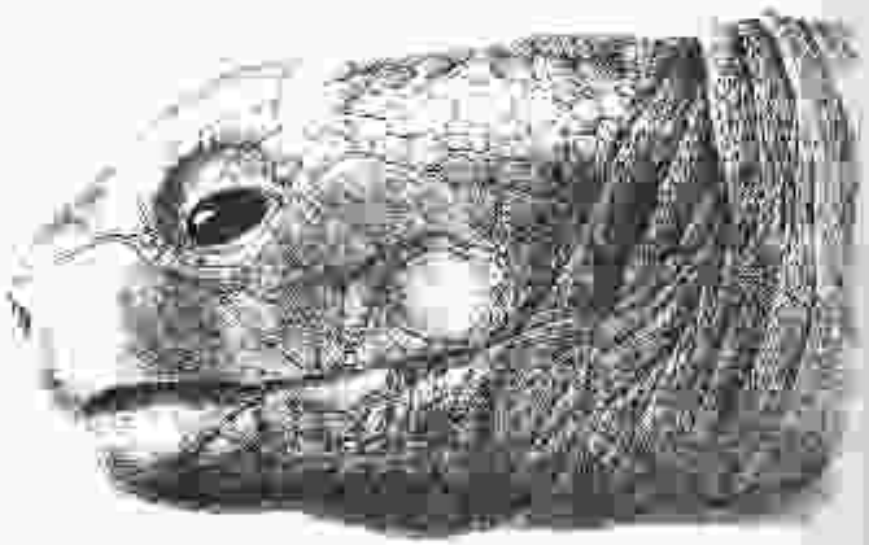
D. G. gigantea (= Testudo elephantina), adult male from Aldabra showing normal dome-shaped shell for this species. (From Günther 1877, Plates 40, 5, and 3.)

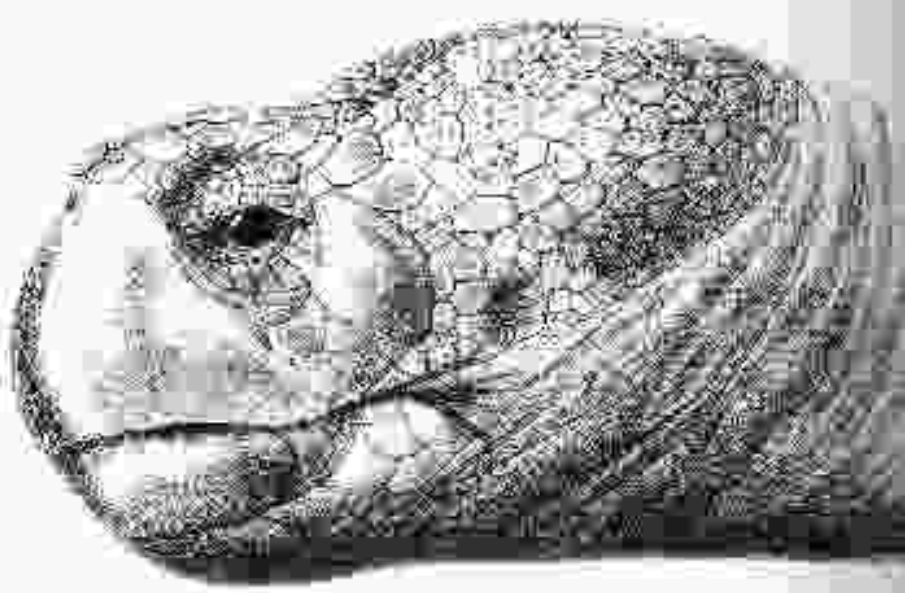
amount of variation in hatchling colouration between the species of Geochelone. The African spurred tortoise, Geochelone sulcata (Miller), has yellow hatchlings, while the leopard tortoise, G. pardalis babcocki (Loveridge), also from Northern Africa, has hatchlings that are light brown with a single central spot on each scale of the carapace. Hatchlings of the southern subspecies G. p. pardalis (Bell) are dull yellow with a pair of spots in each scale of the carapace (Loveridge and Williams 1957, p. 228). In the star tortoise from Ceylon, G. elegans (Schoepff), the hatchlings are dimorphic. There is an orange form which has a yellow vertebral stripe, and a yellow form that lacks the stripe (Deraniyagala 1939, p. 278). Hatchlings of the Galapagos tortoise, G. elephantopus (Harlan), are apparently black with a light ring in each shield (Shaw 1961, p. 11). There has been no attempt to explain this colour variation, and it is not clear what evolutionary or taxonomic significance it has. It is even more surprising that few authors have attempted to explain the bold yellow and black markings that occur on adults of species such as the star, G. elegans, leopard, G. pardalis, and radiated tortoise, G. radiata (Shaw). Wermuth and Mertens (1961) and Pritchard (1967) have pictures of these species.

There is no yellow or light patch on the throat of the Aldabran Giant Tortoise as there is in many of the races from Galapagos (Van Denburgh 1914).

Appendages. The head is covered with large scales, a characteristic of Geochelone; and characteristic of the subgenus Aldabrachelys, the frontal area is rather bulbous (Loveridge and Williams 1957, p. 225), almost forming a proboscis (Figure 33). The neck is long and covered with fine skin that often falls into longitudinal wrinkles.

The anterior (dorsal) of the antibrachium is covered with







C

Figure 33. Close up of giant tortoise heads.

A. Geochelone gigantea (= Testudo elephantina) (adult male)

B. G. elephantopus (= Testudo microphyes) (adult male)

C. G. gigantea from Cousin Island, Seychelles.

Showing probocis-like structure in G. gigantea.

(A and B from Günther 1877, plates 1 and 32.)

stout, tile-like scales that are usually pentagonal or hexagonal. There are very heavy scales on the soles of the feet, while the posterior (ventral) of the front limb is covered mainly with small scales. The front pes is equipped with five stout claws that turn in medially. Only four claws are found on the hind leg, and it is covered almost entirely with fine scales except for the soles of the feet which have very thick scales. The posterior of the hind leg, near the ilium, has large tuberous scales, and these occur right to the base of the tail. This last appendage is covered with large scales and terminates with a long conical scale which is considerably larger in males than in females.

The shell. A tortoise shell, which in fact forms a complete corselet around the animal, can be divided into an upper portion "carapace", and a lower portion, "plastron". The carapace is rather dome-shaped. Down the median line are five large scutes, or shields, called "vertebrals" or "centrals" (Figure 34). Both left and right of this row of vertebrals is a row of four "costals" or "laterals", and around the periphery are 24 small shields, the "marginals" or "peripherals". The medial anterior marginal is the "nuchal" or "precentral" and the medial posterior marginal is the "supracaudal" or "postcentral". Carr (1952, p. 38) and Loveridge and Williams (1957, p. 171) discuss scale and scute terminology.

The presence or absence of a division down the supracaudal and the presence or absence of a nuchal are of taxonomic importance in distinguishing various forms of giant tortoise (Rothschild 1915; Wermuth and Mertens 1961), but there is considerable variation in these characters in the Aldabran population.

The plastron, or ventral portion of the shell, is flat and shaped rather like a rectangle with the four corners removed (Figure 35). In adult males it develops a deep concavity with bulging sides (De Sola 1929; Grubb 1971 a, p. 335). Six pairs of

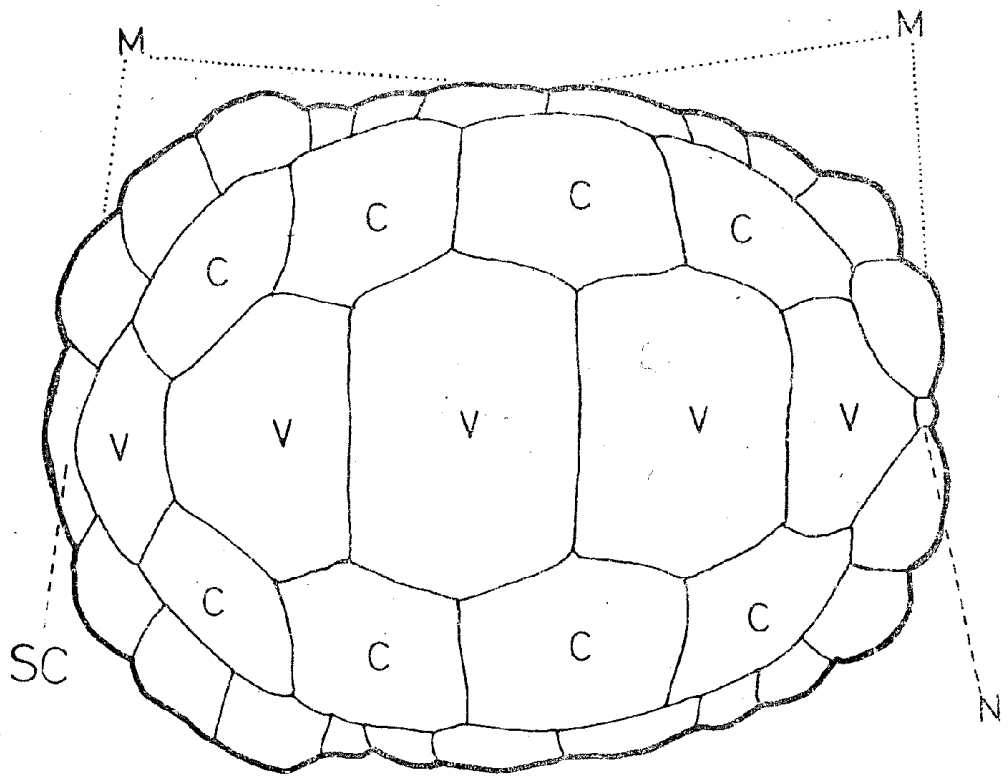


Figure 34. Carapace of giant tortoise (top view) showing epidermal shields.
V = vertebrals; C = costals; M = marginals (11 pairs); N = nuchal; SC = supracaudal.

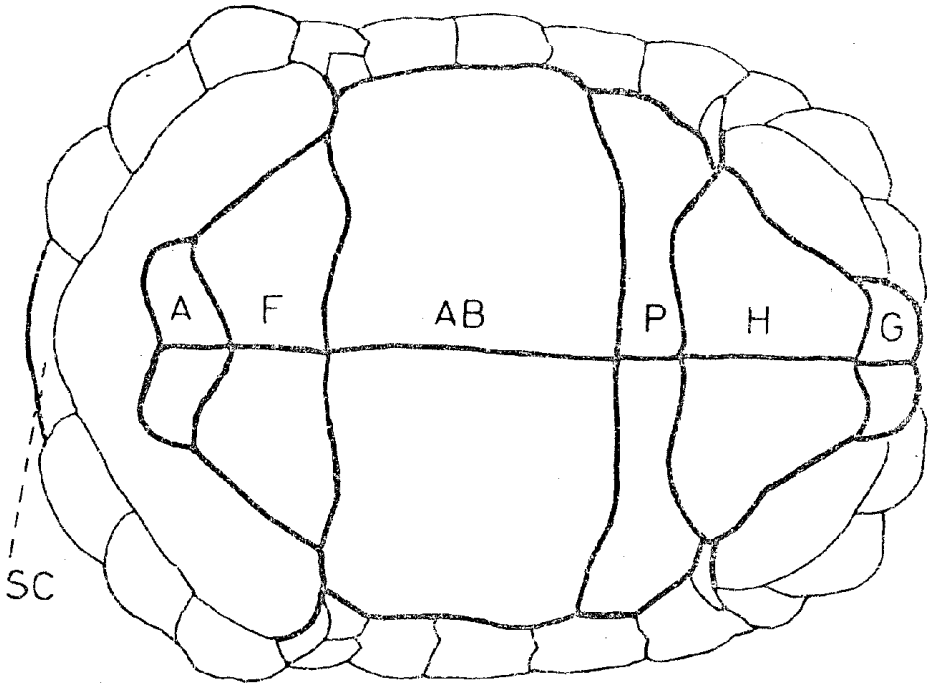


Figure 35. Plastron of giant tortoise. (Ventral aspect of shell.)
G = gular; H = humeral; P = pectoral; AB = abdominal; F = femoral; A = anal.

scutes cover the plastron. From anterior to posterior they are: gulars, humerals, pectorals, abdominals, femorals, and anals. The gulars project forward, but not to the same extent as in other types of land tortoise, e.g. Gopherus (Carr 1952), Geochelone atlas, and subgenus Cylindaspis of Geochelone (Gadow 1894).

Internal Anatomy

Skeletal. Good accounts of chelonian osteology are given by Bojanus (1819), Deraniyagala (1939), Romer (1956), and Gans (1969, 1970). Günther (1877) deals specifically with giant tortoises, including those from Aldabra. Detailed studies on specific aspects of the osteology are Williams (1950 b) - cervical vertebrae; Zangerl (1969) - turtle shell; and Auffenberg (1966) - carpus of land tortoises. The skull has been treated in considerable detail by Loveridge and Williams (1957).

Soft parts. There are few good studies of chelonian soft tissues. Bojanus (1819) wrote an exhaustive monograph on the European pond turtle, Emys orbicularus (L.) and Thom son (1932) studied the Greek tortoise Testudo graeca (L.). There have been a number of studies of musculature in relation to respiratory problems, Gans and Hughes (1967) and Gaunt and Gans (1969) being the most recent. Parsons (1968) investigated the choanal anatomy of a large number of chelonians.

The only detailed anatomical description of giant tortoises that I know of is by Fritsch (1870) who dissected a specimen which he identified as Testudo elephantina; however there is some question as to whether this animal came from the Mascarenes.

I had planned to autopsy two animals a month, but because of a number of setbacks in the other studies it was possible to examine only two adult males. Data on these animals are presented

in Table 2. Detailed discussion of these data must await examination of my histological specimens, but several points are worth noting:

1) there is quite a difference in the size of testis between the two animals;

2) there are certain idiosyncrasies in these animals, for example the much larger size of the right kidney;

3) the gastrointestinal tract is relatively simple but there seem to be two distinct muscular areas; one at the stomach or ventriculus and one at the beginning of the colon.

TABLE 2. Weights and measures of various organs from two adult male tortoises dissected at Dune Jean Louis

Specimen	39	48
Date	4 Nov. 1969	25 Feb. 1970
Total weight (kg)	56·1	38·0
Total shell (kg)		8·95
Carapace (kg)		6·4
Plastron (kg)	3·5	2·55
Front limb girdle, legs and muscles (kg)	8·0	8·16
Hind limb girdle, legs, tail and muscles (kg)	7·55	7·0
Connective tissue and muscle from plastron (kg)	1·379	
Lungs, trunk muscles, & associated connective tissues (kg)	1·3	0·910
Liver (g)		660
Spleen (g)		34·5
Heart (g)	93·0	68·0
Both testes (g)	2·5	13·75
Lf. Testis (g)		7·75
(mm x mm)		66 x 18
Rt. Testis (g)		6·0
(mm x mm)		100 x 11
Lf. Kidney (g)	40·0	23·6
Rt. Kidney (g)	82·0	49·5
Bladder (g)	810·0	270·0
Alimentary canal (kg)	2·12	1·55
(m)	4·27	3·3
Esophagus (cm)	10	@ 10
Stomach (cm)	47	41
thin muscular (cm)	15	8
smooth (cm)	10	9
thick muscular (cm)	22	24
(sphincter)		
Small intestine (cm)	155	98
(sphincter)		
Muscular pouch (cm)	10	
Large intestine (cm)	255	
Contents of alimentary canal (kg)	12·605	5·25
Fluid from body cavity (including blood) (l)	4	3
Blood alone (ml)		700

3A GENERAL POPULATION ECOLOGY

680 tortoises in the immediate vicinity of the Dune Jean Louis plains were marked in 1968 by painting serial numbers on both sides of each animal. This marking was carried out either at night by myself or else very quietly in the daytime by Seychellois assistants; the marking was done in such a way as to reduce disturbance to the animals as much as possible. The object of the marking was to make individuals readily identifiable, and it was hoped that data on population sizes and structure could also be obtained, for I had planned to measure the marked animals at the end of the study.

However, the tortoises did not stay on the plains, but moved some distances, sometimes up to several km, into the mixed scrub. Hence, there was a fair turnover of animals on the Dune Jean Louis plains, and few marked animals were available for measurement at the end of the study.

My intention in this study was to observe undisturbed animals as much as possible. Tortoises often react to being measured by avoiding human beings and even leaving an area entirely. This results in abnormal activity, and since this would have ruined my observations I could not afford to disturb the animals by measuring. Furthermore, abundant information on tortoise measurements already exists (Honegger 1967, Gaymer 1968, and Grubb 1971a); therefore very little emphasis is placed on the major aspects of population ecology in this study.

A representative size-frequency distribution of tortoises along the south coastal area is seen in Figure 35 B. This figure is based on 50 tortoises measured in March 1968 at Dune D'Messe, which has a population similar to that of Dune Jean Louis. The range of the length of the carapace (over the curve) of animals found on open, exposed areas was 30 to 100 cm.

32 tortoises in the Dune Jean Louis area were measured for growth studies (see Chapter 6). These measurements did not involve gross length or width measures, but width of the third vertebral. Grubb (1971a) shows that width of the third vertebral is regularly related to the length of the carapace. Not only is the width of the third vertebral more easily measured, but it can also be more accurately measured and hence is a better datum for growth. For these reasons gross measures of length and width were not made on these

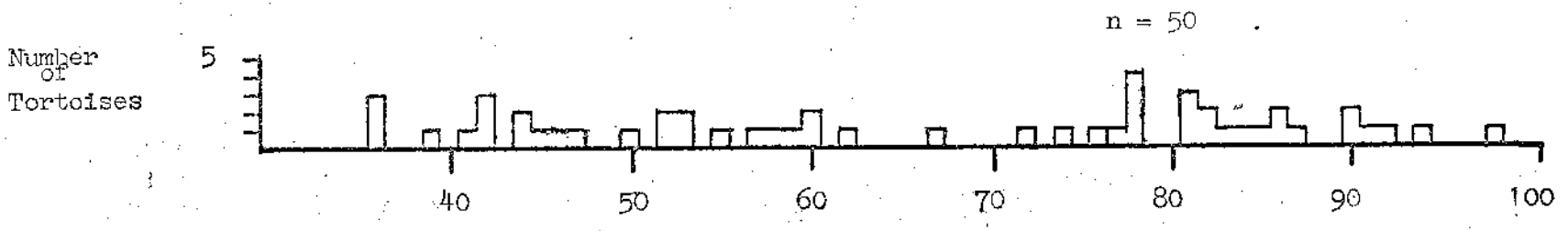


Figure 35 B. Size-frequency histogram of 50 tortoises measured on the coastal area at Dune D'Messe, March 1968.

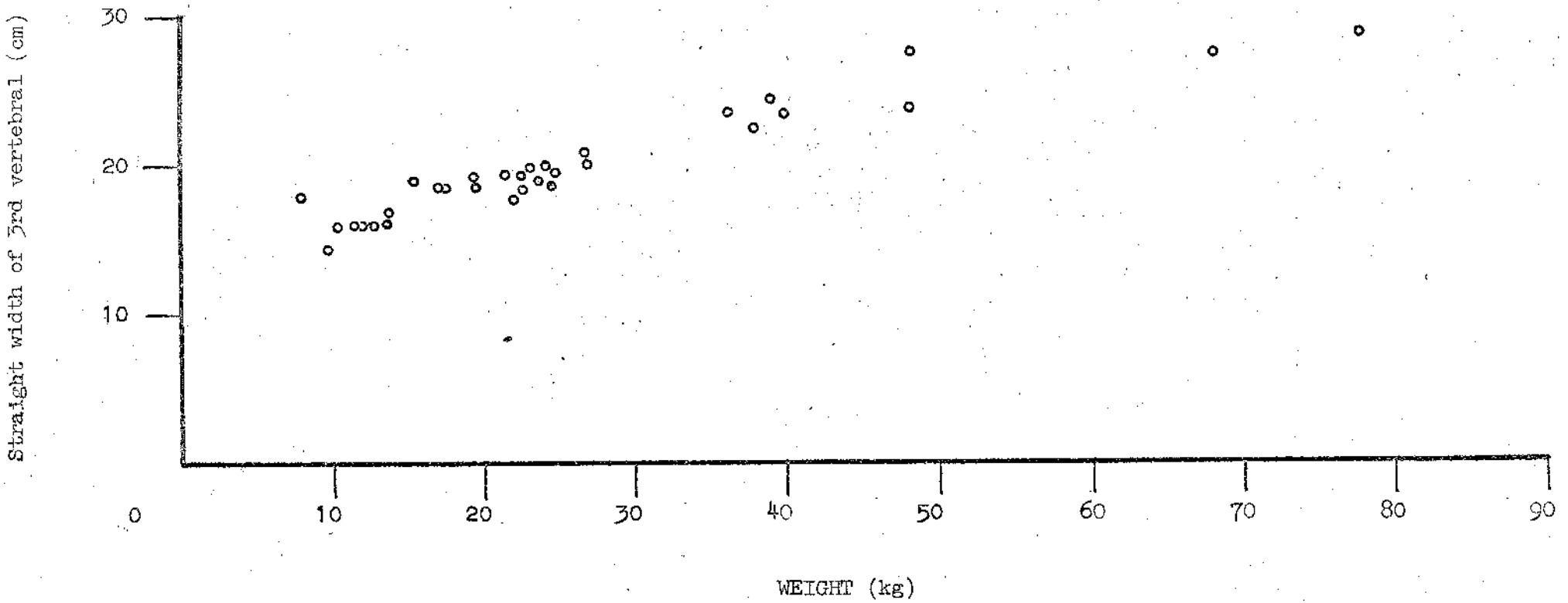


Figure 35 C. Relationship between mass and linear measurements of 32 tortoises measured at Dune Jean Louis, August 1969.

animals.

Figure 35 C shows that the relationship between width of the third vertebral and weight appears to be logarithmic. A word of caution on putting too much importance on measures of weight: a tortoise can void large quantities of both fluid and solid (see Chapter 8), and an animal up to 30 cm long can nearly halve its weight in a matter of minutes. Although the absolute amount of material voided is greater in a large animal, the relative weight is less. Also, the weight of an animal will be greatly influenced by the recent availability of drinking water.

The carapacial scutes of Aldabran tortoises are marked conspicuously with rings, or annuli, in much the same fashion as a tree trunk. Each ring is thought to represent the growth that has occurred in one year, and my data on recaptured individuals (not presented here) substantiate this. Thus, one can estimate the age of a tortoise by counting its rings. However, after about 25 to 30 rings have been formed, the scutes become smoothed, the old rings obliterated, and growth is so slow that subsequent rings are indistinct. Even if the rings are not obliterated and the animal is still growing, it may sometimes only be possible to estimate the age from the rings to within plus or minus five years. Hence, the ageing technique is only valid for animals that are still growing, and even then may yield an estimate within rather wide limits.

At about 25 to 30 years of age, after growth has essentially stopped, the tortoises show secondary sexual characteristics and breeding behaviour. Males characteristically have elongate shells, deeply concave plastrons, long tails, long necks, and massive forearms. Females, in contrast, have more domed shells with flat or slightly concave plastrons, short tails, and lack conspicuously long necks and conspicuously enlarged forearms. But these "female characteristics" are similar to those of all animals less than 20 years old, i.e. immatures. Hence, the sexing technique distinguishes between adult males and others; it is then assumed that animals which have stopped adding annuli, or have 25 to 30 such rings, and lack male characteristics are adult females.

Along with differences in shape, males are on average larger than females; but large females can be several cm longer than small males and there is considerable overlap in the size distributions of the two sexes (Honegger

1967, Gaymer 1968, Grubb 1971a).

Because females and immatures are sometimes indistinguishable, sex ratios can be misleading. What they represent is the proportion of adult males in the population of large animals - not necessarily the proportion of males in the adult population. Gaymer (1968) found 52% and 30% males at two areas near Takamaka and 36% males at Anse Mais.

Average body size varies with locality over the atoll. Straight length of carapace for fifteen-year-olds averages 45 cm at Cinq Cases, 44 cm at Takamaka, 45 cm along the south coast, and 64 cm at Middle Island (Grubb 1971a, personal observation). Animals at Anse Cèdres (in the north-east) are stunted, and this population has some of the smallest adults on the atoll. Many tortoises at Anse Mais (in the south-east) are large, being surpassed in size only by those from Anse Malabar. Thus there seems to be a circular cline of increasing body size from Anse Cèdres in the north-east, clockwise round the atoll to Anse Malabar in the north. The reason for this is not known, but it is interesting that the degree of 'openness' of the vegetation decreases around the same cline.

Concomitant with these locality differences in the body size are differences in population density and structure. Tortoises occur at highest densities in the east and south, averaging about 23 animals per hectare (Grubb 1971a, personal observation), and at the least density in the north. Small tortoises (with less than ten rings) are abundant in the east and south and very rare in the west and north (see also Gaymer 1968 and Grubb 1971a).

At present the population of tortoises on Aldabra is immense. Grubb (1971a, p.366) estimated 92,240 animals on 30.7 sq. km of platin, and my estimate for the south coast of the atoll is 10,000 to 20,000 tortoises. The west and north coast areas may each support less than 1,000 tortoises. Thus, the total population of the atoll is in the order of 120,000 tortoises.

Estimates of the total population in recent times have varied from 80,000 (Palombellia 1954, cited by Gaymer 1968, p.54), less than 80,000 (Honegger 1967), 33,000 (Gaymer 1968) and 100,000 (Grubb 1971a). It seems that each new estimate, based on successively more data and experience, is larger than the previous one. It is unlikely that further estimates will

increase substantially, for most of the atoll has now been covered.

The total population of tortoises on Aldabra has evidently undergone several major fluctuations. Before the atoll was settled in the late 1800's, sailing ships removed large numbers of animals. Sometimes as many as several thousands were taken in a few days (Rothschild 1915, Honegger 1967, Stoddart 1971b). For such large numbers of animals to be collected in such a short period of time, the tortoise population was obviously very large. It is puzzling that in the late 1800's and early 1900's several naturalists visited Aldabra and found very few tortoises (Stoddart 1971b). Sometimes these people went specifically to look for tortoises and visited localities where today it is difficult not to see hundreds of tortoises in an hour's walk. The population seems to have been at a very low level at this time, and the most obvious factor related to this crash is the large-scale removal of tortoises by man. Clearly, if more than a thousand animals could be removed in a few days, many thousands could be removed in a hundred years of exploitation. Man's exploitation of giant tortoises is thought to have led to their total or near extinction in both the Galapagos (Townsend 1928, Perry 1970) and the western Indian Ocean (Rothschild 1915, Honegger 1967, Stoddart 1971b).

Factors involved in the control or limitation of tortoise population are not well understood. On Galapagos it is claimed that habitat destruction and inter-specific competition by introduced animals (goats, pigs and donkeys) is responsible for declines in tortoise populations (Snow 1966). This does not appear to be the case on Aldabra at present, for the goats are at a low level (possibly less than 500 on the whole atoll) and they seem to be taking Sideroxylon inerme as a preferred food. This is one of the few common shrub species not eaten by tortoises (Table 3). Some Seychellois claim that the goat population may have been much larger some years ago, but it is difficult to relate these stories to the tortoise population in a meaningful way. Also, on Galapagos, predation by introduced mammals is said to be responsible for a large proportion of tortoise mortality (Snow 1966). Again, the situation on Aldabra does not seem to be comparable. There are only two dogs (both bitches) on the atoll. Cats and rats are fairly numerous and could prey on small tortoises, but I have no evidence on this point. Later on I will argue that the tortoises appear to be food limited. The intensive

grazing and browsing by such a large population seems to have over-exploited the existing food resources. This is not manifested in mass deaths due to starvation but rather in reduced growth and adult size and reduced reproductive performance. Dead tortoises quickly become conspicuous when the keratinised scutes fall off the carapace leaving a large white shell. However, such 'beacons' are common in only a few restricted localities. In these areas, mainly between Cinq Cases and Takamaka, there are lush ungrazed Sporobolus plains but no shade trees. Death here seems to have been caused by heat prostration (which probably can occur within a few hours - see Part III). The reason animals ventured out into the unshaded area was evidently to graze the lush pastures, and the reason the pastures are lush is evidently because few tortoises stay to graze them for long.

Reproduction seems to be at a low ebb. Only 6 out of 900 observed mating attempts were known to be successful (Part IV, and I have recorded only five nests. Furthermore, egg and clutch sizes from wild Aldabran tortoises are smaller than those from captive Aldabran or wild Galapagos individuals.

A strong indication of the dependence of breeding on food is in the timing of the breeding season. Mating behaviour is observed only during the monsoon, after the rains have fallen and the plants, especially Sporobolus, have begun to produce leaves and flowers. The first mating observed in the summer of 1969-1970 was on 1 January. The peak in mating occurs in March, and about this time successful matings were also seen. As soon as the trades begin the plants dry up and stop producing, and mating attempts subside.

However, it is during the trades, June and July, when conditions are most inhospitable for the tortoises, that nesting occurs. As it takes four to five months for the eggs to hatch and the young to emerge from the nest, nesting during the dry season is a means of ensuring that the young tortoises emerge from the nest at the beginning of the monsoon when food and water are available.

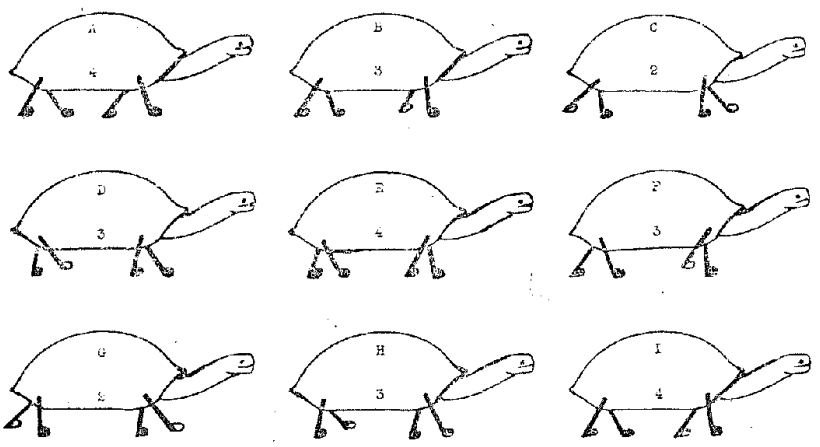
LOCOMOTION

Tortoises usually move by means of the "transverse crawl" (Gray 1968, p. 267). As they advance they balance on four legs, then three, then four, then three, and so on in a series of moving tripods. Occasionally they move the limbs faster and balance on three, then two, then three, then four, then three, then two, etc. (Figure 36). Gray (1968, p. 268) describes the sequence of supporting limbs for the "normal walk" in a generalized quadruped as 3, 2, 3, 2, 3, 2, etc., but tortoises never attain this gait, for it involves balancing on only two legs on the same side. Their slow speed of movement, great width of body and front limbs "akimbo" (see Gray 1959, p. 64) make it impossible for them to balance on two legs on the same side. Consequently, the fastest gait attained by a tortoise is intermediate between a transverse crawl and a normal walk; this intermediate gait is apparently not common, for Gray (1968) does not discuss it.

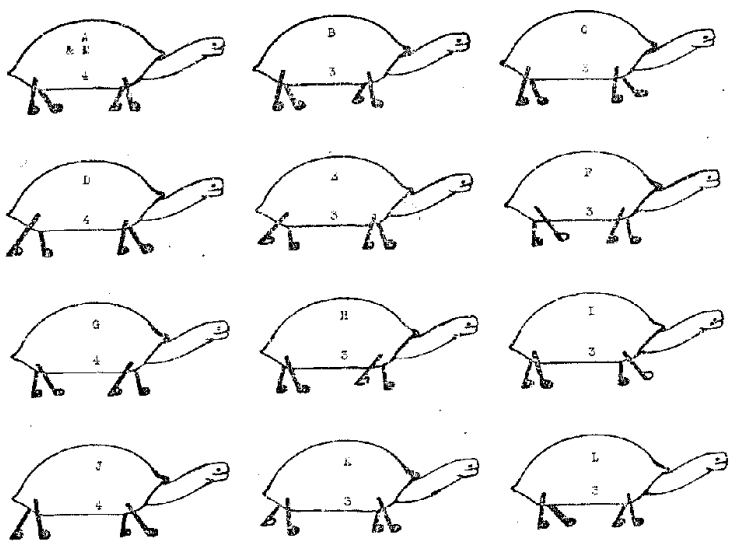
Excellent descriptions of walking in tortoises, reptiles, and generalized quadrupeds are given by Auffenberg (1966), Romer (1956), and Gray (1959, 1968).

The fastest speed observed in an Aldabran tortoise is 12. 1 cm / second; this record is from tortoise T14, a large, 77 kg adult male, who was moving in late morning from bright sunlight into shade. Small tortoises, up to 30 cm long, may sprint away from a disturbance (e.g. a curious naturalist) at two or three times the speed attained by T14, but such rates cannot be maintained indefinitely and deceleration usually begins after several metres.

Speed of limb movement averages about 0.25 cycles per second for 25 observations on a total of 5 different animals. Speed of forward progression is strongly correlated to speed of limb movement ($r = 0.8196$, $p < 0.01$) (Figure 37). Speed of forward



B



A

Figure 36. Locomotory gaits in the giant tortoise.
A. Transverse crawl with 13 phases (A to M)
B. Intermediate transverse crawl/normal walk with 9 phases (A to I).
Numbers (2, 3, or 4) refer to the number of feet on which the animal is balancing; unweighted feet are white.

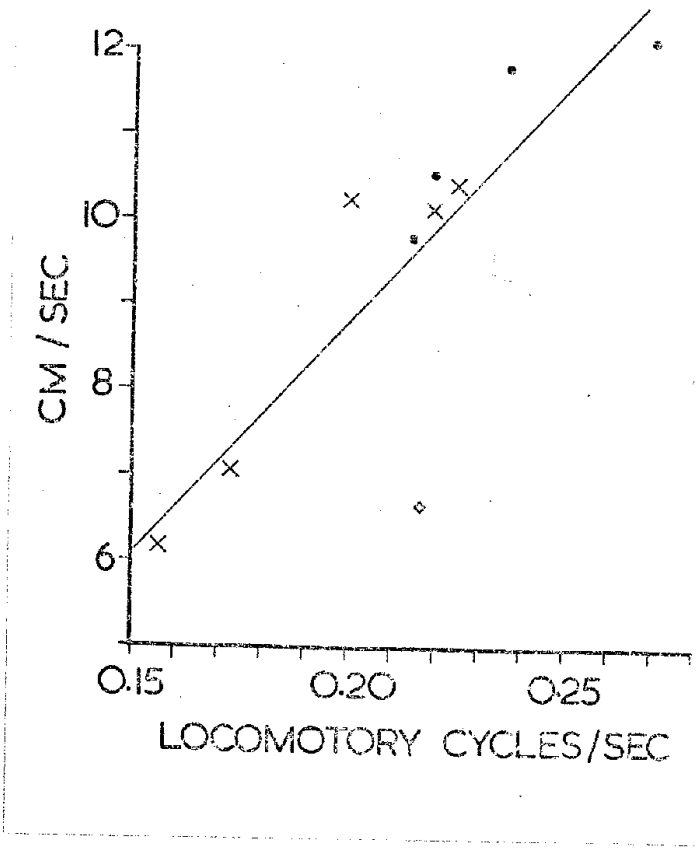


Figure 37. Relationship between rate of forward progression and rate of limb movement.
$y = -2.07 + 54.28\ (x)$ slope is significantly different from 0 ($p < 0.01$)
Tortoises: x = T 14
● = 45
◇ = 99

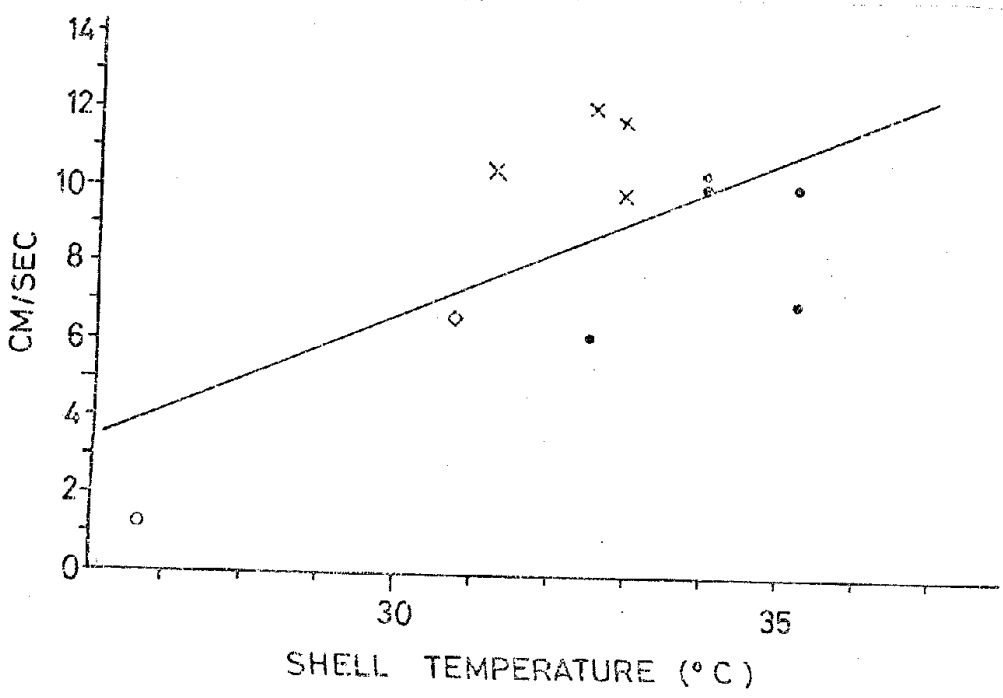


Figure 38. Relationship between rate of forward progression and temperature of the animal's carapace.
$y = -18.24 + 0.831\ (x)$ slope is significantly different from 0 ($p < 0.05$)
Symbols as in Figure 37.
o = Tortoise 297.

movement is also strongly correlated to the animals' shell temperature *($r = 0.6330$, $p < 0.05$) (Figure 38), and substrate temperature ($r = 0.6815$, $p < 0.05$). (But substrate and shell temperatures are themselves strongly correlated [$r = 0.6516$, $p < 0.05$].) In essence, the warmer the tortoise and its environment, the faster it moves. This is consistent with the reports that general physiological processes are often faster when the animal is warmer (Dawson 1967, Templeton 1970).

Speed of movement over long distances is difficult to measure accurately. An adult female moved at <u>least</u> 8 km in 72 days or <u>less</u>, and there are several records of animals moving about 1 km in one or two days. Several tortoises marked at Takamaka in 1968 by Grubb (1971 a, p. 364) turned up at my camp some 7 or 8 km west, within 2 or 3 months. One female marked at Anse Mais in 1967 was seen about two and a half years later at Anse Brigo, some 22 km east. Another animal moved 20 km east from Dune d'Messe to Cinq Cases in 22 months.

Many aspects of locomotion are similar in Aldabran and Galapagos tortoises. My observations on captive Galapagos tortoises (1966) show that rate of limb movement and rate of forward progression are comparable between Aldabran and Galapagos tortoises. Both species use the transverse crawl, can balance on two legs, and have a positive relationship between speed of movement and temperature. It also seems (Snow 1964) that the new world animals move very long distances; however, Darwin's (1900) account that they move at night is unsupported by my findings.

*See thermoregulatory section for details of temperature measurements.

RESPIRATION

Respiratory studies on chelonians are mainly in the realm of physiology. However, one respiratory phenomenon is relevant to the present study. Giant tortoises on Aldabra commonly breath hold for as long as 10 to 15 minutes between rather short periods of breathing. This form of respiration can enable the animals to carry out activities that are incompatible with breathing. For example, in drinking a tortoise may spend three minutes or more with its nostrils submerged while it sucks in water; tortoises bathing in a deep pool may submerge completely and only come up for air at infrequent intervals. Appendix II presents a detailed discussion of testudinate respiration and this breath holding phenomenon.

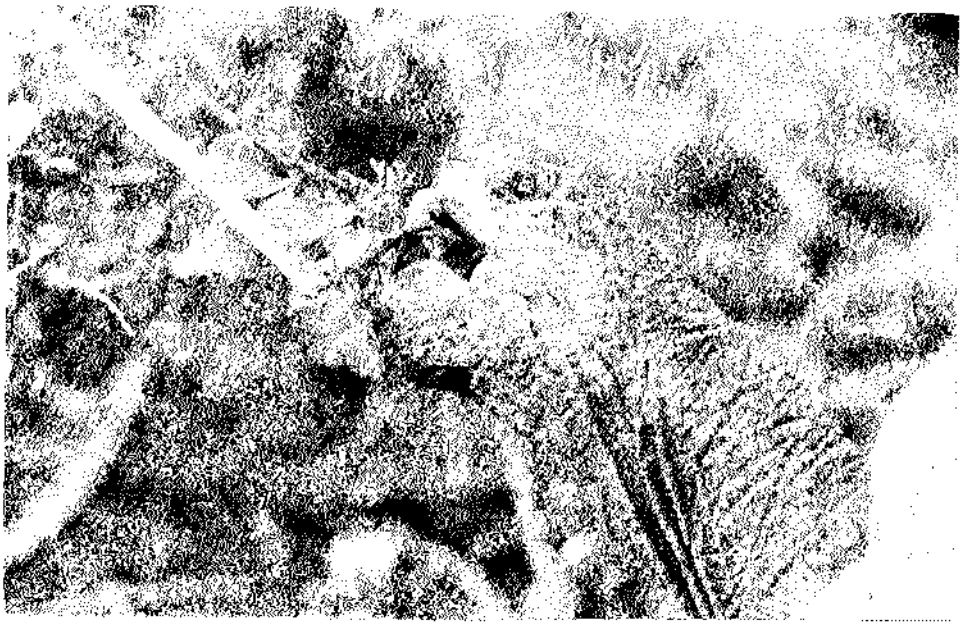
FEEDING

Grazing

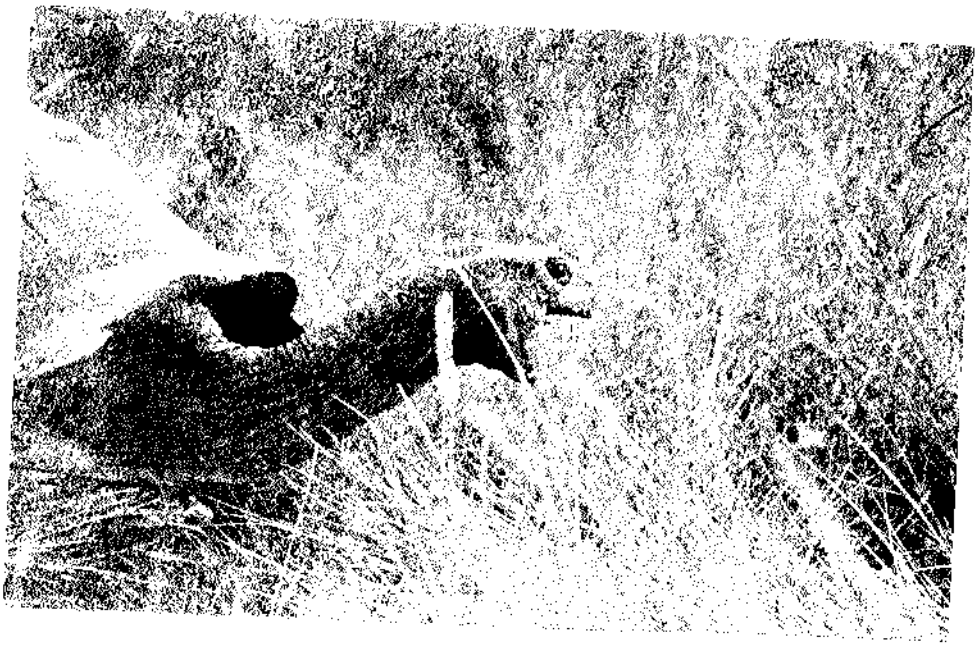
Giant tortoises are just as much grazers as browsers; in fact, it is difficult to tell which mode of feeding is more important to them. In grazing, the animals rest with the plastron on the substrate and the limbs unweighted. The neck is extended and forms an angle between 90 and 135° with the head. The biting movements include closing the mouth, moving the tongue up against the palate, and at the same time moving the mandible backward while keeping the mouth closed. The head is also retracted slightly so that a bobbing or nodding motion is produced. Although the sharp, serrated tomia and double-ridged process in the upper jaw (Figure 39) are instrumental in cutting food objects, grass blades are actually plucked rather than bitten off. Evidence of this is seen in small tortoises, especially immatures such as 244; the head may fly upward if a particularly tough mouthful of grass offers resistance and then suddenly snaps.

As the tortoise extends its neck to bite again, the mandible is moved forward, the mouth opened, and the tongue lowered in the mouth - possibly with the tip protruding. Grazing is usually done with the head held at a slight sideways angle to the substrate so that one side of the mouth takes most of the grass at any one time. Tortoises, like other herbivores, tend to graze in arcs back and forth in front of the body. At times the arc may swing the animal's head 90° out from the anterior. When the grazing arc is finished the animal reaches out with its neck to begin the next sweep and at the same time pushes the body forward with simultaneous thrusts of its limbs.

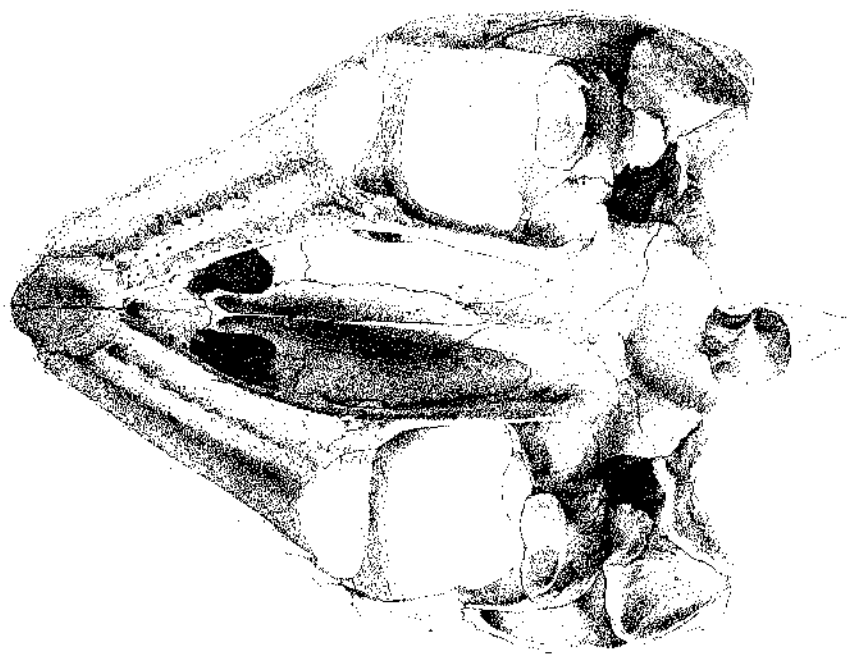
In order to investigate details of grazing behaviour, tortoises were observed from one to three metres away; there was no indication



A



B



C

Figure 39. Feeding adaptations.

A. Browsing Maytenus - note extension of tongue.

B. Grazing Sclerodactylon flowers.

C. Ventral aspect of skull showing ridged process on maxillary into which the mandibular tomia fit (from Günther 1877, plate 9).

that my presence had any major effect on the animals. Infrequently an animal might look up for an instant as I moved, but this investigative behaviour was no different than if a tortoise had moved into the grazing animal's field of view. I kept my movement to a minimum and am convinced that the animals' behaviour was perfectly normal. An observation period consisted of ten minutes' continuous observation, and many such periods were spent on five different tortoises. Twenty-three observation periods were made on tortoise 45, an adult male. During these observations I recorded 8082 distinct behavioural acts, of which 6607 (81·8%) were bites at grass. Other actions included: mandibulations not directed at food objects, "chews" - 471 instances (5·8%); raising the head and neck above the normal grazing posture which is horizontal, and stopping grazing at least instantaneously - 225 instances (3·2%); opening the mouth suddenly just after closing it, to drop small pebbles and other hard objects inadvertently picked up during grazing - 143 instances (1·8%); moving the limbs into a position capable of (but not) supporting the weight of the body - 111 instances (1·4%); moving forward in grazing - 208 instances (2·6%); swallowing - 32 instances (0·4%); and several other infrequent acts.

With over 80% of the behaviours occurring as bites, it is not surprising that biting occurs in long, uninterrupted sequences, or "runs". The average run length for each of the ten minute observations varies from 4 to 12 bites. The distribution of run lengths varies significantly from the predicted geometric distribution (Chi squared = 70·65; $p < 0.001$) (Figure 40). Compared with prediction, the tortoise has a deficiency of short length runs (less than ten bites long), an excess of runs ten to thirty-five bites long, and a deficiency in runs longer than thirty-five. Average run length during a ten minute observation is significantly

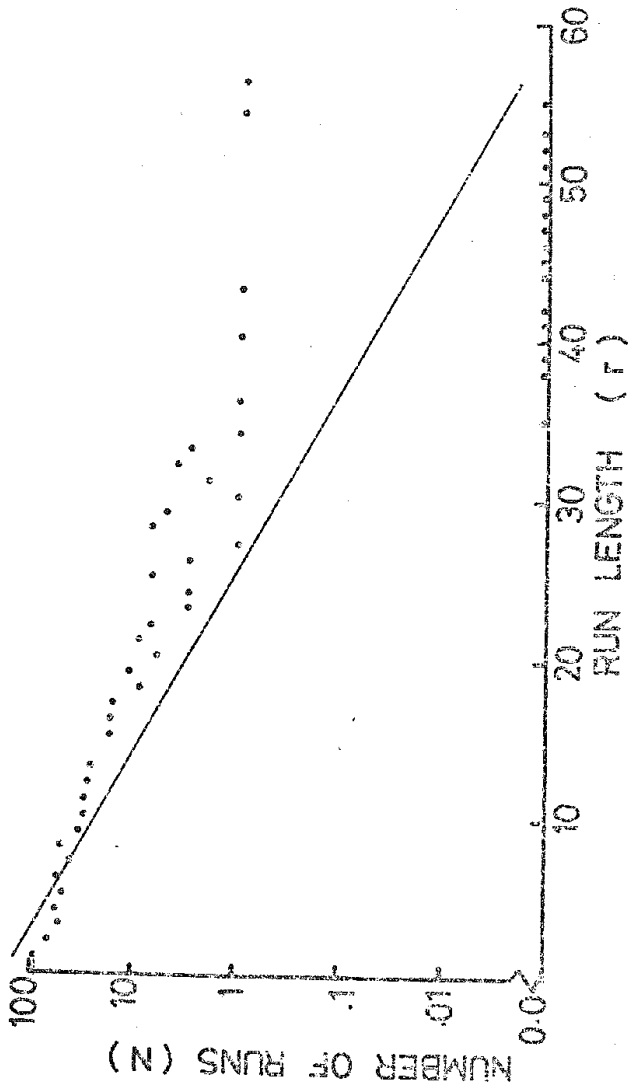


Figure 40. Distribution of runs of bites for Tortoise 45. Grouped data from 23 ten-minute observations.
Line = the expected geometric distribution of the form $y = p^{(r-1)}q$.
p = probability of a single bite occurring in 23 ten-minute observations.
q = 1 - p
r = run length (1 to 54)

Equation for line is : $y = 0.8175^{(r-1)}0.2875$

correlated with the animal's internal body temperature during the observation period ($r = 0{\cdot}4232$; $p < 0{\cdot}05$).

Average rate of biting has also been analysed for each of the twenty-three ten minute observations on this adult male. It takes on average 13·1 to 20·4 seconds to complete 10 bite cycles, or 1 to 2 seconds per bite. Average time per bite is negatively correlated to average run length ($r = -0{\cdot}4778$; $p < 0{\cdot}02$) as well as internal body temperature ($r = -0{\cdot}8272$; $p < 0{\cdot}001$). Thus, the warmer the animal is the faster it bites and the longer its runs of bites. As a consequence, the total number of bites for a period of grazing is strongly correlated to the animal's internal temperature ($r = 0{\cdot}5419$; $p < 0{\cdot}02$).

Clearly, there are other factors that may influence the biting behaviour of a tortoise; the quality of the grass being grazed is probably important, and there may be considerable variation between individuals. Further analysis of the data on other tortoises is still in progress, but the results from animal 45 and impressions from the other data suggest the following:

1) bites at grass are made in runs, and

2) the length of these runs does not fit expectations based on a geometric distribution. There is a paucity of very short runs and an excess of long runs up to thirty-five bites long;

3) run length increases with increasing body temperature, and

4) run length is positively correlated with biting rate; it follows that

5) biting rate increases with increasing body temperature.

Feeding efficiency must be strongly related to the rate at which an animal can take in food. Making long runs of bites is probably an effective way of getting a great amount of food in a short time, for the biting is not interrupted by other behaviours. Biting rate is important for obvious reasons, for it is an indication

of the rate at which the animal can take in food. However, these are indirect measures of food intake and are not terribly useful. Each bite does not represent a standard amount of ingested food, for that matter, every bite does not even take in food. It is not uncommon for a tortoise to bite at grass and break off no blades whatsoever.

I had hoped to use rate of swallowing as another indication of feeding efficiency, but again this is an indirect measure with limited use, for there is no way of knowing the size of a bolus of food. Every bolus is not the same, for a tortoise may swallow shortly after a previous swallow. In fact, swallowing occurs in non-feeding, non-drinking contexts since it is a displacement activity (see section on mating). It is therefore difficult to make a reliable estimate of food intake or feeding rate in undisturbed, free ranging tortoises.

Nevertheless, it is obvious that rate of food intake is very low. Over a period of 230 minutes (nearly four hours) of grazing, tortoise 45 swallowed only thirty-two times. This is an average of once every seven minutes. It is possible that a few swallows were not observed, but still the rate of food input is very slow, considering that a bolus is probably not much more than five by three cm. In a whole day's grazing a tortoise might swallow forty boluses, for daily activity lasts about 5 hours (see activity section).

Browsing

The mouth and head/neck movements involved in browsing are much the same as those used in grazing except that the head is retracted straight back into the shell and there is no nodding or bobbing movement. Also animals usually push the tongue out so that the dorsal distal surface picks up objects (e.g. leaves and small fruits) by adhesion. Browsing animals also tend to stand high off the substrate, often lifting a front foot and forming a tripod so

that they can reach still higher. Carr (1952, p. 144) has even raised the possibility that box turtles (Terrapene carolina carolina (L.)) may stand on the hind legs in reaching up for food! At times a giant tortoise may move under a tree and raise up, actually weighting a low branch with a front leg, and the animal appears to be trying to climb into the tree. The tortoises may also climb up on comrades or rocks in order to reach higher into the vegetation. Grubb (1971, p. 348) has also observed these means of reaching high during browsing. The adaptive value of being able to reach up into vegetation during browsing has been alluded to by Stebbins (1966).

Tortoises have a number of means of breaking off branches or leaves. In addition to biting an object and retracting the head and neck, they also lower the whole body, backing away from the branch. The forelegs can be used in breaking off vegetation. As the animal withdraws its neck, while holding the branch in its mouth, a front leg pushes forward medially and then makes a sweep sideways. Usually the leg hooks the branch and the distal leaf or twig held in the mouth is broken off. However, it is not uncommon for the entire sweeping action to carry the leg past the branch without hitting it at all. The front legs are used also to break away large leaves and other objects that protrude from the mouth, and the motion used is again sweeping the pes from posterior to anterior and then medial to laterial. But, mouth wiping can be just as ineffectual as branch breaking in that the foot never contacts the object to be wiped or broken. It appears that the action has no orientation response (Tinbergen 1969, p. 84).

Feeding habits

The tortoises on Aldabra seem to have fairly catholic tastes. There are some 200 species of Angiosperms on the atoll, many of

them - especially introduced species - very local in distribution. Grubb (1971 a, pp. 355, 358) lists 75 species of flowering plants that are eaten by the tortoises, and my observations add another 7 species (Table 3).

It would be interesting to compare these results with information on feeding habits of African and Madagascan herbivores, e.g. studies such as Gwyn and Bell (1968), Bell (1970), Casebeer and Koss (1970), Goddard (1970), Leuthold (1970), and Sinclair (1970), but this will not be attempted here.

In addition to general feeding studies I also attempted to check for seasonal changes in feeding. I walked a set route through the scrub at hourly intervals on 14 and 15 September, 30 and 31 October, 6 and 7 November, 1969, and 10 and 11 January, 1970. Every instance of feeding on an identifiable plant species was recorded. (See the section on activity census for more details on the habitats involved and the sampling technique.) The results are presented in Table 4.

Only seven species of plant occur 9% of the time (or more) in the observations. Figure 41 illustrates the seasonal changes in the percent occurrence of these seven species in the feeding observations.

The most striking change is the increase in Sclerodactylon. The large number of records on this species are from January when it is fruiting. This confirms general observations that the tortoises begin taking the fruiting bodies of this tall spiky grass as they become available in the summer. Often specialization on Sclerodactylon is such that an animal may spend several days in the swards eating almost nothing but the fruiting bodies. On the whole, animals that feed in this way are large adults, especially males.

The occurrence of Fimbristylis also shows a marked increase from trades to monsoon, and this again is probably related to its production of flowering and fruiting bodies, which are eagerly

TABLE 3

Checklist of genera of Aldabran vascular plants (Fosberg M.S.) in relation to tortoise feeding habits.

CC = Cinq Cases; data from Grubb 1971 a.

DJL = Dune Jean Louis.

Browse/graze line:

++ = very conspicuous browse line
+ = obvious browse line
* = browse line evident
\- = no browse line
g = effect of grazing obvious

Plant part taken:

b = branches
d = dead leaves
f = flowers
l = leaves
p = fruit
r = root
s = dead flowers/seed heads
double letters (e.g. ll) = part taken eagerly
( ) = rarely

TABLE 3 - 1.

	Browse/graze line		Plant part taken	
	CC	DJL	CC	DJL
POLYPODIACEAE				
Acrostichum L. Linn.	-		(l)	
Nephrolepis Schott.				
PANDANACEAE				
Pandanus L. f.	+	+	♂ f.p. (l)	d.l
NAIADACEAE				
Naias Juss. = Najas L.	g			
POTAMOGETONACEAE				
Cymodocea Koen.				d
Halodule Endl.				
Ruppia L.				
Syringodium Kütz.				
HYDROCHARITACEAE				
Thalassia Soland. ex Koenig.				
GRAMINEAE				
Bambusa Schreb.				
Cenchrus L.				
Dactyloctenium Willd.		g		
Daknopholis				
Digitaria Fabr.				
Eleusine Gaertn.				
Interopogon Nees.				
Eragrostis Host. large sp.	g	g		
small sp.	g			
Ischaemum L.				
Lepturus R. Br.	g	g		
Panicum L.	g			
Pennisetum Rich.				
Sclerodactylon Stapf.	g	g		
Sporobolus R. Br.	g	g		
Stenotaphrum Trin.				
CYPERACEAE				
Bulbostylis Kunth.	g	g?		
Cyperus L. dubius	g	?		
ligularis	g	gg		
obtusiflorus	g	?		
Fimbristylis Vahl. cymosa	g	gg		
ferruginea	g	?		
COMMELINACEAE				
Commelina L.				
PALMAE				
Cocos L.			(l)	(l)
LILIACEAE (sensu lats)				
Agave L.				
Asparagus L.		?		
Dracaena L	+		l	
Lomatophyllum Willd.	-	(++)		rr

TABLE 3(contd.) - 2.

	CC	DJL	CC	DJL
DIOSCOREACEAE				
Dioscorea L.				
ORCHIDACEAE				
Acampe Lindl.				
Angraecum Bory.				
CASUARINACEAE				
Casuarina Adans.	- (*)		(1)	
LORANTHACEAE				
Loranthus Jacq.				
VISCACEAE				
Viscum L.				
URTICACEAE				
Laportea Gaudich.				
MORACEAE				
Ficus L. thonningii	++	++	b,l	b,ll,p
aui-aui	++		b,l	
nautarum	++		b,l	
Maillardia Frapp. & Duchartre.	-(*)			
Obetia Gaudich.				
NYCTAGINACEAE				
Boerhavia L.	g	gg		
CHENOPODIACEAE				
Arthrocnemum Moq.				
AMARANTHACEAE				
Achyranthes L.		-		(1)
Amaranthus L.				
Deeringia R. Br.				
Lagrezia Moq.	g	g		
AIZOACEAE				
Mollugo L.	g			
Sesuvium L.				
PORTULACACEAE				
Portulaca L	g	gg		
ANNONACEAE				
Annona L.				
MENISPERMACEAE				
Cissampelos L.				
LAURACEAE				
Cassytha L.	-			
HERNANDIACEAE				
Hernandia L.				
CAPPARIDACEAE				
Capparis L.	(*)	++		ll
Cleome L. DC.				
Maerua Forsk.		++		

	CC	DJL	CC	DJL
MORINGACEAE				
Moringa Adans.				
LEGUMINOSAE				
Abrus L. Adans				
Caesalpinia L.				
Canavalia DC.				
Cassia L.	g			
Crotalaria L.				
Delonix Rafin.				
Erythrina L.				
Gagnebina Neck. ex. DC.				
Pithecellobium Mart.	-			
Sophora L.				
Tamarindus L.				
Tephrosia Pers.	g			
ERYTHROXYLACEAE				
Erythroxylon L. = seq.	-			
ZYGOPHYLLACEAE				
Tribulus L.				
SURIANACEAE				
Suriana L.	+	+[1]	(1)	
EUPHORBIACEAE				
Acalypha L.	++			
Euphorbia L. abbotti	-	-	1	f,1
prostrata	g			
Pedilanthus Neck. ex Poit.				
Phyllanthus L maderaspatensis	g	gg		
casticum	++			
cheloniphorbe	++			
Ricinus L				
Wielandia Baill.				
BURSERACEAE				
Commiphora Jacq.	++			
MELIACEAE				
Malleastrum (Baill.)				
Xylocarpus Koen.				
CELASTRACEAE				
Maytenus Molina	-	+	(1)	1
Mystroxylon Eckl. & Zeyh.	-	-	(1)	(1)
ICACINACEAE				
Apodytes E. May. ex Arn.	-	-	(1)	(1)
SAPINDACEAE				
Allophyllus L.	++			
Macphersonia Blume.	-			
RHAMNACEAE				
Colubrina L. Rich. ex Brongn.	-	+	(1)	1(11)
Gouania Tul.				d(dd)
				f,p
Scutia (DC.) Comm. ex Brongn.	-			

[1] Browse line on Suriana actually due to breakage.

	CC	DJL	CC	DJL
TILIACEAE				
Corchorus L.				
Grewia L.	++			
MALVACEAE				
Abutilon Mill.				
Gossypium L.				
Hibiscus L.				
Sida L.	g	gg		
Thespesia Soland. ex Corrêa. populneoides	-		f,l,p	
GUTTIFERAE				
Calophyllum L.			(l)	
OCHNACEAE				
Ochna L.	-	*	l,p	(l)
FLACOURTIACEAE				
Flacourtia Comm. ex L'Hérit.	+		b,l	
TURNERACEAE				
Turnera L.				
CARICACEAE				
Carica L.				
PASSIFLORACEAE				
Passiflora L.				
CUCURBITACEAE				
Cucumis L.				
Cucurbita L.				
Lagenaria Ser.				
Momordica L.				
Peponium Engl.				
Trichosanthes L.				
COMBRETACEAE				
Lumnitzera Willd.	-			
Terminalia L. fatrea	++			
LYTHRACEAE				
Pemphis J.R. & G. Forst.	*		(l)	
RHIZOPHORACEAE				
Bruguiera Lam.				
Cassipourea Aubl.				
Ceriops Arn.				
Rhizophora L.				
SONNERATIACEAE				
Sonneratia L.				
LETHYCIDACEAE				
Barringtonia J.R. & G. Forst.				
MYRTACEAE				
Eugenia L.				
SAPOTACEAE				
Sideroxylon L.	-	-		

	CC	DJL	CC	DJL
SALVADORACEAE				
Azima Lam.	++			
Salvadora L.				
PLUMBAGINACEAE				
Plumbago L.	g	++		b,l
OLEACEAE				
Jasminum L.				
APOCYNACEAE				
Catharanthus G. Don.				
ASCLEPIADACEAE				
Pleurostelma Baillon.	g			
Sarcostemma R. Br.				
Secamone R. Br.	-			
Tylophora R. Br.				
CONVOLVULACEAE				
Evolvulus L.	g	gg		
Ipomoea L.		gg		
BORAGINACEAE				
Cordia L.			ll	
Ehretia P. Br.				
Tournefortia L.	-	-	d	d,s
LABIATAE				
Leonotis (Pers.) R. Br.				
Ocimum L.				
VERBENACEAE				
Avicennia L.	-		(l),p	
Clerodendrum L.	++			
Lantana L.				
Nesogenes A. DC.	g			
Premna L.	++			
Stachytarpheta Vahl.		-		(l)
SOLANACEAE				
Capsicum L.				
Datura L.				
Solanum L. aldabrense		++	p	l,p
nigrum	g			
SCROPHULARIACEAE				
Bacopa Aubl.	g			
Striga Lour.				
ACANTHACEAE				
Asystasia Blume.				
Barleria L.				
Hypoestes Soland. ex R. Br.	g	gg		
Ruellia L.	g	gg		
RUBIACEAE				
Canthium Lam.				
Guettarda L.	++	++	b,d,f, l,p	d,f,l
Hedyotis L.	g			
Polysphaeria Hook. f.	*	*	(l)	(l)
Psychotria L.				

	CC	DJL	CC	DJL
RUBIACEAE (Contd.)				
Tarenna Gaertn.		++		ll
Triainolepis Hook. f.				
Tricalysia A. Rich.				(l)
GOODENIACEAE				
Scaevola L.	*	++	(l)	d,f,p, ll
COMPOSITAE				
Launaea Cass.		g		
Vernonia Schreb.				
Wedelia Jacq.	g			

TABLE 4. Feeding observations over four different periods

Species of Plant	14 and 15 September		30 and 31 October		6 and 7 November		10 and 11 January		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%
Apodytes dimidiata E. Mey. ex Bernh.	1	1·5							1	0·5
Capparis cartilaginea Decne	2	3·0	2	10·5	10	25·0	6	6·5	20	9·1
Colubrina asiatica (L.) Brong.	18	26·9	1	5·3	10	25·0	6	6·5	35	16·0
Cyperus (*ligularus* L. ?)	3	4·5			1	1·1			4	1·8
Dactyloctenium (*aegyptium*?) (L.) Willd.	8	12·0	3	15·8	2	5·0	1	1·1	14	6·4
Euphorbia abbottii Baker					1	2·5	1	1·1	2	0·9
Fimbristylis sp.	2	3·0	3	15·8			18	19·3	23	10·5
Guettarda speciosa L.	13	19·5	1	5·3	10	25·0	1	1·1	25	11·4
Lagrezia madagascariensis (Poir.) Moq.	1	1·5	1	5·3					2	0·9
Lomatophyllum borbonicum Willd.							3	3·2	3	1·4
Maytenus senegalensis (Lam.) Exell	3	4·5	1	5·3			2	2·2	5	2·7
Mystroxylon aethiopicum (Thunb.) Leosn.	1	1·5					1	1·1	2	0·9
Ochna ciliata Lam.	1	1·5							1	0·5
Phyllanthus maderaspatenis L.							1	1·1	1	0·5
Polysphaeria multiflora Hiern	1	1·5							1	0·5
Portulaca oleracea L.							1	2·5	1	0·5
Ruellia monanthos (Nees) Bojer ex T. Anders.							1	1·1	1	0·5
Scaevola taccada (Gaertn.) Roxb.	1	1·5	5	26·3	4	10·0	13	14·0	23	10·5
Sclerodactylon macrostachyum (Benth.) Camus	3	4·5			1	2·5	28	30·0	32	14·6
Solanum aldabrense C.H. Wright	1	1·5					1	1·1	2	0·9
Stachytarpheta jamaicensis (L.) Vahl					1	2·5			1	0·5
Tarenna sp.	6	9·0			1	2·5			7	3·2
Tournefortia argentea L.f.	2	3·0	1	5·3			1	1·1	4	1·8
"Grass" (possibly *Eragrostis* sp. or *Lepturus repens*)	1	1·5					7	7·5	8	3·7
TOTAL	67	100·4	19	100·2	40	100	93	100·2	219	100·2

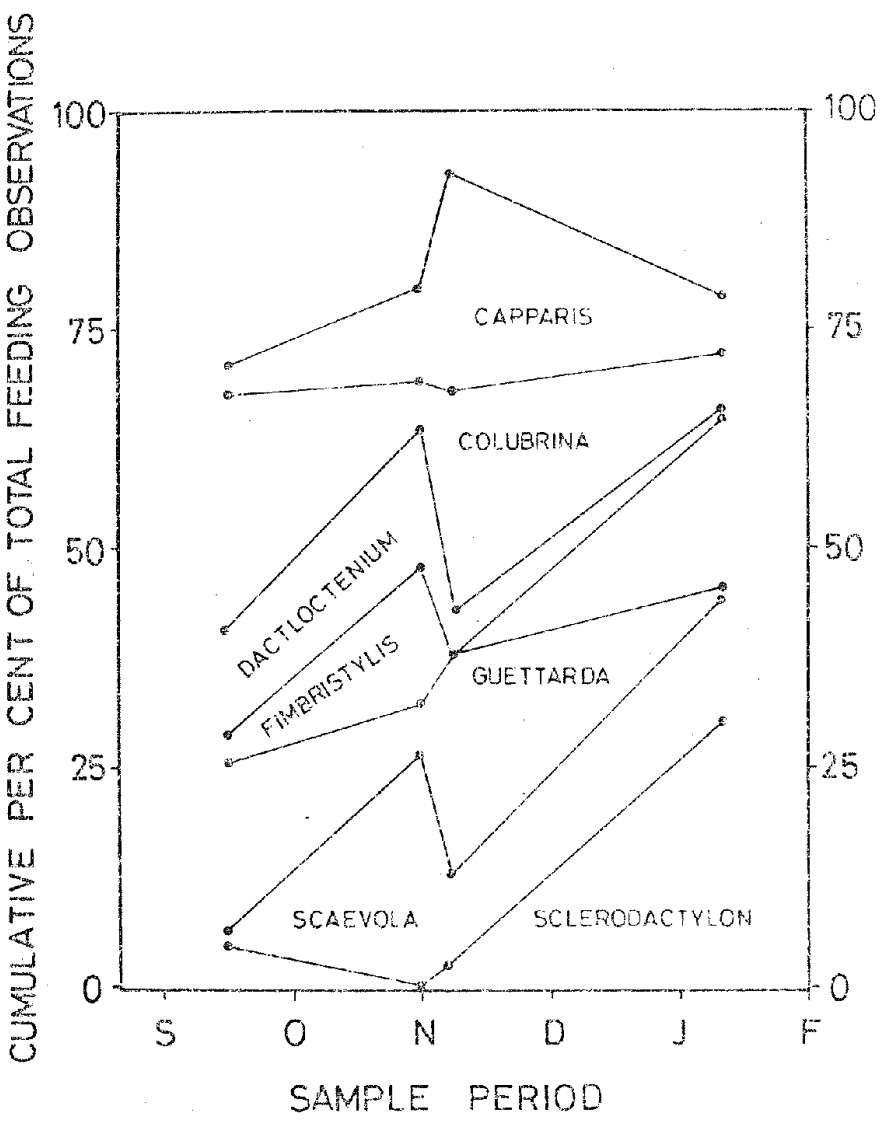


Figure 41. Seasonal change in feeding habits, for seven major food plants.
Plotted as the per cent of total observations for a particular plant. Percentages are plotted cumulatively.

eaten by the tortoises.

Percent occurrence of Guettarda and Dactyloctenium declines from trades to monsoon, and this confirms the general impression that these two species are rather late at flowering and fruiting. Guettarda seems to fruit at the end of the monsoon. Presumably late flowering and fruiting would go together with a late peak in leaf production. Hence the tortoises can feed on early flowering species during the monsoon, and when these resources are depleted they can switch to late producing species. These late producing species may form a major contribution to the food during the trades, as seems to be the case with Guettarda and Dactyloctenium.

Percent occurrence of Scaevola, Colubrina, and Capparis fluctuates greatly between the various sampling periods. These species seem, at least quantitatively, to be consistently available throughout the year. Hence, they may serve as reliable food sources that the tortoises can fall back on when other food plants fail or become depleted. Of course, this is not to say that changes in quality of shrubs such as Scaevola have no effect on their importance as food items.

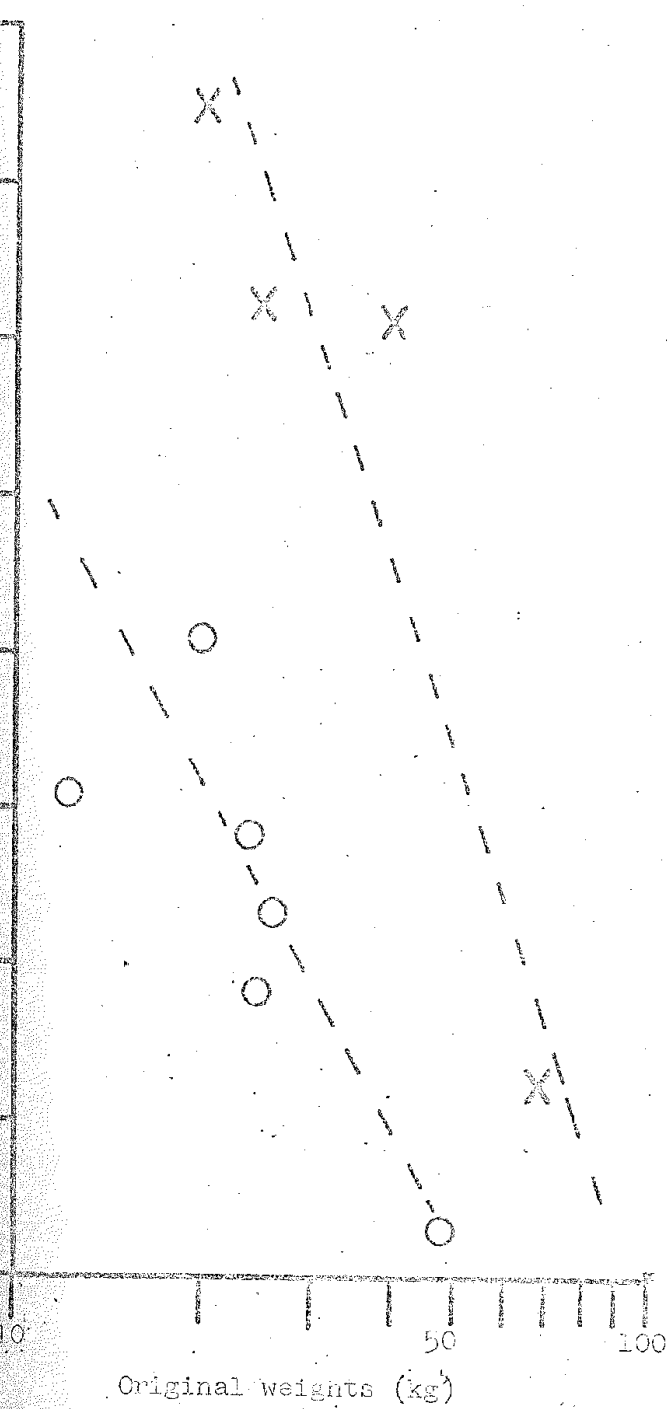
Tortoises are not strictly herbivores, as Beltz (1958) and Mick and Bowman (1960) have pointed out. Both Grubb (1971 a) and I have seen Aldabran tortoises eating a large variety of objects, from animal to inanimate. Colour of an object may be important in stimulating a tortoise to feed (Eglis 1962). Olfaction is evidently of importance as well, for the usual reaction to a strange or potential food object is to push the nares to it while making deep gular movements.

There are almost no limits to the types of animal materials eaten. Muscle, offal, and even skin and shell from crabs, fish, eggs, hatchling and adult sea turtles, tortoises, and goats are all devoured with relish. Human faeces are avidly eaten; Beltz (1958)

has reported an affinity for canid faeces in captive Madagascan and Aldabran tortoises.

A common factor among the inanimate objects eaten, or investigated, is that they are strange to the animals and often not natural to the ecosystem. Plastics, papers, cloth, rope, paint, and even metal foil are bitten at and often ingested. It is also relevant that some plant materials are eagerly eaten when imported into an area. The fronds of coconut palm, coconut endocarp ("meat"), "skins" (pericarp) of various fruits such as oranges, bananas, and papayas, and, perhaps most strange, bark of the mangrove, Rhizophora mucronata and small bits of wood are eaten, often in exceptional quantities if they are available.

The relevance of these unabashed feeding perversions is evidently related to dietary deficiencies rather than to a response to strange objects, for a tortoise will often continue to feed on unfamiliar objects for considerable time. A pilot experiment was run to test the likelihood of this hypothesis. Eleven tortoises living in the Dune Jean Louis vicinity were weighed and measured at the end of August 1969. Four of these animals were resident at my camp and had free access to food scraps; in addition, two cups of dry rice (about 300 g) were boiled in the normal way and placed in a feeding trough for the animals. The rice was offered in the mornings and as a rule the camp tortoises fed voraciously on it. Occasionally, such as after a hard rain, the animals were absent from the camp area and did not partake of the rice. Figures 42 and 43 show that on average the experimental animals grew faster in weight, as well as in linear dimensions, than did the control animals. The large male 183 seems to contradict this trend, but this animal was nearly adult and had essentially stopped growing. However, 183, along with a number of other experimental animals, showed a great amount of mating activity.



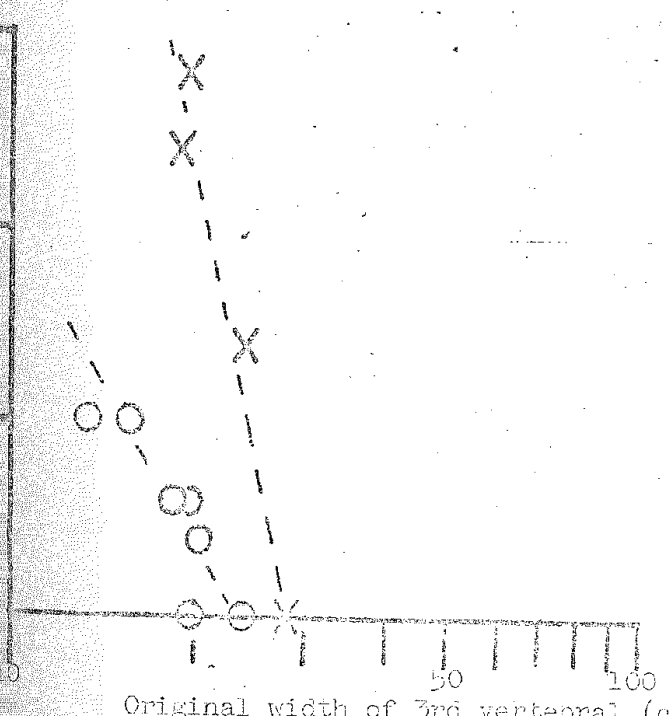


Fig. 42: Change of weight in control (O) and experimentally fed (X) tortoises at Dune Jean Louis from August 1969 to May 1970. The lines are fitted by eye.

Fig. 43: Change in width of 3rd vertebral. Details as in Fig. 42.

That supplementary food increases the tortoises' rate of growth and mating is not surprising. The grass plains where they feed are very heavily populated; sometimes well over 100 animals can be found grazing an area smaller than a football field. The grass is so closely cropped it is difficult to see how the tortoises can get hold of anything to bite, and the shrubs are so heavily browsed that there is generally nothing growing from the ground up to nearly a metre, save the trunk.

To confirm that the vegetational situation just described is due primarily to tortoises and not some other factor an enclosure experiment was run. An 8 x 8 m plot of homogeneous Sporobolus plain was set out into sixteen 2 x 2 m squares. Around eight of these squares a stout bamboo fence was erected to exclude tortoises from the grass (Figure 44). This fence was erected in June 1969, and by January 1970 there was a very conspicuous difference between the grass inside and outside the fence. The grass outside was cropped very short like the rest of the plain. The grass within the enclosure was lush and green. Most dramatic was the occurrence of several hundred fruiting bodies inside the fence and only four outside. Grass samples were taken for more detailed analysis but this is still in progress.

Feeding strategy

Strategies of feeding are usually discussed in connection with predatory animals (Holling 1968; Smith 1971), but although herbivores have stationary food they still have the same basic problems of obtaining sufficient nutrients to maintain bodily activities and form reproductive products; sufficient food must be obtained in a limited amount of time. Successful herbivores must have some strategy that ensures that they meet these demands.

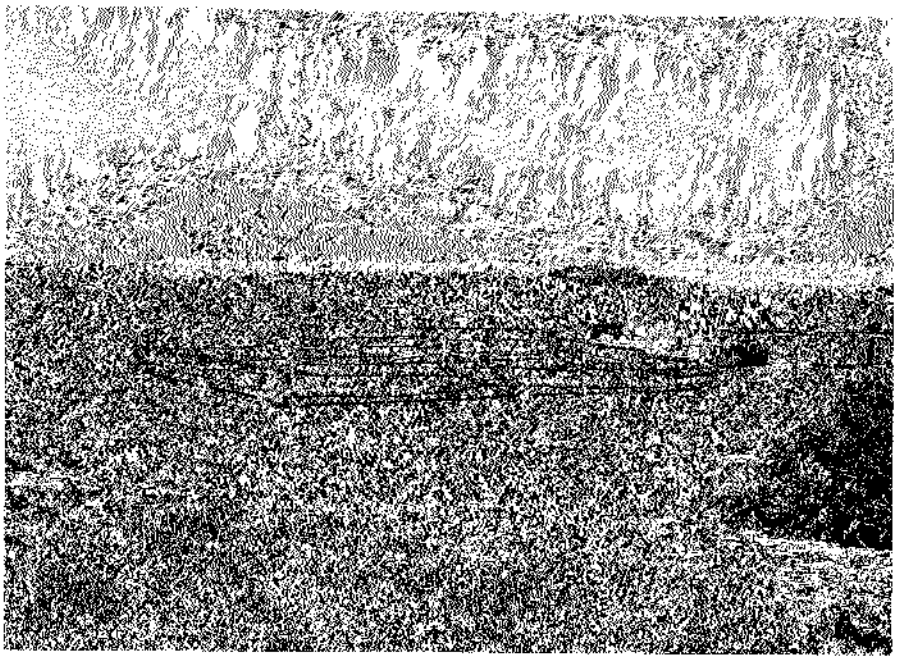


Figure 44. Tortoise exclosure on Sporobolus grassland at Dune Jean Louis. Looking south, onto the Dune Jean Louis beach.

Selective considerations. A fast increasing body of literature clearly shows that feeding in herbivores is not simply a matter of biting off whatever plant or plant part happens to be near, but a large amount of selection and rejection is involved (see Watson 1970 for a collation of recent papers). Several species of African ungulates show a marked selection of particular species of plant, especially grasses (Bell 1970; Casebeer and Koss 1970; Sinclair 1970). Along with species selection there is also component selection; herbivores commonly select leaves and reject stems (Gwyn and Bell 1968; Bell 1970; Sinclair 1970).

I have argued that the tortoises show a seasonal change in feeding habits. This is not always related to changes in availability. The decrease in the relative amounts of Scaevola and Colubrina taken are not because these two species suddenly became rare; they are readily available throughout the year. Instead, the tortoises were selecting other species to feed on. I have no quantitative data on component selection, but it definitely occurs in tortoises. Grazing tortoises will stop grazing and reject Sporobolus stems if they are bitten off. As I have mentioned above, they will selectively take fruiting heads of Sclerodactylon when they first begin to fruit. There is also component selection in browsing. Dry or wilting leaves are often taken in preference to live leaves; fruits are often taken in preference to leaves, and so on.

These selective behaviours are important means by which the tortoises, as well as other herbivores, can obtain nutrient requirements in the most efficient manner.

Spatial considerations. Grazing tortoises do not move randomly about the plains. Instead, most animals have an area of grassland on which each tends to specialise, although there is no exclusion of conspecifics. Tortoise 244 is the most pronounced example of

this. This immature was observed for 14 days; on 12 of these days it grazed a small area of rock rubble about 10 by 20 m in the centre of east plain. On one of the 14 days it did no grazing at all, and another day it grazed another area close to the rock rubble that it often frequented. Tortoise 99 grazed in a similar manner. In the morning she would work up a small depression, in the afternoon she worked down it, and the next day she worked along its side. The males that were observed for long periods of time (297, 45, and T14) showed a distinct tendency to concentrate their grazing efforts in certain areas, but they were not so exclusive as the immature or the female.

This same type of site tenacity was observed in browsing animals. Each tortoise has a tree that it commonly retires to for shade. From this tree it moves out and browses the scrub and the routes to and from the rest tree as well as the routes used while actually browsing are very stereotyped. Tortoise 244, for instance, would, almost as a matter of course, browse a Capparis cartilaginea bush northwest of her accustomed shade tree. The similarity of her browsing routes on different days is quite astounding (Figure 45).

Thus, Aldabran tortoises have specific areas in which they graze and browse. There are several factors that are likely to influence this habit. Many species of animals have home ranges, and the usual explanation for this general phenomenon is that an animal functions better in an area with which it is familiar. Food and water are more easily obtained and more efficiently utilized when the animal is familiar with their location. Escape from predators and other destructive agents (in the case of the tortoises, excess heat and solar radiation) is more effective if the animal knows escape routes and places of shelter.

Benefits accruing from having a home range are not unique to

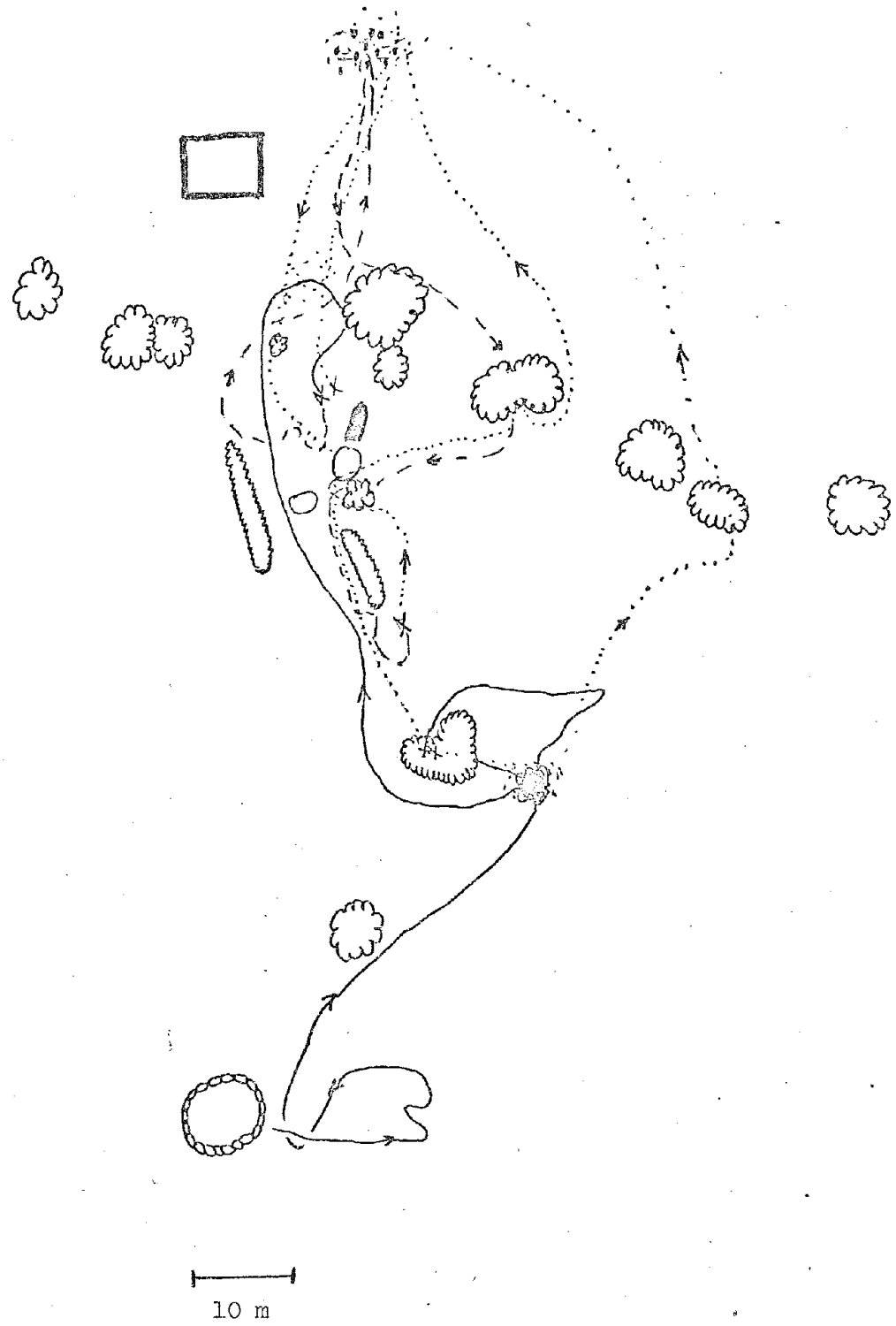


Figure 45. Daily routes of movement of tortoise 244

——— 11th February 1968

– – – – 13th February 1968

. . . . . 14th February 1968

herbivores, but feeding in the same area does have other benefits that are unique. By continually grazing an area, tortoises have a marked affect on the growth habit of the grass. Frequent cropping causes grass to take on a prostrate form; this results in the growing point being close to the ground. Also, the relative amount of stem that is grazable is very low, and flowering and fruiting are inhibited. The net result is that the tortoises are maintaining an area which stays in the vegetative phase of production, produces a small amount of grazable stem compared to leaf, and has a growing point that is essentially protected from cropping as it is very low to the ground. All of these considerations are important in evaluating the quality of food available to the tortoises, and indicate that they are maintaining the grass in a stage of high protein production, but this can only be inferred from studies on other grasses (mostly temperate species) and until data on Sporobolus virginicus (L.) are available one can only speculate. It is also relevant that production is increased with frequency of cropping in some grasses. See Spedding (1970) for a discussion of these points.

The same arguments do not apply to browsing, but there is another aspect to this form of feeding. Quite a bit of browsing consists of picking up dead leaves. This is not simply because they are more easily accessible than live leaves, but the animals show a distinct preference for dead and wilting leaves. The most extreme example of this involves Tournefortia argentea; live leaves of this tree are never eaten, yet it is not uncommon for tortoises to glut on dead leaves and flowers. The way in which tortoises browse involves m u c h branch breaking, and these broken branches provide a source of dead leaves. A tortoise that follows the same browsing route day after day will, in effect, be providing itself with a steady supply of dead and wilting leaves.

However, by following the same browsing route daily there is nothing to stop a tortoise from varying its path slightly and investigating new bushes. The animals are not solely dependent on picking up after the breakage caused the day before, this is merely an advantage in following the same browsing route.

Temporal considerations. A successful grazing strategy must also take into account important problems of time, but the data relevant to this are more applicable to activity and so will be discussed under that section.

DRINKING

Tortoises are often associated with xeric conditions and may have to survive long periods without drinking water. However, when water is available they will make use of it; this is dramatically illustrated after periods of drought. A hard rain is enough to send almost the entire population of grazing tortoises off the plain and into the pavé in search of water. Likewise, a population of sleeping animals awake and rush off in search of drinking water if a midday rain begins after a long dry spell. I have even seen sleeping tortoises rouse and move to the pavé in the depth of night as a hard rain fell.

In drinking, a tortoise lowers the anterior of its face into the water and the hyoid is rhythmically depressed and compressed as it pumps water into the pharynx. Several dozen pumping actions may be made before the animal raises its head to breathe. This may take nearly three minutes with ten to twenty seconds between each swallow. In such a period a tortoise may drink about 300 ml and a large animal might imbibe almost one litre in a drinking session.

By watching colloidal particles one can easily see that the water actually enters the pharynx through the nostrils. Considering the simple anatomy of the chelonian nasal passages (Parsons 1967) this is not at all surprising. Tortoises certainly could not lap water, for the tongue is unsuited for this function. Sucking water up through the mouth would be difficult and ineffective with the horny beak which can neither be shaped to draw water nor made air tight. There is a distinct advantage in drinking through the nose, for the nares are the most anterior part on the face of an Aldabran tortoise; in fact, the head tapers down to the nares almost forming a proboscis (Figure 33). Consequently, it is the nose that is the first organ to contact water, and it can be pushed into small holes where the mouth

cannot reach. I have seen tortoises successfully drinking with the noses pushed into very small depressions and the mouth high and dry. On many occasions animals have been seen with the noses pushed right to the ground sucking up rain water no more than five mm deep as it runs off sand. Clearly it is to the tortoises' advantage to be able to take in water as fast as possible, for the supply is irregular and transient because of rapid evaporation and run off. There is also competition and interference from other tortoises in removal of palatable drinking water and in fouling drinking areas (see section on elimination).

ELIMINATION

Defecation

When defecating, giant tortoises always go into a "defecation posture" (Figure 46). This consists of extending the hind legs and standing so that the posterior of the plastron is elevated while the anterior (the gular scutes in particular) still rest on the ground. The tail is wiggled from side to side in a serpentine manner while the faeces are expelled. As many as four pellets may be voided at once, or the animal may defecate, move ahead, raise its posterior, and defecate again.

Standing with the posterior elevated allows space in which to expel the faeces, and this seems to be the major function of the defecation posture. Although some animals would move ahead before lowering the plastron back to the substrate, many would simply lower the shell or a leg into the fresh faeces. Thus, the defecation posture is not necessarily a means by which the animal keeps itself clean.

Size of faecal pellets is very much related to the size of the animal, but there appears to be individual variation as well as variation related to food and possibly water conditions. Faeces consisting mostly of Sclerodactylon macrostachyum tend to be very large, and faeces from a senile male were very small and compact. It is not known whether or not these size differences in faeces are related to some underlying digestive phenomenon.

Fresh faeces apparently contain a high proportion of water. It is also notable that plant parts in faeces are very little modified from their original condition when first ingested. Beltz (1958) has also commented on this. Faecal analysis (e.g. per cent moisture content and calorific content) is still in progress.

Timing of defecation is coupled closely with the commencement

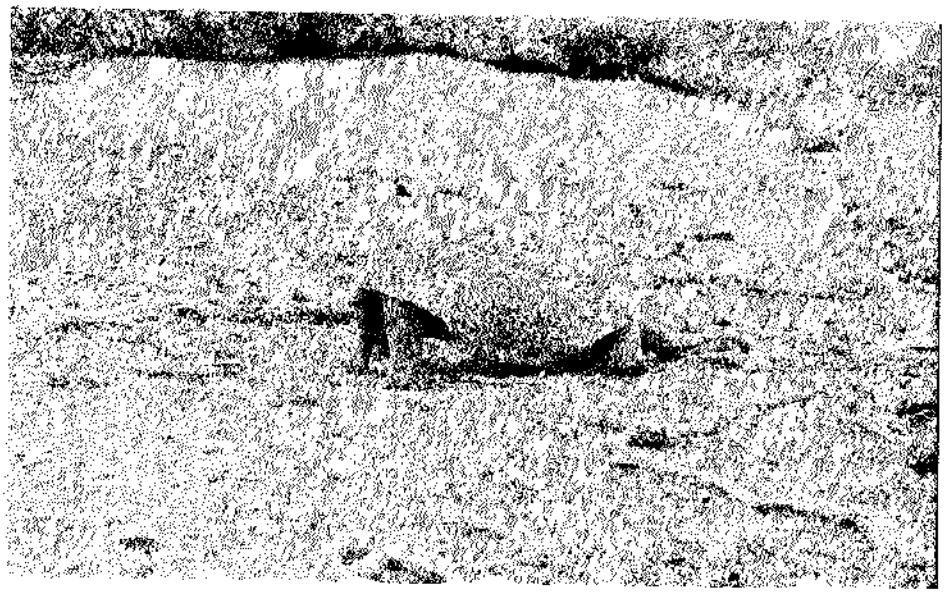


Figure 46. "Defecation posture" and defecation. The adult male is also grazing.

of activity. Of about two dozen observations on defecation in 1968 nearly 68% occurred between 0530 and 0630. In 1969 and 1970, with more detailed observations, it was again found that there was a peak in defecation in the morning, but there is also a peak in late afternoon - again, just as the animals become active. This relationship between defecation and activity has been reported in lizards (Harris 1964, p. 55), and it is not surprising, for many physiological parameters are related to activity and temperature (Dawson 1967, Templeton 1970).

In this context it is interesting that immature tortoises may defecate in the morning and again in the afternoon while large tortoises usually defecate only once a day but may defecate every other day or even every third day. Immatures tend to be more active than adults - especially those adults that go some days without defecating.

Rate of defecation and digestion is amazingly slow. Tortoise 297, a senile male that was not very active, took 34 to 37 days to pass objects fed to him. Tortoise 244, an immature that was very active, took 10 to 12 days; this was the fastest rate of through put observed. There does not appear to be a simple relationship between body size and rate of through put (Figure 47), but there does appear to be a relationship between time spent active per day and rate of through put (Figure 48), as one would expect from the above discussion.

The turds tend to accumulate where the tortoises are when first active. In the morning this usually means that they are left on the plains or in the scrub while the animals are browsing. However, in the afternoon they are commonly left under shade trees. Under some trees there is quite a considerable accumulation of tortoise dung. Grubb (1971 a) also found this.

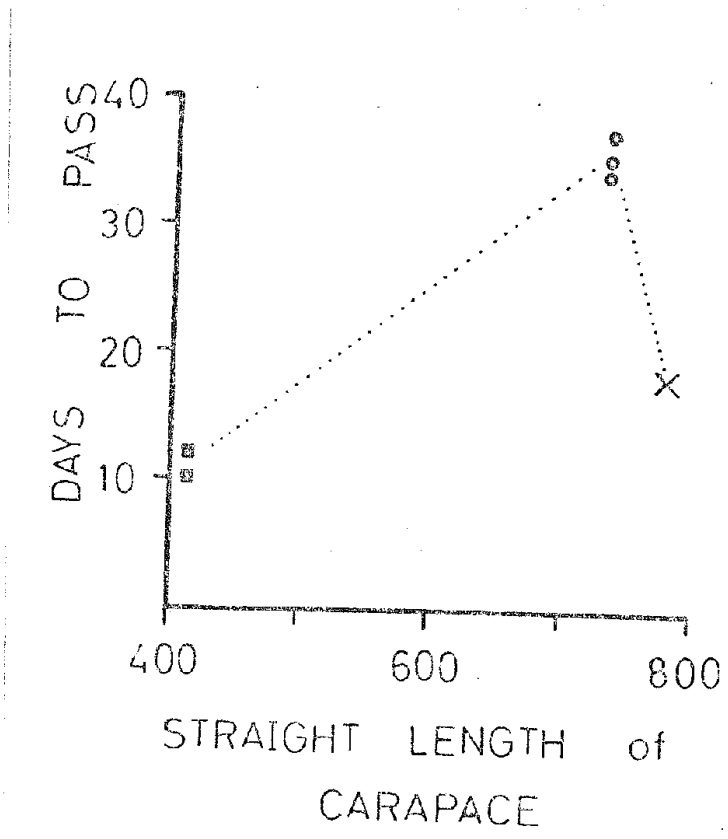


Figure 47. Relationship between rate of digestion ("through put") and body size.
▣ = 244, immature
o = 297, adult (senile ?) male
x = 45, adult male

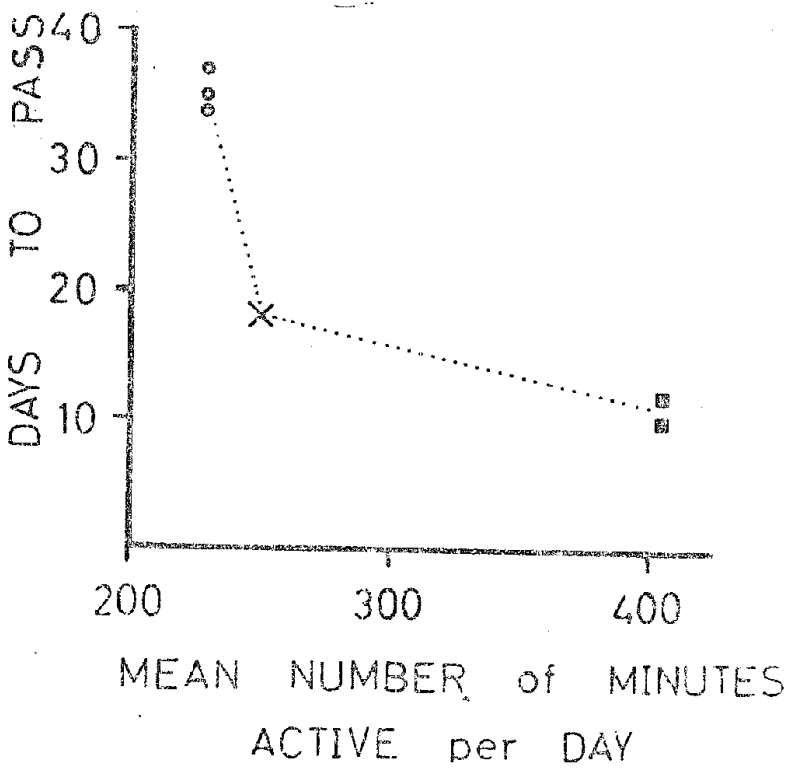


Figure 48. Relationship between rate of digestion ("through put") and average daily activity.

Symbols as in Figure 47.

Urination

Urination occurs very rarely in giant tortoises. Grubb (1971 a, p. 348) never observed it, and I have seen it less than half a dozen times. In an undisturbed tortoise liquid is usually voided while the animal is resting inactive; the fluid may be clear or yellow-brown. Nesting females micturate as part of the nesting process (see the section on nesting). Urination is common in drinking tortoises. Often during a hard rain the animals move *en masse* to the pavé to drink from temporary puddles, and as they are drinking they simultaneously urinate. The liquid voided is frequently brown in colour and has an unpleasant odour. Within minutes of the animals having moved to the pavé to drink, it is usual for many puddles to be tainted brown. This is apparently a contaminant, for tortoises in search of water often reject that which has been urinated in and is brown.

Both urination and defecation seem to be stimulated by handling and disturbing the animal. Tortoises that are being measured or moved void profuse amounts of both liquid and solids. In the psychological literature this would be interpreted as a sign of "fear", "stress", "anxiety", or some other intervening variable usually referred to as "emotionality". It is not clear just how useful this concept is (Hinde 1970, p. 535), but in view of the fact that tortoises under heat stress void a certain amount of fluid (Riedesel et al. 1971), urination does seem to be an indication of at least some forms of physiological stress.

Riedesel et al. (1971) and Cloudsley-Thompson (1968) have shown that micturition in two species of tortoise is important to thermoregulation, in that the animal increases evaporative cooling by spreading fluid over its body. The sudden expulsion of odiferous faeces and fluid could also offset the attack of a predator. Patterson (1971) has shown that canids avoid meat when it is soaked

in tortoise urine, so tortoise urine is repulsive at least to some predators. The sudden ejection of repulsive materials is a common antipredator response in many animals (Eisner and Meinwald 1966). Certainly handling a tortoise that is flowing forth with stinking faeces and urine is not at all pleasant to a human, and some small tortoises have escaped as the result of a sudden blast of urine and faeces.

I do not know what the products of nitrogen excretion are in Aldabran tortoises. In light of work by Rodgers (1966) and especially Kahalil and Haggag (1955) (who worked on two species of land tortoise, one of them a giant species - Geochelone (= Testudo) sulcata), production of ammonia, urea, and uric acid is likely, and the relative proportion of these products is probably related to degree of dehydration. See Cloudsley-Thompson (1970, p. 25) for an analysis of the urine of Geochelone (= Testudo) sulcata. I have seen a small cap of white crystalline substance on fresh faeces, but have no idea what this material was.

Flatus

Cloacal flatus occasionally occurs during defecation by Aldabran tortoises; oral flatus was not recorded. In contrast, I found (1966) that both types of flatus were common in captive Galapagos tortoises, but this may well have been due to conditions of captivity, perhaps diet or excess of water.

My observations on captive Galapagos tortoises show that they are similar to Aldabran tortoises in respect to defecation posture, relationship between activity and defecation, and the occurrence of urination and defecation in response to disturbance.

PERCEPTION

A study of the behaviour and ecology of a species must take into account the sensory capacities of the animals, for this gives some idea of what parts of their world are likely to be important.

Vision

Both Quaranta (1952) and Walls (1942) agree that giant tortoises have retinas rich in cones but poor in rods. Visual acuity is probably good but obviously vision in low light intensities is poor. The ability to discriminate colours is good (Quaranta 1952). My observations on wild tortoises, although not quantified, are consistent with these findings.

Audition

Auditory research on Chelonians has long led to disputes between neurophysiologists on the one hand and naturalists on the other. Physiologists found that the auditory structures of turtles were sensitive to airborne sounds but naturalists had no evidence that the animals could perceive these stimuli.

Patterson and Gulick (1966) found that the problem was not in the animals' ability to perceive but in the experimenters' approach, and they developed a conditioning technique that allowed them to measure auditory thresholds. Patterson (1966) found that the animals were most sensitive to sounds between 200 and 640 Hz. Controlled experiments showed that the responses to these sounds were dependent on auditory sensitivity and not simple vibratory sensitivity. On Aldabra there were occasional indications that the animals might be responding to low frequency sounds.

Chemoreception

I know of no studies of this topic in Chelonians. Observations on mating animals indicate that olfaction is a very important sensory modality in this part of the life cycle (see section on mating). It

has also been shown that there are glandular secretions, and these apparently function as olfactory stimuli (Rose 1970).

My observations indicate that tortoises smell food objects and also conspecifics. They also reject food items after biting into them, indicating that they have a sense of taste.

Tactile Reception

A priori one might imagine that tortoises are fairly insensitive to tactile stimuli, for they are covered with horny scales and a keritinized shell. However, to my dismay, I found this not to be the case. Painting numbers on tortoises invariably leads to their waking up, hissing and moving. The stroke of a paint brush, no matter how softly applied, is responded to. The soft parts of the body are also very sensitive to touch.

PART THREE

GENERAL ACTIVITY

OF

THE GIANT TORTOISE

Chapters 10 to 13

GENERAL ACTIVITY

Activity cycles in animals have received considerable attention lately as these cycles are related to a large spectrum of events in the biology of a species (Cloudsley-Thompson 1961). Phenomena as broad as fluctuations in populations and breeding (see section on breeding) as well as more subtle physiological aspects, such as changes in thermal tolerances (Kosh and Hutchinson 1968), are closely tied to activity cycles. Consequently, investigations on general activity in the tortoises were made at several different levels.

DIURNAL ACTIVITY

Grassland counts

The coastal Sporobolus plains of Aldabra offer a unique opportunity to study tortoise activity. Large areas can be surveyed quickly and details of the animals' behaviour can be observed with ease. As my camp site was situated on the edge of the east plain at Dune Jean Louis, I concentrated my efforts on these 1·5 hectares of grassland. The number of animals active on the plain was counted half-hourly, from about sunrise to sunset, and occasional spot checks were made during the night. The number of sample days for each month varied from three to thirty, but I usually tried to sample at least seven days of each month. In 1968 counts were made from the top of Dune Jean Louis, where the entire east plain could be scanned, during five months from February to July. In 1969 and 1970 counts were made from the east end of the plain, and 100 sq. m at the north-west could not be observed, but this is less than 1% of the total grassland and could not have affected the results very significantly. The 1969 counts involved

only three months: September, October, and November. Counts made in 1970 embraced five months, January to May. There was no indication that my counting had any effect on the animals, and their behaviour is assumed to have been completely normal. The major activity of tortoises on east plain was grazing, but a more detailed account of the actual types of activities observed is presented in the following section on activity census. The average number of animals active at each half hour ($\pm$ one standard error of the mean) are presented by months in Figure 49.

Several trends are obvious for each of these monthly plots. Activity is bimodal, with peaks occurring in early morning and late afternoon. The increase in activity in early morning is sharp, while the decrease in late morning is gradual. The reverse is true for the afternoon peak, where the increase in activity is gradual and the decrease rapid. Thus, changes in population activity tend to be rapid at the ends of the day and gradual toward midday. There is also a strong tendency for the peak of activity to be larger in the morning (Figure 50). Diurnal activity during the trades is not so markedly bimodal although the same general trends are present. Seasonal differences in diurnal activity will be discussed in the section on seasonal activity.

Activity census

In order to examine individual activities in more detail and to investigate activity in several different habitats, I conducted an "activity census". This consisted of walking a set route at about hourly intervals. The route (Figure 51) began at camp, went north-west along east plain by the border of shade trees, and then cut north into the pavé and mixed scrub. Both the south-east and north-east quadrats of Square 1 (each 50 by 50 m) were searched. The south-west quarter of Square 5 was also searched but not regularly. This entire

Figure 49. Mean daily activity curves. Counts of the number of tortoises active on the east plain of Dune Jean Louis.

Mean $\pm$ 1 standard error (thick vertical line) and $\pm$ 1 standard deviation (thin vertical line ended by horizontal bar).

on
Small vertical line/x axis at 0 active (|) = mean, standard error, and standard deviation all = 0.

● = individual observation

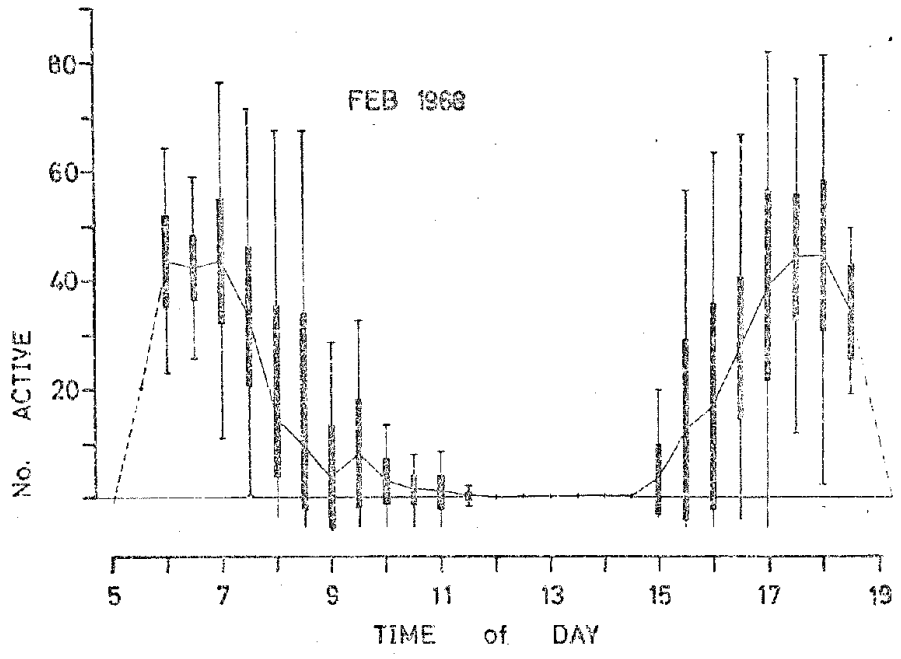
dashed line = estimated mean value

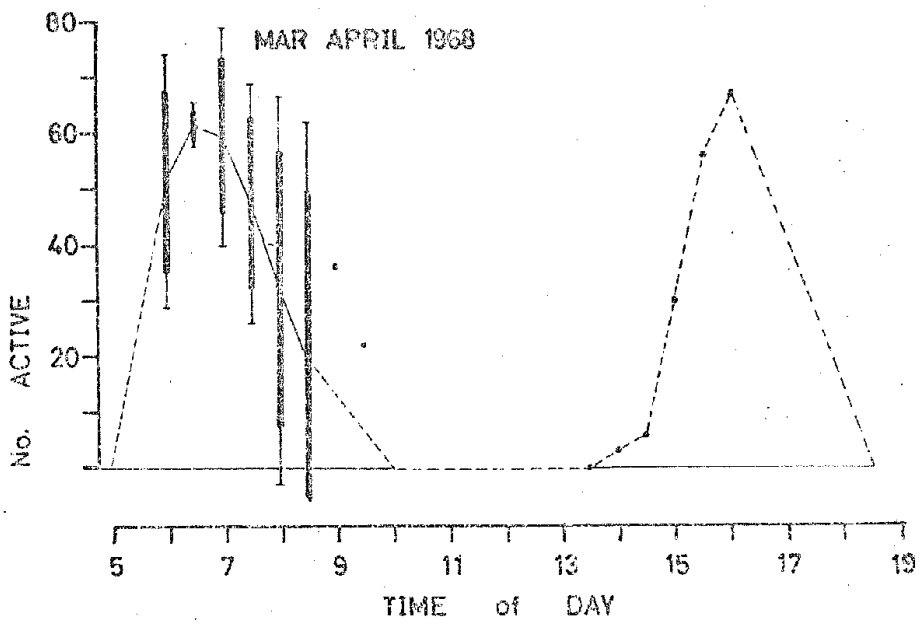
Curves for:

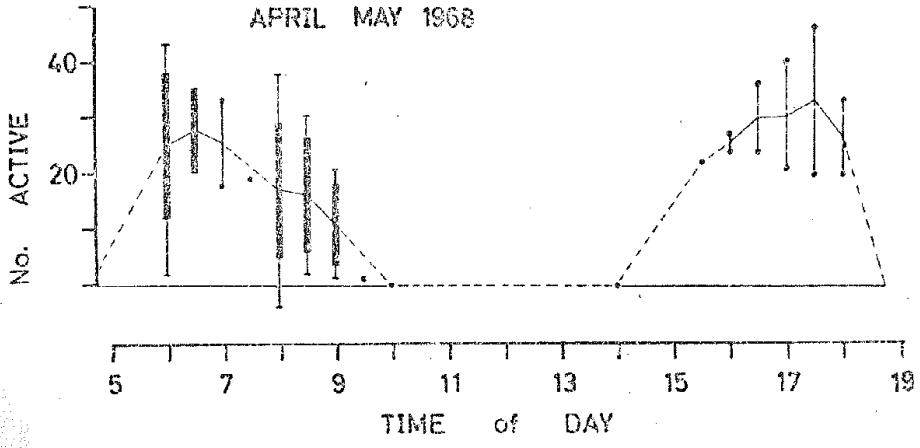
1968 - February; March and early April; late April and May; July

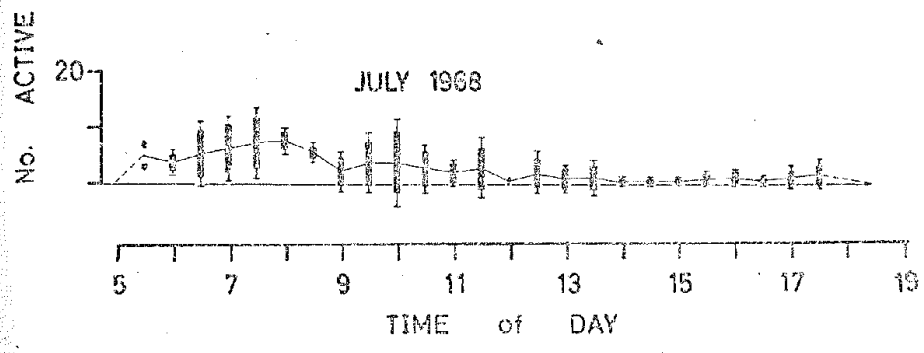
1969 - June, July and August (estimated values); September; late October and early November; late November

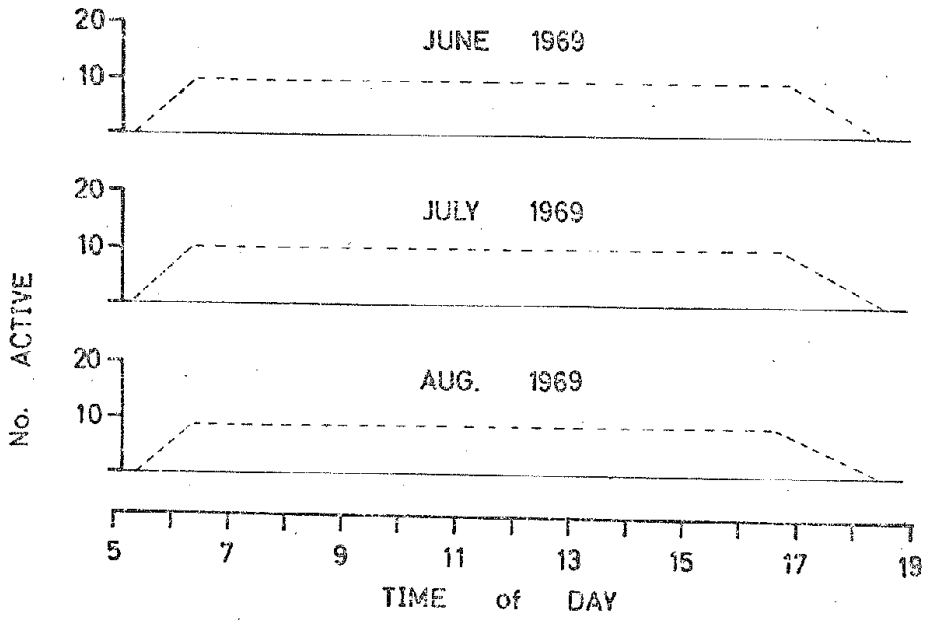
1970 - January; February; March; April; May

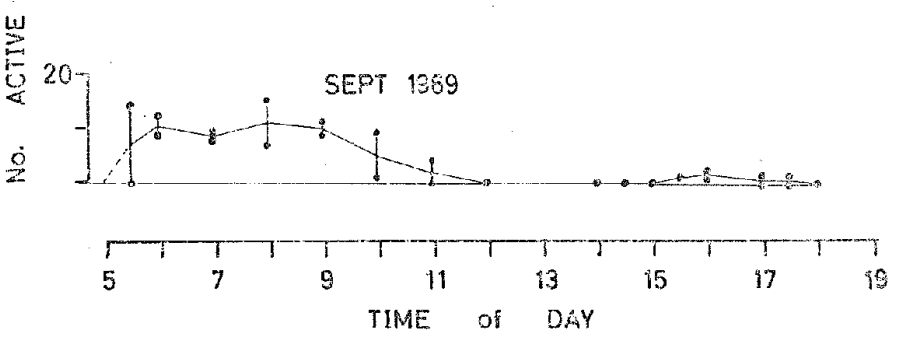

FEB 1968
No. ACTIVE
80
60
40
20
5
7
9
11
13
15
17
19
TIME of DAY

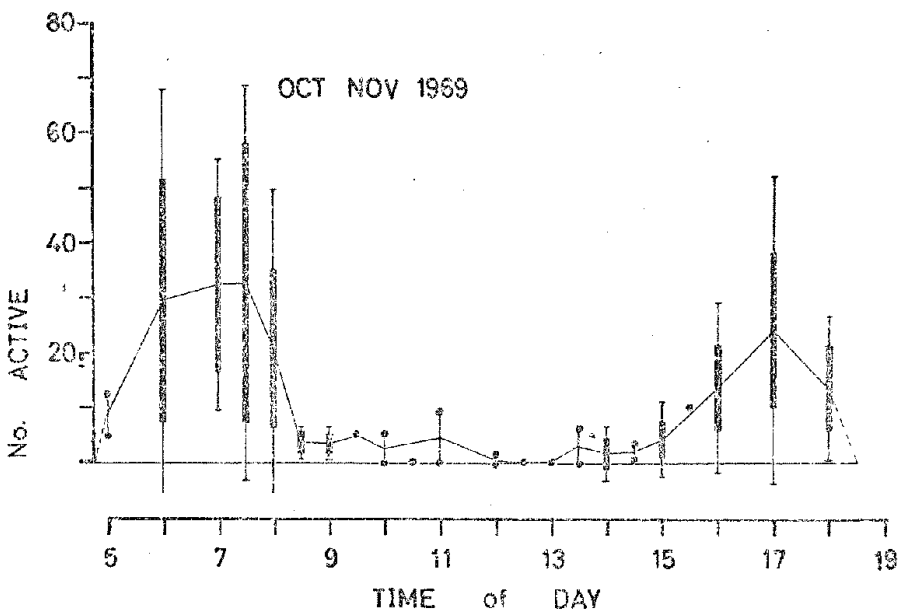

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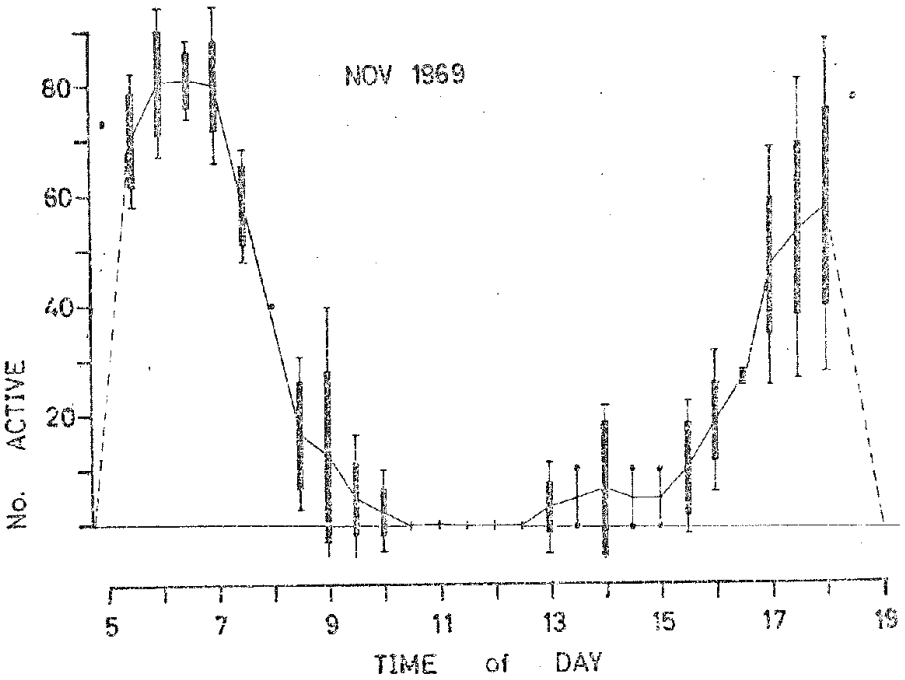

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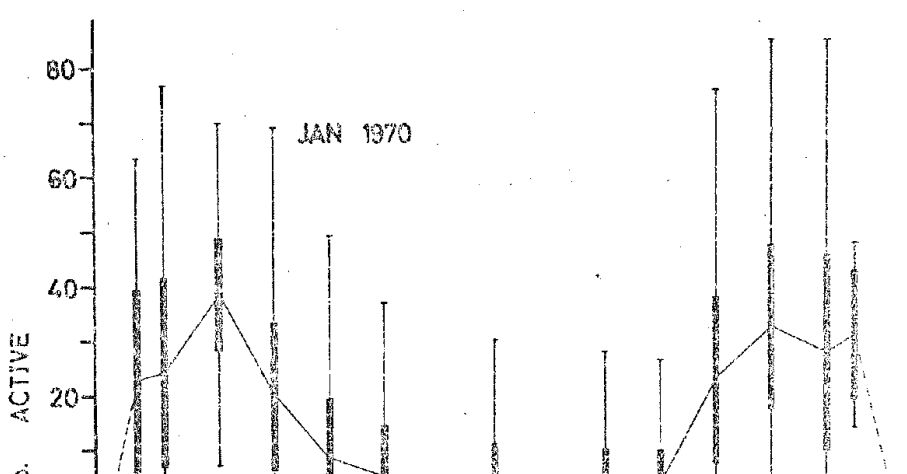

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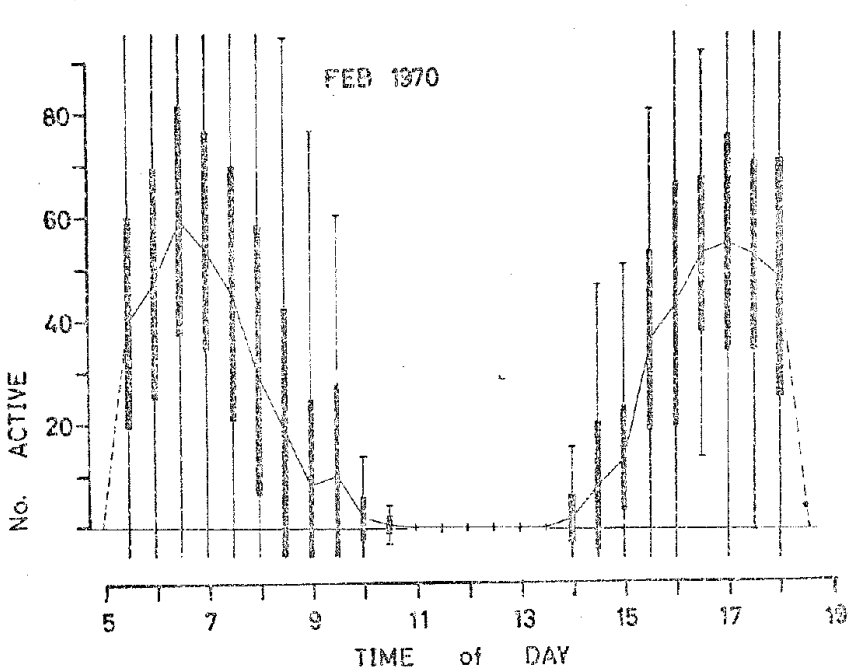

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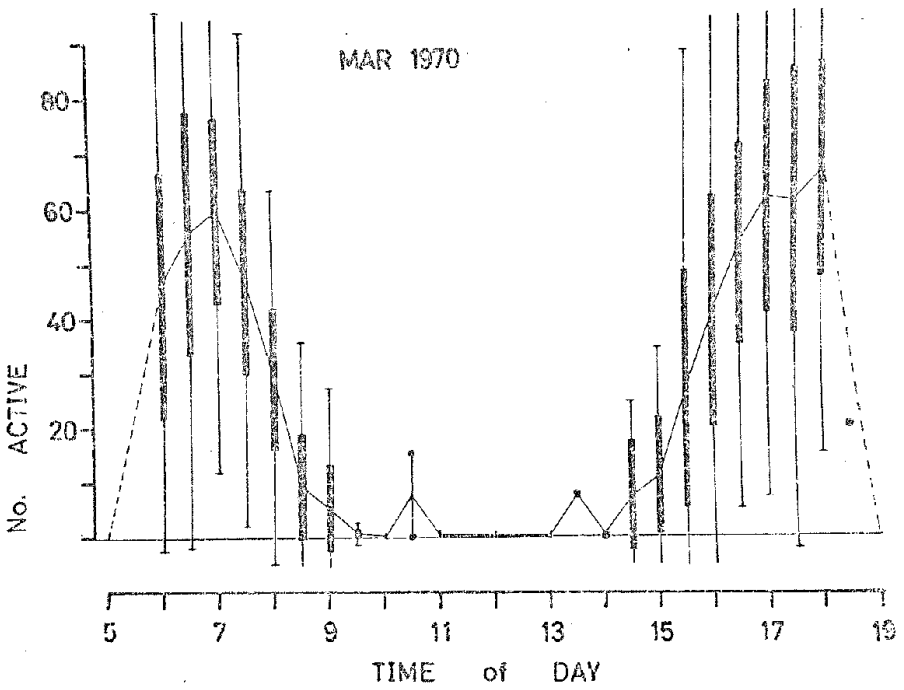

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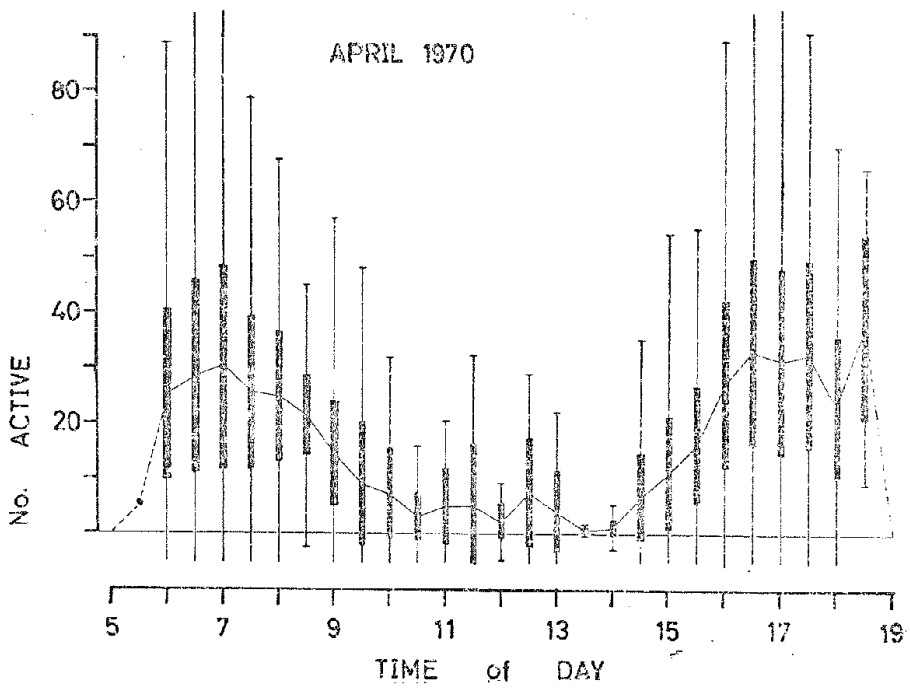

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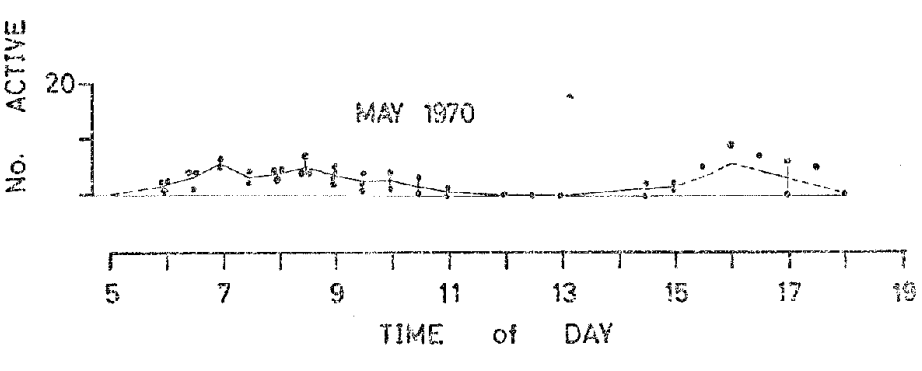

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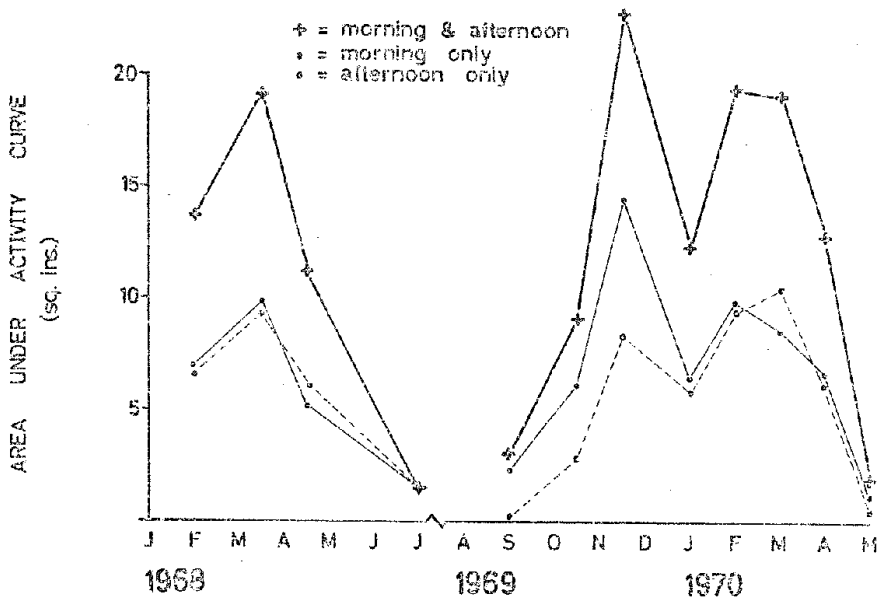


Figure 50. Area under the mean daily activity curves shown in Figure 49.
+——+ = area under the whole curve
⊕——⊕ = area under the curve before 1200 hours
o- - -o = area under the curve after 1200 hours

Figure 2.1 Route taken when conducting the activity census

= Camp

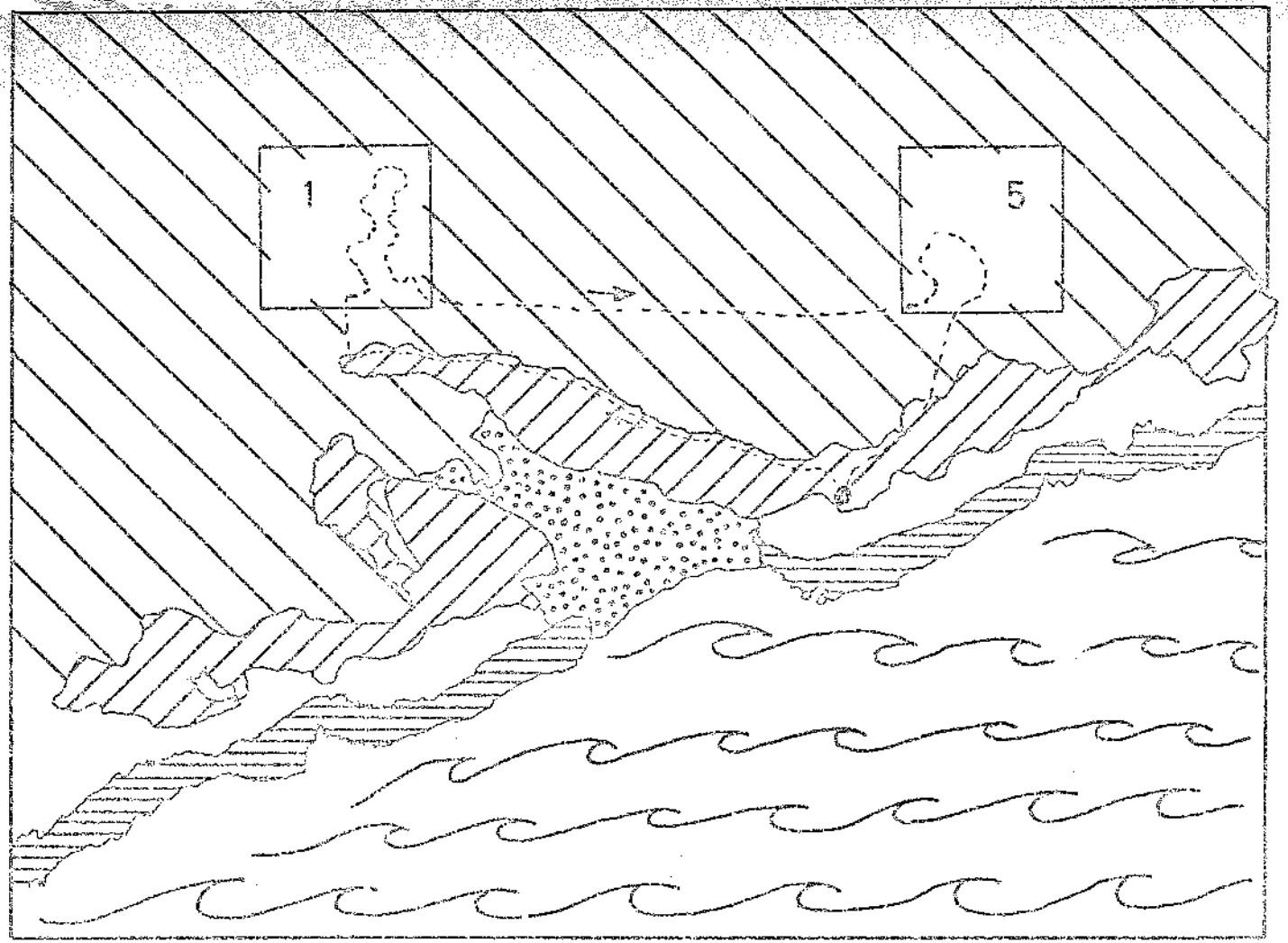
= Mixed scrub

= Sporobolus plain

= Dune & sand

= Coastal champignon

= Coarse grass, sedges, & perched beach



route took about half an hour to complete.

The habitats censused were as follows: 1) east plain - a fully exposed low Sporobolus plain (the same area used in the grassland census) and its immediate border of shade trees, mostly Scaevola taccada; 2) south-east quarter of Square 1 - moderately rough champignon with little soil, few plants at ground level and a sparse to moderate amount of scrub, little shade, and hardly any catchment for rain-water; 3) north-east quarter of Square 1 - nearly half of the terrain is flat and platin-like, providing a good catchment area for rain-water; soil and ground level vegetation are present, and much of the area is vegetated with shrubs or trees, affording a substantial amount of shade; 4) south-west quarter of Square 5 - homogeneous in appearance, the terrain is highly dissected but with considerable soil, most of which is covered with the coarse grass, Sclerodactylon macrostachyum, and the shrub Scaevola taccada. There is almost no catchment of rain-water, and although much shade is available it is not very deep.

Some animals would look up or even move away from me as I walked by in the census, but my disturbance to the tortoises was minimal and had no systematic effect. The days on which activity censuses were carried out and the weather conditions on those days are described in Table 5 below.

TABLE 5. Climatic conditions on days in which activity censuses were made

Day	Month	Wind Direction	Wind Speed (knots)	Rain mm	Temperature in °C Maximum	Minimum	Black bulb	Cloud
	1969							
14	Sept.	ESE	16	0	26·0	23·0	59·6	hazy & cloudy
15	Sept.	ESE	18	0		23·2		
30	Oct.	SE	12	0	30·0	24·0	63·5	cloudy
31	Oct.	SE	12	0	29·1	25·2	63·6	clear
6	Nov.	ESE	9	1·8	28·5	23·5	63·4	cloudy
7	Nov.	SE	11	trace	30·0	23·8	64·0	clear
	1970							
10	Jan.	N	10	1·0	31·2	25·5	65·0	clear
11	Jan.	NNW	15	0	31·8	26·5	66·4	cloudy

The results of the activity census (Figure 52) are consistent with the grassland counts.

Activity tends to occur in two peaks - early morning and late afternoon. Other more detailed trends are evident, and it is possible to generalize the following daily cycle of activity. About an hour before sunrise most animals are asleep, but the population soon wakes up and some animals may spend many minutes holding their heads high, "looking" around, before they become fully active. Just before sunrise there is a marked increase in grazing and browsing, other behaviours are infrequent at this time. The peak in feeding lasts two or three hours and then other forms of activity become common. There are marked increases in the proportions of animals that are moving, "looking", and inactive but awake, but the number of animals engaged in these activities diminishes as sleeping becomes the dominant behaviour. The majority of the population remain asleep for six to eight hours and then the morning pattern repeats itself, in reverse. As the population wakes up there is an increase in the number of animals awake, looking around, and moving; these activities decline as the afternoon peak develops. This peak lasts two or three hours before the population again becomes inactive and goes back to sleep.

Lowery (personal communication 1969) has seen Aldabran tortoises feeding by the light of a full moon, but in many hours of observation I have never witnessed nocturnal feeding. I have seen tortoises moving across the Sporobolus plain as a hard rain fell on a very dark night. I have also seen an occasional individual get up and shift its evening sleeping position a few metres, apparently in response to some disturbance. However, the general rule is that tortoises are inactive at night.

Details of habitat selection in relation to type of behaviour and time of day are also revealed by the activity censuses. In early morning and late afternoon much activity occurs in open sunlight, and

animals are often lying about sleeping and awake in very exposed sites; this virtually never happens at midday when almost all animals are in the shade. The same applies to feeding behaviours, which occurs in open sunlight in early morning and late afternoon, but in shade during the central part of the day, late morning and early afternoon. The bulk of feeding occurs in open sunlight but by browsing in the shade the animals lengthen the total amount of time available for feeding.

This pattern of diurnal activity applies to both the grassland plains and the quadrats in the mixed scrub, and is not peculiar to any special habitat.

There are, however, some days in which this general pattern is absent. On 6 November the activity cycle appears to have broken down. Some behaviours, such as feeding which is normally cyclic and quite predictable, appear very erratic. There is also a great amount of drinking. The 6th of November was a rainy day, and this breakdown in the diurnal activity cycle and the large amount of drinking are clearly related to the rain. Drinking is evidently a high priority behaviour, for it displaces more common activities such as feeding. This is most striking in November which followed a long dry period (see section on climate). The prolonged activity occurring at midday is thought to be related to lowered air temperatures, as discussed later.

Individual activity

To further investigate activity cycles, individual tortoises were followed and observed. The period of observation for each animal ranged from three to fourteen consecutive days, but most observations lasted at least a week. Along with the observations on activity, detailed behavioural, feeding, and temperature observations were made; these results are discussed in the relevant sections.

It is possible to follow quite close to a tortoise, and if one

moves carefully the animal takes no notice. Nevertheless, there are occasionally times when the observer does affect the animal, but such incidents were generally infrequent and had no systematic bias on the activity data presented here.

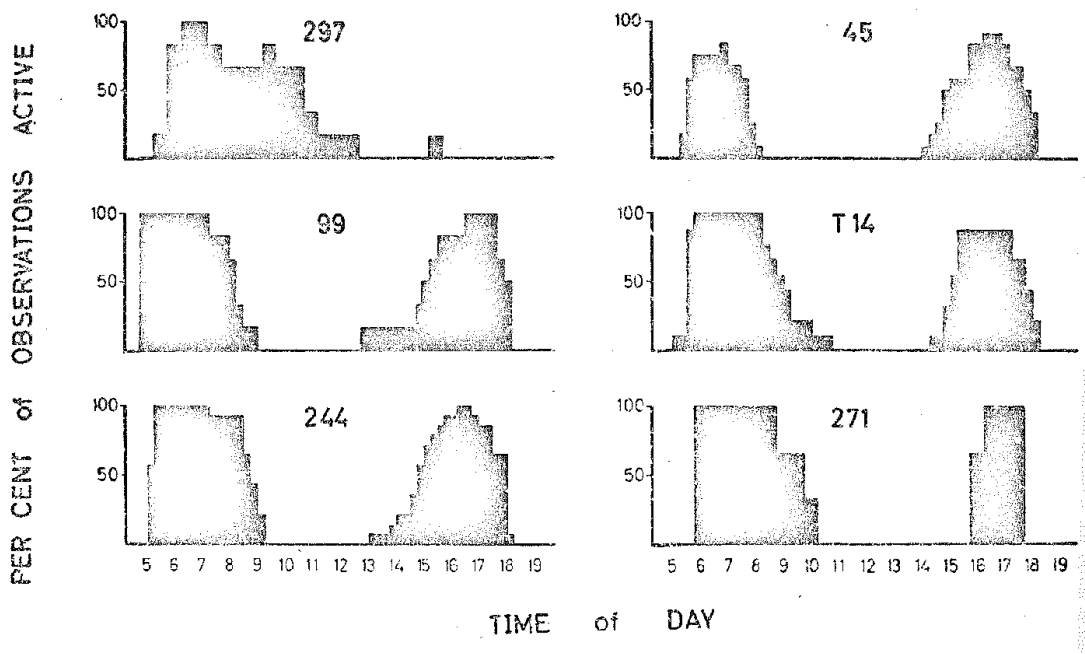
Individual records for the various animals followed are presented in Figure 53 and summarised in Figure 54. These results are consistent with the results of the monthly grassland counts and the activity censuses. There is a conspicuous diurnal pattern of activity. Feeding and other active behaviours occur in early morning and late afternoon, while sleeping and inactive behaviours dominate the midday period.

The consistent exception to this generality is tortoise 297 who was active for long periods during mornings and rarely active in afternoons. This results in a broad dominant peak of activity in the morning, and then a small afternoon peak. Very similar skewed activity cycles can be seen for the grassland counts during winter months: May, June, July, August, and September (Figure 49). Tortoise 297 was observed in August and his general pattern of activity is consistent with that for the rest of the population for this time of year.

Other similarities between populations and individuals are seen in the shapes of their activity curves. Activity increases rapidly in early morning and then decreases gradually before midday. In the afternoon the increase in activity is gradual and the decrease, rapid. Furthermore, the morning peak of activity tends to be longer than the afternoon peak, except in male 45.

Certain behaviours such as moving, feeding, "looking", and lying inactive tend to occur as transitions between the more dominant behaviours of feeding and sleeping. This same pattern was seen in the activity censuses.

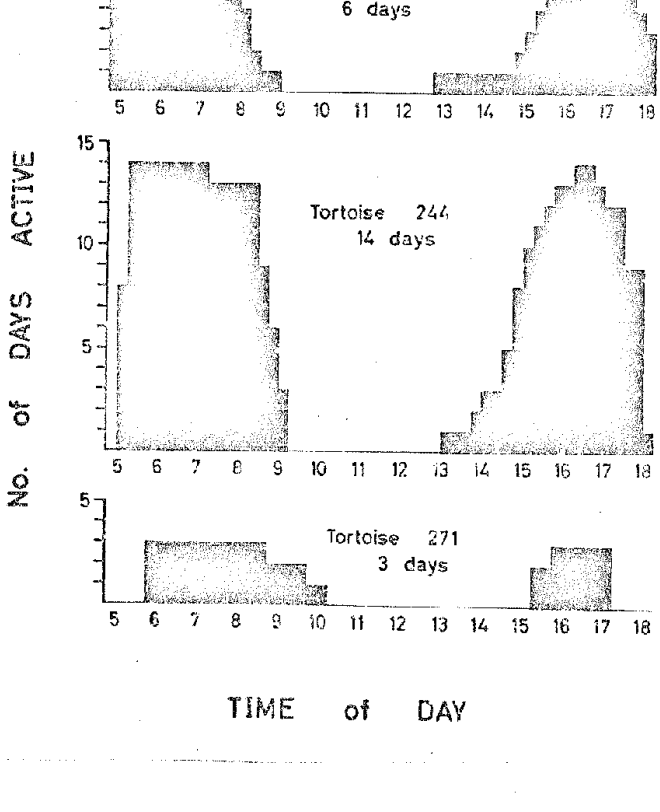
Likewise, details of microhabitat selection by individual tortoises are in agreement with the results from the activity censuses. Animals are in open sunlight during early morning and late afternoon,



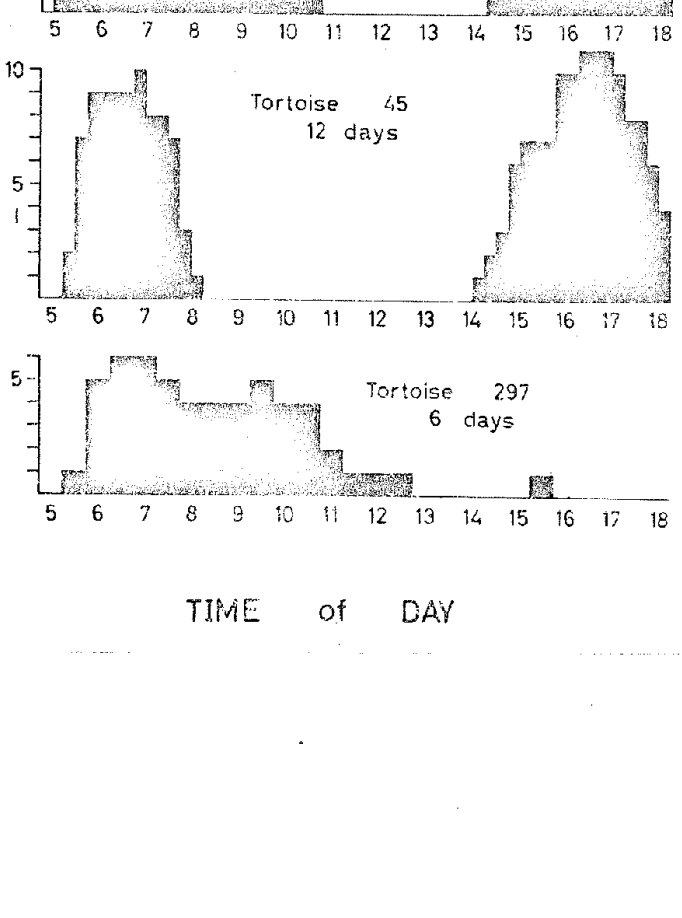
B.

Figure 54. Activity curves for individual tortoises.
A. Number of days active at different times of day (sample period for each tortoise is indicated under its number).
B. Per cent of sample period active at different times of day (e.g. 100% for tortoise 297 indicates that he was active 6 of 6 days at the indicated time).

A 1


Tortoise 99
6 days
Tortoise 244
14 days
Tortoise 271
3 days
No. of DAYS ACTIVE
TIME of DAY

A 2


Tortoise T14
9 days
Tortoise 45
12 days
Tortoise 297
6 days
TIME of DAY

and they are in shade for a long period at midday. Feeding under shade tends to occur toward midday; that is, at the end of the morning session of feeding and at the beginning of the afternoon session.

The sudden but transient occurrence of drinking at midday (see records of tortoises 99 and 244) supports the earlier suggestion that drinking is a high priority behaviour. When rain-water suddenly becomes available for drinking the animals take advantage of it; and thus, drinking displaces other activities, disrupting the general activity pattern.

Discussion of diurnal activity

Total time active. In some species the total feeding time per day is related to the size of the animal. Clough and Hassam (1970) found that large warthogs (Phacochoerus aethiopicus (Pallas)) spent less time feeding than small individuals; the larger teeth of the former apparently allow them to feed more efficiently. My data do not indicate any correlation between body size and total time spent feeding (Figure 55). Very small tortoises, under twenty-five cm long, do not appear to spend much time active. They are difficult to locate, apparently spending most of their time secreted under vegetation. When these small animals are conspicuous, it is only for an hour or so during the cooler part of the day, but I have no quantitative data on their activity. On the other hand, very large adults do not seem to be as active as immatures such as tortoise 244. Consequently, if there is any relationship between body size and total time spent active, it is likely to be complex.

Tortoises on Aldabra are active for less than half of the daylight period. In the six individuals studied the overall average was 5·4 hours of activity per day. Animal 297, the senile male, was active for only 4·4 hours a day, and tortoise 244 the immature, was active for 6·8 hours per day. Although most of this time active was spent

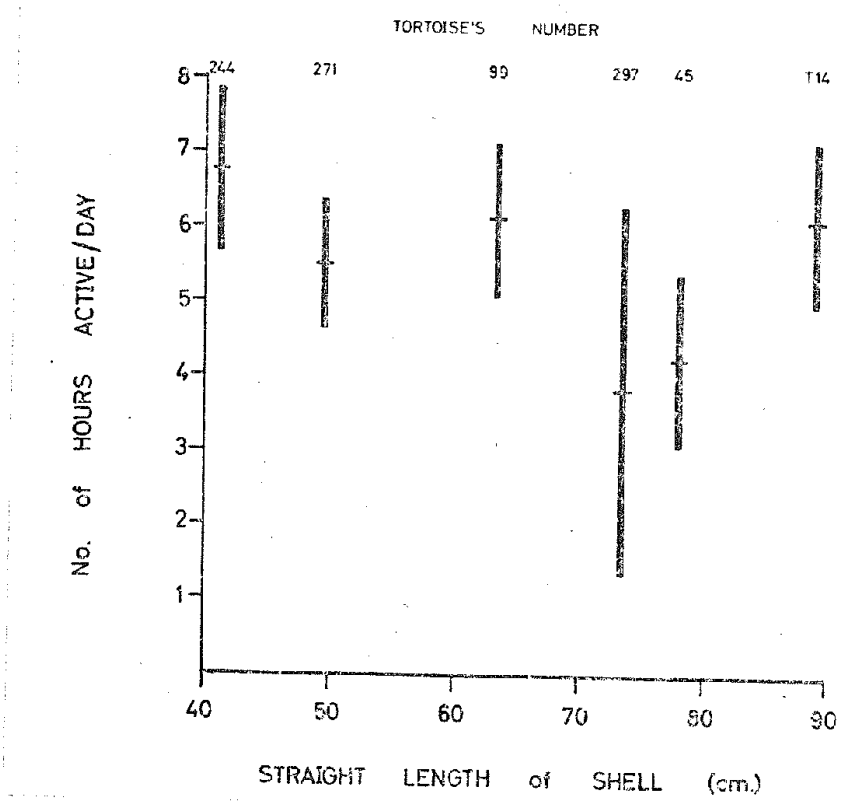


Figure 55. Relationship between body size and time spent active/day.
Mean ± 1 standard error.

either grazing or browsing, tortoises spend a relatively small amount of time feeding. In domestic cattle grazing involves 6·5 to 10·2 hours a day, and an additional 5 to 7 hours are spent chewing the cud. Sheep, which are closer in size to giant tortoises, spend even more time than cattle grazing and ruminating (Table 6). Tropical ungulates likewise spend a great proportion of their time feeding. Spinage (1968) studied waterbucks (Kobus defassa ugandae Neumann) in Uganda, and his results indicate that these antelopes need about nine hours a day for feeding and an additional eight hours for ruminating. Clough and Hassam (1970) found that warthogs spent from four to nine hours feeding during an eighteen hour period.

Tortoises do not ruminate and apparently do not break down cellulose, since plant parts in the faeces are little modified from their original condition. Hence, it is likely that the assimilation efficiency in these reptiles is extremely low in comparison with mammalian herbivores. In addition, the reptiles' rate of digestion, or through-put, is very low - taking up to thirty-six days, so that assimilation rate is evidently also low in comparison with mammals. It may seem curious that tortoises spend so little time feeding in comparison with ungulates, and Aldabran tortoises may be unable to spend more time feeding because of some restriction on their activity. In a few cases, particularly with active animals such as 244 and 99, it seems that an environmental factor is limiting their activity, and, in fact, I will argue just this point in the next section.

Yet, several observations indicate that regardless of environmental restrictions, the animals have a limit to the average amount of time they will spend grazing in a day. That is, there seem to be endogenous as well as exogenous factors limiting feeding activity. On 25 November, tortoise 99 was active for five hours during the morning, but when the rest of the population returned to the plains in the

TABLE 6. Ranges and averages (in brackets) of grazing and ruminating times for cattle and sheep. Comments on pasture types and management conditions have not been included in this summary

Hours / day		Livestock breed	Locality	Source
grazing	ruminating			
7 to 8	7	Beef cattle	New York, U.S.A.	Johnstone-Wallace 1944
4·3 to 10·5 (6·5)	3·7 to 6·8 (5·6)	Dairy cattle	Reading, England	Castle, Foot, and Halley 1950
6·9 to 9·1 (8·4)	6·2 to 7·8 (6·9)	Dairy cattle	New Zealand	Hancock 1954
4·9 to 8 (6·5)	4·7 to 6·5 (5·6)	Dairy shorthorn	England	Castle and Halley 1951
5·9 to 9·6 (7·5)	4·7 to 5·8 (5·4)	Dairy cattle	New Zealand	Corbett 1951
5·7 to 7·5 (6·5)		South Devon cattle	Devon	Halley 1951
7·3 to 11·5 (9·3)		Dairy cattle	Ayr, Scotland	Waite, MacDonald, and Holmes 1951
5·6 to 7·8 (7·)	4·3 to 9·2 (6·3)	Dairy cattle	Somerset,	Wardrop 1951
6·6 to 7·8		Hereford-cross bullocks	Stratford-on-Avon	Tayler 1951
(10·2)		Free range cattle	Ireland	O'Donnell and Walton 1969
9·3 to 13·2	8·2 to 10·3	Blackface sheep	Wales	England 1954
9·8 to 12·6	5·5 to 10·3	Clun sheep	Wales	England 1954
10·4 to 12·2	7 to 8·8	Spanish sheep	Wales	England 1954
8·9 to 10·7	9·1 to 10·2	Suffolk sheep	Wales	England 1954
9 to 11		Sheep and goats		Hafez 1962
10		Merino sheep		Arnold 1963

afternoon, she was inactive. Animal 297 was even more extreme, for he would not only spend whole afternoons, but occasionally entire days inactive. On overcast days I have also seen large males graze from nearly dawn to dusk without interruption, although the remainder of the population had normal biphasic activity. However, after these large animals have gained nearly six "extra" hours of feeding time, they spend the whole of the following day asleep, while the rest of the population is active in the normal way.

From the results of the grassland counts, the activity censuses, and the observations on individuals it is clear that a tortoise is normally active for less than six hours a day. Since a significant increase in feeding on one day (or in the morning) results in a decrease on the next day (or in the afternoon) it appears that six hours' feeding supplies the energy requirements of a tortoise. However, it seems strange that they do not take advantage of opportunities for extended feeding activity, to store up food or fat. Rate of through-put in these reptiles is incredibly slow for a vertebrate and this undoubtedly limits the rate at which they can take in food. If the ventriculus is full after a long period of feeding, it may be useless, or impossible, for the animal to ingest any more. However, this hypothesis needs experimental confirmation.

If, in fact, six hours' grazing or browsing per day does supply the tortoises' energy requirements, these animals are adapted to survive with relatively short periods of feeding activity and low energy intake. (It is questionable whether six hours of feeding per day, under the present conditions on Aldabra, provides sufficient nutriment for maintenance as well as reproduction, see breeding section.) The tortoises can also conserve energy, and further reduce their energy requirements, by going to sleep under a tree for days or hours. Although the input of energy in this situation is nil, output is probably so reduced that the animal may be nearly "switched off"

metabolically and in a semi-torpid state. Again, this must be tested experimentally, but it is known that poikilotherms have relatively low energy demands (see Benedict 1932; McNeill and Lawton 1970; and Appendix II on respiration).

Time of activity. Diurnal activity is common in the Testudinata and has been described in a variety of species, both aquatic and terrestrial: Geoamyda annulata (Gray) (Park et al. 1940); Pseudemys scripta (Schoepff) (Moll and Legler 1971); Pseudemys scripta troosti (Holbrook) (Cagle 1950); Terrapene c. carolina (Stickel 1950); Gophorus agassizii (Cooper) (Woodbury and Hardy 1948); Testudo horsfieldi (Gray) (Sergeyev 1939); Geochelone (= Testudo) sulcata (Cloudsley-Thompson 1970); and Geochelone elephantopus (Frazier 1966). Diurnal activity is to be expected in chelonians for these animals are scotopic, having nearly pure cone retinas, and their vision is greatly handicapped at low light intensities (Walls 1942).

There are however, several exceptions to this general trend for diurnal activity in testudines. Darwin (1900) claimed that Galapagos tortoises moved "by night and day" when they had long distances to cover. It is not clear whether he actually observed this or merely related what the inhabitants told him, but nocturnal activity on Galapagos seems highly unlikely, for (as on Aldabra) the terrain is broken and rough and the animals are subject to death or injury by falling.

Hatchling sea turtles (Chelonidae) are known to emerge from their nests under cover of darkness and make their way to the sea (Hendrickson 1958; Mrosovsky 1968). However, this nocturnal behaviour (which is evidently affected by low temperatures (Mrosovsky 1968)) is a rather special form of activity. Likewise, many species of chelonian nest at night (Park 1941; Carr 1952; Moll and Legler 1971), but this again is a special activity characteristic of a very limited period in the life of the animal.

The only chelonian example of general activity occurring at night is in the desert tortoises (Gophorus agassizii). Woodbury and Hardy (1948, p. 179) found that these animals were active at night during hot, summer months. Normally the animals are diurnal, and this change is thought to be related to high summer temperatures.

THERMOREGULATION AND ACTIVITY

Tortoises, like other reptiles, are endotherms; hence, their body temperature is dependent on environmental temperatures. In order to survive the animals must maintain their body temperature at some "preferred level" between a critical minimum and a critical maximum by "thermoregulation". As so many authors have emphasized (see the literature review in Templeton 1970), a common way for a reptile to regulate its body temperature is to move from one micro-environment to another, and this obviously has a marked effect on the animal's activity. Hence, activity cycles of many reptiles are strongly related to the environmental temperatures in which they live. Klauber (1939), Cloudsley-Thompson (1961), and Heckrotte (1962) discuss this in some detail, although they make no mention of Testudines.

The relationship between activity cycles and environmental temperatures has been examined in two species of tortoise; Sergeyev (1939) studied Testudo horsfieldii from Asia Minor and Cloudsley-Thompson (1970) studied the desert tortoise (Geochelone (= Testudo) sulcata in the Sudan. Both studies showed that the animals had bi-modal cycles of daily activity, and suggested that this was related to the high midday temperatures that occur in the habitats where these animals live.

Observations on populations

The bimodal pattern of daily activity on Aldabra is clearly a means by which the tortoises can be active by day, while avoiding intense solar radiation and high temperatures that occur at midday. Figure 56 illustrates how the tortoises avoid activity during the peak in diurnal air temperature, and concentrate their feeding and other activity into the cooler parts of the day. More direct evidence for the relationship between activity and temperature is the strong

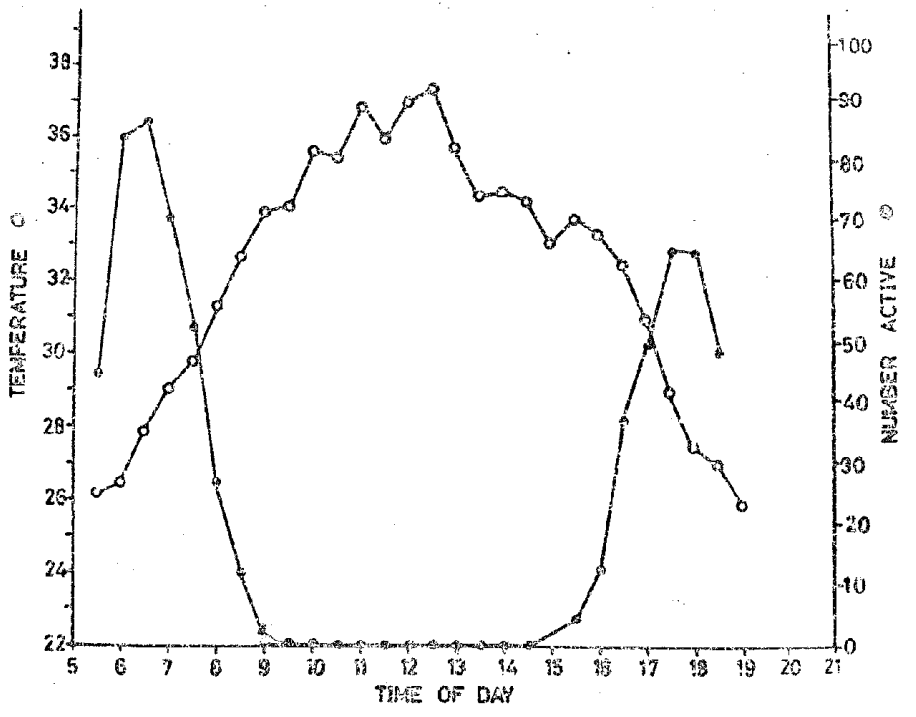
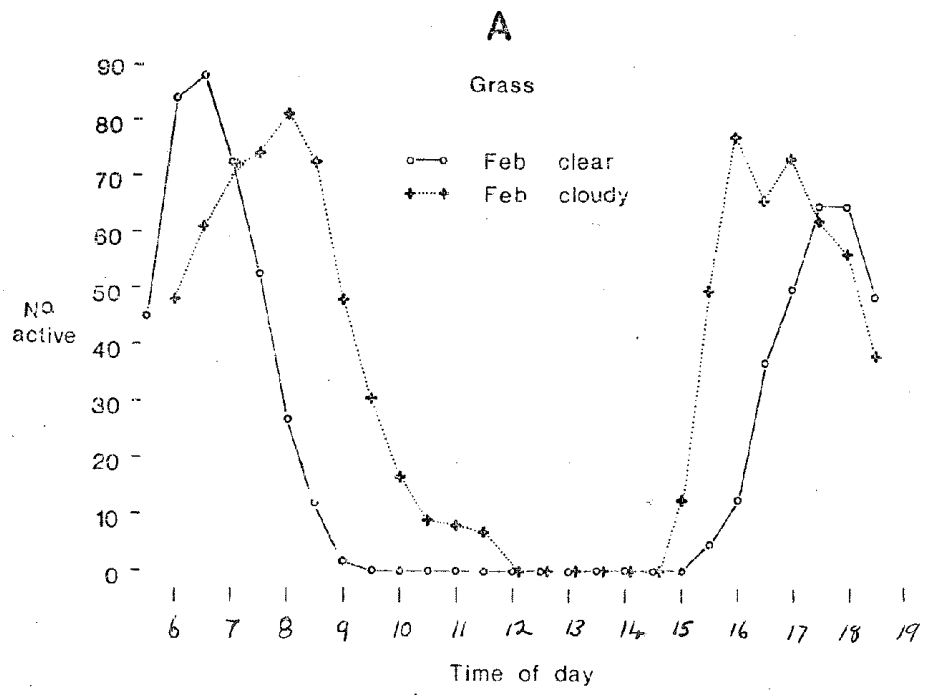


Figure 56. Mean number of tortoises active on the east plain & the plain west of Premier L'Anse (●) and average air temperature (○) at 2 cm above the sand on top of the dune.
Half-hourly readings for 10 clear days (i.e. less than 3 hours of overcast and no rain) in February 1968.

negative correlation between the number of animals active and the air temperature. Counts of the number of tortoises active on the east plain were made in February, March, and April 1968, and at the same time the unshaded air temperature on top of Dune Jean Louis was recorded. In sixteen counts made during mornings the correlation coefficient between activity and temperature was - 0·7750 ($p < 0·001$), for nine counts made during afternoons the value was $r = - 0·7087$ ($p < 0·05$). Thus, the warmer the air temperature, the fewer animals are active on the east plain.

Variations in the diurnal activity cycle are usually accompanied by variations in the pattern of diurnal temperature. If activity counts are separated into those which were made on clear and those made on cloudy days, the results for the two groups are quite different. In counts made during February 1968 (Figure 57) the cloudy days have broad morning and afternoon peaks of activity and a relatively short period of inactivity; clear days have narrow peaks of activity and long periods of inactivity. This difference applies to counts made for grassland as well as for mixed scrub. These points are summarised in Table 7.

The average daily air temperature regimes for clear and cloudy days in February 1968 are shown in Figure 58. As one would expect, cloudy days reach a lower maximum, arrive at this peak later in the day, and are generally cooler than clear days. On cloudy days, when the grassland and scrub populations cease activity, the air temperature is 32·75°C on average; on sunny days the equivalent average temperature is 32·5°C for grassland and 34·5°C for scrub. Thus, when the unshaded air temperature on top of the dune reaches about 33°C the populations on both plains and pavé are inactive and resting in the shade. (As will be seen later, this is about the maximum (preferred) body temperature for these animals.) Because this "threshold temperature" is reached more quickly on clear days, activity ceases



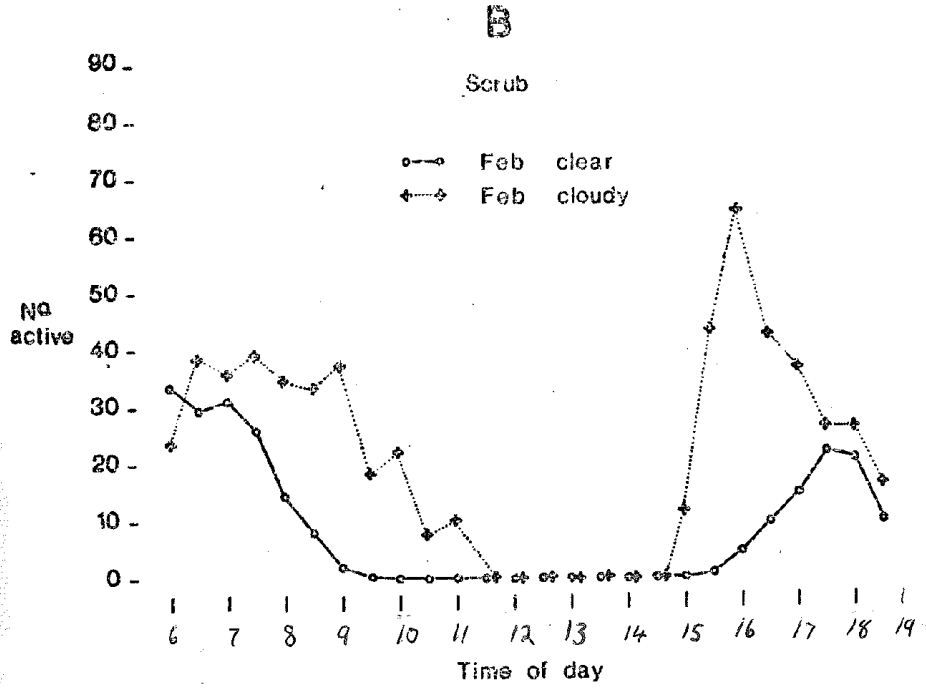


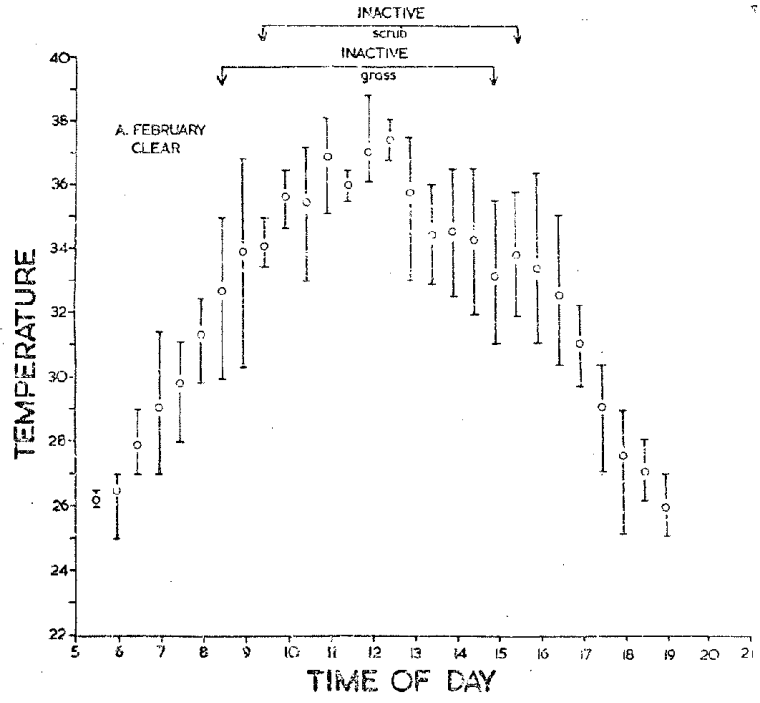
Figure 57. Average number of tortoises active on 10 clear days (o) and 2 cloudy days (+) in February 1968.
A. on the plain at Dune Jean Louis
B. in the mixed scrub adjacent to the plain.

TABLE 7. Summary of activity studies in February 1968, average values for clear and cloudy days

	Habitat			
	Grassland		Mixed scrub	
	Clear	Cloudy	Clear	Cloudy
Morning peak value				
no. active	86·5	81	33·5	39
time of day	0730	0900	0700	0745
Afternoon peak value				
no. active	65	77	21·5	64
time of day	1845	1700	1845	1700
Period of inactivity				
length (hrs.)	6·5	2·5	6	2·5
beginning	0930	1300	1030	1300
end	1600	1530	1630	1530

TABLE 8. Summary of activity studies in July 1968, average values for clear and cloudy days

	Habitat			
	Grassland		Mixed scrub	
	Clear	Cloudy	Clear	Cloudy
Morning peak value				
no. active	8·3	15	30	45
time of day	0900	0830	0700	0930
Afternoon peak value				
no. active	no afternoon activity	no peak	no afternoon activity	73
time of day				1700
Period of inactivity				
length (hrs.)	8	no inactivity	6	no inactivity
beginning	1100		1300	
end	1900		1900	



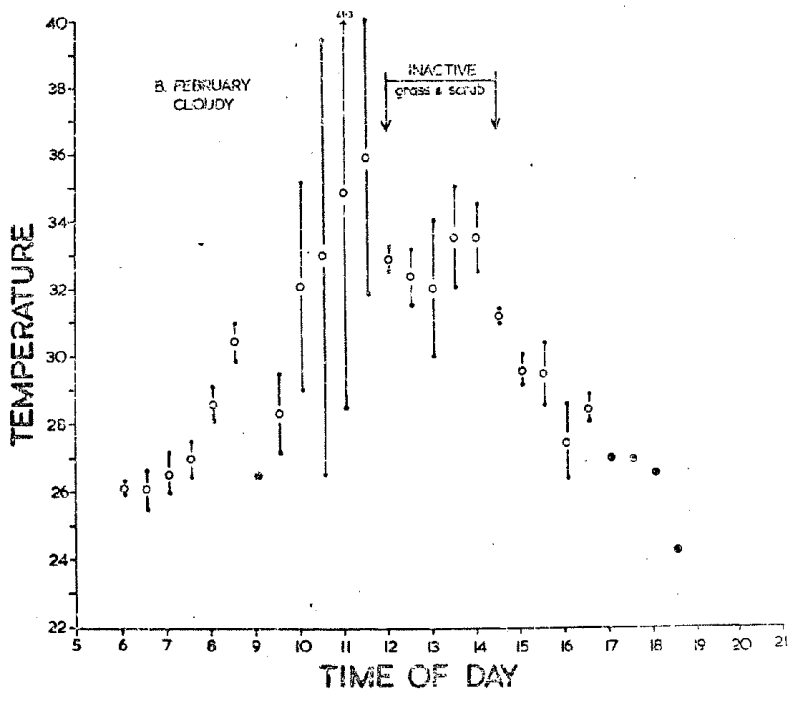


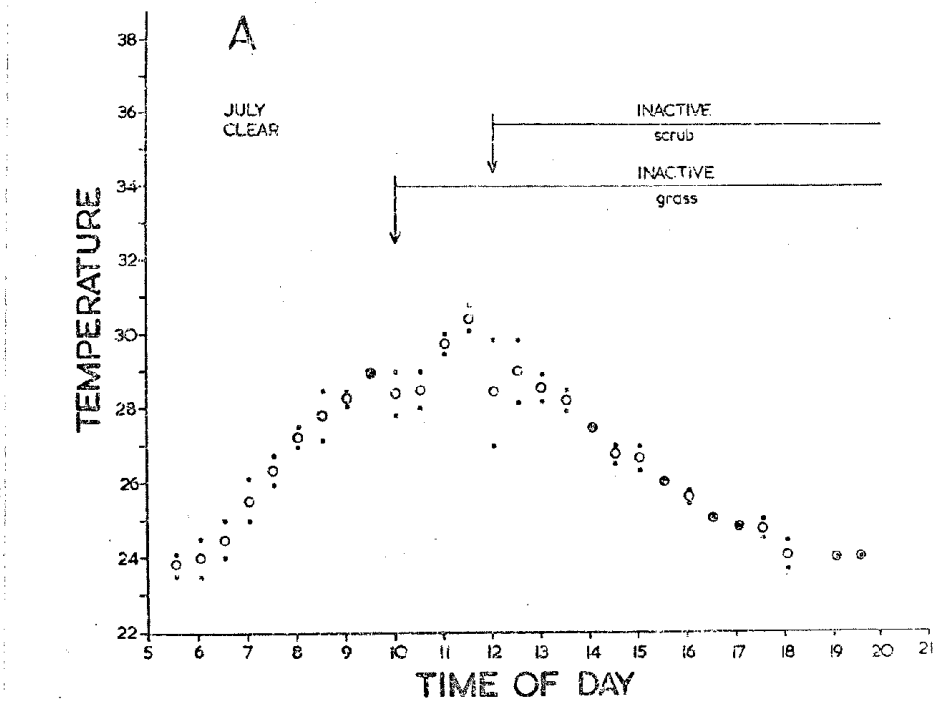
Figure 58. Air temperature in February 1968 on the top of Dune Jean Louis; average and range of measurements for half-hourly intervals. Time during which grassland and mixed scrub populations were inactive is indicated.
A. Clear days; B. Cloudy days.

earlier. Afternoon activity on sunny days begins when the temperature has dropped to between 33°C and 34°C. On cloudy days the plains do not become populated again until the average air temperature has dropped to 31·2°C, but despite this lower afternoon temperature, the tortoises are active considerably earlier in the afternoons of cloudy days. This again illustrates the much cooler air temperatures that occur on cloudy days.

This discussion has been based mainly on the results of observations made in February 1968, and these data are representative of any day in which diurnal temperature peaks about midday and daily activity is bimodal. In fact, this pattern is characteristic of most days on Aldabra; Figure 49 shows the common occurrence of bimodal daily activity in different months. The main exceptions are the midwinter months, where the period of inactivity is not distinct and is often absent. Figure 59 presents the air temperatures for clear days and a rainy day in July 1968. The maximum temperature reaches just over 30°C on the clear days and only comes to 29°C on the cloudy day. This is far cooler than any day, clear or cloudy, in February; and is consistent with the general meteorological data which showed this same seasonal difference in air temperature.

On clear days in July activity did not cease until about noon (Figure 60); on the rainy day there was no period of inactivity. Table 8 summarises these data. The wide peaks of activity in July and the persistent activity during the rainy day appear to be related to the low temperatures that occurred at these times. The generally cool conditions during the winter allow the animals to be active at any time during the day.

However, the effect of rain cannot be ignored. It was suggested earlier that drinking is a high priority behaviour and that animals will disrupt a "normal" activity cycle to take advantage of drinking water when it becomes available. This is the cause of the large peak in animals active during the afternoon of the rainy day; they were



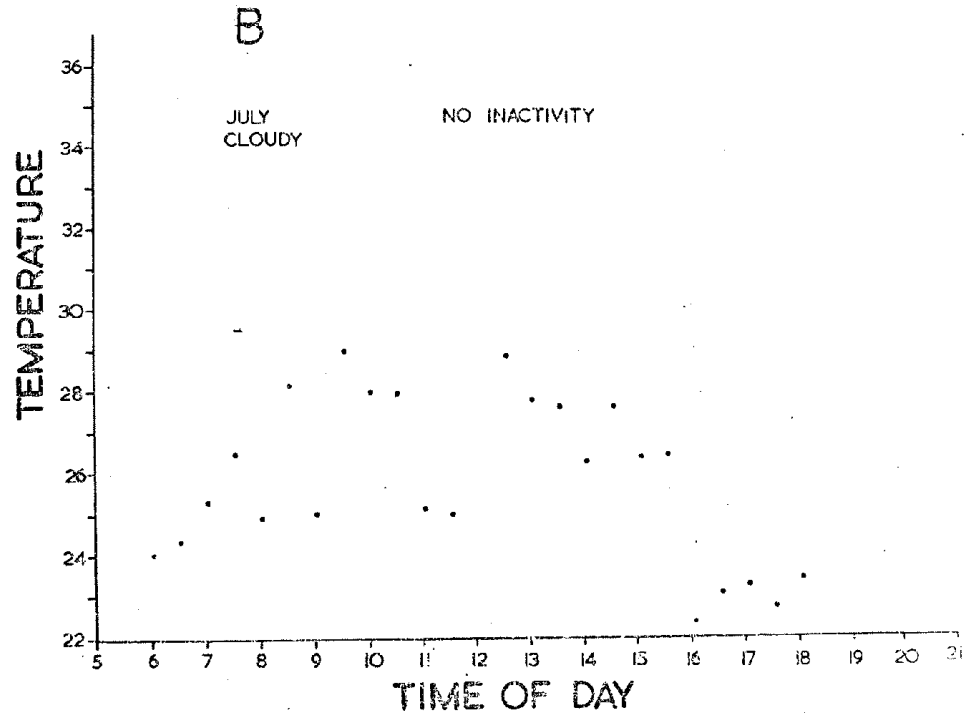


Figure 59. Air temperatures on top of Dune Jean Louis for July 1968.
Details as in Figure 58.

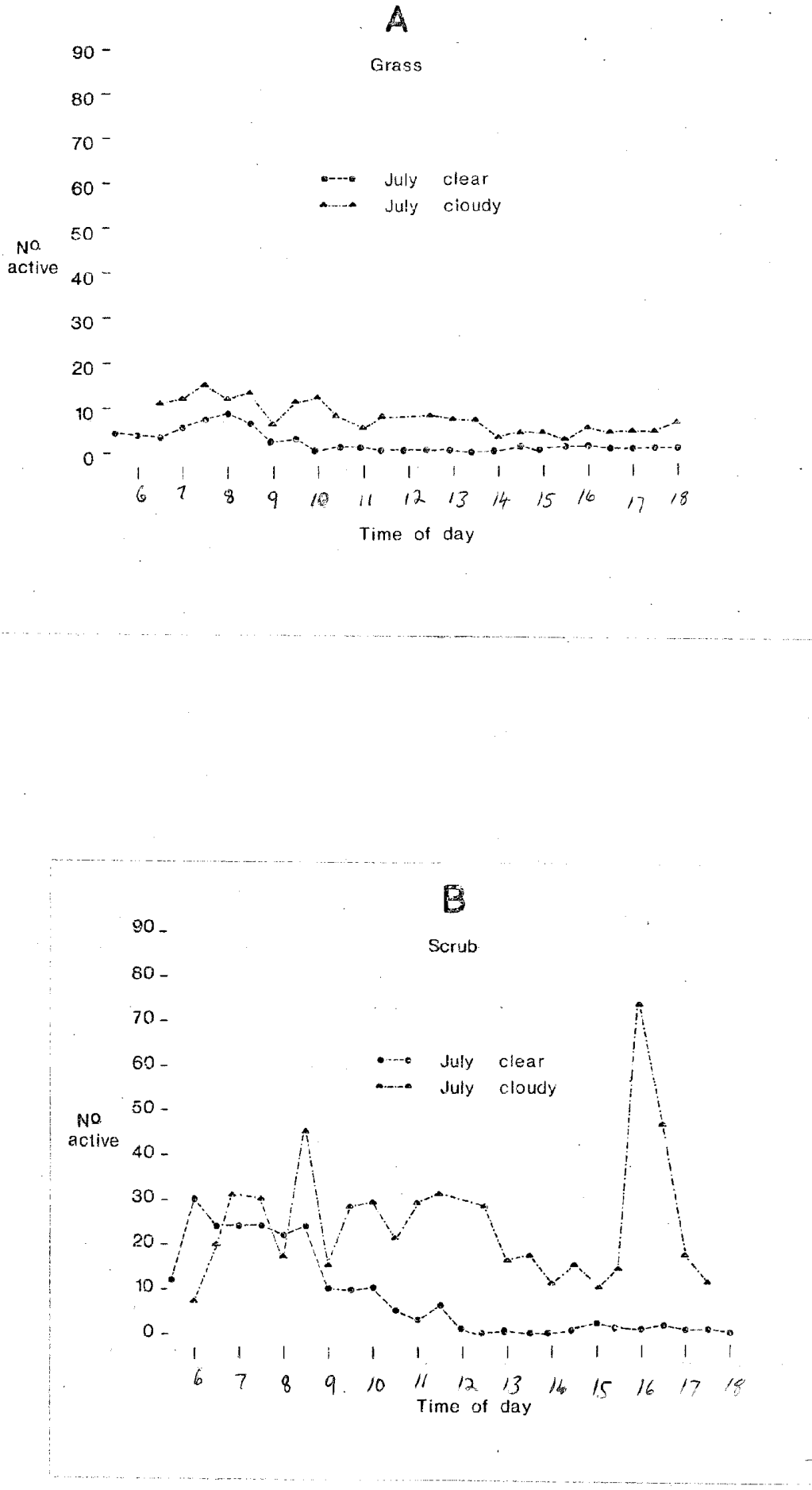


Figure 60. Average number of tortoises active on two clear days (●) and one cloudy day (▲), in July 1968.
A. On the plain at Dune Jean Louis.
B. In the mixed scrub.

all out drinking.

The small amount of general activity that occurs in July is rather an enigma if activity and temperature are negatively related. Winter air temperatures never reach the hypothetical threshold values that were reached in the summer, and animals became inactive under much lower temperature conditions than they did during the summer. The cooler environmental temperatures during the winter would result in the animals having lower body temperatures and hence lower metabolism. This would result in lower activity (see locomotion, feeding, and defecation sections). However, tortoises can be, and are, active under cool environmental conditions (e.g. when nesting), and the paucity of activity in the winter is thought to be due more to reduced food supply than to lowered environmental temperature (see section on seasonal activity).

Observations on Individuals

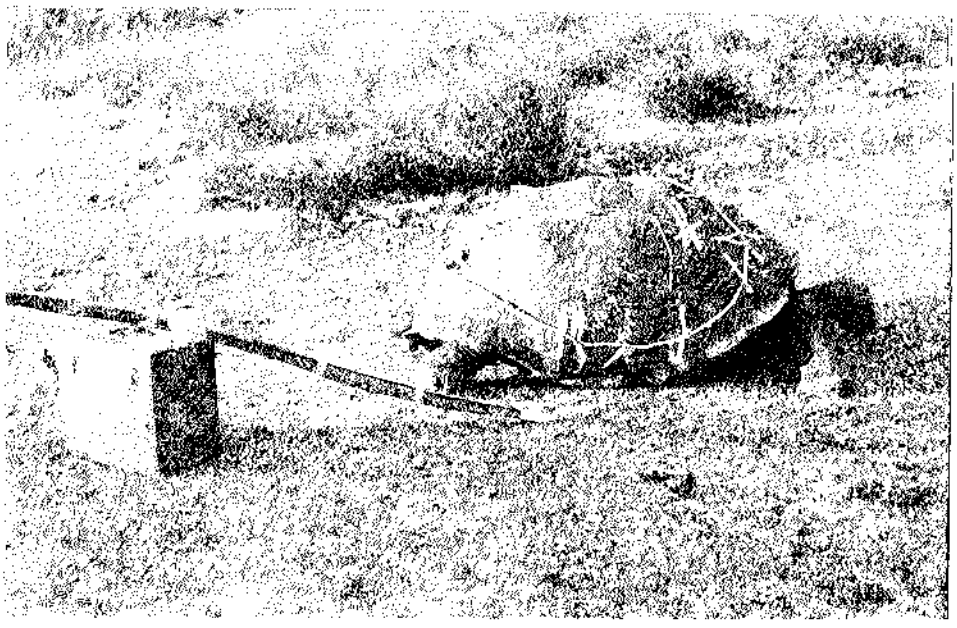
The most detailed investigation of the relationship between temperature and activity was conducted on eight tortoises. Two immatures, two adult females, one subadult male, and three adult males were studied, five in great detail (Table 9).

TABLE 9. Individual tortoises used for detailed temperature study

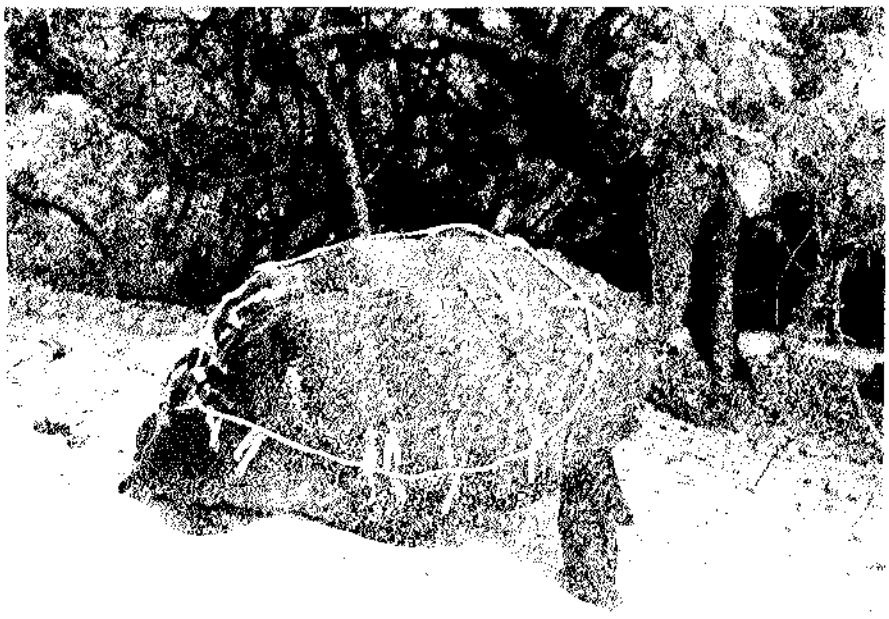
Animal's number	Sex	Age class	Weight (kg)	Length of carapace (cm) Straight	Length of carapace (cm) Curved	Period of observation
297	♂	Adult (senile?)	48	73·5	95·5	4 to 13 August 1969
99	♀	Adult	36	63·3	82·3	17 to 29 November
244	?	Imm.	12	41·2	54·8	10 to 25 February 1970
45	♂	Adult	@ 60	78·0	103·2	22 March to 3 April
T14	♂	Adult	77·5	89·0	113·5	16 April to 2 May

At least two temperature sensitive electrical resistors, "thermistors", were attached to each animal. One was cemented to the top of the carapace so that it varied with the shell's temperature. The other probe was fixed close to the first and covered with a small shield to shade it from the sun; it varied with the air temperature immediately around the animal. Occasionally additional air and surface probes were used and also probes were sometimes affixed to the skin or shaded areas of the carapace where the limbs protrude. A thermistor, fixed into a stainless steel tube, 4 mm in diameter, was attached to a pole. With this I could stand nearly two metres from the tortoise but still insert the probe into the soil or sand by the animal without disturbing it. If the animal was on solid rock with no soil nearby the probe was pushed into a tiny crevice or depression. Because the study was concentrated on the plain at Dune Jean Louis it was usually possible to insert the probe one to two cm into the soil without difficulty. The cables from all these thermistors fed into an automatic chart recorder (Grant Instrument Co.) which made a reading every half-hour, all things being well.

In addition, seven of the eight animals were each fed a radio pill. (See Mackay 1968 for details on these miniaturized radio transmitters.) The simplest way to induce the animals to swallow the pill was to wrap it in the leaf of a highly preferred species of food plant (e.g. Ficus or Guettarda). The pill transmitted a signal whose frequency varied in a direct linear relationship with temperature. This signal was picked up by an aerial that was attached to the animal, and then converted by a receiver to a response simply read off on a galvanometer as degrees Celsius. Figure 61 shows male T14 as he appeared during a recording session. Before recordings on each animal were started, all the probes and the pill to be used were calibrated. If possible the equipment was calibrated at the end of the study to check for any drift that might have occurred.



A



B

Figure 61. Electric tortoise.T14 as he appeared during the temperature recording sessions.

A. Grazing, the chart recorder is in the box and the galvinometer for internal body temperature is on top of the box.

B. Browsing Thespesia.

Each animal was studied for three to fourteen days. Obviously with long-term recordings made half-hourly on eight animals a large amount of information was gathered. A complete analysis will necessitate a considerable amount of computing, but this has not been practicable in the time available. For the present purposes it must suffice to describe the thermal characteristics of the tortoises' environment and the way in which the animals behave in relation to it, and the following description will be based on selected examples that are thought to be representative of the data as a whole.

Two days of temperature data for each of five tortoises are plotted in Figure 62 and summarised in Table 10.

General tendencies. The temperature curves are asymmetric; mornings are characterised by rapid acceleration in temperature, while gradual deceleration occurs in afternoons. This is evidently nothing more than a reflection of the daily temperature regime in which rapid heating takes place just after sunrise, and then gradual cooling begins in late afternoon (see Figure 14 in Farrow 1971).

One noticeable trend in nearly all days plotted is a sharp downward drop in environmental (i.e. air and substrate) temperatures when the tortoise moves from the open plains, or scrub, to underneath the shade of a tree. The opposite occurs when the animal commences activity in the afternoon, and moves back into direct sunlight. In simple terms, the tortoises occur in two habitats - in early morning and late afternoon they are in open plains and scrub, exposed to the sun; at midday they are in the shade of trees. Because of this the animals are experiencing two very different micro-environmental temperature regimes. Rather than staying in the open during the marked peak in daily temperature (see Figure 58), the tortoises change their micro-environment, moving into an area with a cooler temperature regime at midday.

The temperature at which there is a transition from one activity,

Figure 62. Temperature records of individual tortoises.

x = internal body
o = shell
⛰ = air
□ = substrate

The animal's activity and exposure to sunlight are indicated in the pie diagrams.

"Active" = intensive feeding
"Sleep" = sleeping
Intermediate position = moving and feeding, moving, or 'looking'.

Proportion of black in the circle = proportion of body that is heavily shaded.

Records for:

297 - 7th and 12th August 1969

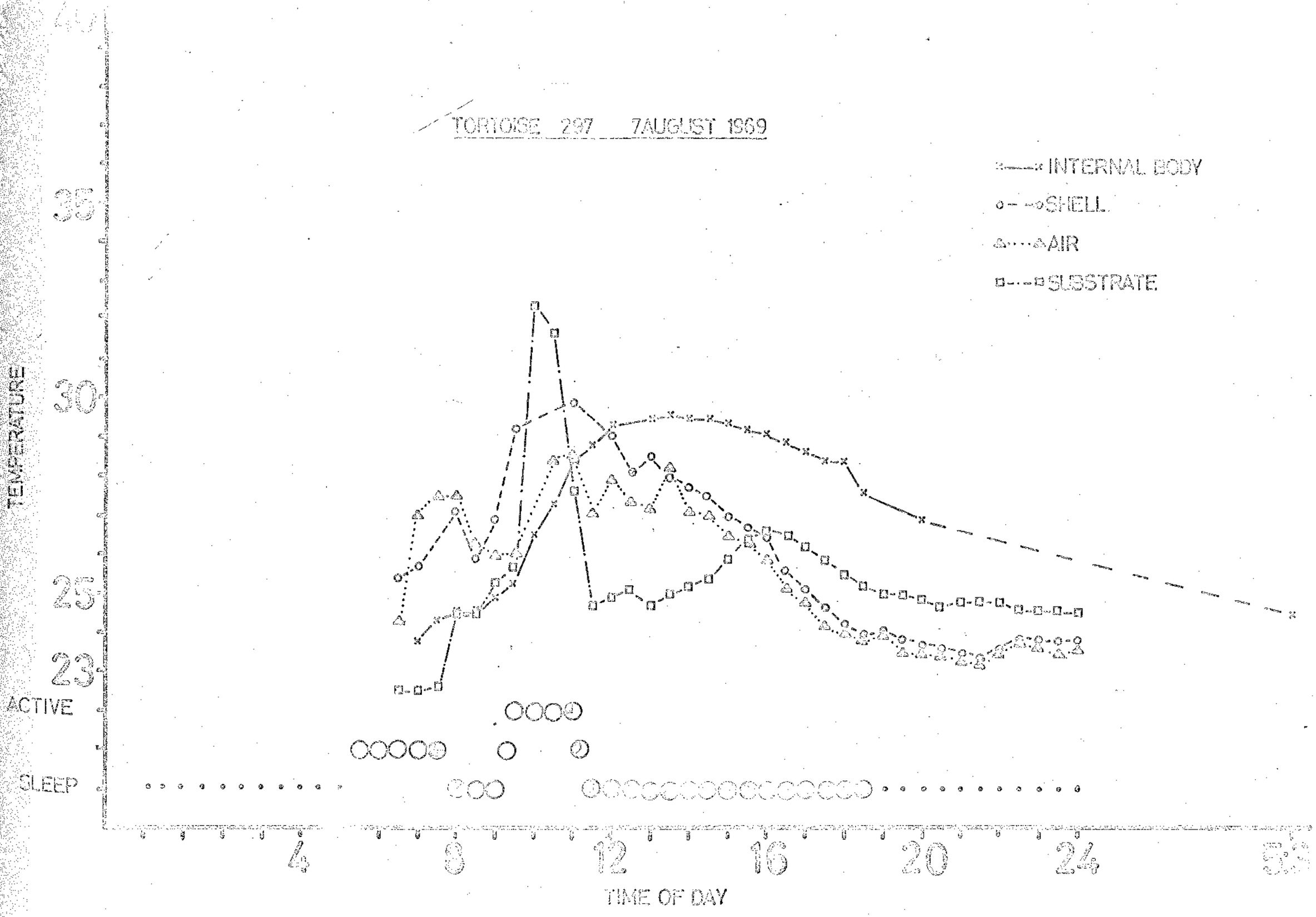
99 - 22nd and 24th November 1969

244 - 12th and 22nd February 1970

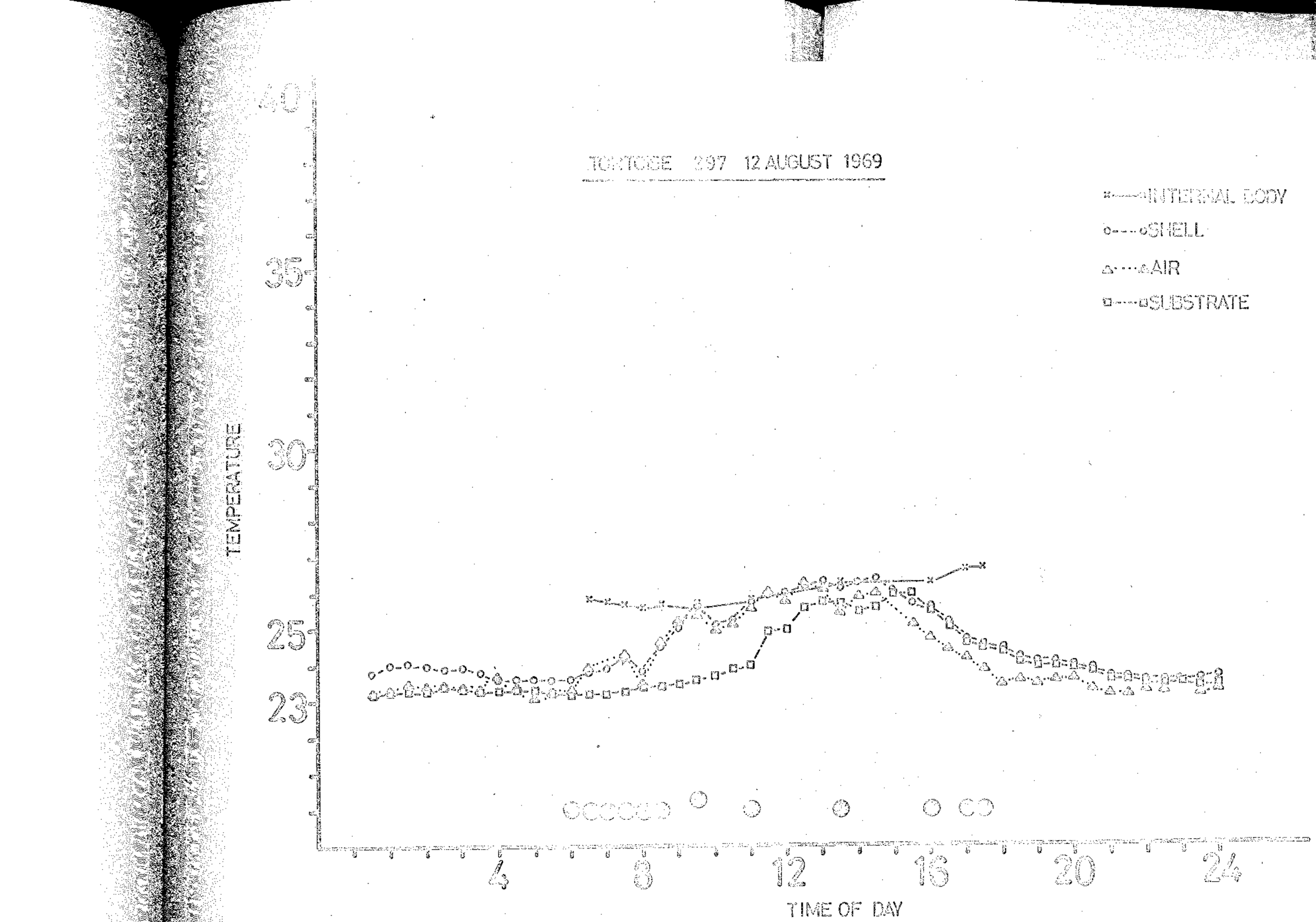
45 - 23rd and 29th March 1970

T 14 - 24th and 29th April 1970

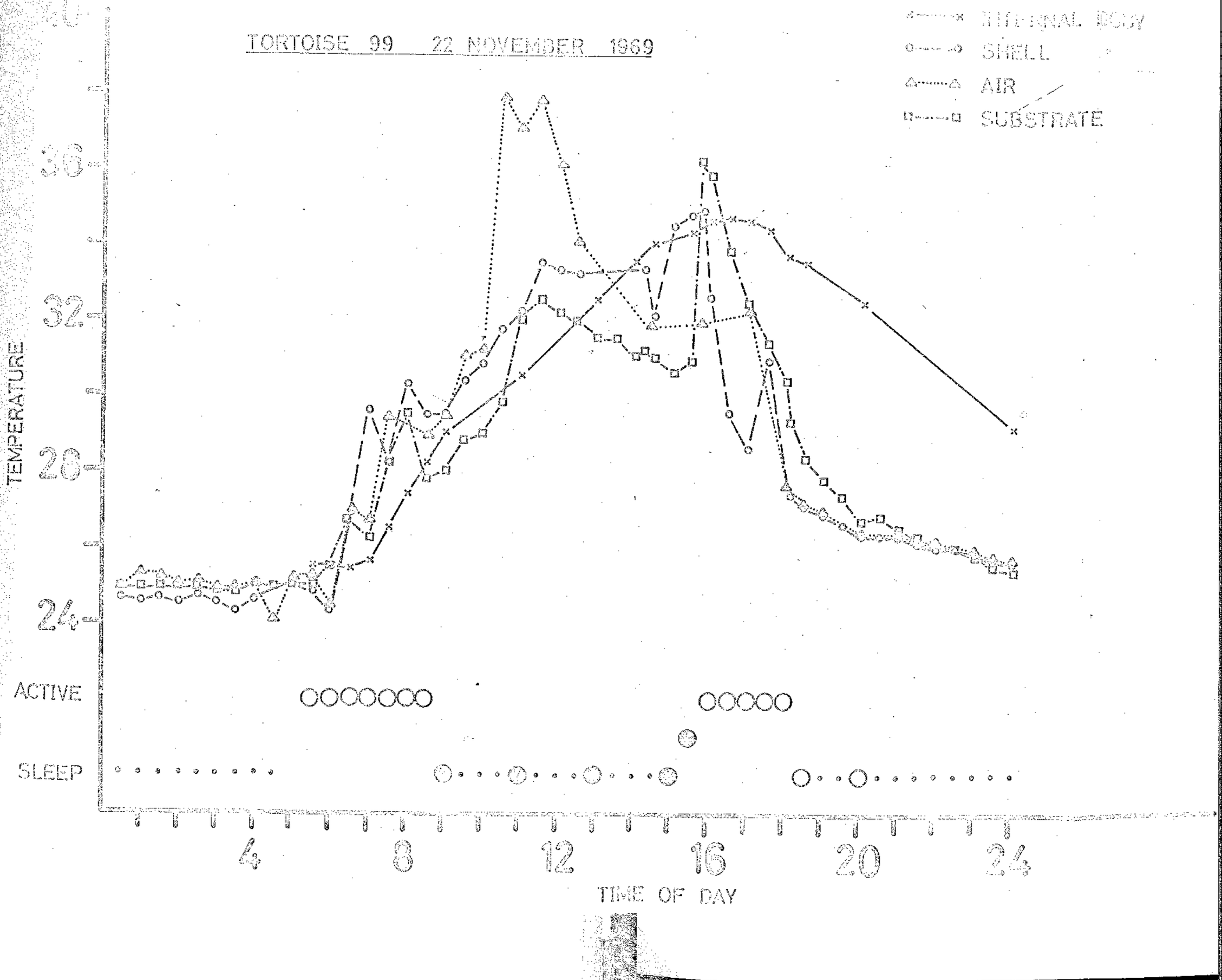
TORTOISE 297 7AUGUST 1969



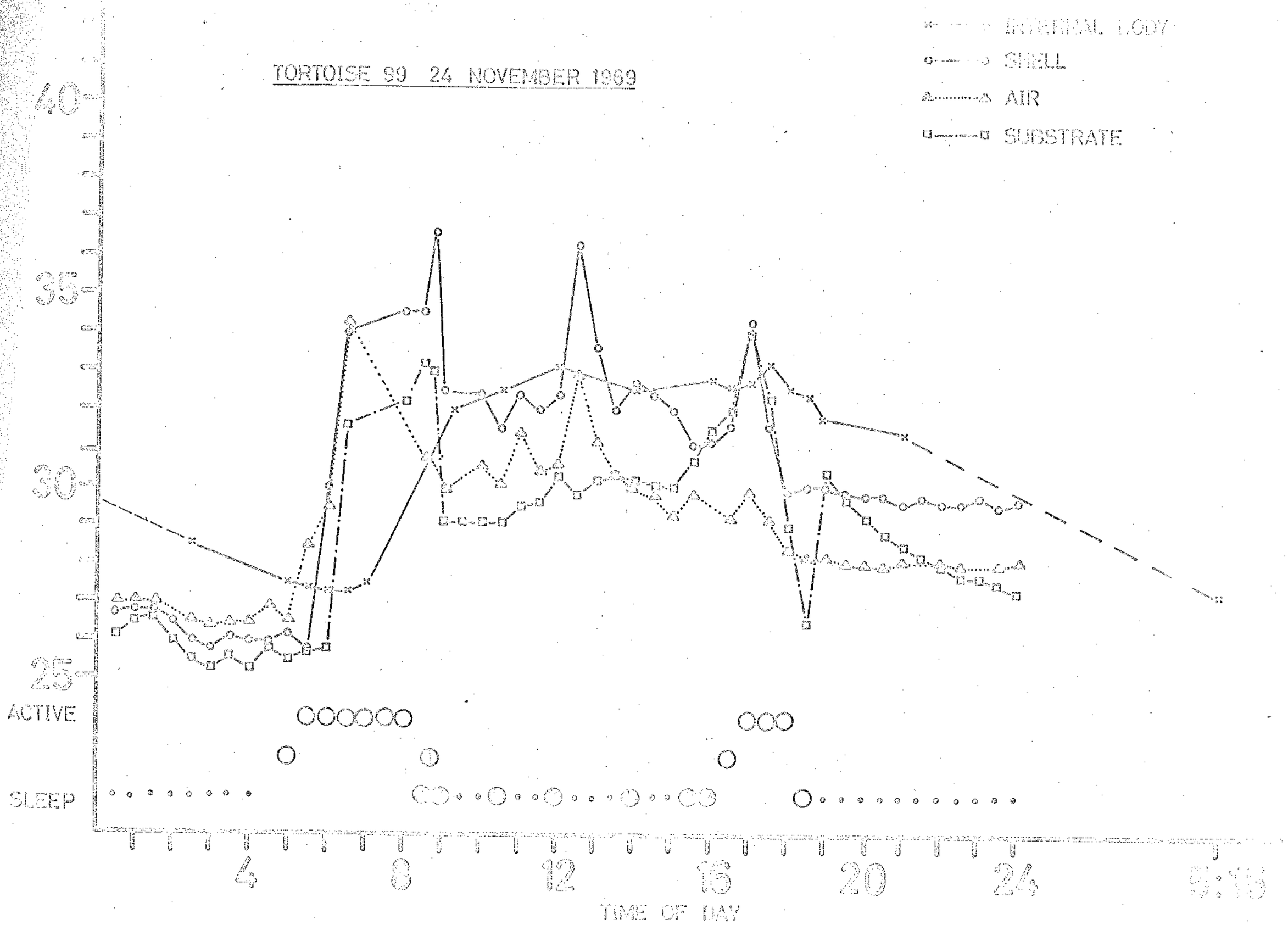
TORTOISE 297 12 AUGUST 1969



TORTOISE 99 22 NOVEMBER 1969



TORTOISE 99 24 NOVEMBER 1969



TORTOISE 244 12 FEBRUARY 1970



TORTOISE 3/4 22 FEBRUARY

SHELL
AIR
SUBSTRATE

TEMPERATURE

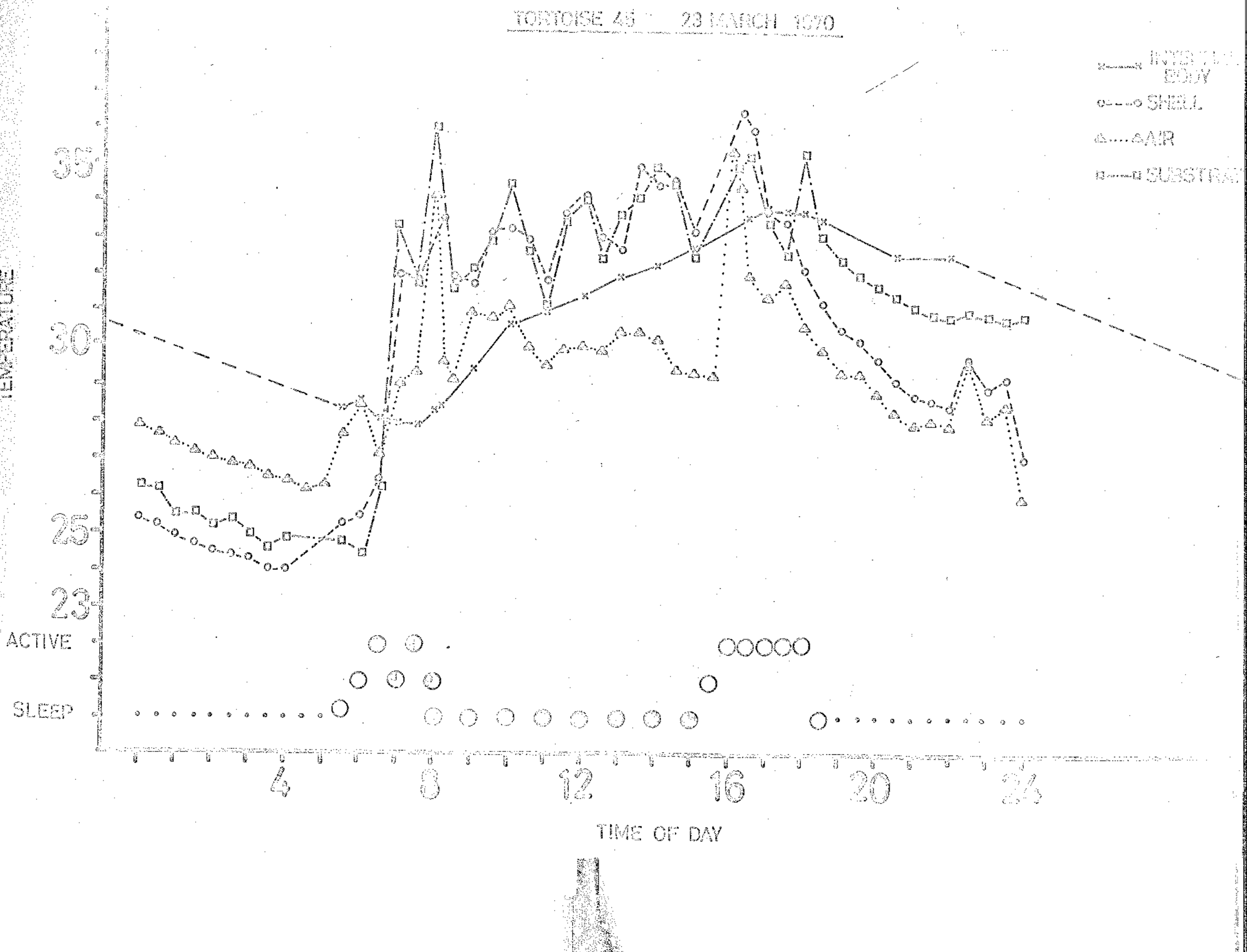
38
34
30
26
22

ACTIVE
SLEEP

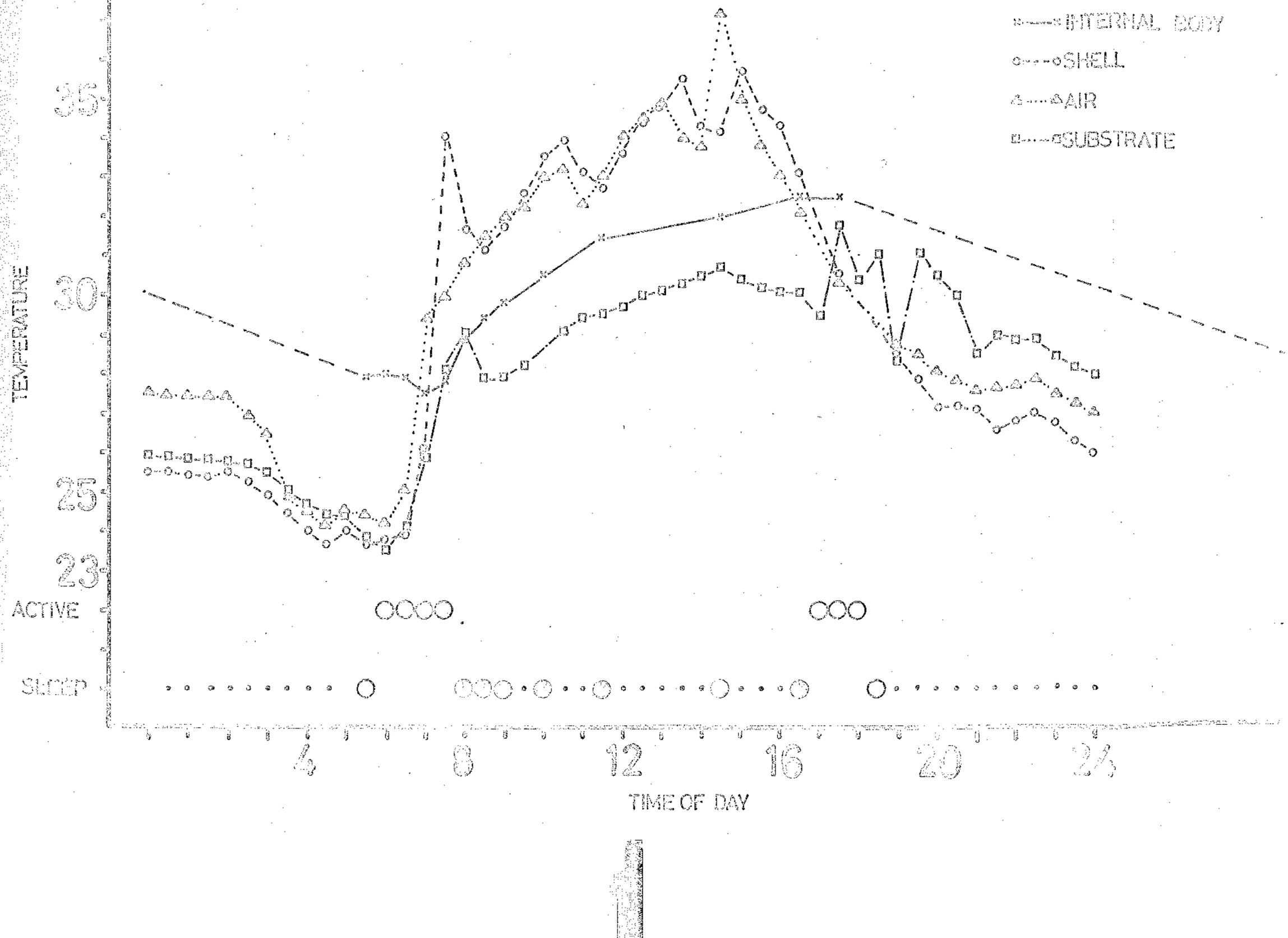
4 8 12 16 20 24

TIME OF DAY

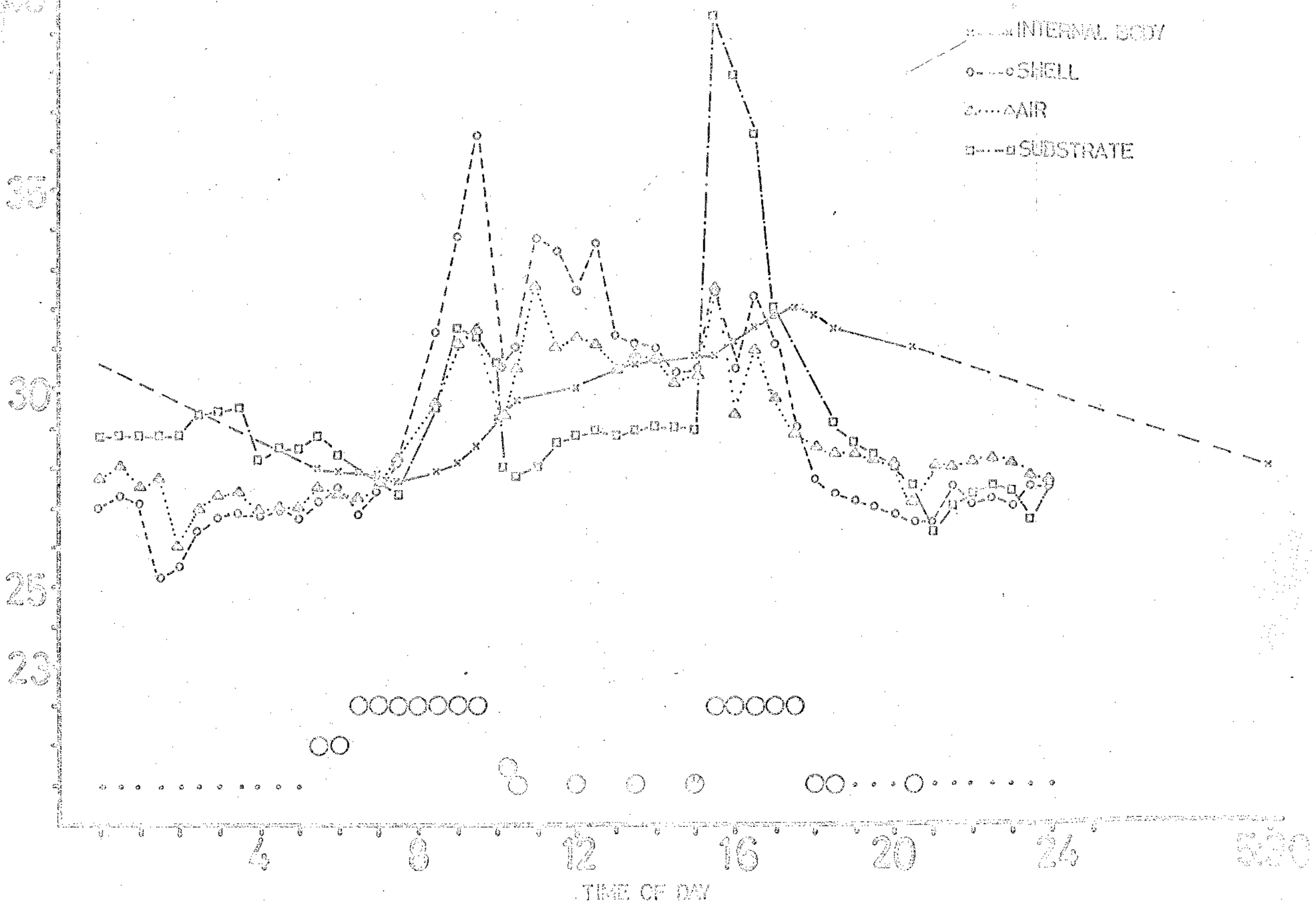
TORTOISE 45 23 MARCH 1970



TORTOISE 45 29 MARCH 1970



TORRODE TTS 24 APRIL 1970



TORTOISE TR 29/APRIL 1970

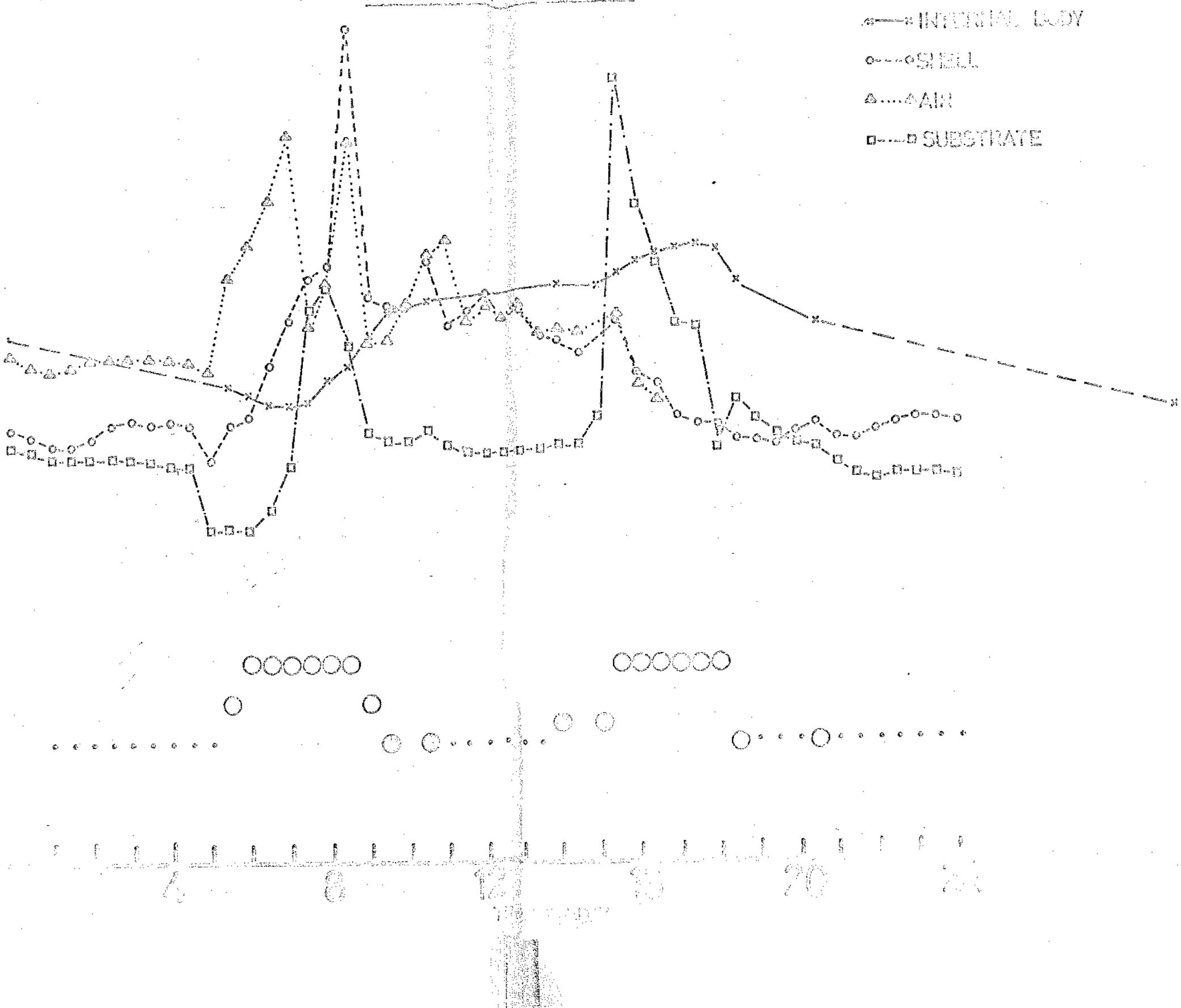


TABLE 10. Summary of temperature data from Figure 62. Times and temperatures of high and low values, daily ranges, and morning and afternoon change points for internal body, shell, air, and substrate temperatures

Tortoise	Date	Internal body temperature					Shell Temperature					Air Temperature					Substrate				
		Low temp. (time)	High temp. (time)	Range	Change point Morn. (time)	Aft. (time)	Low temp. (time)	High temp. (time)	Range	Change point Morn	Aft.	Low temp. (time)	High temp. (time)	Range	Change point Morn	Aft.	Low temp. (time)	High temp. (time)	Range	Change point Morn	Aft.
297	7 Aug.1969	23·8 (0700)	29·6 (1330)	5·8	28·4 (1700)		23·4 (2130)	29·9 (1100)	6·5	29·9		23·2 (2130)	28·6 (1100)	5·4	28·5		22·5 (0700)	32·4 (1000)	9·9	27·6	
297	12 Aug.	25·6 (0800-1000)	26·7 (1400-1600)	1·1			23·6 (0400)	26·4 (1430)	2·8			23·1 (0500)	26·3 (1230)	3·2			23·2 (0100-0700)	26·0 (1500)	2·8		
99	24 Nov.	27·3 (0600)	33·2 (1730)	5·9	29·5 (0800)	32·7 (1700)	25·8 (0530)	36·6 (0830)	10·8	34·5	34·3	26·4 (0300)	34·3 (0630)	7·9	31·6	29·9	25·3 (0300-0400)	34·0 (0830)	8·7	32·2	34·0
99	22 Nov.	25·4 (0630)	34·6 (1630)	9·2	28·2 (0800)	34·6 (1600)	24·3 (0600)	34·9 (1545)	10·6	29·5	32·6	24·0 (0430)	37·9 (1030)	13·9	28·9	32·0	24·9 (0430)	36·1 (1545)	11·2	27·8	35·8
244	12 Feb.1970	27·6 (0630)	33·7 (0900)	6·1	33·6 (0845)	32·8 (1600)	25·9 (0500)	35·6 (0815)	9·7	34	33·1	26·2 (0500)	33·8 (0815)	7·6	31·9	31·1	25·0 (0530)	31·3 (0845)	6·3	31·3	33·2
244	22 Feb.	27·5 (0600)	33·0 (1630)	5·5	30·7 (0800)	32·5 (1500)	24·9 (0500)	36·7 (1500)	11·8	29·4	36·7	25·0 (0500)	32·8 (1030)	7·8	28·5	31·9	25·6 (0700)	31·9 (1000)	6·3	28·8	29·3
45	23 Mar.	28·0 (0700)	33·8 (1700)	5·8	28·0 (0730)	33·3 (1600)	24 (0400)	36·5 (1600)	12·5	31·8	35·8	26·2 (0430)	35·4 (1600)	9·2	29·4	35·4	24·5 (0600)	36·0 (0800)	11·5	31·8	34·6
45	29 Mar.	27·5 (0700)	32·5 (1700)	5	27·8 (0730)	32·5	23·6 (0430)	34·7 (1500)	11·1	34·0	31·7	24·2 (0600)	37·2 (1430)	3·0	30·0	31·2	23·5 (0600)	31·8 (1730)	8·3	28·1	29·5
T14	24 Apr.	27·6 (0730)	32·0 (1730)	4·4	28·5 (0930)	30·8 (1530)	25·2 (0130)	36·4 (0930)	11·2	36·4	32·5	26·0 (0200)	32·5 (1100-1530)	6·5	31·5	32·5	26·3 (2100)	39·4 (1530)	13·1	31·3	39·4
T14	29 Apr.	28·5 (0700)	32·5 (1730)	4	29·5 (0830)	31·8 (1530)	27·1 (0500)	38·0 (0830)	10·9	38·0	30·6	28·6 (1630)	35·3 (0700)	6·7	35·1	30·7	25·4 (0500-0600)	37·7 (1530)	12·3	30·0	36·7

or micro-habitat, to another could be called the "change point". In the morning it is the temperature at which the tortoise leaves the plain; in the afternoon it is the temperature at which the animal comes on to the plain. In effect, this means the last temperature recorded before the animal leaves the plain (or open scrub) and the first temperature recorded after it returns to the plain (or open scrub). The change point, as a rule, is lower in mornings than it is in afternoons. Stated another way, when the temperature is rising the tortoise has a change point that is lower than when the temperature is falling. The morning change point for air temperature varies between 28·5°C and 31·9°C, with one extreme reading at 35·1°C (Table 10). The afternoon change point ranges from 29·9°C to 32·5°C with one extreme point at 35·4°C. In six out of eight instances the morning value is lower than that in the afternoon. For substrate the morning change point varies from 27·6°C to 32·2°C while the afternoon point ranges from 29·3°C to 39·4°C. In all eight instances the afternoon value is higher than the morning value.

There are occasionally instances when the tortoises remain in one micro-environment. On 12 August, tortoise 297 stayed all day in the shade of a tree, and did not once venture out onto the plain. Temperature records from this day are cooler, and have less fluctuation, than any other day plotted in Figure 62. On cloudy days the animals stay on the plain for longer than they do on clear days; and occasionally, as in July (Figure 60), they may stay out all day. On these cloudy days environmental temperatures are generally low. The change point, or threshold, at which activity in the open ceases is not reached; and, furthermore, there is little difference between the temperature regime on the open plains and that under shade trees (cf. Figure 59 with 62).

Individual differences. Certain details of micro-habitat and individual tortoises are revealed by the curves in Figure 62. The

smaller animals, 244 and 99, show very rapid rates of change for core temperatures. On 12 February 244's body temperature rose nearly 6°C in ninety minutes, from 27·8°C to 33·5°C. The body temperature of female 99 rose 4·5°C from 27·5°C to 32°C on 24 November; this also took ninety minutes. The two large males, 45 and T14, had very gradual changes in body temperature, although they show transient increases on exposure to bright sun and high temperatures. This acceleration is most pronounced near the change point. The difference between the immature and female on one hand, and the two males on the other, is not obviously due to a major difference in temperatures experienced by these animals. Quite the contrary, the males appear to have encountered greater environmental heat than did either the female or the immature (Table 10), but the males still had lower body temperatures.

In all the curves of Figure 62 the internal body temperature shows an obvious lag behind external and environmental temperatures, and the degree of lag varies from one animal to another. On 12 August when 297 was totally inactive, his body temperature began rising three to four hours after the midday peak in environmental temperatures. Tortoise 244 lagged only about an hour behind the environment, and male T14 lagged some five hours before his peak body temperature caught up to environmental temperatures. In afternoons this lag effect is also evident, except that there is an inversion, and the core temperatures are now above the other temperatures. The core temperature of tortoise 297 lags some six to ten hours and is 2 to 5°C above environmental temperatures. Female 99 was similar. Tortoise 244 had lags of at least seven hours, but its body temperature was only 2 to 3°C above environmental. Male 45 showed lags in cooling of about nine hours, with his body temperature 3°C above the environment; and male T14 had lags of a similar magnitude, although his substrate temperatures were several degrees cooler.

These results show that large tortoises heat up, but also cool

off, more slowly than do small tortoises. This is consistent with Newton's law of cooling in which heat transfer is a function of surface area divided by the mass of the body (and also proportional to the difference between the temperatures of the body and its environment) (Spanner 1964). Large tortoises have smaller surface to volume ratios, and hence a slower rate of heat transfer. The distinct thermal lags, and the strong relationship between body temperature and environmental temperature, rather than body temperature and state of activity, are good indications that these animals are passive to environmental heating and cooling processes.

This conclusion may sound obvious because tortoises, being poikilotherms, are dependent on their environment for heating and cooling. However, Mackay (1964) suggested that there was some form of active heat transfer mechanism in Galapagos tortoises. My data do not support this, nor can I see how active heat transfer could be effected in these animals, for they have a poorly vascularized dorsum with a large amount of dead bone. Furthermore, Benedict (1932) showed that the metabolic heat produced by large tortoises was minimal; he never recorded production greater than five cal./kg body weight / 24 hours.

It is more exact to state that the tortoises are thermally passive to the micro-environment rather than to the environment as a whole, for they can (and do) change from one micro-environment to another. The importance of this change, in terms of temperature regulation, can be seen by comparing the potential temperatures (Figure 58) with those actually experienced by the tortoises (Figure 62). By moving into shade, the tortoises, while still dependent on the temperatures around them, are at least able to select a cooler place in which to rest. However, just because they are in the shade does not necessarily mean that they are in a particularly cool microhabitat. A midday sleeping position may be adequately shaded from the sun, but it may be fully open to environmental reradiation, which can be quite intense at midday on Aldabra.

On 22 November female 99 went to shelter at midday under a small Scaevola bush instead of a dense Pemphis bush which she usually visited. The Scaevola bush, although affording shade from direct sunlight, was very open, and she was fully exposed to environmental reradiation over an arc of about 120°. There is a marked difference between the temperature plots of this female on 24 and 22 November. On 24th, her temperatures, as well as the environmental temperatures, drop or remain relatively stable at midday. In comparison, there is a steady rise in temperature after she moved into the shade of the Scaevola on 22nd.

The same effect can be seen in immature 244. Its body and environmental temperatures all decreased as the animal moved into dense shade at midday of 12 February, and these temperatures stayed stable with very little increase over the six hour rest period. Ten days later, at midday, the animal chose to rest, first in a fully exposed pool of water, and then underneath a sparsely leafed Colubrina. The tortoise's body temperature rose more than two degrees over the seven hours of rest and other temperatures were relatively much higher than on 12 February.

The trees that the large males sheltered under were often tall and without lower limbs so that there was little protection from reradiation. These animals show a continual, but gradual, increase in body temperature during the midday rest period, but it is not possible to say whether this is due to thermal lag or heat input from reradiation - probably both are involved.

On 29 March, male 45 was under a large Tournefortia on top of the dune, but eight days after the Ides he was under a small Pemphis bush in the scrub. Although the large tree was very open it had low-lying branches with large dense-growing leaves. These afforded shelter from solar and environmental radiation, for the leaves came right down to the ground. The substrate was sand which could be dug into; and,

in general, this tree offered a cool midday retreat. (It was for this reason that I camped here in 1968.) The small Pemphis bush in the scrub, on the other hand, did not afford much cover at ground level, although it provided adequate protection from the sun. Under the small Pemphis bush body temperature rose to a higher peak (33·4°C) and substrate temperatures stayed fairly high. Under the Tournefortia, body temperature did not rise as high (32·5°C) and substrate temperatures stayed low. However, air temperatures were cooler under the Pemphis.

The data on large male T14 also fit this pattern. On 24 April he was under a small Tournefortia with few low-growing leaves. On the 29th he was under the same large Tournefortia on top of the dune as was 45 the month before. The environment under the small tree was much warmer, and the animal's body temperature was much less stable.

These examples illustrate the importance of micro-habitat selection. Not only must the tortoise move from an unshaded to a shaded position, but the shade must be sufficient to shield the animal from environmental as well as solar radiation.

Thermoregulatory behaviours

Besides changing habitats there are several other overt behaviours that a tortoise can use to effect thermoregulation. The animals often dig into the first few cm of soil when they are resting in the shade. This is so common that no trees commonly used for shade have grass growing underneath them. Instead there is an area of disturbed soil ringing the tree to a distance where the canopy no longer offers shade. The lack of grass is not due to some limiting effect of the shade; on the contrary, Sporobolus thrives if protected from direct sunlight. My fly sheet covered an area of Sporobolus grassland, and the grass thus sheltered grew lush despite the lack of rain. A shaded area just outside my fly sheet where tortoises could rest at midday was dug up within weeks of the animals

discovering the shade. This apparently destructive behaviour allows the animals to come into contact with the cool, moist soil that lies under the surface. (See Figure 24 for a plot of soil temperatures at various depths.) As soon as a tortoise settles under a shade tree it begins digging in. This is done by laying the dosal surface of the front leg on the soil and thrusting backwards. With the pes acting like a shovel, the substrate is pushed back against the tortoise's shell. At the same time the hind legs thrust alternately causing the animal to turn back and forth almost screwing its way into the substrate. If the animal does a great deal of digging it may lower itself five to ten cm below the original surface of the soil.

The functional significance of this is easily seen by examining the diurnal variation in soil temperatures; the results from two typical days are shown in Figure 63. In both cases soil near the surface (2 cm deep) heats up to about 35°C at midday. Soil 5 cm below the surface stays about 2°C cooler than the surface soil during the midday period (but from late afternoon to early morning there is an inversion, and soil at 5 cm is warmer than that at 2 cm). Soil 17 cm deep may be as much as 7°C cooler than soil at the surface. Obviously, by digging into the soil at midday, the tortoise comes in contact with a cooler substrate than is available at the surface.

Bathing is another behaviour with important thermoregulatory implications. It is not common along the south coast, for there are few large pools. However, there are a large number of fresh-water pools in the south east, and nearly every one is provided with bathing tortoises. One pool, with an area of no more than 400 sq. m, had nearly 100 animals. Often a bathing tortoise will submerge into the water, head and all, with only the very top of the carapace exposed to the air. Body temperatures of animals in this condition will soon equilibrate with the water temperature. I have no detailed data on this but a few spot checks, from several different pools,

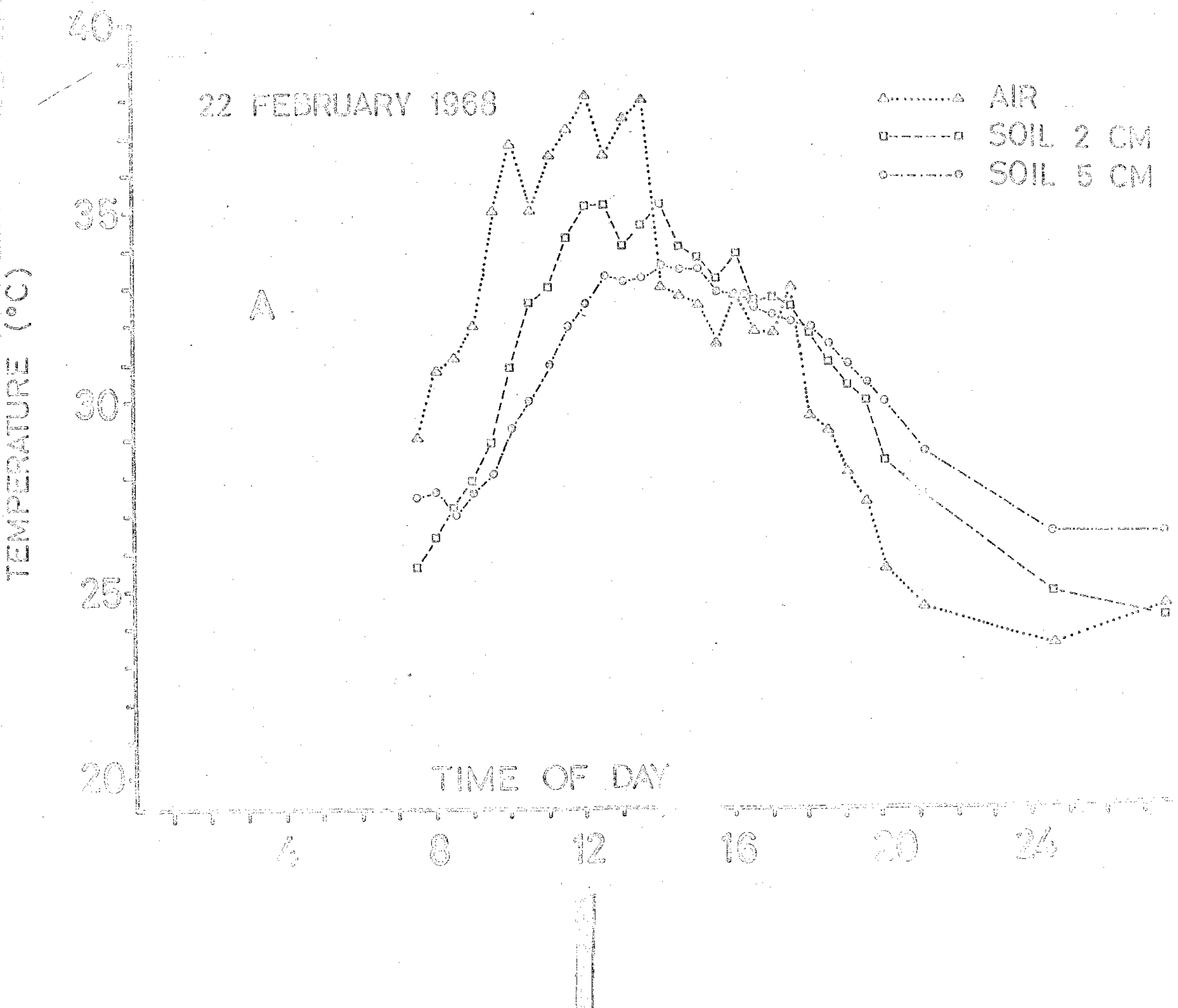
Figure 63. Diurnal variation in air and soil temperatures, recorded at the top of Dune Jean Louis.

A. 22nd February 1968

B. 27th February 1968

22 FEBRUARY 1968

A



27 FEBRUARY 1969

B

AIR
SOIL 2 CM
SOIL 5 CM
SOIL 17 CM

TEMPERATURE (°C)

40
35
30
25
20

TIME OF DAY

4
8
12
16
20
24

yielded water temperatures of 28·4, 29·4, and 40·0°C.

Orientation of grazing tortoises

One very striking feature about a herd of grazing tortoises is that most of the animals face away from the sun. In the morning they face west, in the afternoon, east. As this breaks down on cloudy days, when there is no apparent orientation in the herd, I surmised that orientation was related to thermoregulation. In order to test this hypothesis I counted the total number of tortoises active on the east plain (see grassland counts), and tallied the numbers of animals facing toward and facing away from the sun. If the anterior of the body pointed to within 90° of the sun the animal was classed as facing the sun; if the posterior of the body pointed to within 90° of the sun, the animal was classed as facing away from the sun. Those animals not classed as facing either towards or away, were classed as facing sideways to the sun (Figure 64). Table 11 shows that in sixty-eight such counts, significantly more tortoises face away from the sun than face into it.

TABLE 11. Analysis of observations on the orientation of tortoises grazing on the east plain of Dune Jean Louis

A.	Number of observations	68
B.	Total number of animals tallied (facing either toward or away from the sun)	1256
C.	Average number of animals / observation (= B/A)	18·5
D.	Number of animals tallied as facing the sun	373
E.	% of total number tallied facing the sun (= D/B)	29·7
F.	Average number facing the sun / observation (= D/A)	5·5
G.	1 by 2 Chi squared (D, B-D, B/2, B/2)	207·
H.	Probability that: the number facing the sun = the number facing away	< 0.001

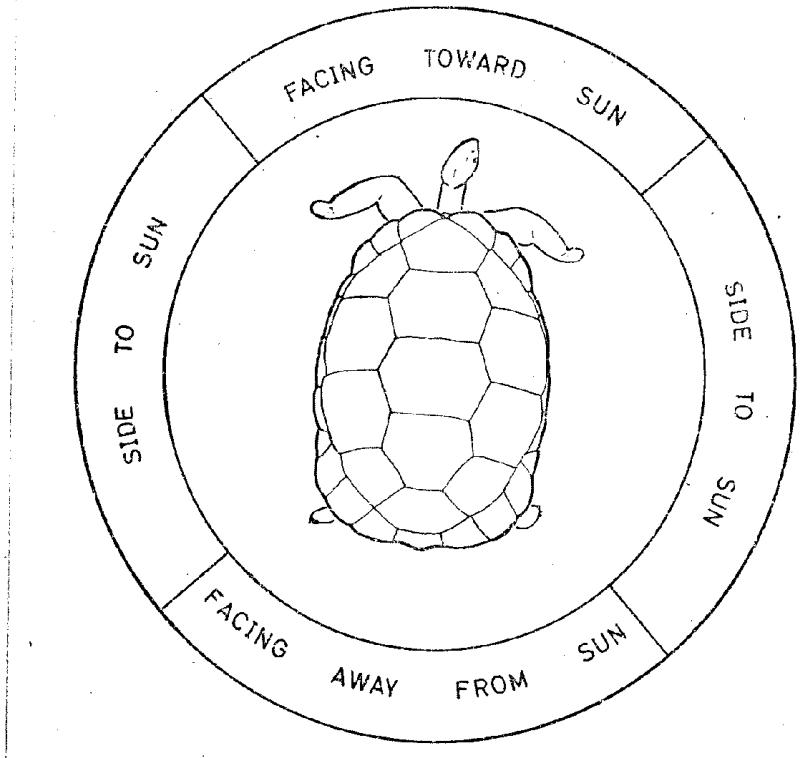


Figure 64. Orientation headings of a grazing tortoise. The sector of the circle in which the sun falls indicates the animal's heading.

Analysis of each of the sixty-eight individual observations gives results fully consistent with the grouped data in Table 11. In sixty of the counts the number facing the sun was less than the number facing away (i.e. in only 11·8% was the general trend reversed; the probability that the ratio 60 : 8 represents a chance departure from 50 : 50 is 0·00001 (binomial test)). A binomial test on the facing away - facing toward ratio for each of the sixty counts reaches significance (i.e. $p \leqslant 0{\cdot}05$) in 39 counts (57% of the total); the failure for more individual counts to reach significance is probably due to small sample sizes of the individual counts.

There is little doubt that more tortoises face away from the sun than face into it, and it is of interest to know what stimulus parameters are related to this orientation response (see Hinde 1970, p. 192). With this goal in mind multiple regression analysis was carried out.

Multiple regression analysis. Three different orientation headings were used as dependent variables: the percent of all animals active that 1) face toward the sun, 2) face away from the sun, and 3) face sideways to the sun. The sum of 1, 2, and 3 is obviously 100%. Five independent variables were used to predict, or "explain", the dependent variable (Tables 12, 13, and 14). Measures of wind speed or direction were not included in any of the regressions, for it was found that they varied too much to have any meaningful relationship with orientation.

Because of inconsistencies in the sampling, some parameters were not measured for all of the 68 counts; for example, temperature was not always recorded. Consequently, the data were divided into various sub-blocks depending on which independent variables were available. This means that as the number of independent variables being tested increases, the sample size decreases. The reason for treating so many different permutations of the data is that the

Explanation for Tables 12, 13, and 14

t values for independent variables:

Time = time of day when observations were made;

Total No. Active = total number of tortoises active on the east plain;

Air Temp. = temperature of the air:
1968 - unshaded and at the top of Dune Jean Louis,
1969 - shaded and at tortoise height on east plain;

Cloud cover = total cloud cover in eights ("oktas");

Month = dummy variable where Dec. & Jan. = 1, Nov. & Feb. = 2, Oct. & March = 3, and Sept. & April = 4.

The t values indicate whether or not the partial regression coefficient for the independent variable is significantly different from 0, i.e. whether there is a regression effect with this variable. "*" = $p \leq 0.05$; "**" = $p \leq 0.01$; "***" = $p \leq 0.001$.

d.f. = Degrees of freedom.

F = Variance ratio for regression sum of squares and residual sum of squares. This indicates whether or not the regression equation accounts for a significant amount of the variation in the dependent variable. "*" = $p \leq 0.05$; "**" = $p \leq 0.01$; "***" = $p \leq 0.001$.

$100xR^2$ = Multiple correlation coefficient times 100, which represents the proportion of variation that is explained by the regression equation.

St.Er. = Standard error of the multiple regression equation.

resid. $\propto$ y = Residual from the multiple regression equation is proportional to the dependent variable? if it is then the variation in the dependent variable can be further explained by other independent variable(s) not included in the analysis;

"++!" = very strong relationship; "++" = strong relationship; "+" = relationship evident but weak; "0" = no apparent relationship.

The data are presented in eight different blocks; "n" = the number of observations for a block of data.

TABLE 12. Results of multiple regression analysis using the per cent of the total number of tortoises active on east plain that face sideways to the sun as the dependent variable

INDEPENDENT Variables									
Time	Total No. Active	Air Temp.	Cloud Cover	Month (Dummy)	d.f.	F	100xR^2	St.Er.	resid. ∝ y
All data n = 68									
0·66	1·42			0·89	3,64	1·43	6	·19	++!
	1·5			0·84	2,65	1·94	6	·19	++!
	1·78				1,66	3·18	5	·19	++!
All mornings n = 39									
1·13	1·92			0·4	3,35	1·28	10	·18	+
1·10	1·91				2,36	1·88	9	·18	++!
	1·59				1,37	2·54	6	·18	++!
Mornings 1968 n=16									
1·4	0·72	1·32			3,12	1·42	26	·19	+
	0·37	1·14			2,13	1·08	14	·20	+
		1·46			1,14	2·15	13	·19	+
Mornings 1969 n = 17									
2·06	0·43	2·41*	1·29	3·21**	5,11	2·29	51	·15	0
2·57*		2·6 *	1·54	3·31**	4,12	3·02	50	·14	+
2·04		2·09		2·88*	3,13	2·93	40	·15	+
		0·5		1·9	2,14	1·88	21	·16	+
				1·9	1,15	3·69	20	·16	+
All afternoons n = 26									
0·99	0·008			0·55	3,22	1·19	14	·20	+
1·11				0·57	2,23	1·87	14	·20	+
1·88					1,24	3·52	13	·20	+
Afternoons 1968 n = 9									
0·26	1·01	0·56		0·48	4,4	1·17	54	·24	+
	1·12	0·54		0·46	3,5	1·89	53	·22	+
	1·28	0·62			2,6	3·15	51	·20	+
	2·55*				1,7	6·48*	44	·19	+ (A)
Afternoons 1969 n = 14									
2·0	0·44	2·25		0·2	4,9	1·61	42	·15	+
2·13	0·43	2·52*			3,10	2·36	41	·14	+
2·55*		2·65*			2,11	3·73	40	·13	+
		0·81			1,12	0·65	5	·16	++
Afternoons 1969 n = 9									
0·03	2·21	0·47	2·45	0·52	5,3	1·87	76	·13	+
	2·59	1·44	2·88*	0·86	4,4	3·11	76	·12	+
	2·84*	1·33	3·09*		3,5	4·11	71	·11	+
	2·77*		3·03*		2,6	4·7	61	·12	+
			0·94		1,7	0·89	11	·17	+

(A) $y = -12·05 + (1·41)$ (total no. active) (non linear).

TABLE 13. Results of multiple regression analysis using the per cent of total number of tortoises active on east plain that face toward the sun as the dependent variable

INDEPENDENT Variables									
Time	Total No. Active	Air Temp.	Cloud Cover	Month (Dummy)	d.f.	F	$100xR^2$	St. Er.	resid. ∝ y
All data	**n = 68**								
-2·09*	0·43			1·84	3,64	2·81*	12	·12	++!
-2·16*				1·80	2,65	4·18*	11	·12	++!
-2·23*					1,66	4·95*	7	·13	++!(A)
All mornings	**n = 39**								
-7·28***	-4·10***			1·29	3,35	20·16***	63	·07	+
-7·53***	-4·66***				2,36	28·89***	62	·08	+ (B)
-4·81***					1,37	23·15***	38	·09	++
Mornings February 1968		**n = 16**							
-0·99	-0·51	-0·87			3,12	1·96	33	·08	++
-0·99		-0·76			2,13	2·97	31	·08	++
-2·35*					1,14	5·53*	28	·08	++ (C)
		-2·23*			1,14	4·97*	26	·08	++ (D)
Mornings 1969		**n = 17**							
1·25	0·23	2·04	0·61	0·85	5,11	2·23	50	·14	+
1·33		2·12	0·74	0·9	4,12	3·02	50	·14	+
1·77		2·61*		1·13	3,13	3·98*	48	·13	+
1·46		3·11**			2,14	5·22*	43	·13	+
		2·78*			1,15	7·72*	34	·14	+ (E)
All afternoons		**n = 26**							
0·13	0·57			0·64	3,22	0·50	6	·11	+
0·41				0·55	2,23	0·61	5	·10	++
				1·04	1,24	1·08	4	·10	++
Afternoons 1968		**n = 9**							
0·31	0·17	0·43		0·17	4,4	0·15	13	·13	++
0·51		0·45		0·15	3,5	0·24	12	·12	++
0·91		0·61			2,6	0·41	12	·11	+
0·71					1,7	0·50	7	·10	+
Afternoons 1969		**n = 14**							
0·95	0·65	1·16		0·34	4,9	0·42	16	·13	+
0·96	0·62	1·17			3,10	0·57	15	·12	+
0·81		1·16			2,11	0·71	11	·12	+
		0·88			1,12	0·78	6	·12	+
Afternoons 1969		**n = 9**							
1·29	1·14	1·99	1·54	1·56	5,3	1·7	73·9	·09	+
1·43		1·81	1·28	1·79	4,4	1·7	62·6	·10	+
1·49		1·80		1·74	3,5	1·49	47·3	·11	
		1·35		0·87	2,6	0·94	24	·12	
		1·08			1,7	1·17	14	·11	+

(A) $y = 26·74 - (0·013)$ (time).

(B) $y = 135·848 - (0·446)$ (total no. active) $- (0·237)$ (time).

(C) $y = 60·01 - (0·101)$ (time).

(D) $y = 88·435 - (2·47)$ (temp.).

(E) $y = 103·56 - (2·59)$ (temp.).

TABLE 14. Results of multiple regression analysis using the per cent of total number of tortoises active on east plain that face away from the sun as the dependent variable

INDEPENDENT Variables									
Time	Total No. Active	Air Temp.	Cloud Cover	Month (Dummy)	d.f.	F	$100xR^2$	St. Er.	resid. ∝ y
All data n = 68									
2·08*	-1·32			0·16	3,64	2·29	10	·19	++!
2·09*	-1·43				2,65	3·48	10	·19	++!
2·20*					1,66	4·83	7	·19	++! (A)
All mornings n = 39									
2·59*	0·31			-0·54	3,35	3·95*	25	·16	++!
3·45**				-0·68	2,36	6·03**	25	·16	++!
3·43**					1,37	11·78**	24	·16	++! (B)
Mornings 1968 n = 16									
0·50	0·62	1·80			3,12	2·28	36	·14	++
	0·37	1·94			2,13	3·50	35	·14	++
		2·70*			1,14	7·30*	34	·13	++ (C)
Mornings 1969 n = 17									
0·83	0·64	0·43	1·84	2·34*	5,11	4·19*	66	15	+
1·00	0·74		1·88	3·79*	4,12	5·57**	65	14	+
1·91			2·18*	3·82**	3,13	7·51**	63	14	+ (D)
			1·80	3·21**	2,14	7·94**	53	15	+
				3·32**	1,15	11·00**	42	17	+ (E)
		2·45*			1,15	6·00*	29	28	+ (F)
All afternoons n = 26									
1·00	0·29			0·84	3,22	1·81	20	21	+
1·25				0·82	2,23	2·79	20	21	+
2·23*					1,24	4·98*	17	21	+ (G)
Afternoons 1968 n = 9									
0·12	1·44	0·19		0·75	4,4	2·41	71	18	+
	1·78	0·47		1·04	3,5	3·99	71	16	0
	3·14*			1·15	2,6	6·76*	69	15	0
	3·41*				1,7	11·6 *	62	16	0 (H)
Afternoons 1969 n = 14									
0·74	0·64	0·78		0·319	4,9	0·4	15	23	+
0·81	0·62	0·95			3,10	0·54	14	22	+
1·15		1·01			2,11	0·66	11	21	+
0·55					1,12	0·30	2	21	+
Afternoons 1969 n = 9									
0·83	2·62	1·65	3·08	1·42	5,3	2·93	83	15	0
	2·90	2·55	3·42*	1·26	4,4	3·78	79	15	0
	2·97*	2·22	3·42*		3,5	4·05	71	16	0
	1·54		2·07		2,6	2·17	42	20	0
			1·28		1,7	1·64	19	22	0

(A) $y = 43·94 + (0·019)$ (time).

(B) $y = -16·05 + (0·16)$ (time).

(C) $y = -97·19 + (5·08)$ (temp.).

(D) $y = 114·74 + 0·077$ (time) $- 4·648$ (cloud) $- 17·837$ (month).

(E) $y = 129· - (17·5)$ (month).

(F) $y = -34·377 - 3·02$ (temp.).

(G) $y = 214·37 - (0·154)$ (time).

(H) $y = 99·369 - (1·534)$ (total no. active).

regressions are more meaningful with large sample sizes, but in order to examine as many independent variables as possible the sample size has to be greatly decreased.

Table 12 shows the results of the analysis for the numbers facing sideways to the sun. Only one regression is statistically significant, the percent facing sideways to the sun on the total number of animals active for afternoons, 1968. I have no simple explanation for this result and fail to see any biological significance in it. The lack of any other statistically significant regressions (especially using the same variables which were tested in eight different blocks of data) is a strong indication that the proportion of animals that are sideways to the sun does not change in any regular way in relation to the variables measured. There is no definitive indication of a sideways orientation in grazing tortoises.

The proportion of animals grazing that face <u>into</u> the sun shows several significant regressions (Table 13). The proportion decreases as time of day increases; this is true for the blocks of all data, all mornings, and mornings in 1968. Air temperature is the most important independent variable for mornings in 1969 and is nearly as good a predictor as is time for mornings in 1968 (Figure 65). Air temperature and time of day are strongly correlated ($r = 0{\cdot}7407$; $p<0{\cdot}01$ for mornings in 1968 and $r = 0{\cdot}6815$; $p<0{\cdot}01$ for mornings in 1969). Thus, temperature and time are both having strong effects on the orientation of the population, but the results suggest that temperature has a more consistent, and probably a more important, relation with the orientation of the population. Air temperature shows significant regressions in both of the two blocks in which it was tested, while time shows significant regressions in three of four blocks. When temperature data are available they seem able to explain most (if not all) of the variation explained by time.

The total number of animals active is an important variable in

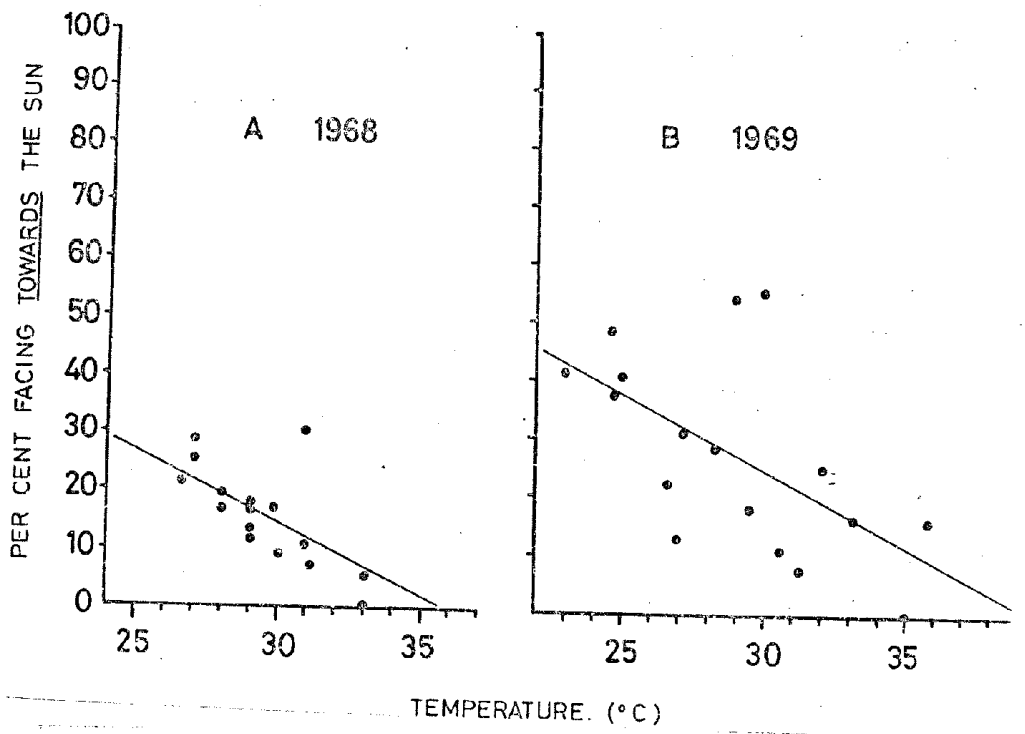


Figure 65. Change in the per cent of total number of animals active on east plain that face towards the sun in relation to air temperature; for mornings.
A. Feb. 1968 $y = 88.435 - 2.47\ (x)$, $(p < 0.05)$
B. 1969 $y = 103.56 - 2.59\ (x)$, $(p < 0.05)$

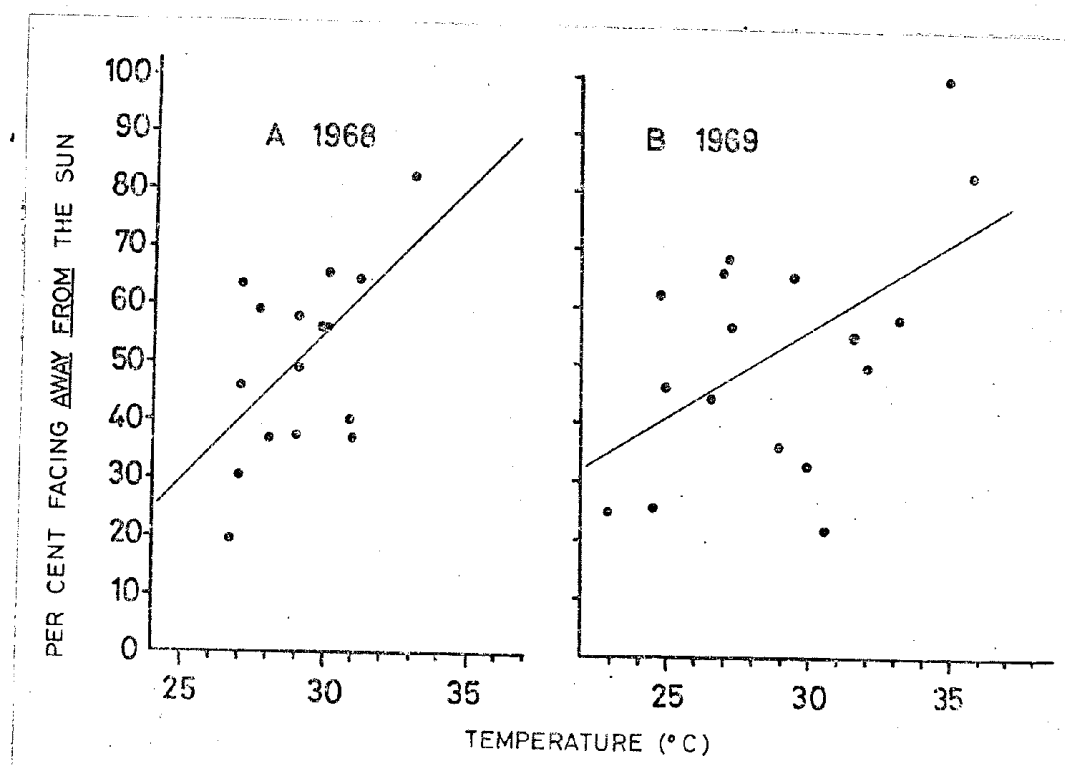


Figure 66. Change in per cent of active animals that face away from the sun in relation to air temperature; for mornings.
A. Feb. 1968 $y = -97.19 + 5.08\ (x)$, $(p < 0.05)$
B. 1969 $y = -34.377 + 3.02\ (x)$, $(p < 0.05)$

one regression, with data from all mornings. However, the number active is highly correlated with time ($r = -0{\cdot}7036$; $p < 0{\cdot}001$ for data from all mornings), and it is inconsistent in its effect on the dependent variable, appearing significant only once. The number active does not generally contribute to the explanation of variation in the orientation response.

There is no indication of any statistically significant regression in the afternoon data.

The proportion of tortoises facing away from the sun also shows several significant regressions (Table 14). Time is an important variable in blocks of all data, all mornings, and all afternoons. However, when temperature data are available in mornings 1968 they are most important; as temperature increases, so does the proportion of animals facing away from the sun (Figure 66). Time is strongly correlated with air temperature for these data ($r = 0{\cdot}7407$; $p < 0{\cdot}01$). The dummy value for months is the most important explanatory variable for the block of data in mornings in 1969. The regression for cloud cover reaches statistical significance once for this block of data, and temperature alone shows a significant regression although it is not as good a predictor as is the month variable. Only two independent variables are significantly correlated with the dependent; they are month ($r = -0{\cdot}6505$; $p < 0{\cdot}01$) and temperature ($r = 0{\cdot}5347$; $p < 0{\cdot}05$). Month and temperature are themselves correlated, but not to a statistically significant level ($r = -0{\cdot}4522$; $0{\cdot}05 < p < 0{\cdot}10$).

With the afternoon data, time produces a significant regression for all the data together, but not for the yearly sub-blocks. The total number of animals active shows a significant regression for afternoons in 1968.

To summarise:

1) There is little evidence for a sideways orientation.

2) Temperature and time are both inversely related to the proportion of tortoises facing toward the sun. These two explanatory variables are closely correlated, but temperature seems to have a more consistent and a stronger effect on the orientation. There is no evidence for an orientation toward the sun in afternoons.

3) The proportion of animals facing away from the sun has rather complex regressions. In the afternoon blocks of data, time of day and total number of animals active each show one significant regression. If these two variables are affecting orientation in the afternoon then they are doing so in an inconsistent manner. The total number of tortoises active is the denominator for the dependent variable and hence is not really independent of it. In this light, two significant regressions out of twenty-four is a strong indication that the total number active is having no consistent effect.

The evidence for an afternoon orientation facing away is slight.

There is very clearly a facing away orientation in the morning, with time, temperature, and cloud cover each showing significant regressions. Time and temperature are significantly correlated and temperature and month are correlated just below statistical significance; temperature and month are the only variables significantly correlated with the orientation response in the data from mornings in 1969. Thus, temperature gives the most consistent results and I will work on the assumption that this variable has the most important effect on the orientation response.

Discussion of orientation and thermoregulation

Orientation in grazing mammals has been described by several authors. Gosling (personal communication 1971) found groups of Coke's Hartebeest facing in one direction and this was thought to be a mechanism to minimise conspecific attacks and also to be related

to a general pattern of movement between grazing and resting areas. Crofton (1958) suggested that each sheep in a flock was orientated with an angle of 110° to two neighbouring sheep, but there was no tendency for all the flock to orientate in the same direction except when facing away from a driving rain. Hunter (1954) also states that sheep face away from driving rain, while Brownlee (1960) claims that cattle face away from strong winds. None of these responses involves an orientation in relation to the sun, nor are any of the statements quantified.

In examples of ungulate orientation, a social effect seems to be important. Although considerable time was spent in direct observation of the tortoise herds, there was no indication of a social effect on orientation. If some social factor were at work one might expect orientation to have a consistent relationship with the total number of animals active, for the number active would be an indication of the size of the social group. Another factor related to ungulate orientation is inclement conditions. Tortoises may face away from strong wind and rain, but this is not invariably so and I have no quantitative data. There was no evidence that they faced away from strong winds alone.

It could be argued a priori that the tortoises' orientation away from the sun is primarily, and simply, to avoid the bright glare. It is not uncommon for the animals to be clearly orientated away from the sun but to graze with necks turned out and heads in direct sunlight. Also, if orientation were to avoid glare then two things should follow. First, time should be an important variable, but instead of orientation away from the sun increasing with time, it should decrease as the sun rises and its rays become more perpendicular to the animal. Second, cloud cover should be more strongly related to the degree of orientation, for it is a direct index of the amount of sunlight striking the animal's face. That these two conditions are not met suggests that avoidance of glare is not a

primary factor in the orientation.

The month variable, tested in nearly every sub-block, only reached significance once. The relevance of the regression on the month variable is that the proportion of animals facing away from the sun decreases as the month value increases, i.e. gets farther from mid-summer. It is relevant that average monthly temperature is highest at mid-summer and decreases in the months before and after (see Farrow 1971, and section on climate). I suggest that the importance of the month variable is due to its relationship with temperature and not to any independent or intrinsic feature of the months themselves, and if there is a seasonal effect on the orientation response then it is probably due to seasonal temperature changes. Certainly temperature is the variable most often involved in significant regressions and seems to be the most important single variable affecting orientation.

The overall activity of the tortoises is dominated by thermoregulation; this is seen especially in the diurnal activity cycle and choice of micro-habitats. That temperature is the most important factor in predicting the degree of orientation strongly suggests that thermoregulation is also the major concern here.

The most important heat source to many reptiles is the sun; Bogert (1959) coined the term "heliotherm" to emphasize this. There are examples, and suggestions, of reptiles orientating with the sun either to increase or decrease solar (heat) input (Weese 1917; Bogert 1959; Heath 1965; Bartholomew 1966). Similar responses have been described in amphibia (Brattstrom 1962) and insects (Clench 1966; see also Fraenkel and Gunn 1960 for a comprehensive review), but few studies have been quantified or tested experimentally.

The carapace of a giant tortoise is roughly a hemisphere, except that the anterior is open and exposes a relatively large amount of soft, vascularized tissue to the environment. The anterior

of a 50 kg tortoise may have 1000 sq. cm of skin exposed to the sun (Table 15). On the other hand, at the posterior virtually no skin is exposed to the sun (except the soles of the feet which are covered by thick, horny scales), for the carapace descends right to the substrate (Figure 67). I postulate, therefore, that heat input from solar radiation is most rapid if the anterior of the body is orientated toward the sun and is least rapid if it is orientated away. This difference would not be as marked if the sun were overhead, but considering the times when the tortoises are actively grazing, this complication does not arise.

TABLE 15. Calculation of the area of skin in the anterior of a 50 kg tortoise

1.	Benedict (1932, p. 365) found the total area of skin of a 5 kg Geochelone (= Testudo) denticulata L. to be 815 sq. cm.
2.	From his figure 85 on page 364 it seems that 472 sq. cm of this is contributed by the front legs and the head and neck.
3.	If one assumes that surface increases as the 2/3 power of weight (Thompson 1917, p. 17), then a 50 kg tortoise would have 2190 sq. cm of skin in the anterior.
4.	This figure could be reduced by $\frac{1}{2}$ since the legs and neck are roughly cylinders and are only half exposed to the sun.

It might be argued that facing sideways to the sun would present the greatest surface area and provide the greatest potential for heat input, as has been described in lizards (Heath 1965; Bogert 1959; Bartholomew 1966). However, this does not seem to be the case in tortoises. First, there is no definitive evidence for a sideways orientation in my data. Second, although the lateral surface of a tortoise does represent more surface area than the posterior or anterior, the relative difference is much less than in a long, thin lizard. Finally, there is a great amount of vascularized area in the anterior but very little in the lateral or posterior. The vascularized tissues will input heat into the animal's core far faster than will

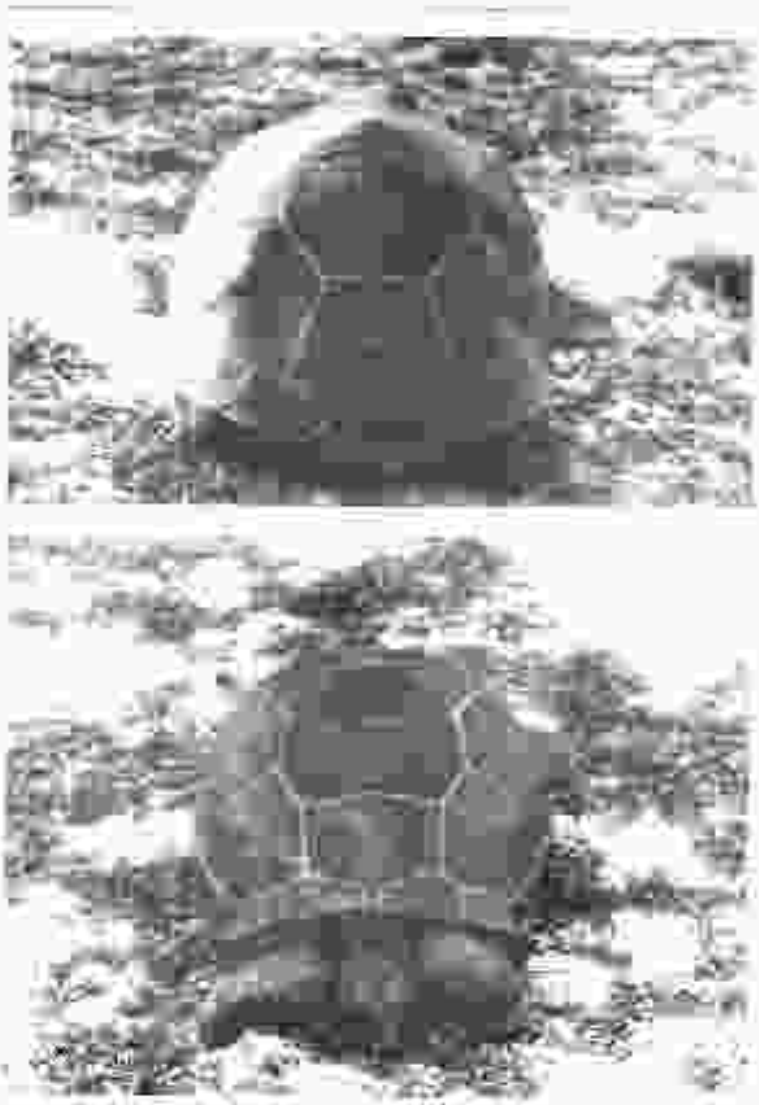


Figure 67. Differences in appearance of vascularized tissues as materials and artefacts.

the horny shell and bone.

The response of the grazing tortoise could be called a "dorsal (or oblique dorsal) light reaction" (Fraenkel and Gunn 1960, p. 120) or simply a "tropotaxis" (Tinbergen 1969, p. 93; Hinde 1970, p. 156) where the light from the sun is the "token" stimulus responded to, but the animals' preferred temperature is the ultimate goal or target value. That is, the light response is proximate, the temperature response, ultimate. This would explain why cloud cover is related to orientation, for it interferes with the proximate stimulus (light) as well as the ultimate stimulus (solar radiation). However, some animals can make adequate temperature reactions without light cues (Fraenkel and Gunn 1960) so the effects of various potential stimuli still need to be experimentally tested.

Nevertheless, the function of the orientation response is clearly a potential means of controlling body temperature in an environment in which solar heat input is of prime importance. The available data indicate that the facing away response is much more common than the facing towards response (cf. Figure 65 with 66), and it appears as if reducing heat input is far more important than enhancing it. This is strange, for although there are good reasons why a tortoise would need to cool off, there are also reasons why it would need to pick up heat. One might expect a tortoise in early morning or late afternoon to have problems in attaining, or maintaining, active body temperature, and means by which it could obtain or conserve heat would seem to be advantageous. Many lizards begin their daily activity by basking to increase their body temperature (Templeton 1970).

Three points seem relevant to this anomaly. Firstly, thermoregulatory response will depend on the temperature of the animal. If some of the animals at the time of an observation are still warming up while others are too warm, there will be a great amount of

variation in the orientation of the herd. Large animals will take longer to heat up than small animals but will retain heat for longer. Thus, all the members of a herd may not be adopting the same thermoregulatory posture. This means that the trends for the groups that I have shown are most probably representative of the dominant size class on the plains. Animals that are larger or smaller than this size class will be out of phase and will be adding a good deal of variation to the data, and making it difficult to show an orientation response with the present analysis.

Secondly, it may be that the rate of heat input is so rapid in the morning that it is disadvantageous to systematically increase the body temperature for that small part of the early morning when the temperature is low. The longer the tortoise can delay heating up, the longer it can stay on the plains.

Lastly, it is difficult to see why the tortoises do not take advantage of the sun's heat in the last hours of grazing in order that they can begin the night at a higher temperature. Interesting comparisons here can be drawn with experimental work on lizards. It has been shown that lizards not only function better (i.e. have increased body weight and more testicular activity) with an alternation in heat-cool regimes of body temperature (Licht 1965), but that they actually select a cool area when they are inactive (Regal 1967). Whether these findings are relevant to giant tortoises is a matter of speculation.

The failure for the afternoon data to show a consistent regression for orientation on any environmental parameter may be related to this last point. At the beginning of the afternoon period of activity, about 1500 to 1600 hours, the air temperature will be at its highest for the rest of the afternoon. Consequently, animals will face away from the sun right after coming out of the shade. If there is no response to face toward the sun as the

temperature drops then there will be no systematic change in the orientation of the herd during the afternoon, and it will remain in much the same orientation in which it began the afternoon period of activity. The orientation away from the sun is significantly stronger in the afternoon than in the morning as seen in grouped data (Table 16); and the same trend is evident in the individual observations (Table 17).

TABLE 16. Comparison of orientation response in mornings and afternoons using grouped data

		Morning	Afternoon
A.	Number of observations	42	26
B.	Number of animals tallied as facing either away from or towards the sun	727	529
C.	Average number counted / observation (= B/A)	17·3	20·3
D.	"p" for 2x2 Chi squared on rows A and B	0.05	
E.	Total number tallied as facing the sun	259	114
F.	% of total tallied facing the sun (= E/Bx100)	35·6	21·3
G.	"p" for 2x2 Chi squared on rows B and E	0.001	

TABLE 17. Comparison of orientation response in mornings and afternoons using individual observations

		Morning	Afternoon
A.	Number of observations	42	26
B.	Instances when the number facing the sun is greater than the number facing away	6	2
C.	Percent of total (= B/A x 100)	15	8
D.	Instances when the ratio of number facing away to facing toward the sun is significantly different from 50:50	21	18
E.	Percent of total (= D/A x 100)	40	69

Summary. There is a distinct tendency for grazing tortoises to face away from the sun. The strength of this response in the herd is related to air temperature and the response is thought to be concerned with thermoregulation, facing away from the sun being a means to

retard heat input. The antithesis, facing towards the sun, is not as marked a response and this may be because: 1) acquiring heat is of far less importance than dispersing it on Aldabra (i.e. there is usually an excess, and rarely a paucity, of heat); and 2) cooling off when inactive at night is advantageous to maintaining a high body temperature during inactivity.

SEASONAL ACTIVITY AND MOVEMENT

Seasonal changes in activity

Diurnal activity. The diurnal pattern of activity is somewhat more complex than outlined in the preceding sections, for there is variation with seasonal factors. Daily activity is distinctly bimodal in summer months. There are sharp peaks, in early morning and late afternoon, separated by broad troughs of inactivity. In the winter, from May to October, this pattern is modified so that the morning peak is broad and constitutes the greater part of daily activity; the period of inactivity is often shorter than in summer and is less well defined (Figure 49).

Counts made in 1968 from the top of Dune Jean Louis show that this summer-winter difference in diurnal activity occurs in mixed scrub as well as on grassland. In February, activity is bimodal; in July it is generally unimodal (Figures 57 & 60 and Tables 7 & 8). The results of the activity census (Figure 52) are further confirmation for this seasonal difference. In September, feeding is restricted mainly to the mornings and the afternoon is spent sleeping. This applies to all habitats. In late October, November, and January (summer months) daily activity is bimodal in all habitats (except on rainy days, as discussed earlier).

The observations on activity of individuals likewise show a seasonal difference in daily activity pattern (Figure 53). Tortoise 297 who was observed in August was active for long periods during mornings and hardly at all during the afternoons. Incidental observations on 297 during the summer showed that he was biphasic in this season. The other individual tortoises watched for long periods of time were all biphasic, and they were all observed in the summer. Incidental observations on tortoise 99 in the winter indicated that she was active mainly during the morning in this season.

General activity. The grassland counts show a very distinct monthly trend in general activity (Figure 49). This can be easily seen by plotting the area under the mean monthly activity curves (Figure 50). The greatest number active at any one time in each month also shows a similar trend (Figure 68), as does the monthly average of the greatest number active (Figure 69). Large numbers of animals are active on east plain during the monsoon, from November until April. There is a very high peak in November, a slight depression in January and a peak again in March. During the trades, from May to early October, there is very little activity on east plain.

Frequent counts were made on other south coast plains to check how widespread this seasonal change is. Plains both east and west of Dune Jean Louis were checked (Figure 70) and the results are fully consistent with the findings from east plain (Figure 71). Incidental observations were also made on coastal plains in the east, by Cinq Cases, and on plains to the west, at Dune D'Messe. The general pattern of activity on these more distant plains was just the same as on the plains studied in detail, for they were densely populated with tortoises during the monsoon and nearly devoid of animals during the trades.

In order to quantify seasonal movement in the scrub, six hectare squares were marked out (Figure 70), and the total number of tortoises within each square was counted several times a month, if possible. Counts were made by my Seychellois field assistants but unfortunately I was not allowed to keep the same men so counts on different occasions were done by different pairs of men, or even a single man in a few instances.

The results from these counts are shown in Figure 72. All squares but number 5 show a decline in the number of tortoises present at mid-summer. This effect cannot be explained solely on the basis of less comprehensive counting by one man, for often counts by two men

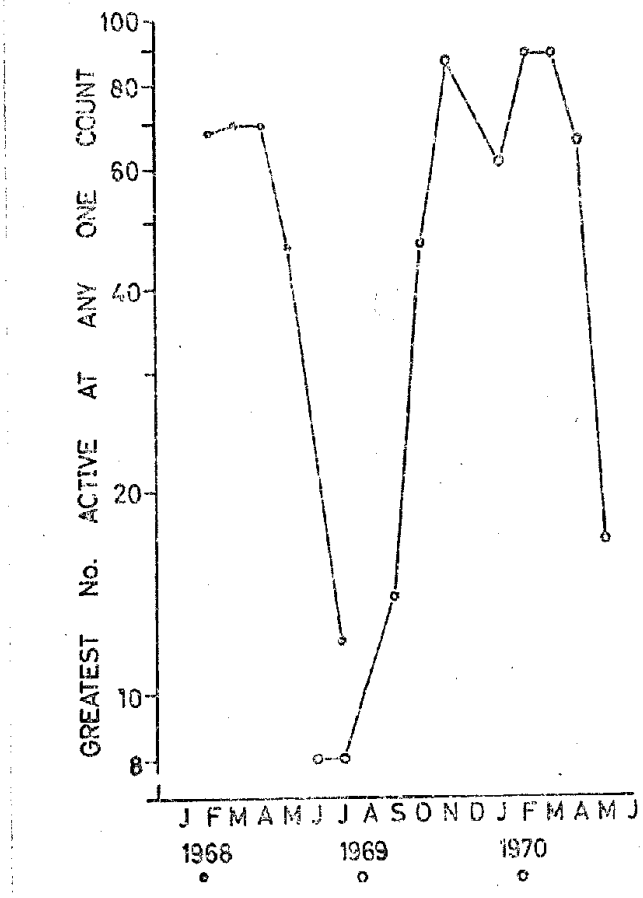


Figure 68. The extreme monthly value for the greatest number of tortoises active on east plain at any one time. (Note the y axis is logarithmic.)

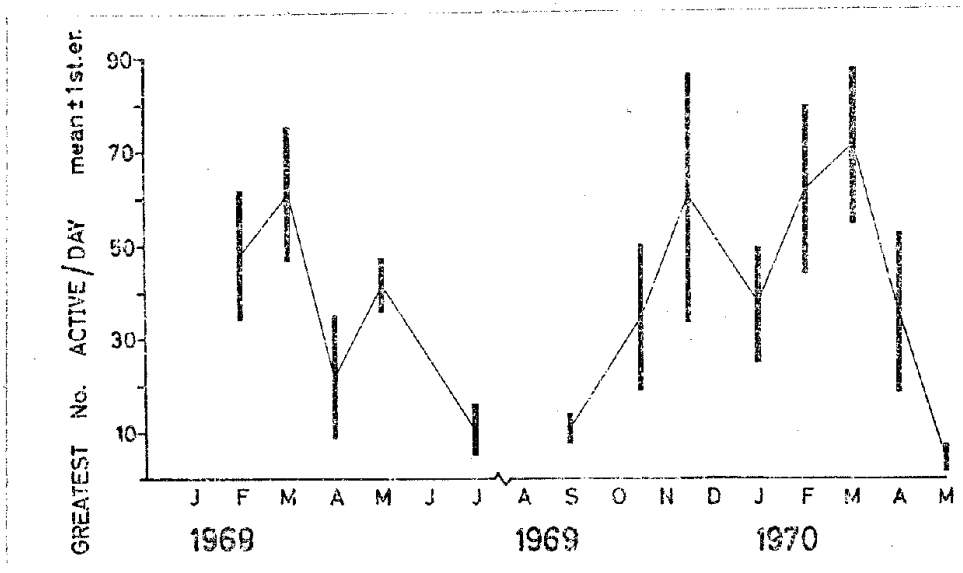


Figure 69. Average monthly value for the greatest number of tortoises active on the east plain. (± 1 standard error)

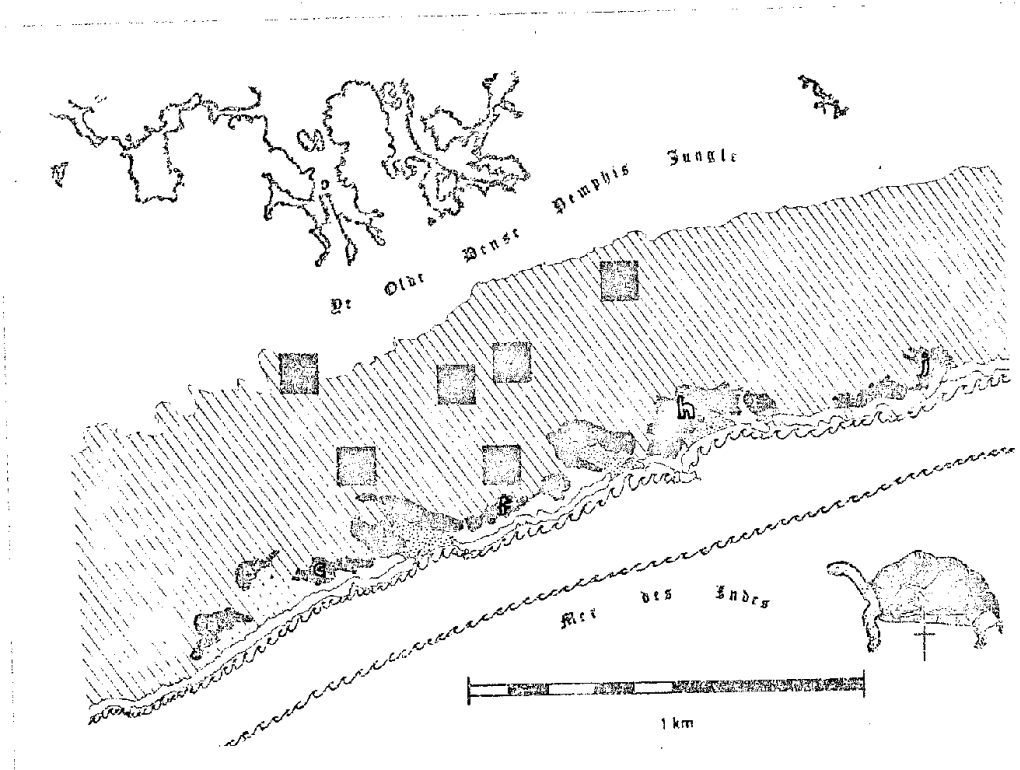


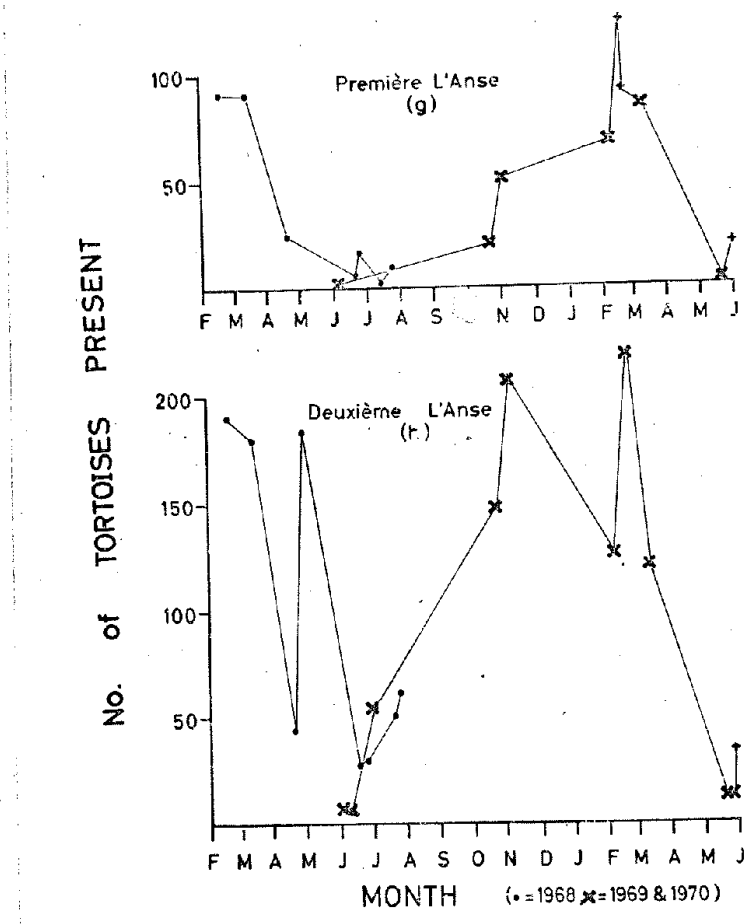
Figure 70. Map of South coast study area.
Grassland plains are indicated by letters a. to j.; e. is the east plain at Dune Jean Louis.
One hectare sample squares in the mixed scrub and pavé are indicated by numbers.
Stippling = sand and dunes
Oblique parallel lines = mixed scrub
Lagoon and mangrove creeks are shown in the top left.

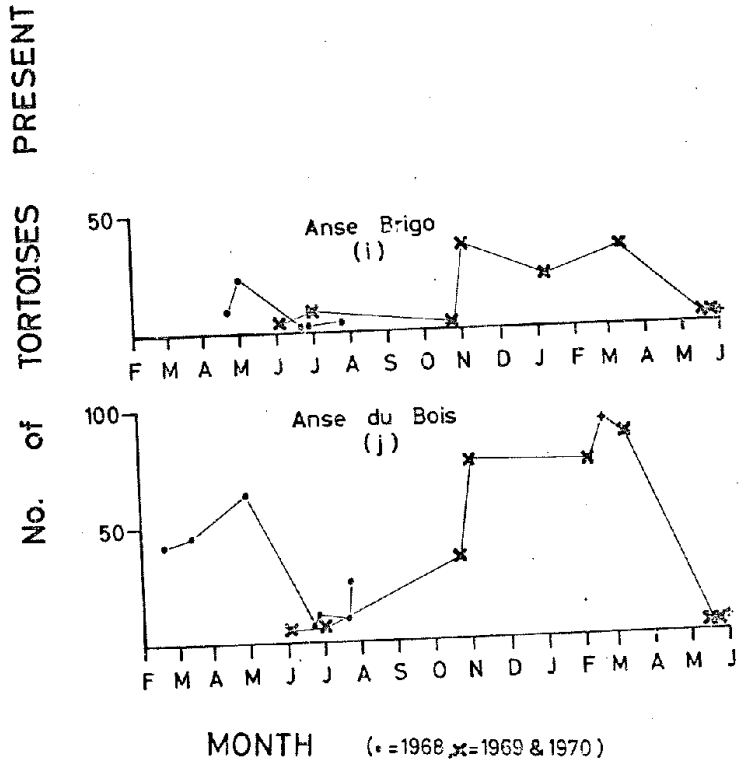
Figure 71. Seasonal changes in the number of tortoises active on the ten grassland plains indicated in Figure 70. plus Dune le Rat and Dune Au Pic which are 1 km west of Dune Jean Louis.

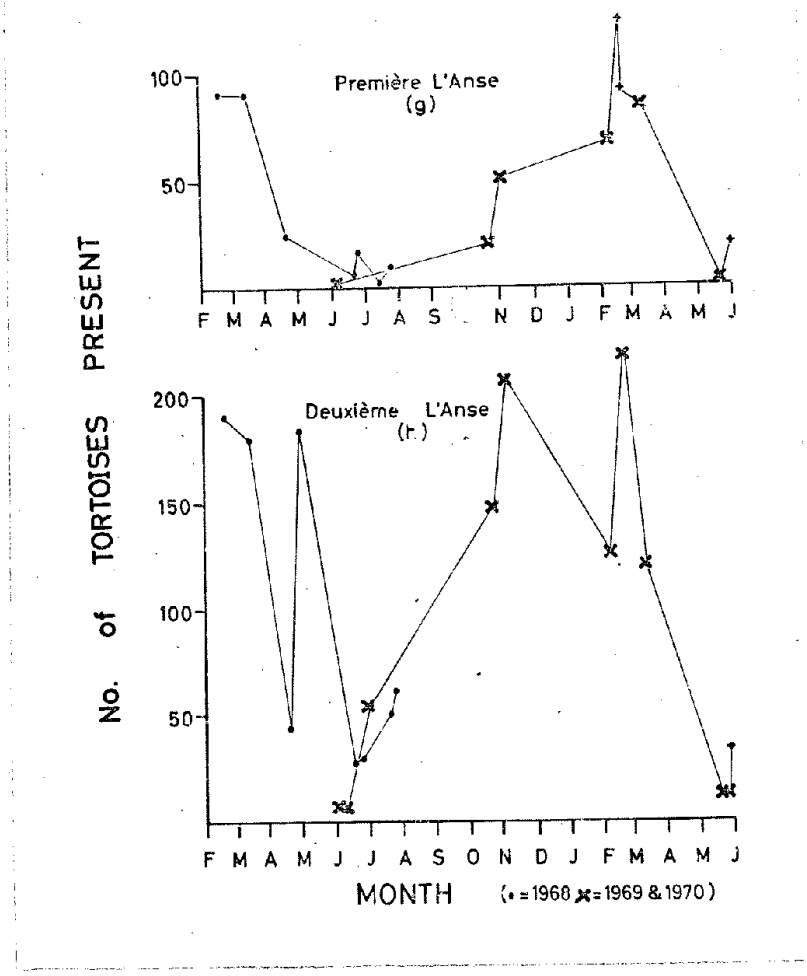
⊛ = counts made in 1968

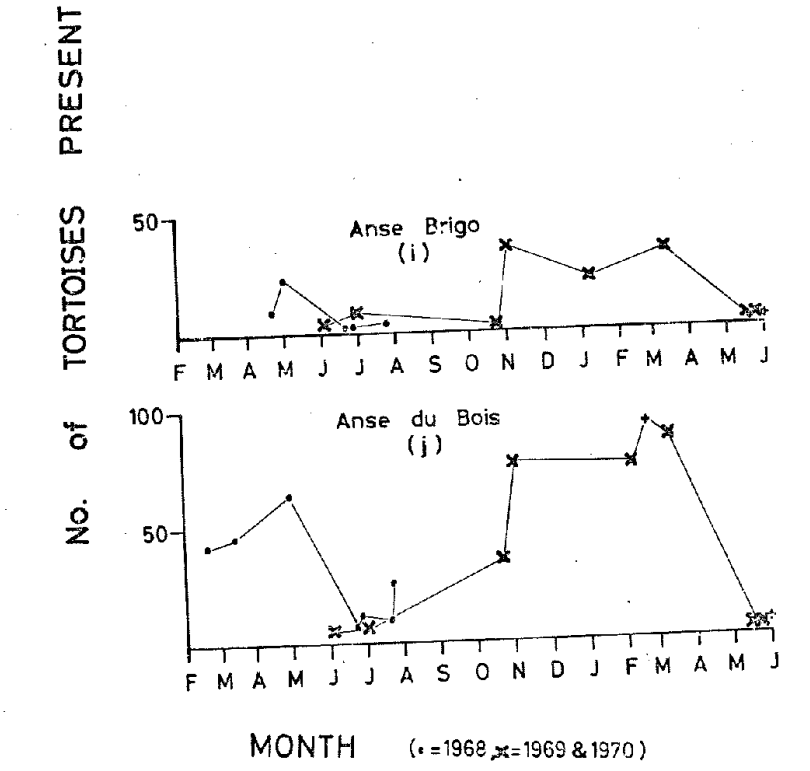
x = counts made in 1969 and 1970

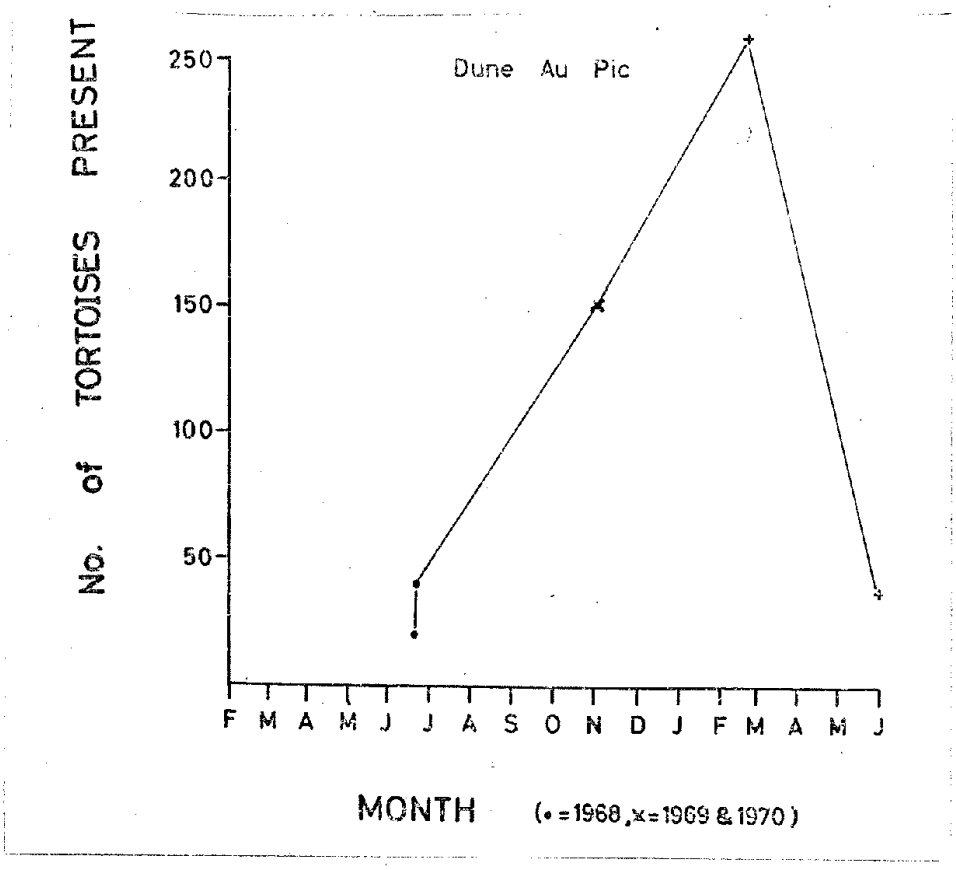
+ = counts made in 1970 by Seychellois field assistants


Première L'Anse
(g)
100
50
F M A M J J A S O N D J F M A M J
Deuxième L'Anse
(h)
200
150
100
50
F M A M J J A S O N D J F M A M J
No. of TORTOISES PRESENT
MONTH
(• = 1968 x = 1969 & 1970)


Anse Brigo
(i)
50
F M A M J J A S O N D J F M A M J
Anse du Bois
(j)
100
50
F M A M J J A S O N D J F M A M J
No. of TORTOISES PRESENT
MONTH
(• = 1968 x = 1969 & 1970)


Première L'Anse
(g)
100
50
Deuxième L'Anse
(h)
200
150
100
50
No. of TORTOISES PRESENT
F M A M J J A S O N D J F M A M J
MONTH
(• = 1968 ✕ = 1969 & 1970)


Anse Brigo
(i)
50
Anse du Bois
(j)
100
50
No. of TORTOISES PRESENT
F M A M J J A S O N D J F M A M J
MONTH
(• = 1968 ✕ = 1969 & 1970)


Dune Au Pic
No. of TORTOISES PRESENT
250
200
150
100
50
F M A M J J A S O N D J F M A M J
MONTH
(• = 1968, x = 1969 & 1970)

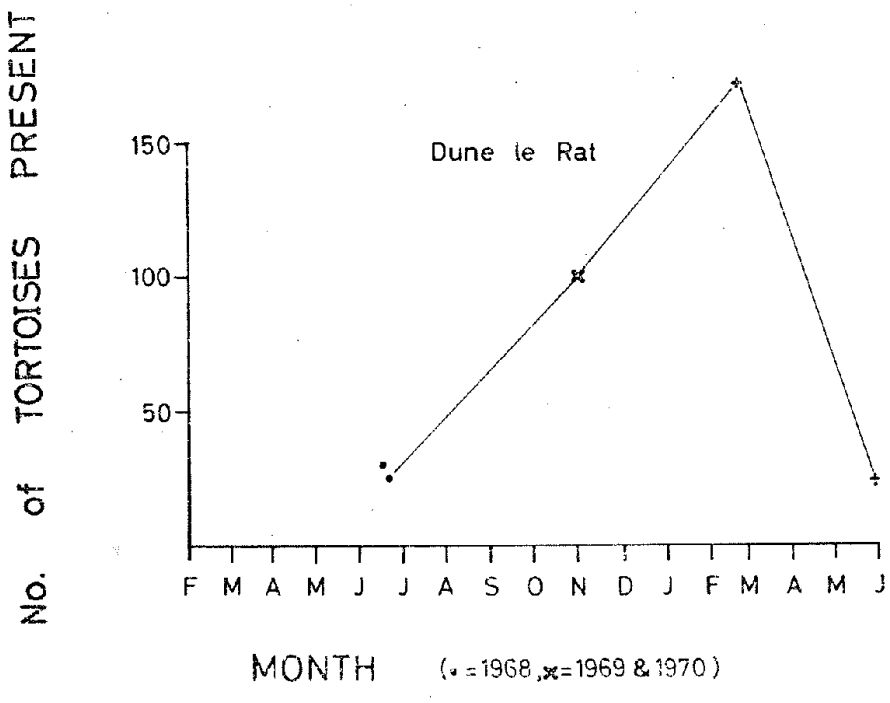
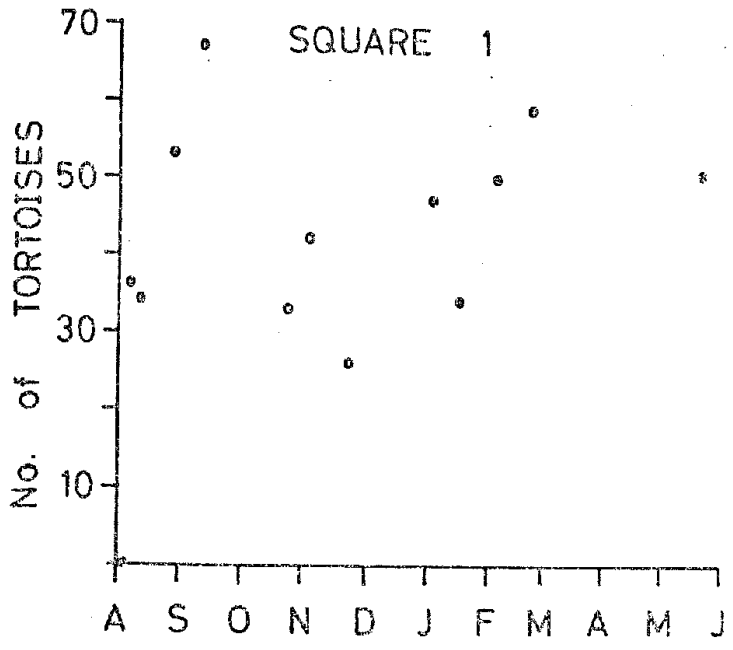

Dune le Rat
No. of TORTOISES PRESENT
150
100
50
F M A M J J A S O N D J F M A M J
MONTH
(• = 1968, x = 1969 & 1970)

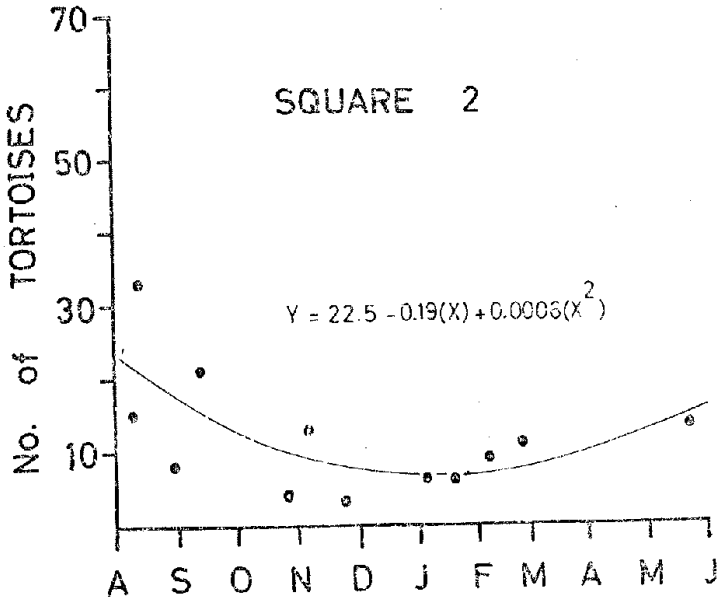
Figure 72. Seasonal changes in numbers of tortoises present in six hectare quadrats in the mixed scrub at Dune Jean Louis.

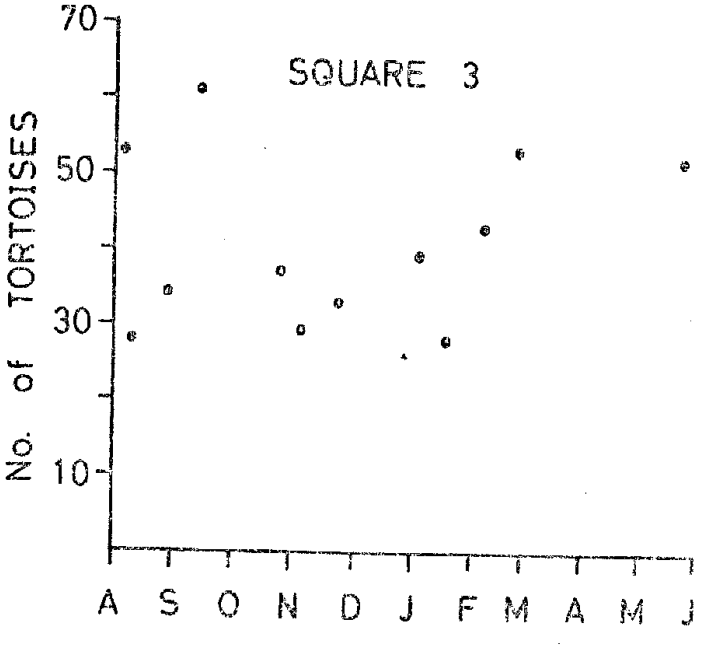
● = counts made by two field assistants working together

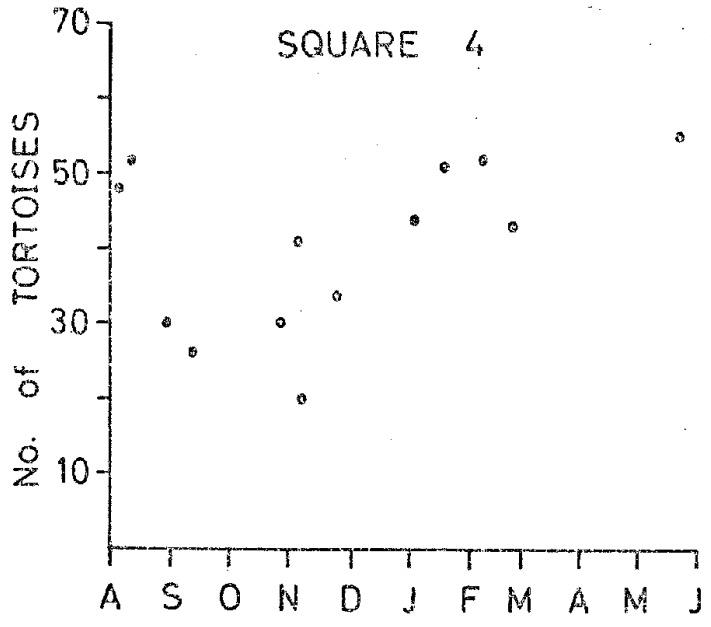
o = counts made by one field assistant working alone

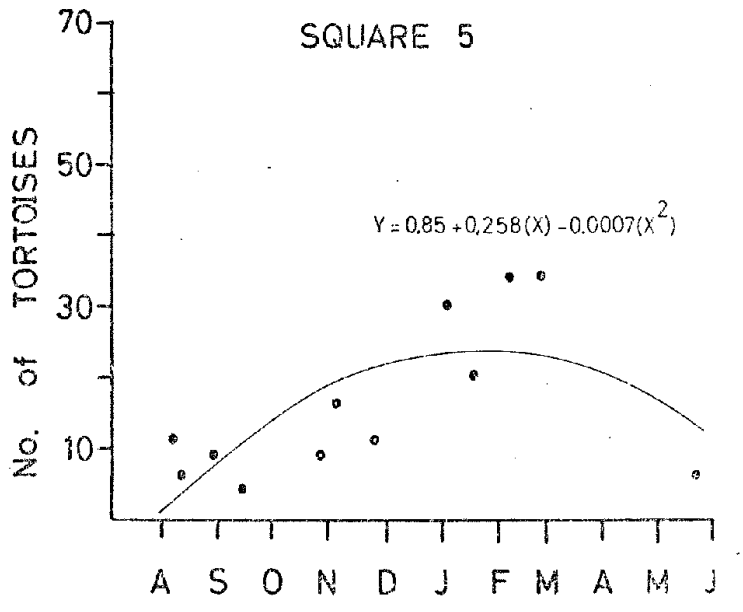
Lines and equations are drawn in where the regression coefficients were found to be significantly different from 0. Where no line appears, neither a linear nor quadratic expression described a significant amount of the variation in the number of tortoises.

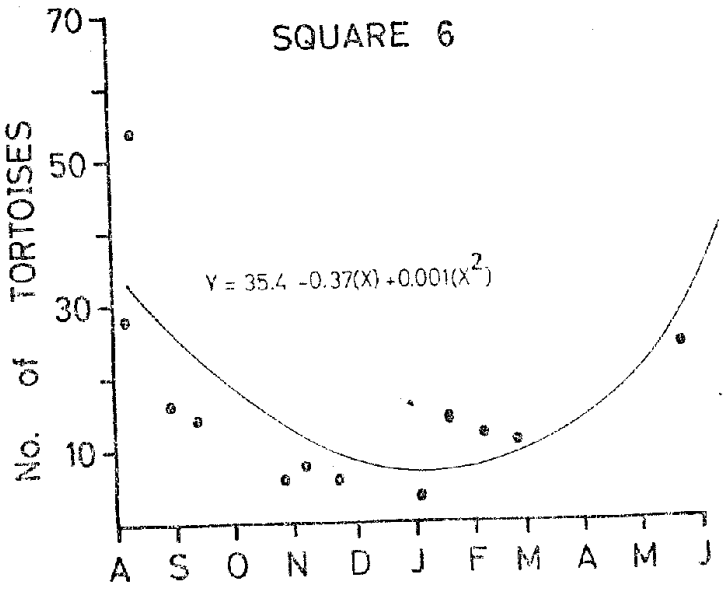

SQUARE 1
No. of TORTOISES
70
50
30
10
A S O N D J F M A M J


SQUARE 2
No. of TORTOISES
Y = 22.5 - 0.19(X) + 0.0006(X²)
70
50
30
10
A S O N D J F M A M J


SQUARE 3
No. of TORTOISES
70
50
30
10
A S O N D J F M A M J


SQUARE 4
No. of TORTOISES
70
50
30
10
A S O N D J F M A M J


SQUARE 5
No. of TORTOISES
70
50
30
10
Y = 0.85 +0,258(X) -0.0007(X^2)
A S O N D J F M A M J


SQUARE 6
No. of TORTOISES
70
50
30
10
Y = 35.4 -0.37(X) +0.001(X^2)
A S O N D J F M A M J

are as low as, or lower, than one man counts. For squares 2 and 6 regression analysis shows that quadratic functions can account for 46% and 56% of the variation in number of tortoises, indicating that is a regular cycle in the numbers present. In squares 1, 3, and 4 a horizontal line explains as much of the variation in numbers as does any other line or a quadratic function. Square 5 is unique in that it is the antithesis to the other squares, showing a mid-summer increase in numbers present; the indicated curve accounts for 51% of the variation.

Discussion of seasonal activity and movements

Seasonal movement. The well documented changes in number of animals active on east plain are common to east and south coastal plains, and are certainly not due to some herd of tortoises revolving around the atoll at the rate of one r.p.y. This is not to say that individuals do not move from one plain to another, for they do. But there is no regular evacuation of one plain, and subsequent population of another, that would account for these seasonal changes. Instead, there is a general movement onto the east and south coast plains during the monsoon and off the plains during the trades. Although the distances moved are not great, especially in relation to the size of the animals, this regular phenomenon of yearly movements to and from particular area is best defined by the term "migration" (Landsborough Thomson 1964).

If the tortoises are migrating on and off the plains then a reciprocal movement must be occurring in another habitat. On the south coast the major habitats from sea to lagoon are: sand beaches; coastal champignon and perched beach; coastal Sporobolus plain; mixed scrub and pavé; dense Pemphis and dissected champignon; and mangrove and dissected champignon. Tortoises are rarely on the coastal sand and champignon, and they seldom occur in the dense

Pemphis or in the mangroves. Along the south coast the tortoises occur regularly only on the Sporobolus plain and in the mixed scrub. Hence, the plains migration should be mirrored by a reciprocal movement in the mixed scrub. Yet, the results of the scrub counts do not show this and the problem is not as simple as it first appeared.

It is as certain that the plains tortoises do come from the scrub as it is that they do not come from the sea; there simply is nowhere else that they could come from so quickly. Records on individually marked animals (not presented in this study) show indisputably that plains animals move to and from the scrub. To assume that the mixed scrub is a homogeneous habitat and that the tortoises in it are all behaving the same way is evidently erroneous. The very different pattern of seasonal change in the sample squares is evidence for a very distinct difference in these squares.

Squares 2 and 6 were at the northern edge of the dense Pemphis. The terrain is well dissected in Square 6 and barren of vegetation for a large part of Square 2. The shrubs are dense and low, but shade is not readily available. Few of the shrubs are eaten by the tortoises; soil is not common and ground level vegetation is sparse. Rain-water catchment is not good either. In short, the habitat in which Squares 2 and 6 are found is not an exceptionally good one for tortoises.

Square 5 is at the southern edge of the mixed scrub bordering the Sporobolus plain. The terrain is very dissected and large pits are frequent. In the south-west, soil is reasonably deep and it is covered extensively with Sclerodactylon macrostachyum. However, most of the square lacks any soil or ground cover. The shrub Scaevola taccada is extremely common and occurs over most of the square, but although shade is available, it is never very deep. Rain-water catchment is not very good in this square either. Like Squares 2 and 6, Square 5 occurs in a poor habitat for tortoises.

Square 1 is just north of Dune Jean Louis on the border of the Sporobolus plain. The terrain is very dissected except in the north-east where it is flat and pavement-like. There is a wide variety of shrubs which fall into wind rows on the west side of the square. Shade is available and quite deep in places. Ground level vegetation is common in the north-east and herbs in crevices are common over the rest of the square. Rain-water catchment is good in the north-east. Thus, this square has both good and poor quality tortoise habitat, and it borders both good and poor quality areas. Squares 3 and 4 are in the centre of the mixed scrub zone and very close to one another. The terrain ranges from moderately dissected to flat and pavement-like. Both squares are very open, 3 especially. There is little soil but herbs are common. Shrubs are not common, but there are a number of Guettarda trees on which the tortoises feed and under which they sleep. Catchment of rain-water is good in these squares. The habitat containing Squares 3 and 4 is very similar to the platin in the south-east of the atoll, and is good tortoise habitat.

TABLE 18. Summary of counts in sample squares

Square	Location	Habitat quality	Regular yearly movement	In or out of phase with plains
1	edge of plain	good & poor	no	
2	edge of Pemphis	poor	yes	out
3	middle of mixed scrub	good	no	
4	middle of mixed scrub	good	no	
5	edge of plain	poor	yes	in
6	edge of Pemphis	poor	yes	out

Regular movement in the mixed scrub is seen in areas of poor habitat; in areas of good habitat the density of animals is usually

quite high throughout the year (Table 18). Mixed scrub areas that are distant from the plains have a migration that is reciprocal to that of the plains. Areas that are adjacent to the plains have a migration that occurs at roughly the same time as on the plains.

The area of mixed scrub is far greater than the area of plains, and the mixed scrub holds a much larger population of animals than the plains. Hence, changes in the number of animals on the plains may not necessarily be reflected as a general phenomenon throughout the mixed scrub. In addition, there are evidently areas in the scrub that offer food of equal quality and quantity to that found on the plains. They also have ample shade and, unlike the plains, have good catchment of rain-water. One would not expect tortoises to leave these areas for areas of poorer quality.

However, if animals live in an area of poor quality one would expect them to move off to better areas, if available. If the poor area is some distance from the good area then the animals will simply exit from one to the other. This seems to be the case with squares 2 and 6. If the poor area is at the edge of a good area it will act as a buffer, for animals moving to and from the good area will pass through the poor one. This seems to be happening in Square 5.

Without details of individually marked animals it is not possible to say whether the tortoises that leave the poor quality habitats move directly to the plains, or whether they move to good areas in the scrub, displacing other animals which in turn move to the plains. Undoubtedly, both types of movement occur. Data on marked animals, relevant to this problem, have not yet been analysed, but it is my impression that many animals move directly from poor areas in the scrub to the plains.

Thus far I have argued, without precisely stating it, that the seasonal movements in the tortoises are related to seasonal changes in food. Evidence for this point has been discussed in the feeding

section, where it was argued that there are seasonal changes in feeding habits which reflect changes in food availability. The movements of the tortoises on and off the coastal plains likewise reflect changes in the growth and availability of the Sporobolus. During the winter the grass grows very little and may even turn brown. As the rains begin at the onset of the monsoon the grass begins to grow, apparently quite suddenly; and, almost as suddenly, the tortoises appear on the plains. The grass continues producing, and tortoises are on the plains in large numbers throughout the monsoon, but as the trades begin the Sporobolus stops growing and the reptiles abandon the grassland for the scrub.

Areas in the scrub that offer all the necessary requisites (except possibly nest sites) are heavily populated throughout the year (e.g. Squares 1, 3, and 4). Other scrub areas, especially those adjacent to the dense Pemphis, serve as refuges during the dry season when the plains are no longer suitable because of lack of food, water, and shade, and probably also because the coastal areas are exposed to continual high winds and salt-water spray.

Migrations have been described in numerous Testudinates. Galapagos tortoises make migrations from highlands to lowlands for nesting (Porter 1822; Heller 1903; Van Denburgh 1914; Snow 1964; Hendrickson 1965, 1966), but the most dramatic examples are in the breeding and nesting migration of sea turtles, which may cross hundreds of miles of open ocean (Carr 1965, 1969). Fresh-water terrapins also make nesting migrations (Gibbons 1968; Moll and Legler 1971) as well as regular yearly movements to and from hibernacula (Cahn 1937; Cagle 1944; Carr 1952).

The coastal plains on Aldabra have large areas suitable for nesting but a cursory examination of the sex ratio in July (during the nesting season) 1969 did not indicate an abnormally high proportion of females. Because frequency of nesting is so low (see

nesting section) it is unlikely that nesting has a major effect on tortoise migration, although gravid females may well have their own small migrations.

I know of no other example of a migration related mainly to food in testudinates, although this is very common in other herbivores (Bell 1971).

Seasonal changes in diurnal activity. Seasonal changes in diurnal activity seem to be due to several factors. Tortoises are, on the whole, less active during the winter. The ambient temperature is lower, so presumably their general metabolism is lower than in the summer (Kenyon 1925). Food is not readily available, for most plants appear to have stopped, or reduced, production, and water is scarce, for little rain falls. Winter is a time of year when requisites are likely to be in short supply, and with reduced activity and metabolism the tortoises need less to stay alive, as discussed earlier.

The disproportionate amount of activity in mornings is probably also due to food. Plants are likely to be more palatable, more nutritious, and have more moisture in the morning than in the afternoon. The twelve hours from dusk to dawn have high humidity, absence of light (which generally inhibits growth) and no grazing by tortoises. Plants in the afternoon have experienced: morning grazing by tortoises, high temperatures, light, and humidity (especially during the midday) and hence have not had very much time, nor very good conditions, in which to grow (although there has been an excess of light for photosynthesis). Plants in the afternoon are likely to be badly desiccated; hence, morning grazing probably gives better yields of food per unit of effort.

A concentration of activity in mornings, but a general reduction of the amount of activity, results in a diurnal cycle with a single peak of activity in the morning.

Modification of diurnal activity in relation to food quality,

especially moisture content, has been suggested in other animals. Taylor (1969) found that a preferred food plant of the Oryx (Oryx gazella L.) had only 4% water during the day, but at night it could contain up to 42% due to hygroscopic absorption. If these animals were to feed at night they could obtain their daily water requirements without drinking.

SUMMARY OF PART III

Throughout the three preceding chapters I have merely alluded to the underlying factors involved in the pattern of diurnal activity, thermo-regulation, and seasonal activity. In its quest for food, water, and mates, the giant tortoise exposes itself to intense solar radiation. It is, in some ways, at a distinct disadvantage in being a poikilotherm, for the animal can regulate its body temperature with few direct physiological mechanisms; and, thus, its activity is dependent on the temperature regimes in the micro-environments in which it is living. As soon as ambient temperatures, and more important, the animal's body temperature, reach critical limits, it must find a cool retreat.

I have no data on the critical thermal maxima for this species, but one incidental observation is relevant. On 23 February 1968, at about 11.00 hours, I encountered an immature tortoise (with a carapace 66.5 cm long over the curve) on the coastal plain between Takamaka and Cinq Cases. This animal was apparently heat prostrated, for fluid was streaming from its eyes; the mouth was foaming; and its motor movements were not normal, but unco-ordinated and unusually fast. The cloacal temperature, with the thermometer inserted about ten cm, was 37.5°C.

This temperature is well within the daily range of environmental temperatures at Aldabra and shows that the animals must guard against overheating. In endotherms, or "homoiotherms", the animal can make use of sophisticated physiological mechanisms to facilitate heat loss. Ultimately, these mechanisms depend on evaporative heat loss, which is brought about by panting, sweating, and increasing the moist area available for evaporation. But, in reptiles, these mechanisms are relatively ineffective.

Reptiles do pant, but increased respiratory heat loss (i.e. panting) just about compensates for increased metabolic heat production at higher body temperatures (Templeton 1960, Schmidt-Nielsen 1964). Very little heat is lost by panting and it seems to be a last-minute emergency effort, not effective as a regular means of cooling. (See below.)

As Benedict (1932), Schmidt-Nielsen (1964), and Schmidt-Nielsen and Bentley (1966) have emphasised, reptiles lose considerable quantities of water through the integument. Schmidt-Nielsen even claims that, contrary to the conventional view, some reptiles have a larger cutaneous water loss

than some mammals. However the rate of heat/water loss is apparently not under delicate physiological control as in mammals and birds. Moreover, the amount of water normally lost cutaneously is about the same as that lost in respiration and is not sufficient to act as an effective cooling mechanism.

Benedict (1932) experimented with two South American tortoises (Geochelone denticulata) weighing 4422 and 3856 g and found that they lost respectively 0.20 to 0.53 and 0.19 to 0.45 per cent of their total body weight per day by "insensible perspiration" (i.e. respiratory and cutaneous water loss). Schmidt-Nielsen and Bentley (1966) found that cutaneous water loss amounted to 0.18 per cent of total body weight per day in American desert tortoises (Gopherus agassizi) at 35°C. Cloudsley-Thompson (1970) tested Sudanese desert tortoises (Geochelone sulcata) at the same ambient temperature; small animals with a mean weight of 42.7 g lost 0.16 per cent of the body weight from cutaneous transpiration, while an animal weighing 303.4 g lost 0.39 per cent of its body weight.

The above studies indicate that about 0.3 per cent of total body weight can be lost through the skin in a day. (Figures for respiratory water loss are of the same order of magnitude.) This means that a 1000 gram tortoise would lose approximately 3 g water a day, which would take 2400 cal in latent heat of vaporisation. If 70 per cent of a small tortoise is flesh (Benedict 1932), with a specific heat similar to that of water, then its cutaneous water loss could lower its body temperature about 3°C in 24 hours. Having seen the speed with which the Aldabran environment heats up and also realising that half of the day is thermally neutral, or cool, for the tortoises, this potential heat loss is hardly sufficient to enable a tortoise to thermoregulate by cutaneous or respiratory transpiration.

Increasing the area for evaporative heat loss by salivation and/or urination has been described in two Chelonians: Geochelone sulcata (Cloudsley-Thompson 1970) and Terrapene ornata (Riedesal, Cloudsley-Thompson and Cloudsley-Thompson 1971). In both species this is brought on by heat stress and is an emergency means of cooling the body when it is near the critical maximum. However, increasing the area for evaporative heat loss expends large amounts of water. Cloudsley-Thompson (1970) describes a 57 g tortoises that lost about 10 per cent of its body weight in an hour and even then it was only able to maintain its body temperature just over 40°C, which is above the

preferred level.

All these means of cooling demand ample supplies of water to evaporate, and the cooling effect is often insufficient for effective thermoregulation. Evaporative cooling is used by tortoises mainly in situations of heat stress, at a time of emergency, and cannot be used as a normal means of cooling. A common way for reptiles to counteract high heat loads in one habitat is to move to a cooler habitat. With tortoises on Aldabra, this amounts to leaving the open plains and scrub and moving into the dense shade of trees and bushes. Not only is this an efficient means of keeping the body temperature at a preferred level, it alleviates the paradoxical problem of having to expend precious water in order to thermoregulate. It would be very difficult for a tortoise to lose 10 per cent of its body weight per day and still remain active; under conditions of dehydration tortoises become inactive and lethargic (Benedict 1932). Thus, behavioural thermoregulation has a number of distinct advantages for the tortoise; it accomplishes thermoregulation efficiently and also conserves water.

The effect of changing habitats is dramatically illustrated by examining the temperature differences between exposed and shaded areas. Table 19 gives a typical example, showing that the temperature difference between the two micro-environments is as much as 10°C. More extensive recordings show that differences of this magnitude are not uncommon.

TABLE 19. Temperatures recorded at 1200 hours on 14 February 1968 by a large Tournefortia tree, commonly used for shade by tortoises

	Temperature °C		
	A In sun	B In shade	Difference between A and B
Air at 10 cm above sand	41·0	34·1	6·9
Surface of sand	41·6	31·6	10·0

In order to avoid heat prostration the tortoises must be fairly sensitive to environmental temperatures, for the ambient temperature on Aldabra increases very rapidly. An animal that does not move into the shade soon enough will be liable to heat prostration. Consequently, the change from activity on the open plains to inactivity in the shade is very rapid, both in individuals (Figure 53) and in populations (Figure 52). If ambient temperatures suddenly begin to rise, such as after the clearing of overcast conditions, the major exodus from the grassland plains may occur in less than an hour. At one observation the peak in activity is reached, half an hour later the grazing population has dwindled to less than half its peak size, and after another half hour there are only a few stragglers left.

The gradual decline in activity that is indicated in the morning peaks of the grassland counts is not an indication that there is a gradual transition from activity in exposed habitats to inactivity in shaded ones. Instead, it is the variation in daily temperature regimes that causes this gradual decline in morning activity. One day the population may be able to stay out until 0900 hours but the next day they might only be able to stay out until 0700. The same argument applies to the increase in activity in late afternoon. Daily variation in temperature results in a gradual increase in the

mean daily activity.

Change from inactivity to activity in early morning and the cessation of activity in the evening is probably not related to temperature. It could be argued that during these times of day the environmental temperature is too low for the tortoises to be active, but they are active with very low temperatures on winter afternoons, especially after rain. More probably, activity is restricted from dusk to dawn because the animals have poor vision at low light intensities, and movement over the broken terrain at Aldabra is dangerous in the dark. Activity begins as soon as there is sufficient light to see and ceases when there is insufficient.

The gently sloping mean daily activity cycles in the winter are due to great variability in daily activity. Because diurnal temperatures are much lower, they are less restrictive to the animals, and they can be active nearly any time in the day. The reason they are not active throughout the day in these conditions is an enigma. I suggest that food and water are in such short supply during the winter that the tortoises may have to spend more energy searching for nutrients than they would obtain by eating and drinking. In other words, they would produce an energy deficit if they were active a full day in the winter.

That the tortoises are poikilotherms is, at this point, a distinct advantage. Rather than having to maintain high rates of activity when environmental conditions become unfavourable, they can simply spend most of their time inactive, thus conserving energy. This is impossible for a homiotherm, because it has to find nutriment to fuel the high energy needs of its sophisticated physiology - even if only maintaining its somatic condition and not reproducing or growing.

PART FOUR

MATING BEHAVIOUR OF THE GIANT TORTOISE

Chapter 14

MATING BEHAVIOUR

Description of mating behaviours

A successful mating can be organized into five sequential phases, based on the actions of the male. For purposes of discussion it is simplest to take a "perfect" mating which runs from start to finish without complications. This is outlined in Table 20.

Phase I: Premounting or approach. This phase is simply a means of getting the two members of the pair together. Most often it begins when the male merely looks up and moves to the "partner" (which may or may not be a female). On reaching the partner the male may pass directly to the next phase, by mounting, or he may "noze" the partner. Nozing involves a slow, deliberate extension of the neck so that the external nares are brought very close to, or even touching, an object; at the same time the floor of the mouth moves in deep, rhythmic pulsations.

Nozing can be directed at the partner's limbs, head, neck, or the side or posterior of its carapace. It is not uncommon in the first phase of the mating sequence, and was recorded in nearly half of the matings I observed. The nozing may be transitory, lasting only a few seconds, or it may go on for several minutes.

On rare occasions nozing may evolve into slow, deliberate biting movements directed at the head, neck, limbs, or shell of the partner; usually biting is directed at the anterior appendages. On one occasion the male actually succeeded in biting the soft skin on the partner's neck. Biting is rare in the first phase of mating, occurring less than 5% of the time. Most biting that was recorded in the first phase of mating was initiated by males that were either stunted, immature, or had been unsuccessful in mating.

The actions of the partner during the first phase of the mating

Table 20. Summary of mating behaviour in the giant tortoise.

Phase	♂ Always	♂ Sometimes	'♀' Optional actions * = most common
Premounting	Look up Move to ♀		Withdraw limbs Move away Stand No response (graze)
courtship		Noze Bite	Look up Noze Move to ♂
Mounting	Extend neck over '♀' Step up Step on	Step down Pivot	Withdraw limbs Move away Budge out from under *Protect posterior *Wiggle posterior Stand Look up No response (graze)
Groan and Thrust Up	Extend hind legs Extend neck Manoeuvre tail	Bite	Withdraw limbs Move away Budge out from under Spin Protect posterior
Down	Swing front legs forwards Unweight hind legs Groan Thrust with tail Recycle	Hit '♀'s' head or legs Lift hind legs	Elevate posterior Wiggle tail Defecate, flatus
Coition	Evert penis	Insert penis Groan and thrust	Elevate posterior Wiggle tail Withdraw limbs Spin Budge
Dismount	Stop Withdraw penis	Rest on '♀' Back off Slide off Fall off	Move away Budge Spin Wiggle posterior Look up Graze

sequence can, for convenience, be listed as a series of options. It may extend all four limbs, "standing" with the plastron elevated as high off the ground as possible. While standing, the neck may be fully extended and the head held aloft, or it may be held horizontal with the ground. The partner may also noze with the male or merely "look" at him. It may move away from the male, or even withdraw its appendages into its shell. Most often, however, the partner makes no overt response to the courting animal, but simply continues with whatever it may be doing - usually grazing. Some of these options (e.g. moving away) are exclusive; that is, if they occur no others can. On the other hand, some options may occur in conjunction with something else (e.g. nozing and then standing).

On several occasions a mating sequence seemed to be initiated by the partner moving away from the male. A typical sequence would be: male and partner both grazing; partner in its apparently normal grazing activity moves away from male; male suddenly looks up and moves to partner. Also, when animals were leaving shade trees at the beginning of the afternoon session of activity they would occasionally be "chased" by males. However, in the great majority of cases, it seems to be wholly the actions of the courting male that initiate the mating.

Phase II: Mounting. Having moved to the partner, and possibly nozed it, the male may now mount. In mounting, the neck is extended its full length over the carapace of the partner (Figure 73). The male then steps up with a front leg and moves his body forward over the carapace of the partner until he actually steps onto it with the front leg. Stepping on with the other front leg, he continues to move forward on the partner's carapace, finally resting his plastron on it.

In not all cases, however, is the mounting so direct. The male may extend his neck over the partner but not step up; this is most

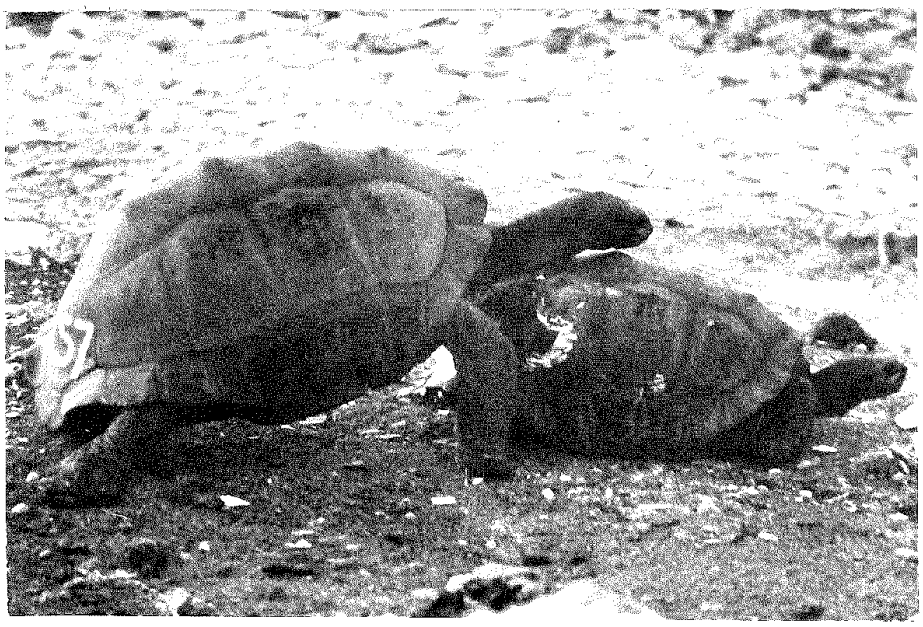


Figure 73. Mounting, neck extended over female, stepping up with left front foot. Female is "looking up". This pair mated successfully.

common if the partner is moving away and the male cannot get his body far enough over it - but it may also occur when the partner is perfectly still. In addition, the male may extend his neck, step up with his front leg, but not actually step onto the partner. He may then lower his leg back to the ground, lift it again, lower it, etc. This action looks much like prancing or working a treadmill; such behaviour is commonly called "ambivalent" (Hinde 1970).

The male may not necessarily mount the partner's posterior, but climb onto its anterior or side (Figure 74). If the mounted male is not facing the partner's anterior, he may pivot on its carapace to orient properly before beginning the next phase of the mounting.

During the mounting the partner may do most of the options previously listed for the premounting phase: stand, "look" up, move away, withdraw its appendages, or make no response. There are also two additional options which can occur during mounting. The partner may stand and at the same time, while keeping the four feet stationary on the ground, swing its posterior from side to side in short alternate arcs, occurring about once a second. This "tortoise twist" makes it very difficult for the male to remain on the partner and usually he is dislodged or comes off of his own accord.

The most common response to being mounted is to push up with the front legs, raising the anterior of the body and at the same time wedging the posterior of the carapace into the substrate (Figure 75). The front legs are often slightly spread to the sides forming a broad base. This "protecting" posture is made when the male mounts from the posterior. If he mounts from the anterior, the partner will most likely elevate its posterior, thereby "protecting" its anterior. Similarly, if the male mounts from a side, the partner will raise the opposite side, lowering the "attacked" side into the substrate. In this way the partner reduces the exposure of its soft parts at the site of "attack". In relation to mating, the protecting posture takes



A



B

Figure 74. Mounted sideways.

A. Groan-thrusting, with mouth open.

B. Mounting with mouth open.

Female in A is elevating her posterior slightly.



Figure 75. Female protecting posterior.



Figure 76. Male covering female, neck fully outstretched, mouth open, and head nearly touching female's. Head of female completely withdrawn into shell.

advantage of a built-in chastity belt, for when the posterior is wedged into the substrate the supracaudal scute forms an impenetrable barrier to the cloaca.

While "protecting" is the most common posture in this phase, it is intriguing that some animals make no overt response to the initial mounting; they simply continue to graze. If the male is clumsy or very active during mounting, he will probably scratch and generally hit the partner which will almost certainly lead to its adopting the protecting posture.

Phase III: Groan and Thrust. The most conspicuous aspect of this phase is described in the name. To begin with, the male moves forward on the partner by extending his hind legs; with his front legs he stands on the first pair of costal scutes on the partner's carapace. His neck is fully outstretched and hung down so that it is as close as possible to the head of the partner (Figure 76); in fact, the anterior of his plastron may be in the way, with his neck pressed hard against the gular scutes. The mouth is often open, and as the male's body moves forward he may make biting movements at the head, elbows, or anterior of the carapace of the partner. Some males even drool which gives the whole action a very lustful appearance.

At the same time the male is manoeuvering his tail at the posterior of the partner. It winds back and forth probing for a way round the partner's supracaudal scute. Often his tail curves to one side of the supracaudal, going under the upturned marginals behind a hind leg.

Once the tail succeeds in making contact with the soft parts of the partner's posterior it begins to "hook". In hooking, the tail is formed into a letter "J", and the distal end, which is covered with a stout scale, is pressed into the base of the partner's tail, prodding upward with considerable force.

When the male reaches the limit of his forward body movement, the

front legs are alternately swung forward. The hind legs are then unweighted, usually by lifting them simultaneously off the ground, and at the same time the front legs pull backwards and inward, against the partner's carapace, slowing the male's backward fall. In so doing, his front legs commonly hit the partner's head and front legs, often quite forcibly. As the male descends posteriorly, he produces a loud, low frequency groan or bellow (Figure 77).

As his body rocks back, his tail thrusts forward into the partner. At the end of the thrust, with his hind legs raised off the ground and the body rocked back so far that the front legs have lost contact with the partner's carapace, the male may be supported by only his tail. One cycle now completed, the male extends his hind legs and begins another groan and thrust cycle. One cycle takes about five seconds (Table 21).

TABLE 21. Rate of groan thrusting

Male	Date	Time	Cycle(s) per seconds
	1969		
T14	25 April	0610	1 / 4·5
"	" "	0650	1 / 5
"	" "	0740	5 / 30
"	" "	"	"
"	" "	"	"
"	" "	"	"
"	" "	"	"
"	" "	"	"
	27 April	1745	6 / 25
unmarked	1 May	1610	5 / 21·5
"	" "	"	5 / 22·5
"	" "	"	5 / 23·5

During the groan and thrust phase the partner may perform many of the options of phases one and two: stand, withdraw its appendages, look up, protect its soft parts, or move away. Standing is rare, for

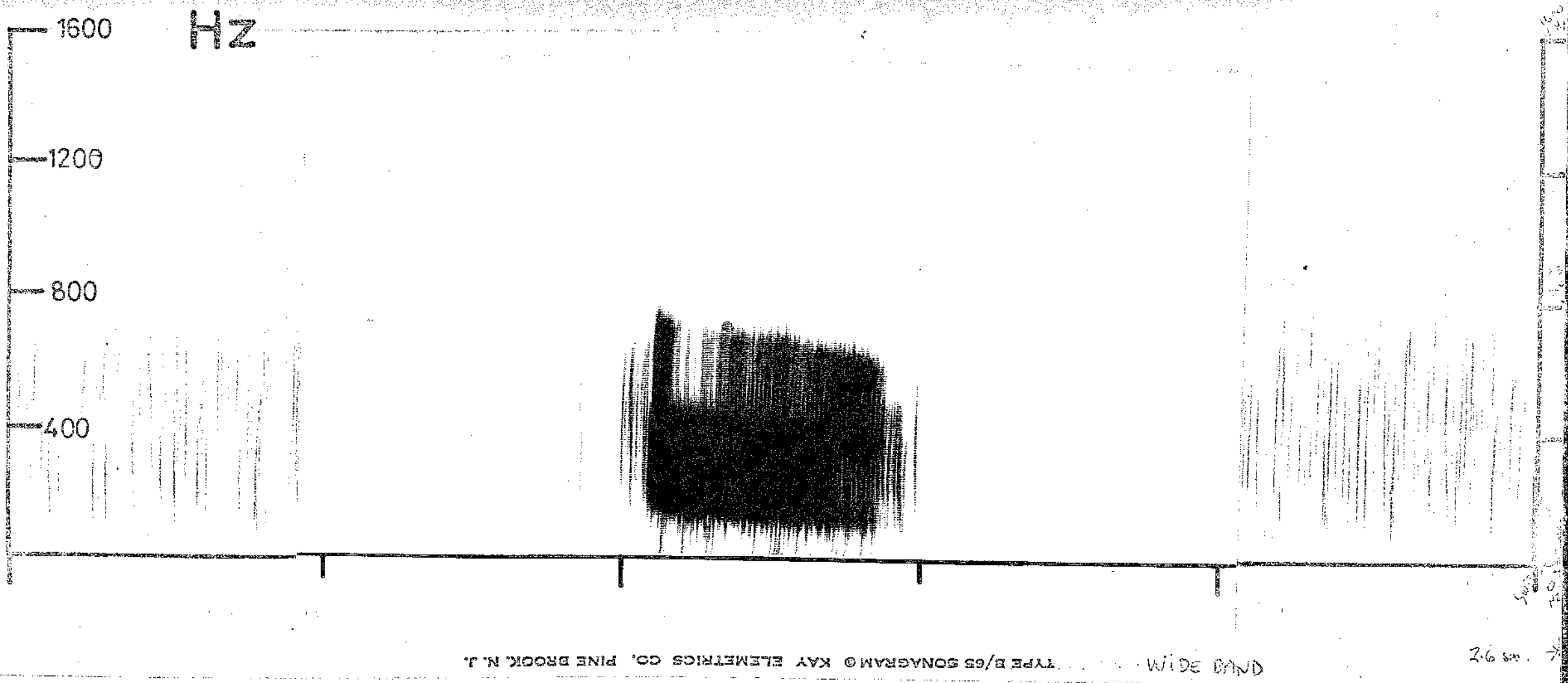


Figure 77. Sonagram of Male 45 groaning while mounted on an immature male 30th March 1970 at 1620 hours. Horizontal axis is marked off in half-second intervals. Recorded on a Phillips cassette recorder - EL 3301/220.

it can only occur when the partner is larger than the male. Withdrawing is not uncommon, especially after the male has smashed the partner's anterior with his massive front limbs. Again, it is intriguing that in this phase of the mating, with the male actively thrusting, the partner may make no more response than to simply stop grazing and slightly lift its head. However, once the male begins "hooking" with his tail, the partner will almost certainly respond by either protecting its posterior or moving away.

Protecting is the most common response and it is often followed by the partner suddenly bolting out from under the groan-thrusting male. It is not always easy for the partner to escape from the male; often it appears to be pinned to the ground by the mere force of his weight. It also seems that the deeply concave plastron of the male may "trap" the partner, and in such a case the partner will only be able to make small movements under the male. It may push or budge forward with all four limbs, moving just a few cm, or it may turn or spin sharply under him. Spinning can be very effective in dislodging the male. If suddenly the lower animal spins sharply to one side, the male will have to reposition himself on its carapace. As he is pivoting he will be offbalance and if the partner suddenly spins back the other way the male may be dislodged or caused to fall off.

If the partner does manage to break out from under the male, it will usually move only a few steps before immediately beginning to graze. If it continues to move forward, and the male is nearby, it is highly likely that he will suddenly move to it and possibly remount. (As stated above, moving away by the partner often results in the male approaching and mounting.)

If the partner moves a great deal under the male, or maintains a very steep protected posterior, he simply stops groan-thrusting and dismounts. Otherwise, he will carry on groaning and thrusting, and as the hooking continues, the female will begin to exhibit behaviours commonly seen during defecation. Her tail, instead of

being tightly tucked to one side under her shell, will be wiggled from side to side, and cloacal flatus or defecation may even occur. But, most important to the copulation, the female will, as in a normal defecation, elevate her posterior by extending her hind legs (Figure 78). This exposes her posterior and allows coition, the next phase, to occur.

Phase IV: Coition. After groan-thrusting has occurred for several minutes the female may be flat on the substrate or even elevating her posterior. At the end of a thrust the male will suddenly evert his penis, often with an explosive sound. If properly guided, it will find the female's cloaca and coition will be effected. However, the phallus does not always strike the target; on one occasion, for example, it shot forward, missed the cloaca, turned to the left, and evidently became wedged between the female's knee and her shell. In this situation the male must stop, withdraw the penis, resume groan-thrusting, and try again.

Once coition is effected the male may stop groan-thrusting and remain quiet upon the female. More frequently, however, he will continue groaning and thrusting, but not as rapidly or rhythmically as he did before coition. Both the amplitude and frequency of the thrusts are much reduced. Yet, the male's posture on the female remains the same with his neck fully outstretched and his head near to hers; he may even make biting movements.

In some copulations there was no noticeable activity at the male's tail. In others, there were obvious "peristalic" movements, and the midpiece, or stalk, of the penis (which can be clearly seen Figure 79) seemed to be thrust forwards and backwards by muscles in the tail.

Coition lasts about five minutes.

During coition the female sits quietly, but towards the end she may begin to squirm. After several minutes of coition the male may



Figure 76. Female showing posterior.
The same pelt as in Figure 73.



Figure 77. Caliban, the puppies in marbled.

suddenly withdraw his neck and expire or groan. The groan is not the same as that heard in "groan-thrusting" but is more like a groan of "effort". Finally, the male will withdraw his penis from the female's cloaca into his own. This is done quickly except for the distal end ("glans") which, when engorged, may be more than five cm wide - possibly too wide to be redrawn into the cloaca. It will thus lay on the ground and may become covered with sand or other debris. At the same time as the male withdraws his penis, he also withdraws his neck (Figure 80). Thus, the position of a mounted male's neck is a good indicator of his activity.

Phase V: Dismount. This is the last phase in the mating sequence. Having stopped his activities, the male may simply rest stationary on the female. When he does dismount he steps back simultaneously with both hind legs, sliding his plastron down the partner's carapace. If the partner moves under him, his departure may not be quite so elegant, for he may either slip to a side or fall off.

In this last phase the partner's actions may again involve most of those mentioned before: protect, spin, budge, move away, wag posterior, look up, or no response. Moving away is the most common. As the mated female moves off, her tail typically hangs down vertically (rather than being tucked up as usual), and her tail and posterior are often wet.

Once separated, the male may begin to graze, but usually he will just sit quietly; he may sit for five or ten minutes, or even half an hour. The female, on the other hand, will usually begin grazing right away. She may even begin while the male is still resting upon her or she may graze close beside him.

General considerations. A complete mating, if there are no complications, may take ten minutes or more. I have records of over 900 matings, about a third of which are from vocalizations, and I

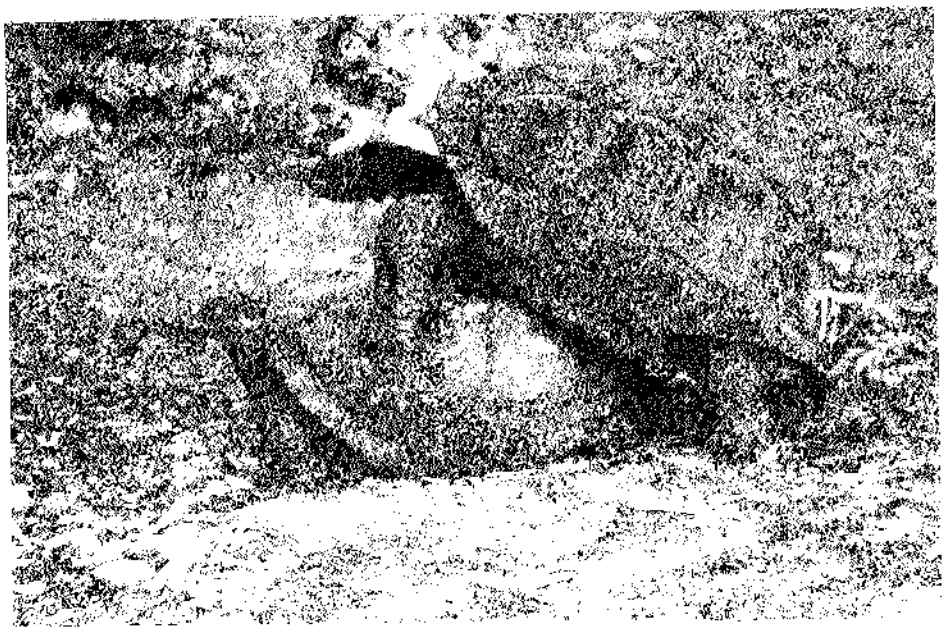


Figure 80. Coition finished, male's neck is withdrawn. Female is "looking up".

have recorded only six matings in which insertion was certain. The vast majority of tortoise matings that I have witnessed were unsuccessful and most were far more complicated than the brief sequence described above. The male may recycle within a phase or to various other phases in the sequence. He may, for example, move to the partner, mount and begin groan-thrusting. The partner may protect its posterior and then suddenly bolt out from under the male. He may approach again, remount, and so on. Large males, especially, are very persistent, some spending half an hour or more attempting to inseminate a female.

It is not uncommon for the male to stop of his own accord, before the end of the mating sequence. He may move to a female, noze, and then move on; or he may mount, stop on the female, and then just dismount. Occasionally the male may do a few groan-thrusts and then dismount. If the lower animal holds the anterior of its body high off the substrate, in an intense protecting posture, this wedges the supracaudal shield firmly into the substrate and makes coition impossible; likewise, many spinning and budging movements under the male make it difficult for him to stay upright and impossible for him to inseminate. These vigorous rejections invariably lead to the male terminating the mating of his own accord. In the few successful copulations I have seen the female did not vigorously reject the male, although she may have elevated her anterior slightly in the early phases of the mating.

On every occasion that I could verify, an unsuccessful male mandibulated either after stopping on the partner or after dismounting. Occasionally he would mandibulate while still on the female and then again after dismounting. When mandibulations did occur, there were usually two or three given together in a "bout", and whenever it was possible to observe, swallowing was recorded at the end of the mandibulations. Occasionally, an unsuccessful male

would also eye blink conspicuously, making long, deliberate, frequent blinks. Likewise, a female that has been pinned to the ground during groan-thrusting might also mandibulate and/or eye blink, but because it was difficult to observe the lower animal in detail I do not know how often these behaviours occurred.

The partner. I stated in the beginning of this section that the partner might be either male or female. Breeding males do not seem to discriminate on the basis of sex when selecting a mate. A male may complete a successful copulation one day and then spend the next day trying to mate with males or immatures. However, there is a distinct discrimination on size, a male will rarely select a female larger than himself. Matings involving known animals were recorded forty-eight times; in only three instances was the female the larger member of the pair. Nine cases in which the exact measurements were known are plotted in Figure 81. It is highly unlikely that this consistent size difference arose by chance ($p = \cdot 002$, sign test).

Other than coition, the sequence of events in a homosexual mating are indistinguishable from that in a heterosexual mating, for male partners behave just like female partners.

Masturbation. This behaviour has been recorded three times in 1970. On 28 January, at 1740 hours, a subadult male was seen standing in a "defecation posture" with the posterior of his plastron elevated ten to twenty cm off the ground. For several minutes he thrust his penis in and out of the cloaca; this was done at a rate no faster than about once every ten seconds. At one point the penis was out nearly fifteen cm lying on the ground, and the animal stood on all four legs. After about a minute he lowered his anterior and resumed the in and out thrusting. This animal masturbated for at least five minutes and for the duration of this time there was a conspicuous amount of eye blinking and mandibulating.

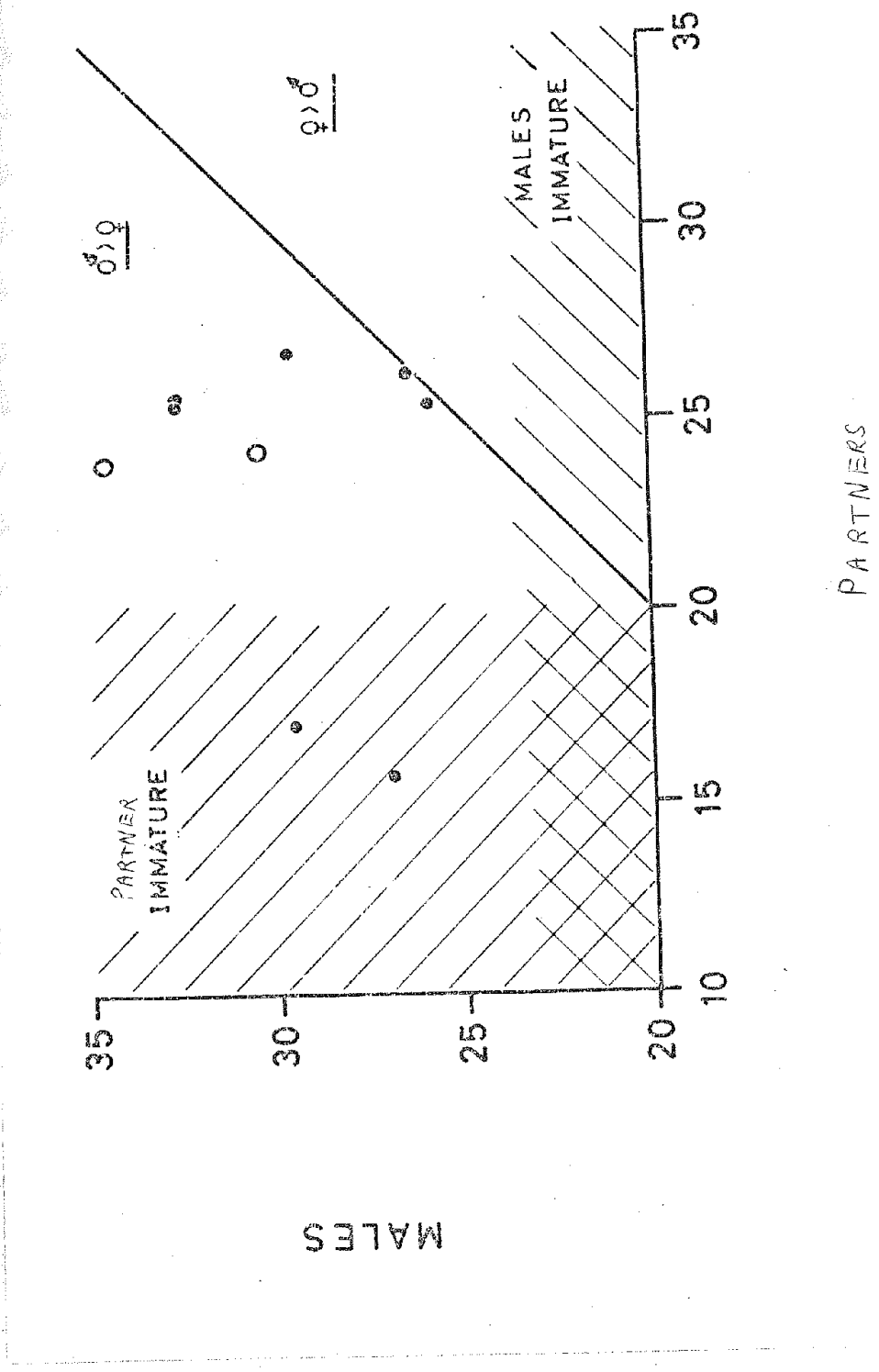


Figure 81. Curved width of the third vertebral scute (in cm) in copulating males and their partners
● = unsuccessful
o = successful
Above the diagonal males are larger than females, below females are larger.
Females are thought to mature at about 20 cm, males between 20 and 25 cm.
(See Grubb 1971a)

On 12 March, at 1830 hours, an adult male about 80 cm long was observed masturbating on the east plain. He was grazing in a defecation posture; but rather than voiding faeces, as it first appeared, he was thrusting the penis in and out. The phallus was everted ten to fifteen cm. His tail hung down vertically and the tip jerked up convulsively but also rhythmically. After several minutes he lowered his plastron onto the substrate. Since his tail was left outstretched, with the tip pointing forward, he actually pressed his tail between substrate and plastron. Rhythmic, almost peristalic-like, movements in the base of the tail indicated that the penis was being thrust in and out. After several minutes he elevated his posterior and resumed penial thrusting with the convulsive rhythmical tail jerks. After about five minutes of observation I had to leave the animal masturbating since the twilight had come.

On 22 March, at 1830 hours, a large male about 80 cm long was moving over the east plain in a peculiar manner. He walked in short strides with the posterior unusually elevated; his tail was extended and the penis everted so that it ploughed along the ground as he moved forward. He stopped walking, and lowered his body to the ground, pressing the outstretched tail between plastron and substrate. After a minute he stood on all four legs, everted the penis, and then lowered his body, again pressing the phallus between plastron and substrate. As with the previous observation, the light was failing and I had to leave the animal after five minutes.

Discussion of Mating Behaviour

The mating behaviour of giant tortoises, although simple in comparison with other vertebrates, raises a number of problems in interpretation. In order to discuss these in a frame of reference I will consider mating behaviour under four major headings: function, causation, development, and evolution (as per Dilger 1962).

Functional aspects of mating behaviour.

The female or partner. The immediate functions of the partner's behaviour are, on the whole, fairly obvious. Moving away, budging, and spinning are ways in which the partner can break contact with the courting male and reject him. It is important to note, however, that once this contact is broken the partner does not continue to move away from the male, but usually halts soon after separation. This is probably related to the fact that moving away from the male often results in his following or mounting.

"Standing" is another means of interfering with the male's mating attempts. In order to mount he must elevate his plastron over the partner's shell, and this will be impossible if the top of its carapace is higher than he can raise his plastron. On some occasions standing appears to be a threat (i.e. occurring in "conflict situation"), but the response of the "threatened" animal is extremely inconsistent. It may move away, sit quietly, or even approach or noze the standing animal.

The posture which involves elevating the anterior, while at the same time depressing the posterior into the substrate, I have called "protecting", for this is just what it does. It is not only adopted in mating situations, but may occur in response to many forms of disturbance. Protecting is an especially common response to tactile stimulation. Eibl-Eibesfeldt (1960, p. 53) describes a wallowing Galapagos tortoise that adopted this posture simply in response to the author's approach.

Withdrawing within the shell is another way of protecting the soft parts, but in this posture, with all the appendages inside the shell, the animal is depending solely on its shell and heavily scaled legs as armour. The substrate is not used in conjunction with the shell to form a barrier to the animal's soft parts, as is done in the "protecting" posture.

"Looking" up and nozing do not have any clear functions, other than the obvious one of the partner perceiving the male either visually or by scent. Grazing, which involves no overt response to the male, has no apparent function in the sexual context for grazing females may either reject the male vigorously or allow him to copulate. The females that were involved in successful copulations were grazing before (and sometimes while) they were mounted, but some of the most uncooperative females were also grazing before being mounted. Moreover, the female may commence grazing immediately after a mating, and sometimes even while the male is still mounted on her.

The above behaviours occur in the same form and have the same function, regardless of whether the partner is male or female. The only mating behaviour specific to a female partner is that involved in coition, i.e. elevating the posterior, uncurling the tail, and exposing the cloaca. This, quite simply, allows access to the cloaca. The courting male. Nozing behaviour clearly involves the exchange of air, for soft whistling can be heard in rhythm with the pulsations of the throat, and at close range air currents from the nostrils can be felt. This air exchange, however, is almost certainly not related to respiration, but to olfaction (see Appendix II).

The importance of olfactory cues in mating have been shown (or indicated) in a number of reptiles: snakes (Baumann 1929; Noble 1937); lizards (Goin and Goin 1962); and especially tortoises (Auffenberg 1964 a; 1965; 1966; Moncayo 1966; Rose 1970).

Hence, nozing is probably a means of olfactory sampling. Its usual function is for species and/or sex discrimination; and it may also function for discrimination of receptive versus non-receptive females. In the above chelonian studies at least one of these three functions has been shown or implicated. However, only one species of tortoise exists on Aldabra, and males will often mount

other males or unreceptive females. Homosexual behaviour is not uncommon in captives either (Noegel 1967; personal observation). It is difficult to say what function nozing has in the Aldabran tortoise.

The actions of the male during "groan-thrusting" have one thing in common - they break down the female's resistance. Biting and pawing are means of irritating and hitting the female's head and front limbs; this causes her to withdraw these appendages and thus to lower her anterior. In this way she is "tricked" into exposing her posterior.

Thrusting, by its sheer force, also breaks down the female's resistance. When the male thrusts, suddenly shifting his weight, it is not uncommon for the female to lose her balance and be knocked flat, thus exposing her posterior. It is also possible that thrusting may stimulate the female to cooperate in the mating, for there is considerable tactile stimulation of her carapace with the male moving forward and backward on it. After a mating the partner's carapace is often extremely scratched.

Like persistent pawing and biting, groaning may also result in an avoidance or withdrawal response by the female, causing her to draw her anterior appendages into her shell and abandon the "protecting" posture. Groans are very loud and are emitted when the male's head is extremely close to the female's (Figure 76). The sound has most of its energy concentrated between 100 and 500 Hz (Figure 77) which, on the basis of other chelonian studies, is probably the animal's most sensitive auditory region (see section on perception).

One might argue that the groans are merely a respiratory by-product of the effort involved in thrusting. On the two males that I dissected there was no indication of any vocal apparatus in the windpipe. The low frequency sound of the tortoise is probably

produced much like that of geese and swans where the resonating characteristics of the long tubular windpipe are important in the formation of the sound (Sutherland and McChesney 1965). (However, see Greenewalt (1968) for a criticism of this view.)

Nevertheless, the vocalisations do seem to be intentional. On many occasions a groan-thrusting male would not be able to complete a thrust because of some obstacle under his carapace, or because he was slipping offbalance; if groaning were merely an accident of the male's physical efforts it would not occur in such instances. But it did, and usually it was in perfect rhythm with previous groans. Campbell and Evans (1967) have also argued that sound production during mating in two smaller species of tortoise is not accidental.

It is also significant that many species of tortoise vocalise when mating (Table 22). It is dubious whether those sounds produced by the smaller species, described as "gasps" and "whistles", are audible to, or have much effect on, the female; but the vocalisations must, on the whole, serve some function or they would not be so widespread. Some sounds, such as those of Geochelone carbonaria seem very specialized (Campbell and Evans 1967), sounding much like a chicken clucking (Goin and Goin 1962; personal observation).

Hooking is yet another method of breaking down the female's resistance, but in this case it is the ultimate goal which is being exposed - the female's cloaca. The constant prodding by the male's tail apparently stimulates the female to make what is normally an autonomic response, i.e. defecation. This response serves two functions. First, it obviously exposes the posterior and particularly the cloaca. Second, it clears the cloaca of faeces. A common response of a tortoise being disturbed, especially around its cloaca, is to void copious amounts of faeces and fluids. Clearly this is incompatible with insemination. Thus, it is advantageous for the female to void what she can before coition, then "the path is clear".

Table 22. Summary of Testudinate mating behaviour.

Taxa	Pre-mounting									Post-mounting					Source
	Chase	Noze	Bite	Ram	Head bob	Vocalize	Titilate head	Other	None	Bite	Groan thrust	(Tail) Hook	Vocalize	Other	
Testudo graeca graeca	+		+	+									+		1
" kleinmanni													+		2
Geochelone elegans									?				+	S	3
" tranvancorica		+	-	+	+			X					+		4
" radiata													+		5
" pardalis babcocki				+				O ♀					+		6
" denticulata			+		+								+		7
" "				+											8
" "					+	+									9
" carbonaria			+		+	+							+		10
" sulcata													+		11
" elephantopus		+		+		+		O ♀			+	+			12
" " vandenburgii									*						13
" " "			+	+		+					+		+		14
" " vicna									*						15
" gigantea	+	+	(+)	-	-	-	-			+	+	+	+		16

X = Seasonal colour change
O ♀ = Circle female
S = Stamps with front feet
\+ = Present

(+) = Infrequent
\- = Definitely absent
* = No pre-mounting courtship
? = Probably no pre-mounting courtship

Sources for data presented in Table 22.

1. Bailly-Maitre 1928 and Astre 1948 (cited by Loveridge and Williams 1957, p. 270); personal observation.
2. Flower (? date) (cited by Loveridge and Williams 1957, p. 281).
3. Theobald (? date) (cited by Deraniyagala 1939, p. 287).
4. Auffenberg 1964, 1964b.
5. Baudy 1970.
6. Leakey 1944 and Archer 1948 (cited by Loveridge and Williams 1957, p. 243).
7. Auffenberg 1965; personal observation.
8. Beltz 1954.
9. Snedigar and Rokosky 1950.
10. Auffenberg 1965; Campbell and Evans 1967; personal observation.
11. Cloudsley-Thompson 1970.
12. Ditmars 1927; Mowbray (cited by Hendrickson 1966, p. 255); Moncayo 1966; personal observation.
13. Evans 1949.
14. De Sola 1930.
15. Evans 1949.
16. This study.

I have only considered what effects the male's behaviour may have on the female, but it is also possible that there is some form of positive feedback within his own sequence of behaviour. Positive feedback could be important in the erection of the phallus. Walton (1955) has described how the foreplay of the stallion is important in the preparation of the copulatory organ, and it is not unlikely that the male tortoise may need similar preparation. On numerous occasions, when the male had been groan-thrusting for some time, the penis could be seen protruding periodically from his cloaca, and this may be evidence that it was becoming more rigid. Clearly, the penis must be erect to successfully penetrate the female's cloaca.

The mandibulation and eye blinking that occur at the end of the mating sequence have no apparent function, in either male or female.

Causal implications of mating behaviour.

The question of causation has received considerable attention in the ethological literature, often to the point of overbalancing the science, as Tinbergen (1969) has described. It is not my intention to immerse the reader into hypothetical/theoretical discussions of causation, however it is instructive to examine a few aspects of tortoise mating in the light of conventional concepts of the causation of courtship and mating behaviour.

The female's behaviour. The possible responses of a mating female can be represented in an avoidance/non-avoidance dicotomy (Figure 82). This model is obviously a gross simplification, and I have made no effort to actually quantify the behaviours or to find their "co-ordinates". The postures have all been placed "by eye". Nevertheless, this may help to organize the mating behaviours of the female in relation to conventional interpretations.

It would be useful to quantify the postures and plot them

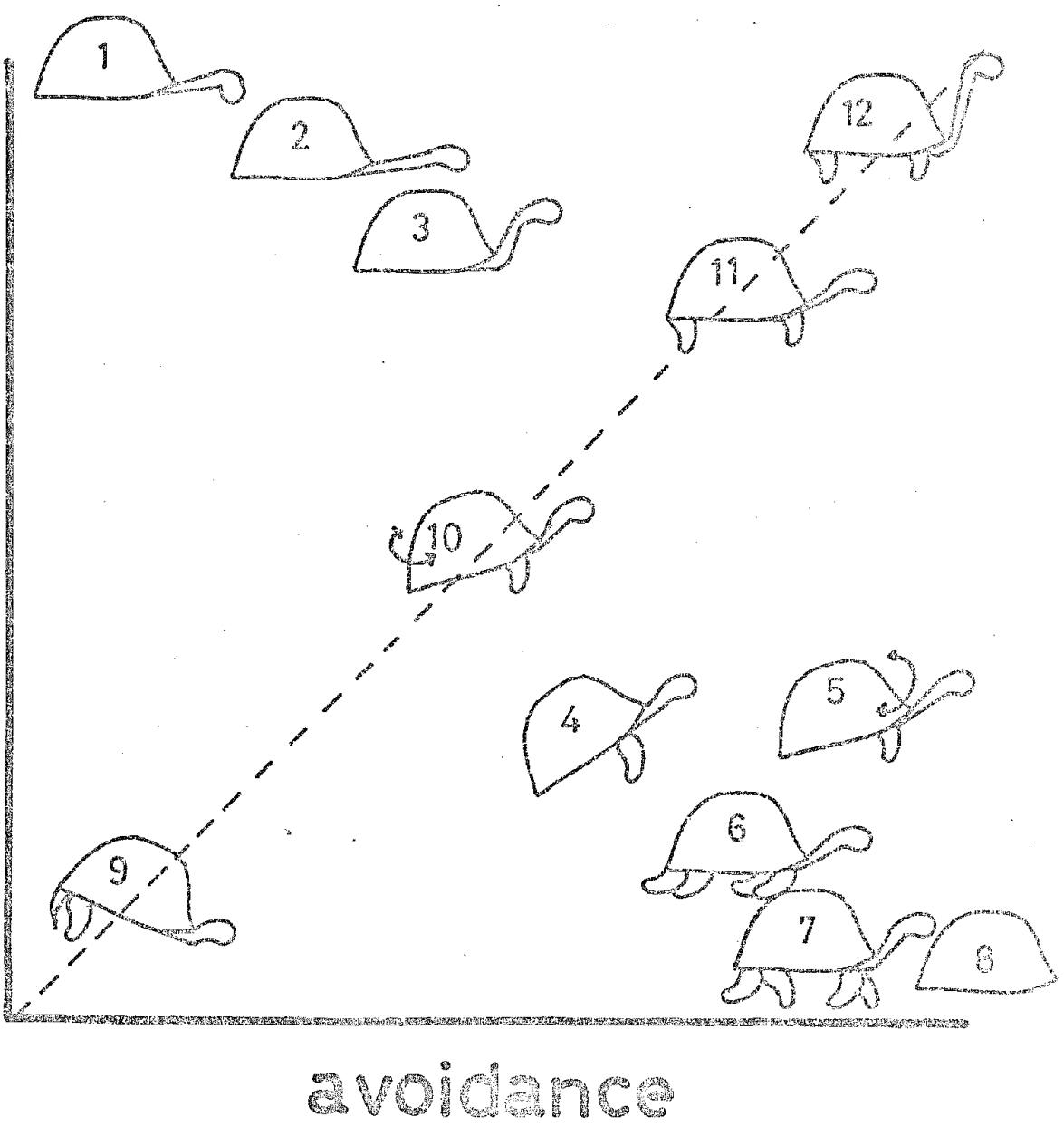


Figure 82. Postures of female tortoise during mating, plotted as to the 'strength' of the avoidance or non-avoidance response to the mating male.

1. grazing
2. nozing
3. looking up
4. protecting posterior
5. spinning under male
6. budging under male (thrusting forward with all four limbs)
7. walking away
8. withdrawing appendages into shell

9. elevating posterior
10. wiggling posterior while protecting posterior
11. standing, neck level
12. standing, neck erect

objectively, but without experimental manipulation this is not easy. Nor is it easy to see what parameters should be quantified to verify this graph. If one uses transition probabilities of two distinct events, each exclusive of the other, the two coordinates must always sum to 100, and this places strict limitations on where a posture can be "plotted".

Those behaviours grouped in the lower right are clearly responses to avoid the male - becoming more intense farther to the right. Those behaviours in the upper left are responses of non-avoidance to the male. It is the behaviours that I have placed on the diagonal that are most perplexing. Standing is a response that can precede either avoidance or non-avoidance behaviours. A standing tortoise may either resume the behaviours it was engaged in before being disturbed by the male (usually grazing), or alternatively it may suddenly withdraw and move away. Considered in this light, the occurrence of standing fits with the conventional concept of behaviour elicited in a state of "conflict" (Hinde 1970), and from this, and other observations in a non-mating situation, standing seems to be a threat posture (although, as I have stated above, it has a dubious function as such).

Two standing postures have been represented in Figure 82, head/neck erect and head/neck horizontal. In fact, intermediate forms may also occur, implying that different intensities of "conflict" result in different intensities of display, rather than a "typical intensity" as described by Morris (1957). The usefulness of the concept of "typical intensity" in bird displays has been challenged by Hinde (1953).

The behaviour of the female, just before coition, is similar to normal defecation (see defecation section), and hence is compatible with what Morris (1956 a) describes as an "autonomic response". This behaviour is also seen in non sexual situations. If a tortoise

(of either sex) is sitting quietly and is touched lightly on the soft parts of its posterior, the usual response is to elevate its back end by extending the hind legs. At the same time the tail is wiggled from side to side as would occur in defecation. Also, a common response to light rain is to elevate the posterior; however, I do not know if tail wiggling occurs in this situation.

The primary autonomic responses listed by Morris (1956 a) are thought to be stimulated by "thwarting situations". However, I have just described how an autonomic response can be elicited by simple tactile stimuli. If a tortoise is stimulated somewhat more vigorously it may not only raise its posterior, but also its anterior. With further stimulation the neck may even be raised; this is the posture I have called "standing" and have interpreted as a threat. As Hinde (1970) elaborates, threat displays occur in a state of "conflict", so that if one assumes a simple continuum of stimulus-response relationships, the posture with the posterior elevated could be considered as being elicited by "low intensity thwarting". However, this discussion is merely academic until some method is developed for obtaining an objective measure of intervening variables or hypothetical constructs such as "conflict" and "thwarting".

The male's behaviour. The male's first obvious response in the mating sequence is to look up and then to move to the female. This is clearly an approach response, and in successful matings it is carried through to the point where the male is fully in contact with the female.

One intriguing feature about tortoise copulation is the simplicity and directness of the mating sequence prior to mounting; there is virtually no premounting courtship. ("Courtship" being a set of signals, or behaviours, by which the male can: 1) test a potential partner for acceptability, i.e. if it is a conspecific female, and receptive; and 2) increase his chances of a successful

copulation by modifying the female's behaviour /Morris 1956 b; Assem 1970/. I shall not use the restriction that courtship occurs only before mounting, as does Bastock /1967 a, b/.) According to conventional views (Hinde 1953; 1970; Morris 1956 b; Bastock 1967 a, b) courtship occurs as the result of behavioural "conflict". I have described above how some males exhibit ambivalent behaviour in the mounting phase (Phase two), extending the neck over the female but not mounting, and stepping up but not onto the female. Similar ambivalent behaviours in a premounting context have been described in finches, and are called the "pivot dance" (Morris 1954; Hinde 1955).

Often the males that exhibit ambivalent behaviour also indulge in nozing and biting before attempting to mount. Immature and stunted males, as well as males that have previously been unsuccessful in mating, are the types of animals most often involved in this behaviour, that is those animals most likely to be unsuccessful in mating. They appear to be trying to mate, but something is evidently interfering. This reticence to mount seems to be due to an avoidance of the mating situation, "fear".

Living inside a rigid corslet, with its limb girdles inside the ribs, a mounted male tortoise is in a very precarious position. He is balanced by a minimum of supports, often at an angle of 45^{o} or more with the substrate. In addition, one very important support - the female under his plastron - is not only unstable but is actively trying to dislodge him. It is not surprising that many mating attempts end with the male falling off the female. Allard (1939) even postulated that death due to falling was a common end to copulation in the male box turtle (Terrapene carolina). Clearly, if a giant tortoise falls upside down and cracks his shell, lands in a pit, is heat prostrated before he can right himself, or is simply unable to right himself - his chances of survival will be greatly reduced. On two occasions I have seen groan-thrusting males fall

over upside down as the partner moved suddenly under him. Although I have never witnessed death by this means, many animals had very large gashes, holes, cracks, and other scars in the carapace which could well have resulted from falling off a female. For the sake of the male's safety, it would be highly adaptive for him to mount the female after he had made some precursory examination or action to reduce the chances of his being vigorously rejected. There is good reason for a male to "fear" the mating procedure.

Other evidence that the mating male is "fearful" is seen in his response to moving partners. When an animal moves away from him he commonly follows and mounts it, but if the partner suddenly stops moving away, a following male may also halt. Conventionally, this could be interpreted as evidence that the partner's moving away reduces the male's "fear" and allows his mating "tendency" to dominate. This explanation is consistent with an "approach/avoidance conflict" as discussed by Hinde (1970) (if "non-approach" is substituted for "avoidance"). In this model increased distance from the adversive stimulus decreases the avoidance (or non-approach) response and results in the approach response. The partner's moving away increases the distance and according to the hypothesis could decrease the non-approach response. The interrelationship between approach and non-approach however, must be a dynamic one, for otherwise the male would never get within a fixed limit to the female before the approach response were overcome by the increasing closeness of the female. As before, this model is hypothetical, for I have no measures of any of the intervening variables involved.

It could be said that before mounting a male is both "fearful" of the situation and at the same time strongly "motivated" to mate. This could be referred to as "FaM" conflict (Morris 1956 b) - Fear and Mating tendencies are strong, while aggression is weak. Hinde (1953; 1970) and Morris (1956 b) have both emphasised that the

occurrence of courtship necessitates behavioural "conflict". It seems that some form of conflict may be present in the male tortoise before mounting. Thus the behavioural potential for courtship is present.

On examining the mating behaviours of other testudinata it is clear that the evolutionary or phylogenetic potential for premounting courtship is also present (Table 22). Many tortoises bite the legs of the female or ram her before mounting.

In the Aldabran tortoise there is the long term evolutionary potential, the immediate behavioural potential, and the apparent adaptive value for premounting courtship. Yet its occurrence is rare and even inversely related to success. Why?

Is the lack "normal" or is it an artifact produced by some environmental conditions - e.g. the high population density? It is known that intense conditions, such as high density or lack of food, can have drastic effects on breeding (Watson 1970).

While the question of abnormality cannot be ruled out, it is significant that captive giant tortoises have essentially the same breeding behaviour (Noegel 1967; personal observation) as I have described for wild ones. Also, while some of the descriptions of mating in the Galapagos giant tortoise involve precopulatory courtship, many do not (Table 22). Thus, it is consistent with the available facts to assume that the mating sequence described above is normal.

"Rape" seems an appropriate description of the giant tortoise's mating, and curiously, this is very similar to the situation in some insects. In longicorn beetles the male must take the female by surprise when mounting. She actively rejects him at first, but once mounted he performs various behaviours to appease her (Michelsen 1964). Successful copulations in a cynipid wasp are initiated by quick antennal contact and then proceed directly to mounting; the

mounted male then performs various actions before coition (Assem 1969). Barrass (1960 a) found that the courting male Pteromalid wasp chases the female, but if she stops moving, he also stops (the males cease any moving object which is about the size of a female, but they will stop if it stops moving). Mounting in these animals follows directly after chasing. Parker (1969, p. 316) claims that "most calypterate courtship behaviour lacks display before mounting". Good evidence for this is seen in courtship descriptions of the house fly (Rogoff et al. 1964), the blowfly (Parker 1968), and the yellow dung fly (Parker 1969).

(Insects further parallel the tortoises in that there is no apparent selection for females over males - even at close range. Instead the male's choice of a partner is based primarily on visual cues - especially those of size (Parker 1968; 1969). Assem (1969) even reports that male cynipid wasps mount and court dead females or parts of their corpses. In the blowfly the parallel runs even closer; the female's role could be described as either passively accepting or actively rejecting the male (Parker 1968).)

Mating behaviour of Aldabran tortoises is more similar to some insects than to many other vertebrates and while this is interesting, it still does not explain why tortoises lack premounting courtship - especially when it is quite capable of occurring and has an obvious adaptive value.

Bastock (1967 b) has pointed out that while courtship is the result of "conflict" it need not always appear in a mating. She lists numerous studies (p. 18) in which the male reduces the amount of courtship with reduced opposition from the female and increases courtship with increased opposition. If there is no opposition, "conflict" is reduced and hence courtship may not occur.

In those few tortoises that did exhibit premounting courtship, animals were least successful in mating, while males that approached the female and mounted directly were most likely to be successful.

Thus, there is an inverse relationship between the occurrence of premounting courtship and success in mating, and it could be argued that the successful male has no opposition to mounting, hence does not court before climbing onto the female.

Subsequent behaviours seen in groan-thrusting appear to be aggressive, for the male bites, paws, prods, and hits the female. In Morris' (1956 b) terminology a groan-thrusting male would be described as "fAM", i.e. Aggression and Mating "tendencies", or "drives", are strong, while "fear" is weak. Adult male tortoises are very persistent at mating attempts; in one morning a large male may make as many as six attempts to mate. I have seen a male follow and attempt to mount with a female for ten minutes. Another expression of their libido is in masturbation.

The occurrence of mandibulation and intense eye blinking during mating is enigmatic, for, as I stated earlier, it has no obvious function, and it certainly has no relevance to the mating situation. Mandibulation and eye blinking occur in a situation conventionally described as "thwarting" (Delius 1970), for the male has (apparently) attempted to inseminate the female (the "goal") but has failed. Enigmatic behaviours that occur in situations such as this are termed "displacement activities", and are thought to indicate that the animal is in a state of high "arousal" (Delius 1970), although there is some question as to how "arousal" is measured (Hinde 1970).

Development of mating behaviours. Some authors have claimed that mating is completely "innate"; however experience is important in, at least perfecting, the mating of many species. Barrass (1960 b) found that courtship in a Pteromalid wasp was affected by both maturation and experience. Coulson and White (1958) have shown that breeding success is related to age in the Kittiwake (Rissa tridactyla L.), and Frazer (1968) lists a number of examples in the ungulates, where

mating success and age are related. Experience seems to play an important role in the mating of the giant tortoise.

The female. On escaping from the male, immature females often walk a considerable distance. Although this results in temporarily getting away from the male, in the end it usually leads to his following and remounting. Large (adult) females do not often make this "mistake", but usually stop just after separating from the male. These older animals seem to be more effective in rejecting the male. Whether or not they are more effective at cooperating in mating is not known. The elevated posterior, necessary for coition, is a posture which doubtless requires a considerable amount of strength, for the female has to lift 70 Kg of groan-thrusting male. Strength will be related to size, and size to age, but any age effect here is more a matter of maturation than experience. However, it is not unlikely that an experienced female can acquire a technique for facilitating mating.

The male. The mating attempts of the immature males I observed were awkward and ineffective. The young animals had a great deal of difficulty in mounting the partner, and before actually mounting they often spent considerable time moving about, nozing and making rather gentle biting movements at the partner's shell or limbs. Once mounted the young tortoises did not seem to know what to do next. If thrusting occurred it was of low amplitude and arhythmic; and the movements were uncoordinated. The groans were high pitched in comparison to those of adults, sounding much like a cough. The neck was not extended fully over the female (Figure 75). Most important, the tail was not held in the correct orientation but often stubbed the partner's carapace or the ground.

It is interesting to speculate that the lack of precopulatory ambivalence and courtship in adult males is a product of experience. After many attempts at mating the male may become practiced enough to have learned a technique. This might decrease his avoidance

response to mating, enabling him to proceed directly from approach to mounting, which is the most successful method.

Evolutionary aspects of the mating

The female There are essentially two major evolutionary questions in regard to female mating behaviour: 1. How did the precoital posture, with elevated posterior, evolve? 2. Why are the females so uncooperative?

The behaviours exhibited by a mating female are not unique to the breeding situation. The escaping and protecting behaviours are seen in other intra- and interspecific contexts. Both males and females have the same means of escaping and protecting. The only behaviour peculiar to the female partner is the precoital posture, but even this is indistinguishable from the defecation posture or the posture elicited by light tactile stimuli. Moreover, the response to rain is just like the precoital posture. Several species of African tortoise also elevate the posterior in response to rain. In those species with upturned marginals the shell actually functions for the catchment of rain. The water runs down the carapace to the marginals and then flows forward in the 'gutter' formed by these scutes. Draining off the shell at the anterior, the rain-water is immediately available for the animal to suck up from the ground. Although this behaviour would be highly adaptive in areas where there are sudden rains and little standing water, it is unlikely that the response to rain evolved primarily as a means of collecting drinking water. Tortoises, such as those on Aldabra, having rounded carapaces without marginals that form 'gutters', also make this response. In these species the reaction to rain does not have any apparent function. Hence, it seems likely that the posture is primarily a response to light tactile stimulation, the collection of rain-water being merely a secondary adaptation.

I do not know if the precoital posture illustrated by the Aldabran tortoise is common to the genus or land tortoises as a whole, for there are few detailed descriptions of mating in these animals. In small chelonians, such as Terrapene carolina and Geochelone tranvancorica,

insertion can be effected when the male is nearly vertical on the female (Carr 1952; Auffenberg 1964), and in this way he is not weighting the female down. In large tortoises it would be difficult for a male to maintain a vertical posture because of his great weight. During copulation, the giant tortoise covers the female with his body (Figures 74, 75, 76, 78, and 80) putting considerable weight on her. Thus, in these large animals insertion is not possible unless the female adopts the precoital posture. It would be of interest to compare the mating of large and small species to investigate the origin of this posture but this must await comparative studies.

The uncooperative nature of the female is an enigma; how can a species exist when only 1% of the mating attempts are successful? I argued that the mating sequence in regard to the male was not obviously abnormal. The same, however, may not apply to the female. I have argued that the tortoises on Aldabra appear to be food limited. There is also strong evidence that the reproductive output of Aldabran tortoises is less than either conspecifics in captivity or wild Galapagos tortoises. It would follow that the females are also less receptive if they are not receiving sufficient nutriment.

It is interesting that tortoise 99 was very active, and spent a large proportion of the day grazing; she appeared to be well-fed. Tortoise 99 was unreceptive to mating attempts initially, but she adopted the precoital posture several times and mated successfully at least twice in 1969.

I suggest that the lack of cooperation by the female giant tortoise during mating is a function of harsh environmental conditions - not an indication of some unusual adaptation.

The male Mating behaviour of the male tortoise is somewhat problematical in that there is a lack of premounting courtship. It would seem highly adaptive for the male to immobilize the female before mounting, as is done in other species of tortoise (Table 22).

Possibly the female giant tortoise is too strong for this to be of any use.

Giant tortoises, because of their great size, may have fewer predators than do smaller species, hence the giants may not react to disturbance by withdrawing within their shell but instead move away from the irritating stimulus. In this case premounting courtship would not help to keep the female quiet, and the best approach would be a direct mounting.

The published accounts of mating in Galapagos giant tortoises indicate that the occurrence of premounting courtship is very irregular. It seems that the giant tortoises do not court before mounting. Whether this involved an omission in the evolution of tortoises or whether the small tortoises evolved premounting courtship is not known.

The occurrence of other behaviours in the mating, such as biting, hooking, etc., serves rather a special funtion, and it is difficult to suggest from what they might have evolved without comparative material from other species.

Groaning in tortoises occurs in two contexts, during mating and during physical exertion. The two vocalisations are very similar and it is not unlikely that groaning may have first occurred in the mating sequence as accident. If loud, low frequency vocalisation helped to trick the female into protecting her anterior and exposing her posterior then groaning would be selected for in the mating.

The major weakness in studying the evolution of tortoise behaviour is that there is very little detailed material on other species with which to make comparisons, and the above discussion can serve mainly to draw this problem out into the open.

Admiralty Chart 2899 1965 Chagos Archipelago to Madagascar 1 : 3,500,000. Hydrographer of the Navy, Taunton, England.

Admiralty Chart 718 1967 Islands North of Madagascar. Hydrographer of the Navy, Taunton, England.

Allard, H.A. 1939 Mating of the box turtle ending in death of the male. Copeia 1939 : 109.

Arnold, G.W. 1963 Wool Technol. Sheep Breed. 10 : 17-19. Cited by Spedding, C.R.W. 1970 p. 110.

Assem, J. Van Den 1969 Reproductive behaviour of Pseudeucoila bochei (Hymenoptera: Cynipidae). I. A description of courtship behaviour. Neth. J. Zool. 19 : 641-648.

Assem, J. Van Den 1970 Courtship and mating in Lariophagus distinguendus (Först.) Kurdj. (Hymenoptera, Pteromalidae). Neth. J. Zool. 20 : 329-352.

Auffenberg, W. 1963 Fossil testudinine turtles of Florida genera Geochelone and Floridemys. Bull. Florida State Mus. 7(2) : 53-97.

Auffenberg, W. 1963 b A note on the drinking habits of some land tortoises. Anim. Behav. 11 : 72-73.

Auffenberg, W. 1964 Notes on the courtship of the land tortoise Geochelone travancorica (Boulenger). J. Bombay nat. Hist. Soc. 61(2) : 247-253.

Auffenberg, W. 1964 b A first record of breeding colour changes in a tortoise. J. Bombay nat. Hist. Soc. 61(1) : 191-192.

Auffenberg, W. 1965 Sex and species discrimination in two sympatric South American tortoises. Copeia 1965 : 335-342.

Auffenberg, W. 1966 The carpus of land tortoises (Testudininae). Bull. Florida State Mus. 10(5) : 159-192.

Auffenberg, W. 1971 A new fossil tortoise, with remarks on the origin of South American testudinines. Copeia 1971 : 106-117.

Barrass, R. 1960 b The effect of age on the performance of an innate behaviour pattern in Mormoniella vitripennis (Hymenoptera, Pteromalidae). Behaviour 15 : 210-218.

Barrass, R. 1960 a The courtship behaviour of Mormoniella vitripennis (Hymenoptera, Pteromalidae). Behaviour 15 : 185-209.

Bartholomew, G.A. 1966 A field study of temperature relations in the Galapagos Marine iguana. Copeia 1966 : 241-250.

Bastock, M. 1967 a Courtship: A zoological study. London; Heinmann.

Bastock, M. 1967 b The physiology of courtship and mating behaviour In McLaren, A. Ed. Advances in Reproductive Physiology Vol. II : 9-51. London: Logos Press.

Baudy, R.E. 1970 In quest of Geochelone radiata. Int. Turtle and Tortoise Soc. J. 4(1) : 19-23, 27.

Baumann, F. 1929 Experimente uber den geruchssinn und der Beuteerwerb der Viper (Vipera aspis). Z. vergl. Physiol. 10 : 36-119.

Bell, R.H.V. 1970 The use of the herb layer by grazing ungulates in the Serengeti. Brit. Ecol. Soc. Symp. No. 10.

Bell, R.H.V. 1971 The grazing ecosystem in the Serengeti. Scient. Am. 225(1) : 86-93.

Beltz, R.E. 1954 Miscellaneous observations on Testudinidae. Herpetol. 10 : 45-46.

Beltz, R.E. 1958 Eating habits of some captive Testudines. Herpetol. 13 : 272.

Benedict, F.G. 1932 The physiology of large reptiles. Washington: Carnegie Institution.

Benson, C.W. and Penny, M.J. 1971 The land birds of Aldabra. Phil. Trans. Roy. Soc. Lond. B 260 : 417-527.

Blanc, C.P. 1971 Les reptiles de Madagascar et des iles voisines. Annales de L'Université de Madagascar No. 8 : 95-178.

Bogert, C.M. 1959 How reptiles regulate their temperature. Sci. Amer. 200(4) : 105-120.

Bojanus, L.H. 1819 Anatome Testudinis Europaeae. Vilnae reprinted by Society for the study of Amphibians and Reptiles 1970.

Boulenger, G.A. 1889 Catalogue of the Chelonians, Rhynchocephalians and Crocodiles in the British Museum (Natural History). London 8 : 167-173.

Boulenger, G.A. 1894 On remains of an extinct gigantic tortoise from Madagascar (Testudo grandidieri, Vaillant). Trans. Zool. Soc., Lond. 13(8) : 305-327.

Brattstrom, B.H. 1962 Thermal control of aggregation behavior in tadpoles. Herpetol. 18 : 38-46.

Brownlee, A. 1960 Studies in the behaviour of domestic cattle in Britain. Anim. Behav. 8 : 11-20.

Cagle, F.R. 1944 Home range, homing behavior, and migration in turtles. Misc. Publ. Mus. Zool. Univ. Mich. 61 : 1-34. Cited by Moll and Legler 1971, p. 67.

Cagle, F.R. 1950 The life history of the slider turtle Pseudemys scripta troostii (Holbrook). Ecol. Monogr. 20 : 32-54.

Cahn, A.R. 1937 The turtles of Illinois. Ill. Biol. Monogr. 16 (1-2) : 1-218. Cited by Carr 1952.

Campbell, H.W. and Evans, W.E. 1967 Sound production in two species of tortoises. Herpetol. 23(3) : 204-209.

Carpenter, C.C. 1965 Notes on the behavior and ecology of the Galapagos Tortoise on Santa Cruz Island. Proc. Okla. Acad. Sci 46 : 28-32.

Carr, A. 1952 Handbook of turtles. New York: Cornell University Press.

Carr, A. 1965 The navigation of the green turtle. Scient. Am. 212(5) : 79-86.

Carr, A. 1969 So excellent a fishe. New York: Natural History Press.

Casebeer, R.L. and Koss, G.G. 1970 Food habits of wildebeest, zebra, harbe beest and cattle in Kenya Masailand. E. Afr. Wildl. J. 8 : 25-36.

Castle, M.E., Foot, A.S. and Halley, R.J. 1950 Some observations on the behaviour of dairy cattle with particular reference to grazing. J. Dairy Res. 17 : 215-230.

Castle, M.E. and Halley, R.J. 1951 The grazing behaviour of dairy cattle at the National Institute for Research in Dairying. Brit. J. Anim. Behav. 1 : 139-143.

Clench, H.K. 1966 Behavioral thermoregulation in butterflies. Ecology 47 : 1021-1034.

Cloudsley-Thompson, J.L. 1961 Rhythmic activity in animal physiology and behaviour. London: Academic Press.

Cloudsley-Thompson, J.L. 1968 Thermoregulation in tortoises. Nature 217 : 575.

Cloudsley-Thompson, J.L. 1970 On the biology of the desert tortoise Testudo sulcata in Sudan. J. Zool., Lond. 160 : 17-33.

Clough, G. and Hassam, A.G. 1970 A quantitative study of the daily activity of the warthog in the Queen Elizabeth National Park, Uganda. E. Afr. Wildl. J. 8 : 19-24.

Cogan, B.H., Hutson, A.M. and Schaffer, J.C. 1971 Preliminary observations on the affinities and composition of the insect fauna of Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 315-325.

Corbett, J.L. 1951 Grazing behaviour in New Zealand. Brit. J. Anim. Behav. 1 : 67-71.

Coulson, J.C. and White, E. 1950 The effect of age on the breeding biology of the kittiwake Rissa tridactyla. Ibis 100 : 40-51.

Crofton, H.D. 1958 Nematode parasite populations in sheep on lowland farms IV Sheep behaviour and nematode infections. Parasitology : 48(3 & 4) : 251-260.

Darwin, C. 1900 Journal of Researches into the natural history and geology of the countries visited during the voyage of H.M.S. "Beagle" round the world. London: Ward, Lock & Co., Ltd.

Dawson, W.R. 1967 Interspecific variation in physiological responses of lizards to temperature. In Milstead, W. (ed.) Lizard Ecology: A symposium. Columbia: Univ. of Missouri Press.

Delius, J.D. 1970 Irrelevant behaviour, information processing and arousal homeostasis. Psychol. Forsch 33 : 165-188.

Deraniyagala, P. 1939 Tetrapod reptiles of Ceylon. London: Dulau & Co., Ltd.

De Sola, R.C. 1929 Notes on sex determination in a species of the Galapagos Tortoise. Copeia 1929 : 54-55.

Diamond, A.W. 1971 The ecology of the sea birds of Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 561-571.

Dilger, W.C. 1962 Methods and objectives of ethology. Living Bird. First Ann. Pub. Cornell Lab. of Orn. : 83-92.

Directorate of Overseas Surveys 304 (Series Y852) 1964 Aldabra Island (Sheets 1 and 2) 1 : 25,000. Directorate of Overseas Surveys; Tolworth.

Ditmars, R.L. 1927 Reptiles of the world. New York: MacMillan Co.

Duméril, A.M.C. and Bibron, G. 1835 Erpétologie générale ou Histoire naturelle complète des Reptiles. Paris Vol. 2. Cited by Loveridge and Williams 1957, p. 512.

Eglis, A. 1962 Tortoise behaviour: A taxonomic adjunct. Herpetol. 18 : 1-8.

Eibl-Eibesfeldt, I. 1960 Galapagos. London: MacGibbon and Kee.

Eisner, T. and Meinwald, J. 1966 Defensive secretion of arthropods. Science 153 : 1341-1350.

England, G.J. 1954 Observations on the grazing behaviour of different breeds of sheep at Pantyrhuad Farm, Carmarthenshire. Brit. J. anim. Behav. 2(2) : 56-60.

Evans, L.T. 1949 The reproductive behavior of the Giant Tortoises, T. vicna and T. vandenburghii. Anat. Rec. 105 : 579-580.

Farrow, G.E. 1971 The climate of Aldabra Atoll. Phil. Trans. Roy. Soc. Lond. B. 260 : 67-91.

Fosberg, F.R. 1971 Preliminary survey of Aldabra vegetation. Phil. Trans. Roy. Soc. Lond. B. 260 : 215-225.

Fraenkel, G.S. and Gunn, D.L. 1960 The orientation of animals. New York: Dover.

Fraser, A.F. 1968 Reproductive behaviour in ungulates. London: Academic Press.

Frazier, J. 1966 Observations on captive Galapagos tortoises. Typescript.

Frazier, J. 1971 Observations on sea turtles at Aldabra Atoll. Phil. Trans. Roy. Soc. Lond. B. 260 : 373-410.

Fritsch, A. 1870 Zur Anatomie der Elephanten-Schildkröte Testudo elephantina. Abh. K. Bohm. Ges. Wiss. 3(4) : 1-18.

Fryer, J.C.F. 1911 The structure and formation of Aldabra and neighbouring islands - with notes on their flora and fauna. Trans. Linn. Soc. Lond. (2) 14 : 397-442.

Gadow, H. 1894 On the remains of some gigantic land tortoises and of an extinct lizard recently discovered in Mauritius. Trans. Zool. Soc. Lond. 13(8) : 313-324.

Gans, C. (ed) 1969, 70 Biology of the reptilia. Vols. I, II. London: Academic Press.

Gans, C. and Hughes, G.M. 1967 The mechanism of lung ventilation in the tortoise Testudo graeca Linné. J. Exp. Biol. 47 : 1-20.

Garman, S. 1917 The Galapagos Tortoises. Mem. Mus. Comp. Zool. 30(4) : 257-296.

Gaunt, A.S. and Gans, C. 1969 Mechanics of respiration in the snapping turtle, Chelydra serpentina (Linné). J. Morph. 128 : 195-228.

Gaymer, R. 1968 The Indian Ocean Giant Tortoise Testudo gigantea on Aldabra. J. Zool. 154: 341-363.

Gibbons, J.W. 1968 Reproductive potential, activity and cycles in the painted turtle, Chrysemys picta. Ecology 49: 399-408.

Goddard, J. 1970 Food preferences of Black Rhinoceros in the Tsavo National Park. E. Afr. Wildl. J. 8 : 145-161.

Goin, C.J. and Goin, O.B. 1962 Introduction to Herpetology. London: W.H. Freeman & Co.

Gray, J. 1959 How animals move. London: Penguin.

Gray, J. 1968 Animal locomotion. London: Weidenfeld and Nicolson.

Greenewalt, C.H. 1968 Bird song: acoustics and physiology. Washington: Smithsonian Institution Press.

Grubb, P. 1971 a The growth, ecology and population structure of giant tortoises on Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 327-372.

Grubb, P. 1971 b Ecology of terrestrial decapod crustaceans on Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 411-416.

Günther, A.C.L.G. 1877 The gigantic land-tortoises (living and extinct) in the collection of the British Museum. London: Trustees of the British Museum.

Gwyn, M.D. and Bell, R.H.V. 1968 Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature, Lond. 220 : 390-393.

Hafez, E.S.E. (ed) 1962 The behaviour of domestic animals. London: Baillière, Tindall, & Cox.

Halley, R.J. 1951 The grazing behaviour of South Devon cattle under experimental conditions. Brit. J. Anim. Behav. 1 : 156-157.

Hancock, J. 1954 Studies of grazing behaviour in relation to grassland management. I. Variations in grazing habits of dairy cattle. J. Agric. Sic. 44(4) : 420-433.

Harris, V.A. 1964 The life of the rainbow lizard. London: Hutchinson.

Hay, O.P. 1908 Fossil turtles of North America. Washington: Carnegie Inst. No. 75 : 1-568.

Heath, J.E. 1965 Temperature regulation and diurnal activity in horned lizards. Univ. Calif. Publ. Zool. 64(3) : 97-136.

Heckrotte, C. 1962 The effect of the environmental factors in the locomotory activity of the Plains Garter Snake (Thamnophis radix radix). Anim. Behav. 10 : 193-207.

Heller, E. 1903 Papers from the Hopkins Standford Galapagos Expedition, 1898-1899. XIV. Reptiles. Proc. Wash. Acad. Sci. 5 : 39-98.

Hendrickson, J.D. 1958 The green sea turtle, Chelonia mydas (linn.) in Malaya and Sarawak. Proc. Zool. Soc. Lond. 130 : 455-535.

Hendrickson, J.D. 1965 Reptiles of the Galapagos. Pacific Discovery: Calif. Acad. Sci. 18(5) : 28.

Hendrickson, J.D. 1966 The Galapagos Tortoises, Geochelone Fitzinger 1835 (Testudo Linnaeus 1758 in Part). In Bowman R.I. Ed. The Galapagos. Proceedings of the Symposia of the Galapagos International Scientific Project. Los Angeles: Univ. of Calif. Press.

Hill, J.E. 1971 The bats of Aldabra Atoll, western Indian Ocean. Phil. Trans. Roy. Soc. Lond. B. 260 : 573-576.

Hinde, R.A. 1953 The conflict between drives in the courtship and copulation of the chaffinch. Behaviour 5 : 1-31.

Hinde, R.A. 1955 A comparative study of the courtship of certain finches (Fringillidae). Ibis 97 : 706-745.

Hinde, R.A. 1970 Animal behaviour. London: McGraw-Hill.

Holling, C.S. 1968 The tactics of a predator. Symp. R. Entomol. Soc. Lond. 47-58.

Honegger, R.E. 1967 Beobachtungen an der Reisenschildkröten (Testudo gigantea Schweigger) der Inseln im Indischen Ozean. Salamandra 3 : 101-201.

Hunter, R.F. 1954 Some notes on the behaviour of hill sheep. Brit. J. anim. Behav. II(2):75-78.

Johnstone-Wallace, D.B. 1944 The grazing habits of beef cattle. Proc. Brit. Soc. Anim. Prod. : 74-84.

Kenyon, W.A. 1925 Digestive enzimes in poikilothermal vertebrates. Bull. U.S. Fish. 511 : (977). Cited by Cagle 1950 : 45.

Khalil, F. and Haggag, G. 1955 Ureotelism and uricotelism in tortoises. J. exp. Zool. 130 : 423-432.

Klauber, L.M. 1939 Studies of reptile life in the arid southwest. Bull. Zool. Soc. San Diego 14 : 1-100. Cited by Heckrotte 1962, p. 193.

Kosh, R.J. and Hutchinson, V.H. 1968 Daily rhythmicity of temperature tolerance in eastern painted turtles, Chrysemys picta. Copeia 1968 : 244-246.

Landsborough Thomson, Sir A. 1964 A new dictionary of birds. London: Thomas Nelson & Sons Ltd.

Legrand, H. 1965 Lépidoptères des Iles Seychelles et d'Aldabra. Mém. Mus. natn. Hist. nat., Paris (A), Zoologie 37 : 1-210.

Leuthold, W. 1970 Preliminary observations on food habits of Gerenuk in Tsavo National Park, Kenya. E. Afr. Wildl. J. 8 : 73-84.

Licht, P. 1965 The relation between preferred body temperature and testicular heat sensitivity in lizards. Copeia 1965 : 428-436.

Loveridge, A. and Williams, E.E. 1957 Revision of the African tortoises and turtles of the Suborder Cryptodira. Bull. Mus. Comp. Zool. 115(6) : 161-557.

Mackay, R.S. 1964 Galapagos Tortoise and Marine Iguana deep body temperatures measured by radio telemetry. Nature 204 : 355-358.

Mackay, R.S. 1968 Bio-medical telemetry. London: John Wiley & Sons.

Macnae, W. 1971 Mangroves on Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 237-247.

McKenzie, K.G. 1971 Entomostraca of Aldabra, with special reference to the genus Heterocypris (Crustacea, Ostracoda). Phil. Trans. Roy. Soc. Land. B. 260 : 257-297.

McNeill, S. and Lawton, J.H. 1970 Annual production and respiration in animal populations. Nature 225 : 472-474.

Michelsen, A. 1964 Observations on the sexual behaviour of some longicorn beetles, subfamily Lepturinae (Coleoptera, Cerambycidae). Behaviour 22 : 152-166.

Mitchell, S.W. and Morehouse, G.R. 1863 Researches upon the anatomy and physiology of respiration in the Chelonia. Smithsonian Contrib Knowl. 13(159) : ix-43.

Moll, E.O. and Legler, J.M. 1971 The life history of a neotropical slider turtle Pseudemys scripta (Schoepff) in Panama. Bull. Los Ang. Co. Mus. Nat. Hist. Sci. No. 11.

Moncayo, G. 1966 In Carpenter 1966, pp. 28-32.

Morris, D. 1954 The reproductive behaviour of the Zebra finch (Poephila gutta), with special reference to pseudofemale behaviour and displacement activities. Behaviour 6 : 271-322.

Morris, D. 1956 a The feather postures of birds and the problem of the origin of social signals. Behaviour 9 : 75-113.

Morris, D. 1956 b The function and causation of courtship ceremonies. Fondation Singer-Polignac, Colloque Internat. sur L'Instinct (Paris, 1954), 261-266.

Morris, D. 1957 "Typical Intensity" and its relation to the problem of ritualization. Behaviour 11 : 1-12.

Mrosovsky, N. 1968 Nocturnal emergence of hatchling sea turtles: control by thermal inhibition of activity. Nature 220 : 1338-1339.

Noble, G.K. 1937 The sense organs involved in the courtship of Storeria, Thamnophis and other snakes. Bull. Amer. Mus. Nat. Hist., 73 : 673-725.

Noegel, R.P. 1967 Scanning the Indian Ocean Islands. Int. Turtle and Tortoise Soc. J. 1(6) : 30-36, 44-45.

O'Donnell, T.G. and Walton, G.A. 1969 Some observations on the behaviour and hill-pasture utilization of Irish cattle. J. Brit. Grassland Society 24(2) : 128-133.

Park, O. 1941 Concerning community symmetry. Ecology 22 : 164-167.

Park, O., Barden, A. and Williams, E. 1940 Studies in nocturnal ecology, IX. Further analysis of activity of Panama rain forest animals. Ecology 21 : 122-134.

Parker, G.A. 1968 The sexual behaviour of the blowfly, Protophormia terrae-novae R. - D. Behaviour 32 : 291-308.

Parker, G.A. 1969 The reproductive behaviour and the nature of sexual selection in Scatophaga stercoraria L. (Diptera: Scatophagidae) - III. Apparent intersex individuals and their evolutionary cost to normal, searching males. Trans. R ent. Soc. Lond. 121(8) : 305-323.

Parsons, T.S. 1967 Evolution of the Nasal Structure in the Lower Tetrapods. Am. Zool. 7 : 397-413.

Parsons, T.S. 1968 Variation in the choanal structure of recent turtles. Canad. J. Zool. 46(6) : 1235-1263.

Patterson, R. 1971 The role of urination in egg predator defense in the desert tortoise (Gopherus agassizi). Herpetol. 27(2) : 197-200.

Patterson, W.C. 1966 Hearing in the turtle. J. Aud. Resh. 6 : 453-464.

Patterson, W.C. and Gulick, W.L. 1966 A method for measuring auditory thresholds in the turtle. J. Aud. Resh. 6 : 219-227.

Peake, J.F. 1971 The evolution of terrestrial faunas in the western Indian Ocean. Phil. Trans. Roy. Soc. Lond. B. 260 : 581-610.

Penny, M.J. 1971 Migrant waders at Aldabra, September 1967 - March 1968. Phil. Trans. Roy. Soc. Lond. B. 260 : 549-559.

Penny, M.J. and Diamond, A.W. 1971 The white-throated rail Dryolimnas cuvieri on Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 529-548.

Perry, R. 1970 Tortoise rearing in the Galapagos Islands. Noticias de Galapagos. No. 15/16; 3-7.

Piggott, C.J. 1963 Seychelles - Soils Sheet 3 (to accompany "A soil survey of Seychelles" 1968). Directorate of Overseas Surveys.

Piggott, C.J. 1968 A soil survey of Seychelles. Tech. Bull. Land Resour. Div. Dir. Overseas Surv. No. 2.

Porter, D. 1822 Journal of a cruise made to the Pacific Ocean by Captain David Porter, in the United States frigate Essex, in the years 1812, 1813, 1814. 2 vols. New York: 2nd Edition. Cited by Van Denburgh 1914; p. 215.

Price, J.H. 1971 The shallow sublittoral marine ecology of Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 123-171.

Pritchard, P.C.H. 1967 Living turtles of the world. Jersey City: T.F.H. Publications.

Quaranta, J.V. 1952 An experimental study of the colour vision of the giant tortoise. Zoologica 37 : 295-312.

Regal, P.J. 1967 Voluntary hypothermia in reptiles. Science 155 : 1551-1553.

Renvoize, S.A. 1971 The origin and distribution of the flora of Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 227-236.

Rick, C.M. and Bowman, R.I. 1961 Galapagos Tomatoes and Tortoises. Evol. 15(4) : 407-417.

Riedesel, M.L., Cloudsley-Thompson, J.L. and Cloudsley-Thompson, J. Anne 1971 Evaporative thermoregulation in turtles. Physiol. Zool. 44(1) : 28-32.

Rodgers, L.J. 1966 The nitrogen excretion of Chelodina longicollis under conditions of hydration and dehydration. Comp. Biochem. Physiol. 18 : 249-260.

Rogoff, W.M., Beltz, A.D., Johnsen, J.O. and Plapp, F.W. 1964 A sex phermone in the housefly, Musca domestica L. J. Insect. Physiol. 10 : 239-246.

Romer, A.S. 1956 Osteology of the reptiles. Chicago: University of Chicago Press.

Rose, F.L. 1970 Tortoise chin gland fatty acid composition: behavioral significance. Comp. Biochem. Physiol. 32(3) : 577-580.

Rothschild, Lord W. 1906 Giant land tortoises. Nov. Zool. 13 : 753-754.

Rothschild, Lord W. 1915 On the gigantic land tortoises of the Seychelles and Aldabra-Madagascar group with some notes on certain forms of the Mascarene group. Novit. Zool. 22 : 418-442.

Rothschild, Lord W. 1928 Notes on gigantic land tortoises. Proc. Zool. Soc., Lond. : 658-660.

Sauzier 1892 Cited by Blanc 1971, p. 115.

Schweigger, A.F. 1812 Monographiae Cheloniorum. Königsberger Arch. Naturwiss. Math. 1 : 271-368, 406-458.
Cited by Loveridge and Williams 1957, pp. 225, 533.

Sergeyev, A. 1939 The body temperature of reptiles in natural surroundings. C.R. (Doklady) d'Acad. des Sci. De l'Urss 22(1) : 49-52. Cited by Cagle 1950, p. 45.

Shaw, C.E. 1961 Another generation of Galapagos giants. Zoonooz 34(12) : 10-15.

Sinclair, A.R.E. 1970 Studies of the ecology of the East African buffalo. Oxford: Unpublished D. Phil. thesis.

Smith, J.N.M. 1971 Studies of the searching behaviour and prey recognition of certain vertebrate predators. Oxford: Unpublished D. Phil. thesis.

Snedigar, R. and Rokosky, E.J. 1950 Courtship and egglaying of a captive Testudo denticulata. Copeia 1950 : 46-48.

Snow, D.W. 1964 Research Station in the Galapagos. ORYX 7(6) : 277-291.

Spanner, D.C. 1964 Introduction to thermodynamics. London: Academic Press.

Spedding, C.R.W. 1971 Grassland Ecology. Oxford University Press.

Spinage, C.A. 1968 A quantitative study of the daily activity of the Uganda Defassa Waterbuck. E. Afr. Wildl. J. 6 : 89-93.

Stebbins, G.L. 1966 Processes of organic evolution. New Jersey: Pentice-Hall, Inc.

Stickel, L.F. 1950 Populations and home range relationships of the Box Turtle, Terrapene c. carolina (Linnaeus). Ecol. Monog. 20 : 351-378.

Stoddart, D.R. 1968 The conservation of Aldabra. The Geographical Journal. 134(4) : 471-486.

Stoddart, D.R. 1971 a Scientific studies at Aldabra and neighboring islands. Phil. Trans. Roy. Soc. Lond. B. 260 : 5-29.

Stoddart, D.R. 1971 b Settlement, development and conservation of Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 611-628.

Stoddart, D.R. 1971 c Place names of Aldabra. Phil. Trans. Roy. Soc. Lond. B. 260 : 631-632.

Stoddart, D.R. 1971 d Rainfall on Indian Ocean coral islands. Atoll. Res. Bull. 147 : 1-21.

Stoddart, D.R., Taylor, J.D., Fosberg, F.R. and Farrow, G.E. 1971 Geomorphology of Aldabra Atoll. Phil. Trans. Roy. Soc. Lond. B. 260 : 31-65.

Stoddart, D.R. and Wright, C.A. 1967 Geography and ecology of Aldabra Atoll. Atoll Res. Bull. No. 118 : 11-52.

Stoddart, D.R. and Yonge, M. (eds) 1971 Regional variation in Indian Ocean coral reefs. Symp. Zool. Soc. Lond. No. 28. London: Academic Press.

Sutherland, C.A. and McChesney, D.S. 1965 Sound production in two species of geese. The Living Bird 4 : 99-106.

Swinton, W.E. 1965 Fossil amphibians and reptiles. British Museum (Natural History).

Tayler, J.C. 1951 The grazing behaviour of bullocks under two methods of management. Brit. J. Anim. Behav. 1 : 72-77.

Taylor, C.R. 1969 The Eland and the Oryx. Scient. Am. 220(1) : 89-95.

Taylor, J.D. 1971 Intertidal zonation at Aldabra Atoll. Phil. Trans. Roy. Soc. Lond. B. 260 : 173-213.

Templeton, J.R. 1970 Reptiles. In Whittow, G.C. (ed.). Comparative Physiology of Thermoregulation. London: Academic, pp. 167-221.

Thompson, D.W. 1917 On growth and form. Cambridge University Press, Cambridge.

Thomson, J.S. 1932 The anatomy of the tortoise. Sci. Proc. Roy. Dub. Soc. 20(28) : 359-461.

The Times 1967 Atlas of the World (comprehensive edition). Edinburgh: The Times and John Bartholomew and Son Ltd.

Tinbergen, N. 1969 The study of instinct. London: Oxford University Press.

Townsend, C.H. 1925 The Galapagos Tortoises in their relation to the whaling industry. Zoologica 4(3) : 55-135.

Townsend, R. 1795 Physiological observations on the Amphibia. Dissertation the third, on the respiration of the tortoise. Göttingen. Cited by Mitchell and Morehouse 1863, p. 1.

Van Denburgh, J. 1914 The gigantic land tortoises of the Galapagos Archipelago. Proc. Calif. Acad. Sci. 2(1) 203-374.

Waite, R., MacDonald, W.B. and Holmes, W. 1951 Studies in grazing management III. The behaviour of dairy cows grazed under the close-folding and rotational systems of management. J. Agric. Sci. 41 : 163-173.

Walls, G.L. 1942 The vertebrate eye. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

Walton, A. 1955 Sexual behaviour. In Hammond, J. (ed.) Progress in the physiology of farm animals. Vol. 2 : 603-616. London: Butterworth and Co.

Wardrop, J.C. 1951 Studies in the behaviour of dairy cows at pasture. Brit. J. Anim. Behav. 1 : 23-31.

Watson, A. (ed) 1970 Animal populations in relation to their food resources. (Brit. Ecol. Soc. Symp. No. 10.) Oxford: Blackwell.

Weese, A.O. 1917 The reactions of the horned lizard, Phrynosoma modestum. Biol. Bull. 32 : 98-116.

Wermuth, H. and Mertens, R. 1961 Schildkröten Krokodile Brückenechsen. Gustav Fischer: Jena.

Williams, E. 1950 a Testudo cubensis and the evolution of western hemisphere tortoises. Bull. Amer. Mus. Nat. Hist. 95(1) : 1-36.

Williams, E. 1950 b Variation and selection in the cervical central articulations of living turtles. Bull. Amer. Mus. Nat. Hist. 94(9) : 505-562.

Williams, E. 1952 A new fossil tortoise from Mona Island, West Indies, and a tentative arrangement of tortoises of the world. Bull. Amer. Mus. Nat. Hist. 99(9) : 541-560.

Woodbury, A.M. and Hardy, R. 1948 Studies of the desert tortoise, Gophorus agassizii. Ecol. Monog. 18(2) : 145-200.

Wright, C.A. 1971 Bulinus on Aldabra znd the subfamily Bulininae in the Indian Ocean area. Phil Trans. Roy. Soc. Lond. B. 260 : 299-313.

Zangerl, R. 1969 The turtle shell. In Gans, C. Biology of the reptilia. Vol. I. London: Academic Press.

APPENDIX I

Itinerary

1968

Jan.	8	Settlement
	9	Moustique
	10-12	Cinq Cases
	13-17	Middle Camp (Point Ile Malabar)
	18-19	Anse Cèdres
	20-21	Cinq Cases
	22	Cinq Cases to Dune D'Messe
	23-31	Settlement
Feb.	1-22	Dune Jean Louis
	23-24	Cinq Cases
	25-27	Dune Jean Louis
	28- 3	Settlement
March	4- 6	Astove and Cosmoledo Atolls
	7-12	Settlement
	13-20	Dune Jean Louis
	21-24	Dune D'Messe
	25-31	Settlement
April	1- 9	Settlement
	10-11	Middle Camp
	12-30	Dune Jean Louis
May	1- 3	Dune Jean Louis
	4-10	Settlement
	11	Middle Camp
	12-18	Dune Jean Louis
	19-20	Middle Camp
	21-31	Settlement
June	1-19	Settlement
	20-31	Dune Jean Louis
July	1- 6	Dune Jean Louis
	7-14	Settlement
	15-16	Dune D'Messe
	17-18	Ile Esprit, Settlement
	19-20	Anse Malabar
	21-25	Dune Jean Louis
	26-31	Settlement

1969

June	3- 4	Settlement
	5-15	Dune Jean Louis
	16-17	Settlement
	18-21	Astove
	22-27	Settlement
	28-30	Dune Jean Louis
July	1-31	Dune Jean Louis
Aug.	1-12	Dune Jean Louis
	13	Middle Camp
	14-20	Settlement
	21-23	Anse Mais & Settlement
	24-31	Dune Jean Louis
Sept.	1-14	Dune Jean Louis
	15	Middle Camp
	16-30	Settlement
Oct.	1-24	Settlement
	25-31	Dune Jean Louis
Nov.	1-28	Dune Jean Louis
	29-30	Settlement
Dec.	1-31	Settlement

1970

Jan.	1-31	Dune Jean Louis
Feb.	1-26	Dune Jean Louis
	27-28	Settlement
March	1-11	Settlement
	12-31	Dune Jean Louis
April	1-30	Dune Jean Louis
May	1- 6	Dune Jean Louis
	7-19	Settlement
	20	Tambalico
	21	Settlement
	22-31	Dune Jean Louis
June	1	Dune Jean Louis
	2	Cinq Cases
	3	Dune Jean Louis
	4-23	Settlement

APPENDIX II

RESPIRATION

Studies of respiration in Testudinates have long aroused interest in several major areas. Living inside rigid shells, these animals have peculiar problems in breathing. There are also characteristics in their breathing cycles, gas exchange mechanisms, and metabolism that are uncommon in other vertebrates.

Breathing movements

Breathing movements and mechanics in turtles and tortoises have been studied for some time (Townsend 1795; Mitchell and Morehouse 1863; Gans and Hughes 1967), but misunderstandings still appear in recent writings. Numerous authors have asserted that these animals pump air in and out of the lungs by up and down movements of the gular or throat area (called by various names: "throat pumping" (Bellairs 1957, p. 66), "pumping of the pharynx" (Young 1962, p. 397), "deglutition" and "hyoid pumping" (Mitchell and Morehouse 1863, pp. 1, 25), and "air swallowing" (Lüdicke 1936)).

Although this view has been held until recently (e.g. Negus 1965, p. 57), the bulk of evidence indicates that it is in error. Townsend (1795), by a series of simple yet ingenious experiments, showed that the swamp turtle (Emys orbicularis (L.)) uses various trunk muscles for powering different phases of its breathing cycle. Townsend's work was largely ignored until Mitchell and Morehouse (1863) drew attention to and verified his findings (Gans and Gaunt 1970). They argued that Testudinates are not equipped to pump air into the lungs with the throat alone, for the jaws are horny and cannot be made air-tight. Furthermore, there are no valves in the nares, and the laryngeal cavity is too small to act as a pumping chamber since its volume relative to the windpipes is too small to accomplish exchange of air in the lungs. Mitchell also showed that severing the trachea of a snapping turtle (Chelydra serpentina (L.)) did not arrest breathing; hence the pumping force was inside the shell and not in the throat. McCutcheon's (1943) findings on the diamondback terrapin (Malaclemys terrapin centrata (Latreille)) were in agreement with this; he showed that throat movements do not accompany changes in intertracheal pressures, but cease before breathing begins. Root (1949), working on the musk turtle (Sternothaerus), and Vos (1936) produced similar results.

The actual pumping mechanism has been studied in detail in both the Greek tortoise (Testudo graeca L.) (Gans and Hughes 1967) and the snapping turtle (Gaunt and Gans 1969). In both species the ventilating cycle is composed of three phases, each powered, at least in its initiation, by specific trunk muscles. Buccal movements were thought to be olfactory rather than respiratory in function, a view also maintained by Mitchell and Morehouse (1863), Luddicke (1936), and McCutcheon (1943). Thus, a number of workers, using several species of turtles and tortoises, have found strong evidence that throat movements are not responsible for, and are unrelated to, air exchange in the lungs.

Gaunt and Gans (1969) however, did allow for the possible exception that gular pulsations may have a respiratory function during aquatic respiration in that they provide circulation of water over the vascularized pharyngeal mucosa. This is consistent with Belkin (1968 a) who felt that buccopharyngeal movements were necessary for water ventilation during aquatic respiration in the musk turtle. Girgis (1961) also supports this interpretation of buccal movements, but the most convincing evidence for buccopharyngeal water exchange is the work of Cahn (1937) who showed that carmine particles flow in and out of the nares in rhythm with gular movements.

Some authors (e.g. Tauvery 1701 and Wolf 1933) have claimed that limb movements, and even walking, are necessary for breathing. Townsend (1795) disproved this by binding a tortoise, thus making limb movements impossible, and finding that it could still effect air exchange. The work of Gans and Hughes (1967) supports Townsend's findings.

Although breathing is not caused by limb movements, the two occur together in time. Gans and Hughes (1967) showed conclusively that movements of the front limbs in the Greek tortoise are associated with phases of respiration and that these movements are caused by the rotation of the pectoral girdle, not by the limbs themselves. In the snapping turtle, Gaunt and Gans (1969) concluded that although movements of limbs and limb girdles were capable of effecting respiratory exchanges, these animals use a diaphragm-like muscle within the body for breathing. Movements of the soft skin in the abaxillary and abinguinal areas also occur synchronously with breathing movements. Townsend (1795) observed that movements of paper flaps over the nostrils correlated with movements of the posterior body wall; and work by Mitchell and Morehouse (1863) and McCutcheon (1943) showed similar phenomena in other species.

Breathing rhythm

A second major area of study in Testudinate respiration is in the patterns of breathing. Many workers have noted that turtles have periods of breathing interspersed with breath holding (apnoea). Apnoea often, but not necessarily, occurs during diving. Shaw and Baldwin (1935), using an unnamed species of turtle, found that a dive with breath hold lasted 0·75 to 4 minutes, but if the ventilation was "thorough" apnoea could last twenty to thirty minutes or even three hours in a frightened animal. Belkin (1964) found dives where breath holding lasted about one hour in the river turtle (Pseudemys concinna (Le Conte)). The matamata (Chelys fimbriata (Schneider)) has breathing cycles that average 2·2 minutes of ventilation followed by thirty-five minutes of breath hold, while diving (Lenfant et al. 1970). Girgis (1961) describes periods of six hours' voluntary submergence in the Nile soft-shell turtle (Trionyx triunguis (Forskal)), and Berkson (1966, 1967) studied prolonged submergence in the green sea turtle (Chelonia mydas L.). While observing the diamondback terrapin on land, McCutcheon (1943) recorded pauses in breathing that lasted fifteen to sixty seconds or more.

Boyer (1963) and Gaunt and Gans (1969) also found apnoea interspersed with periods of breathing in the snapping turtle. The last two authors claimed that this respiratory rhythm is typical of all diving turtles but not of terrestrial tortoises which "ventilate more or less continuously" (Gans and Gaunt 1970, p. 17). Evidence for this statement is found in Gans and Hughes (1967) whose study of the Greek tortoise lead them to conclude that "the respiratory rhythm does not appear to be composed of brief periods of ventilatory activity followed by prolonged pauses ..." (p. 17). However, it is confusing to note that previously (p. 6) they state "the breathing rhythm of tortoises consists of pauses, interrupted by ventilatory movements, here referred to as ventilatory cycles. These pauses lasted between four seconds and twenty-three minutes." These authors seem to have overlooked the work of Atland and Parker (1955) which showed that the box turtle (Terrapene carolina (L.)) (a terrapin which is very tortoise-like and terrestrial in its habits) has a breathing pattern consisting of three or four ventilation cycles followed by a "postinspiratory pause" which could last half a minute or longer.

Metabolic adaptations

A third major area of Chelonian respiration studies involves the physiological adaptations that enable these animals to maintain the respiratory rhythms that they use. These adaptations involve mechanisms for aerobic respiration, anaerobic respiration, treatment of waste metabolites, and control of breathing.

Aerobic respiration. Oxygen uptake is very efficient in testudines, for it is only slightly decreased after lowering atmospheric oxygen from 21% to 2% (Boyer 1963). Belkin (1964) claimed that turtles can use about 90% of the oxygen in the lungs, extracting it at extremely low partial pressures. McCutcheon (1943) and later Robin (1962) and Boyer (1963) have suggested a means by which such efficient oxygen uptake could be effected. The internal lung pressure in resting turtles and tortoises is often greater than atmospheric (McCutcheon 1943; Gans and Hughes 1967; Gaunt and Gans 1969) and this would effectively increase the partial pressure of oxygen, enabling more oxygen to be extracted from the alveolar air. Furthermore, levels of haemoglobin are very high in terrapins (Klicka and Mahmoud 1971), thus facilitating rapid oxygen uptake.

Once oxygen has been picked up by the blood, there are various adaptations for effective distribution. Lenfant et al. (1970) found the rate of oxygen dissociation from haemoglobin to be very rapid in aquatic species; this, along with the large Bohr effect that they found, would facilitate the unloading of oxygen during breath holding. Boyer (1963) showed that heart rate increases with a decrease in ambient oxygen, although oxygen pulse (i.e. amount of oxygen used per gram of body weight per heart beat) decreases.

Belkin (1964) discovered a rapid increase in heart rate during the transition from breath holding to breathing, and he argued that this was not bradycardia during apnoea, but tachycardia during breathing. This would enable rapid equilibration of gases during the short period of breathing. Gaunt and Gans (1969) have described tachycardia at the end of apnoea in the snapping turtle.

The high levels of both haemoglobin and myoglobin that occur in turtles are possibly adaptations for greater oxygen storage and more effective diffusion of oxygen through the tissues (Klicka and Mahmoud 1971). There are also means for conserving oxygen stores while breath holding. Berkson (1966) observed that lactate appeared in the blood very late after the commencement of breath holding, and hence argued that peripheral shunts must be used during apnoea.

He also found bradycardia; most notable is a record of nine minutes between heart beats in a deep diving sea turtle (1967). Lowered metabolic rate (i.e. lowered oxygen consumption) in breath holding turtles has also been described by several workers (Atland and Parker 1955; Berkson 1966; Belkin 1968 a).

Special adaptations which enable certain species of turtles to take oxygen directly from the water have received little attention. Girgis (1961) describes aspects of aquatic respiration and details of the pharyngeal cavity in the Nile soft-shell turtle. Despite the fact that there are highly vascularized papillae in the pharynx, most oxygen during aquatic respiration seems to come in through the soft skin on the body, but oxygen absorption must be reasonably efficient as these animals can stay submerged for at least six hours. Root (1949) investigated aquatic respiration in the musk turtle, but he felt that the efficiency of oxygen uptake was too low to be of any significance in explaining the long submergence times that occur in these turtles. This is difficult to reconcile as Belkin (1968 a) found that the same species could live for over six months in oxygen-equilibrated water, without access to free air. Some species also seem able to extract oxygen via the cloaca (Smith and James 1956). These adaptations, although peculiar to fresh-water species, must be kept in mind when considering apnoea under water.

Anaerobic respiration. Many species of chelonian have been shown to be very tolerant of low oxygen conditions (Atland and Parker 1955; Boyer 1963; Berkson 1966; Lenfant et al. 1970). Experiments run on twenty-seven species of turtles and tortoises, in seven different families, showed that most of these animals could survive for ten hours in an atmosphere of nitrogen; some turtles even lived up to thirty hours in these conditions (Belkin 1963). In order to explain large "discrepancies" in the relative amounts of oxygen and carbon dioxide (i.e. abnormal R.Q.s) produced during low oxygen conditions, Atland and Parker (1955) suggested that anaerobic metabolism was being utilised by the box turtle. Belkin (1962) provided direct evidence for anaerobic respiration by showing that the survival time of musk turtles injected with iodoacetic acid (which prevents anaerobic glycolytic energy production) was unaffected in air, but reduced to twenty minutes under anoxic conditions. Controls lived for at least twelve hours in anoxic conditions. He later (1968 b) found that these animals are better able to withstand anoxic anoxia (breathing without oxygen) than stagnant anoxia (stopping of circulation), and suggested that

perfusion of the tissues by blood is more important than supply of free oxygen. This hypothesis has been supported by a series of experiments which showed that painted turtles (Chrysemys picta (Schneider)) could survive three days if the brain was perfused with plasma free of oxygen, but rich in glucose (1970). Without glucose the anoxic turtles lived less than two hours. Belkin concluded that metabolism of plasma glucose is sufficient for anaerobic brain function in these animals.

Waste metabolites. Turtles can hold large amounts of carbon dioxide in the blood (Wilson 1939), and it has been shown that the bicarbonate ion (HCO_3^-), used in the transport of carbon dioxide, is highly concentrated in their body fluids (Southworth and Redfield 1926; Smith 1929; Lenfant et al. 1970). In addition, carbon dioxide concentration in the blood is apparently not controlled by the central nervous system, as it is in most vertebrates, but rather is related to the animal's temperature (Robin 1962). Thus, the warmer and more active the turtle, the more carbon dioxide is carried in the blood. Increased heart rate (tachycardia) during breathing is thought to be an adaptation for the rapid unloading of this waste gas (Belkin 1964).

Belkin (1963) suggested that anoxic turtles might produce something less toxic than lactic acid during anaerobic metabolism, but there is no data to support this. His own findings (1968 b) and those of Berkson (1966) later showed that lactate levels in the blood greatly increase during anoxia.

Control of breathing. It has been shown by several workers, in several species of turtles, that the length of a dive with breath hold is correlated to the level of atmospheric oxygen (Atland and Parker 1955; Boyer 1963; Gaunt and Gans 1969; Lenfant et al. 1970). Also, carbon dioxide and pH levels in the blood are related to the animal's temperature and apparently not controlled centrally (Robin 1962). Consequently, several authors have suggested that central control for breathing is affected by oxygen level (Boyer 1963; Lenfant et al. 1970).

This is of interest in the light of work done by van Sommers (1962, 1963) on the lever pressing behaviour of the red-eared turtle (Pseudemys scripta elegans (Wied)) in response to various regimes of air reward. Duration of access to air was inversely related to amount of lever pressing (i.e. the less air, the more lever pressing). Rate of lever pressing increased with both increased temperatures and added meat in the diet, indicating that more air (oxygen) was needed with increased metabolism. He also found that rate of lever pressing decreased with

added carbon dioxide in the air. Air with a high level of carbon dioxide is not a good reward, but it is not clear whether this is because partial pressure of carbon dioxide is high or because partial pressure of oxygen is low (due to the displacement of oxygen by carbon dioxide in the air).

Most of the above discussion is related to aquatic rather than terrestrial species as there is a paucity of information on the latter. Also, some of the above discussion (e.g. that on aquatic respiration) is not directly relevant to tortoises, although it does show the wide range of respiratory adaptations that these animals have. Certainly, there are major differences between aquatic and terrestrial species. Agassiz (1857) showed that there is a tendency for relative lung capacity to be larger in terrestrial species, and some authors have interpreted this to mean that physiological demands on terrestrial species are less intense. Gaunt and Gans (1969) and Lenfant et al. (1970) have made physiological comparisons between terrestrial and aquatic species, finding that the latter have distinct respiratory adaptations facilitating survival in the aquatic environment. Comparisons between species, however, must be interpreted with care so that effects of taxonomy and ecology are not confused (see Belkin 1963).

Observations on Giant Tortoises

Both throat movements and movements of the posterior body wall were observed in Aldabran giant tortoises. Throat movements usually occurred when the animal was investigating some aspect of its environment (e.g. food, water, or another tortoise), but these movements did not always occur during breathing, especially when the animal was inactive. Throat movements did not correspond to obvious respiratory exchanges, such as the sound of expirations. However, movements of the body wall, i.e. the ballooning in and out of the soft skin at the base of the limbs, correlated with the passage of air out of the nostrils. Thus it was assumed, on the basis of the present observations as well as those of other workers, that limb and body movements were related to breathing, while throat movements were not. Observations on the posterior body wall are the basis of the following results.

In the adult giant tortoise, while resting apnoea constitutes 48 to 76 % of the breathing cycle (Figure II-1, Table II-1). After the breath hold the first few breaths are very rapid and then the intervals between breaths gradually increase (Figure II-2). This was observed in a large number of animals in the field and appears to be the normal pattern of breathing in resting adult tortoises. The rhythm in active animals could not be observed accurately, but it also appeared to

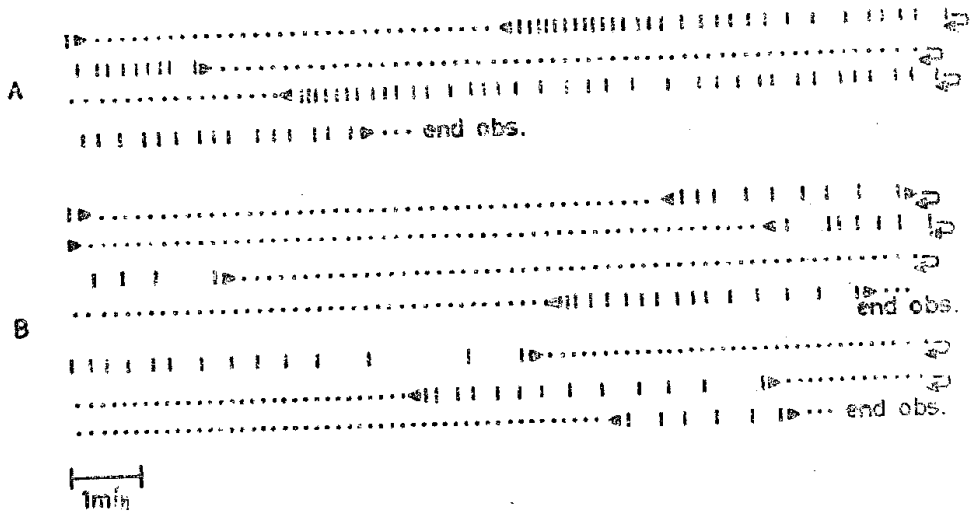


Figure II - 1 Occurrence of breaths. | = one breath; apnoea is bounded by inward facing arrows; dots are spaced at 10-second intervals.
A. Tortoise 99.
B. Tortoise 297. (See Table II - 1)

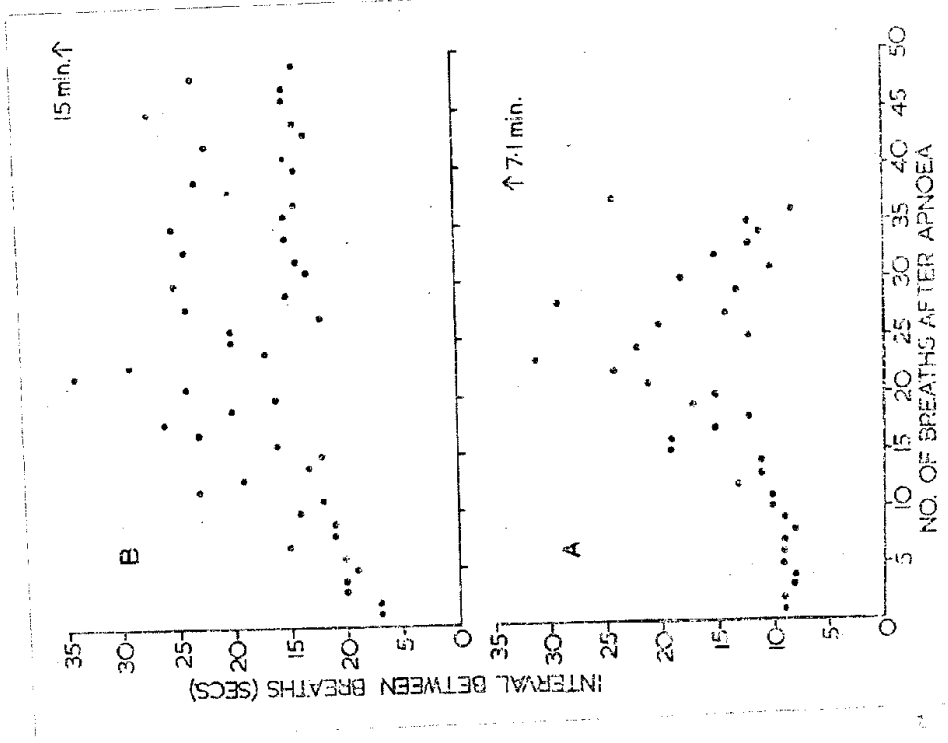


Figure II - 2 Interval between breaths in relation to number of breaths after apnoea.
Tortoise 99 on 23rd November 1969, 2000 hours;
A. after a breath hold of 7.1 minutes
B. after a breath hold of 15 minutes.

TABLE II - 1. Proportions of the total breathing cycle spent in apnoea and ventilation for two Aldabran tortoises and an aquatic terrapin

	Length of apnoea			Length of ventilation			Total length of breathing cycle	
	min.	sec.	% of total	min.	sec.	% of total	min.	sec.
Tortoise 297	6 August 1969		1630 to 1730 hrs.					
	9	35	74%	3	22	26%	12	57
	11	30	71%	4	36	29%	16	66
	18	42	81%	4	16	19%	23	
	11	52	69%	5	14	31%	17	6
	11	13	82%	2	24	18%	13	37
mean	12	34	76%	3	59	24%	16	33
Tortoise 99	23 November 1969		2000 hrs.					
	7	6	42%	9	45	58%	16	51
	15		51%	14	35	49%	29	35
mean	11	3	48%	12	10	52%	23	13
Matamata turtle	Lenfant et al. 1970							
	35		94%	2	12	6%	37	12

TABLE II - 2. Hypothetical units of heat/water lost by respiratory evaporation during three hypothetical heat/water loss - time functions; and the per cent of heat/water loss during regular ventilation (B) that is lost with apnoea(A)

Curve from Figure II-2	With apnoea (A)			Without apnoea (B)	A/B x 100
	18 breaths made at regular 30 second intervals	1 breath hold 10 minutes long	Total	19 breaths made at regular 1 minute intervals	
a	99	7	106	114	92·98
b	18	7	25	66·5	37·59
c	3·6	7	10·6	11·4	92·98

involve a breath hold. The pattern in immature animals is much more difficult to observe, but the rate of respiratory exchanges was clearly more rapid than in adults, and if there were breath holds in these small animals, they were very short in duration. Unfortunately, efforts to collect more detailed data were foiled by instrument failure.

Although the results are not extensive, they warrant discussion because they contradict the conventional view (e.g. Gans and Hughes 1967; Gaunt and Gans 1969; Gans and Gaunt 1970) that tortoises have a regular breathing rhythm. The breathing pattern described here for the giant land tortoise is what one would expect to find in an aquatic animal where there is a need to refrain from breathing. Clearly, the relative length of breath hold is much longer in the aquatic matamata turtle than it is in the giant tortoise (Table II-1), but this does not make it any simpler to explain why the terrestrial animal spends such a large proportion of its breathing cycle in apnoea.

In attempting a functional explanation of this apparent anomaly two points seem relevant: the conservation of heat and the conservation of water. Both of these points are intimately related to respiration, because ventilation results in evaporative water loss from the surfaces of the respiratory passages. By panting, heat-stressed lizards (Templeton 1960, 1970) and birds (Dawson and Hudson 1970) make use of this evaporative cooling to increase the rate of heat loss. However at times the loss of either heat or water is a distinct disadvantage and in order to decrease these losses an animal may abate its rate of breathing. Breath holding not only reduces the number of respiratory exchanges in a period of time but also concentrates breaths into a small portion of the breathing cycle. This reduces the interbreath interval in all instances but that immediately after apnoea.

The effects of such a breathing pattern can best be illustrated with a hypothetical example. Over a period of twenty minutes a tortoise could make twenty ventilatory exchanges. If breathing were regular, the interval between each breath would be one minute, and there would be nineteen such intervals. On the other hand, if 50% of the twenty minute period were spent in apnoea, there could be eighteen inter-breath intervals of thirty seconds and one interval of ten minutes.

The rate at which heat and water are dissipated from the animal's respiratory passages to its environment is dependent on the magnitude of the heat/water differential between the tortoise and the air. This differential will itself be dependent on how much time the system has had to reach equilibrium, air which has been in contact with the respiratory passages for ten minutes will have effected more evaporative water loss than air which has been in contact with the passages for

only one minute.

The amount of heat or water lost to the environment is thus related to the interbreath interval. Without direct measurements it is impossible to say what this relationship is; however, three generalised heat/water loss - time functions could be postulated (Figure II-2). Table II-2 illustrates the different quantities of heat or water lost to the environment under the three conditions illustrated in Figure II-2. If curve II-2 b is the best representation of the real situation then breath holding results in a considerable saving of heat and water; if either of the other curves (II-2 a and c) is more realistic, then breath holding has no apparent effect on this problem.

Should breath holding in fact conserve heat and water, it will be necessary to explain the functional significance of this. Conservation of heat would be important to a tortoise from late afternoon to early morning when its body is often considerably warmer than the environment (see section on thermoregulation). However, since the animals do not seem to conserve heat by other means (e.g. facing into the sun to facilitate solar heat input - see section on orientation) heat conservation does not seem to be an important problem to the animal. Furthermore, about the last thing a tortoise needs at midday is conservation of its body heat. Animals in the middle of the day are most liable to heat stress, but tortoises resting in the shade during the midday heat at Aldabra do breath hold.

This is not to say that respiratory heat dissipation is unimportant. Heat stressed giant tortoises do pant, as well as spreading saliva over their legs and neck which further increases evaporative cooling. This has also been experimentally demonstrated in the spurred tortoise (Geochelone (= Testudo) sulcata Miller) by Cloudsley-Thompson (1968, 1970) and in the ornate box turtle (Terrapene ornata ornata Agassiz) by Riedesel et al. (1971).

Conservation of water, on the other hand, is a crucial problem to tortoises which live in xeric conditions. Cloudsley-Thompson (1968, 1970) and Riedesel et al. (1971) have shown the large demands made by evaporative cooling on the animals' somatic water supply. The desert tortoise, when supplied with moist food, usually does not imbibe; however, after being heat-stressed and increasing its evaporative heat and water loss it drinks deeply when water is available (Cloudsley-Thompson 1968). Riedesel et al. (1971) suggested that the bladder in testudines is an important source of fluid that can be used in emergencies for evaporative cooling.

If breath holding results in a significant reduction of evaporative water loss, which is more important than the possible disadvantage of

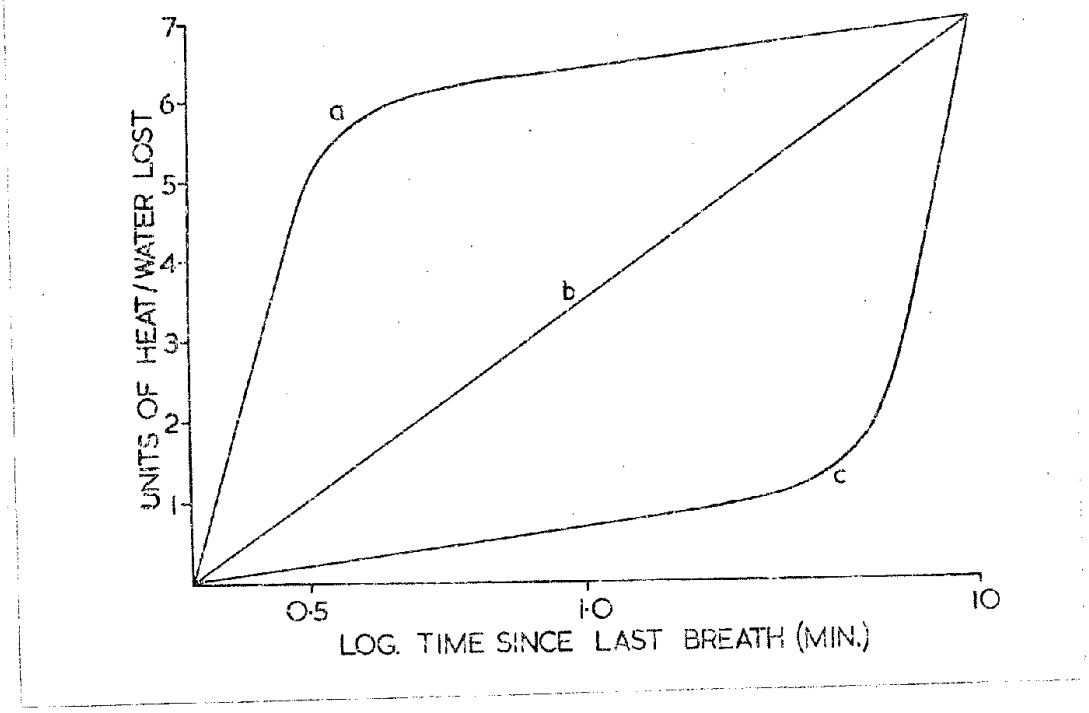


Figure II - 3 Hypothetical units of heat/water lost by evaporation from respiratory passages in relation to time since last breath (in minutes).

heat conservation, then the adaptive role of apnoea may be to conserve precious water. It may also be relevant to compare the tortoises' physiology with that of comatose animals in which general physiological processes (e.g. respiration) are depressed, but the interpretation of this respiratory anomaly in the giant tortoise must await experimental investigation.

REFERENCES

Agassiz, L. 1857 Contributions to the natural history of the United States of America. Boston: Little, Brown & Co.

Altland, P.D. & Parker, H. 1955 Effects of hypoxia upon the box turtle. Amer. J. Physiol 180 : 421-427.

Belkin, D.A. 1962 Anaerobiosis in diving turtles. Physiologist 5 : 105.

Belkin, D.A. 1963 Anoxia: tolerance in reptiles. Science 139 : 492-493.

Belkin, D.A. 1964 Variations in heart rate during voluntary diving in the turtle Pseudemys concinna. Copeia 1964 : 321-330.

Belkin, D.A. 1968 a Aquatic respiration and underwater survival of two freshwater turtle species. Respir. Physiol. 4 : 1-14.

Belkin, D.A. 1968 b Anaerobic brain function: Effects of stagnant and anoxic anoxia on persistence of breathing in reptiles. Science 162 : 1017-1018.

Belkin, D.A. 1970 Plasma glucose can support long-term anaerobic brain function in turtles. Physiologist 13 : 146.

Bellairs, A. d'A. 1957 Reptiles: Life history, evolution, and structure. New York : Harper and Brothers.

Berkson, H. 1966 Physiological adjustments to prolonged diving in the Pacific green turtle (Chelonia mydas agassizii). Comp. Biochem. Physiol. 18 : 101-119.

Berkson, H. 1967 Physiological adjustments to deep diving in the Pacific green turtle (Chelonia mydas agassizii). Comp. Biochem. Physiol. 21 : 507-524.

Boyer, D.R. 1963 Hypoxia: Effects on heart rate and respiration in the snapping turtle. Science 140 : 813-814.

Cahn, A.R. 1937 The turtle of Illinois. University of Illinois Bulletin 35 : 175-207. Cited by Girgis 1961.

Cloudsley-Thompson, J.L. 1968 Thermoregulation in tortoises. Nature 217 : 575.

Cloudsley-Thompson, J.L. 1970 On the biology of the desert tortoise Testudo sulcata in Sudan. J. Zool., Lond. 160 : 17-33.

Dawson, W.R. & Hudson, J.W. 1970 Birds. In Whittow, G.C.(ed.) Comparative Physiology of Thermoregulation. Vol. I : 224-310. London : Academic Press.

Gans, C. & Gaunt, A.S. 1970 Shell and physiology of turtles. Int. Turtle and Tortoise Soc. J. 4(1) : 14-18, 32-33.

Gans, C. & Hughes, G.M. 1967 The mechanism of lung ventilation in the tortoise Testudo graeca Linné. J. Exp. Biol. 47 : 1-20.

Gaunt, A.S. & Gans, C. 1969 Mechanics of respiration in the snapping turtle, Chelydra serpentina (Linné). J. Morph. 128 : 195-228.

Girgis, S. 1961 Aquatic respiration in the common Nile turtle, Trionyx triunguis (Forskal). Comp. Biochem. Physiol. 3 : 206-217.

Klicka, J. & Mahmoud, I.Y. 1971 A comparative study of respiratory pigment concentrations in six species of turtles. Comp. Biochem. Physiol. 38 (A) : 53-58.

Lenfant, C., Johansen, K., Petersen, J.A. & Schmidt-Nielsen, K. 1970 Respiration in the fresh water turtle Chelys fimbriata. Resp. Physiol. 8 (3) : 261-275.

Lüdicke, M. 1936 Über die Atmung von Emys orbicularis L. Zool. Jb., Abt. allgem. Zool. Physiol. 56 : 83-106. Cited by Gans and Hughes 1967, p. 5.

McCutcheon, F.H. 1943 The respiratory mechanism in turtles. Physiol. Zool. 16 : 255-269.

Mitchell, S. & Morehouse, G.R. 1863 Researches upon the anatomy and physiology of respiration in the Chelonia. Smithsonian Contrib Knowl. 13 (159) : ix-43.

Negus, V. 1965 The biology of respiration. London : Livingston, Ltd.

Riedesel, M.L., Cloudsley-Thompson, J.L. & Cloudsley-Thompson, J. Anne. 1971 Evaporative thermoregulation in turtles. Physiol. Zool. 44 : 28-32.

Robin, E. 1962 Relationship between temperature and plasma pH and carbon dioxide tension in the turtle. Nature 195 : 249-251.

Root, R.W. 1949 Aquatic respiration in the musk turtle. Physiol. Zool. 22 : 172-178.

Shaw, R.J. & Baldwin, F.M. 1935 The mechanics of respiration in turtles. Copeia 1935 (1) : 12-15.

Smith, H.M. & James, L.F. 1958 The taxonomic significance of cloacal bursae in turtles. Trans. Kans. Acad. Sci. 61 : 86-96.

Smith, H.W. 1929 The inorganic composition of the body fluids of the Chelonia. J. biol. Chem. 82 : 651-661.

Southworth, F.C. Jr., & Redfield, A.C. 1926 The transport of gas by the blood of the turtle. J. Gen. Physiol. 9 : 387-403.

Tauvery, D. 1701 A new rational anatomy. London: Midwinter and Leigh. Cited by Gans and Hughes 1967 , p. 5.

Templeton, J.R. 1960 Respiration and water loss at the higher temperatures in the desert iguana, Dipsosaurus dorsalis. Physiol. Zool. 33 : 136-145.

Templeton, J.R. 1970 Reptiles. In Whittow, G.C. (ed.) Comparative Physiology of Thermoregulation. London : Academic ; pp. 167-221.

Townsend, R. 1795 Physiological observations on the Amphibia. Dissertation the third, on the respiration of the tortoise. Göttingen. Cited by Mitchell and Morehouse 1863, p. 1.

van Sommers, P. 1962. Behavioral regulation of the respiratory environment in three vertebrate species. Unpublished doctoral dissertation. Harvard University. Cited by van Sommers 1963.

van Sommers, P. 1963 Air motivated behavior in the turtle. J. comp. physiol Psychol. 56 (3) : 590-596.

Vos, H.J. 1936 Over ademhaling en Reukzin bij Reptielen en Amphibien. Acad. Proefschrift, Rijksuniv. Groningen. Cited by Gans and Hughes 1967, p. 5.

Wilson, J.W. 1939 Some physiological properties of reptilian blood. J. Cell. & Comp. Physiol. 13 : 315-326.

Wolf, S. 1933 Zur Kenntnis von Bau und Funktion der Reptilienlunge. Zool. Jb., Abt. Anat. Ont. 57 : 139-190. Cited by Gans and Hughes 1967, p. 5.

Young, J.Z. 1962 The life of vertebrates. Oxford : Oxford Univ. Press.

APPENDIX III

Activity census.

Per cent of the total number of tortoises censused that were engaged in various activities.

□——□ = per cent in the sun
●-----● = per cent in the shade

Censuses conducted in four areas at Dune Jean Louis: the eastern Sporobolus plain; the SE quarter of Square 1; the NE quarter of Square 1; the SW quarter of Square 5.

Census dates:

14th and 15th September 1969 (No data for SW Square 5)

30th and 31st October 1969 " " " " " "

6th and 7th November 1969

10th and 11th January 1970

EAST PLAIN

14 SEPT

15 SEPT

SLEEP 75%

50

25

AWAKE 75%

50

25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

BROWSE 25%

GRAZE 75%

50

25

5 7 9 11 13 15 17 19

TIME OF DAY

PER CENT OF POPULATION

EAST PLAIN

30 OCT

31 OCT

SLEEP 75% 50 25

AWAKE 75% 50 25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

BROWSE 25%

GRAZE 75% 50 25

5 7 9 11 13 15 17 19

TIME OF DAY

PER CENT OF POPULATION

EAST PLAIN

6 NOV

7 NOV

SLEEP 75% 50 25

AWAKE 75% 50 25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

BROWSE 25%

GRAZE 75% 50 25

PER CENT OF POPULATION

5 7 9 11 13 15 17 19

TIME OF DAY

5 7 9 11 13 15 17 19

EAST PLAIN

10 JAN

11 JAN

SLEEP 75%

50

25

AWAKE 75%

50

25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

BROWSE 25%

GRAZE 75%

50

25

5 7 9 11 13 15 17 19

TIME OF DAY

PER CENT OF POPULATION

N.E. OF SQ. 1

14 SEPT

15 SEPT

SLEEP 75% 50 25

AWAKE 75% 50 25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75% 50 25

PER CENT OF POPULATION

5 7 9 11 13 15 17 19

TIME OF DAY

N.E. OF SQ.1

30 OCT

31 OCT

SLEEP 75%
50
25

AWAKE 75%
50
25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75%
50
25

5 7 9 11 13 15 17 19

TIME OF DAY

PER CENT OF POPULATION

NE OF SQ1

6 NOV

7 NOV

SLEEP 75%
50
25

AWAKE 75%
50
25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75%
50
25

5 7 9 11 13 15 17 19

TIME OF DAY

PER CENT OF POPULATION

N.E. OF SQ.1

10 JAN

11 JAN

SLEEP 75%

50

25

AWAKE 75%

50

25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75%

50

25

5 7 9 11 13 15 17 19

TIME OF DAY

PER CENT OF POPULATION

S.E. OF SQ.1

14 SEPT

15 SEPT

SLEEP 75% 50 25

AWAKE 75% 50 25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75% 50 25

PER CENT OF POPULATION

5 7 9 11 13 15 17 19

TIME OF DAY

5 7 9 11 13 15 17 19

SE OF SQ1

30 OCT

31 OCT

SLEEP 75%
50
25

AWAKE 75%
50
25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75%
50
25

5 7 9 11 13 15 17 19

TIME OF DAY

PER CENT OF POPULATION

S.E. OF SQ.1

6 NOV

7 NOV

SLEEP 75% 50 25

AWAKE 75% 50 25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75% 50 25

5 7 9 11 13 15 17 19

TIME OF DAY

PER CENT OF POPULATION

S.E. OF SQ.1

10 JAN

11 JAN

SLEEP 75%

50

25

AWAKE 75%

50

25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75%

50

25

PER CENT OF POPULATION

5 7 9 11 13 15 17 19

TIME OF DAY

5 7 9 11 13 15 17 19

S.W. OF SQ. 5

6 NOV

7 NOV

SLEEP 75% 50 25

AWAKE 75% 50 25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75% 50 25

5 7 9 11 13 15 17 19

TIME OF DAY

PER CENT OF POPULATION

S.W. OF SQ.5

10 JAN

11 JAN

SLEEP 75%
50
25

AWAKE 75%
50
25

LOOK 25%

MOVE 25%

MOVE/ FEED 25%

DRINK 25%

BROWSE 75%
50
25

PER CENT OF POPULATION

5 7 9 11 13 15 17 19

TIME OF DAY

APPENDIX IV

Daily activity of individual tortoises.

Activities, indicated on vertical axis, include:

F = Intensive feeding
M & F = Moving and feeding
M = Moving only
L = 'Looking' (i.e. holding the head and neck erect for periods of several minutes)
A = Awake but inactive
S = Sleeping (i.e. eyes closed)

Infrequent activities include:

B = Bath
C = Copulate
D = Drink
N = Noze

o = Activity indicated carried out in sun
● = Activity indicated carried out in shade

Individuals recorded:

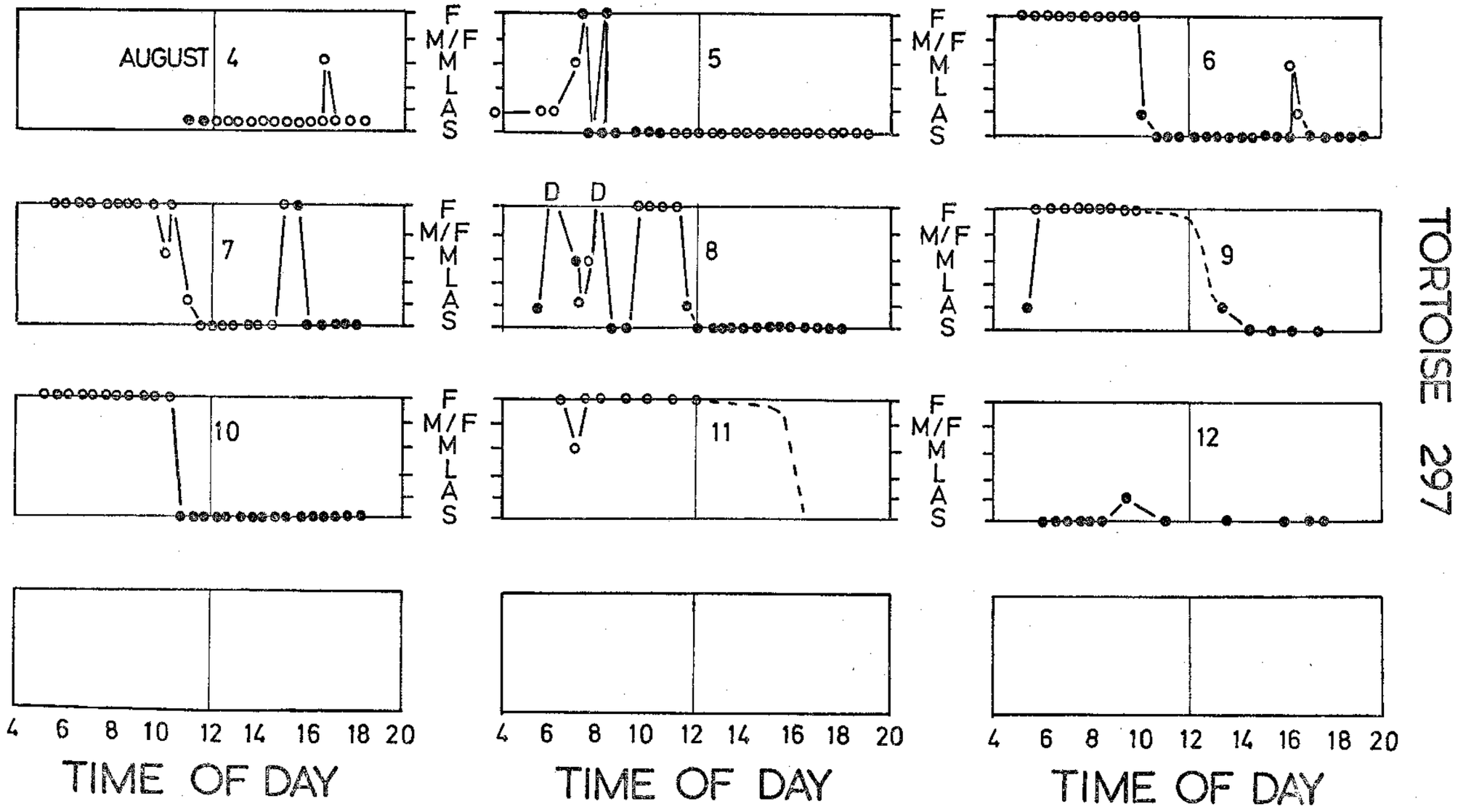
297 - 4th to 12th August 1969

99 - 17th to 28th November 1969

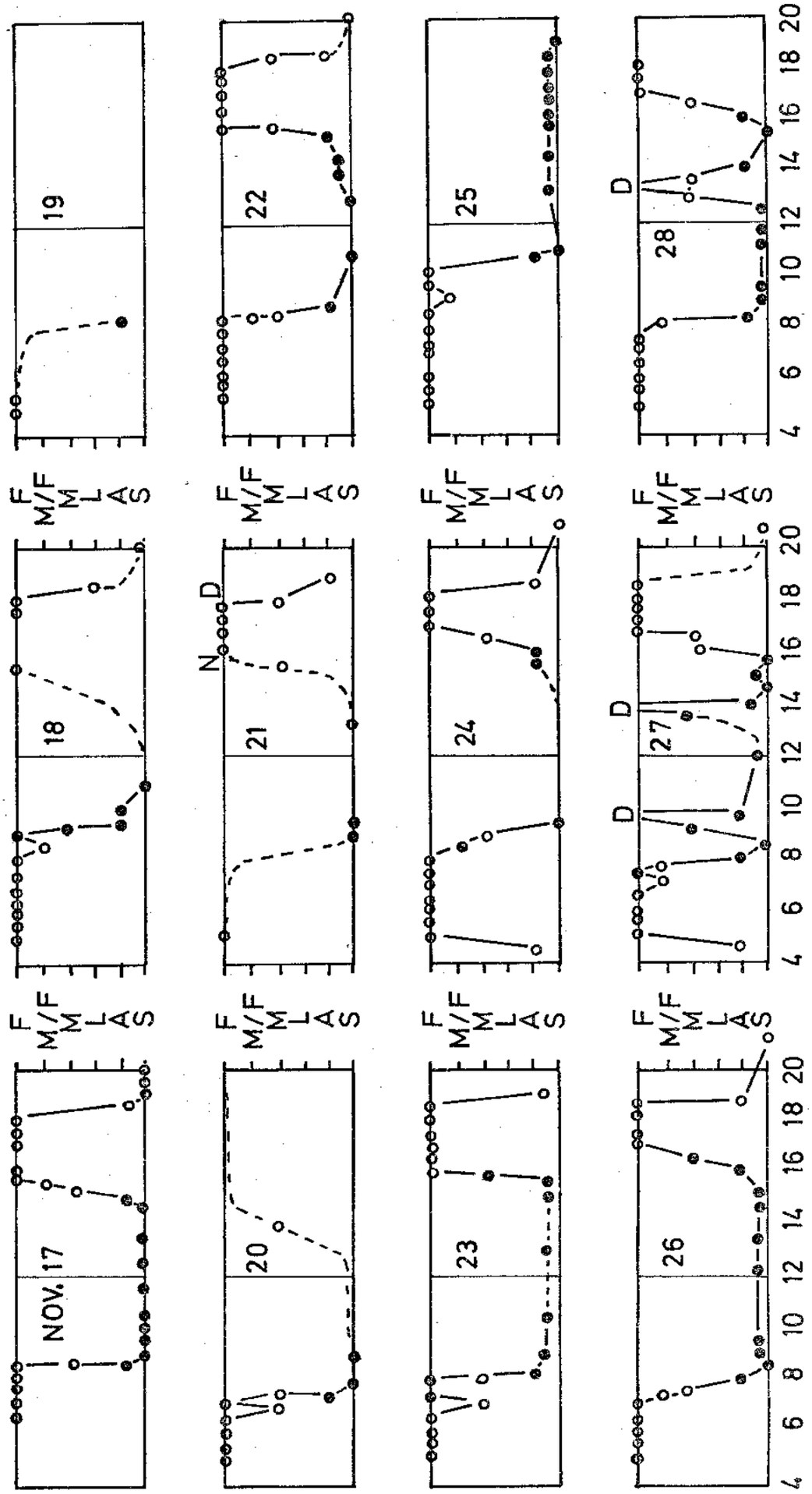
244 - 10th to 24th February 1970

45 - 22nd March to 2nd April 1970

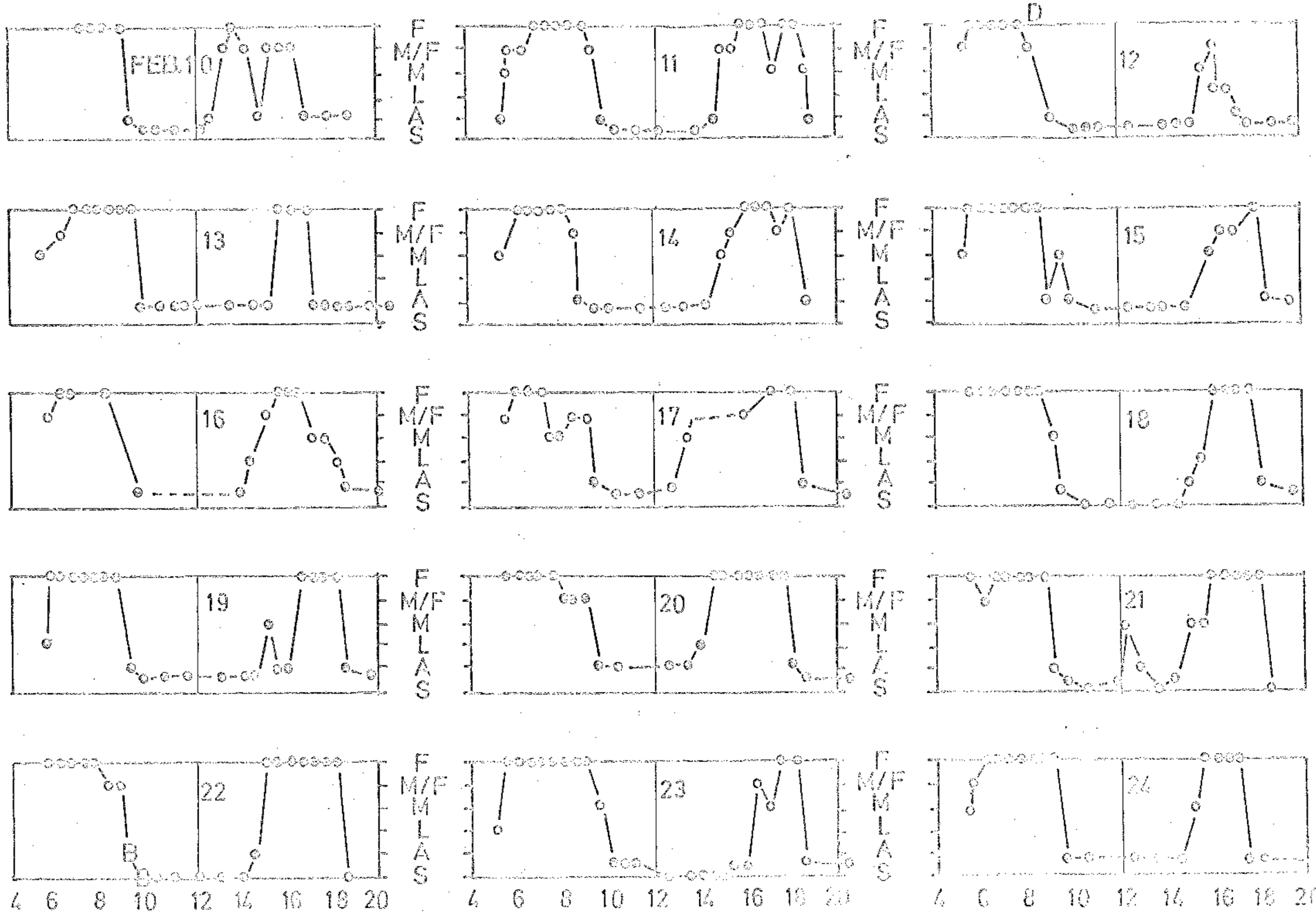
T 14 - 17th April to 1st May 1970


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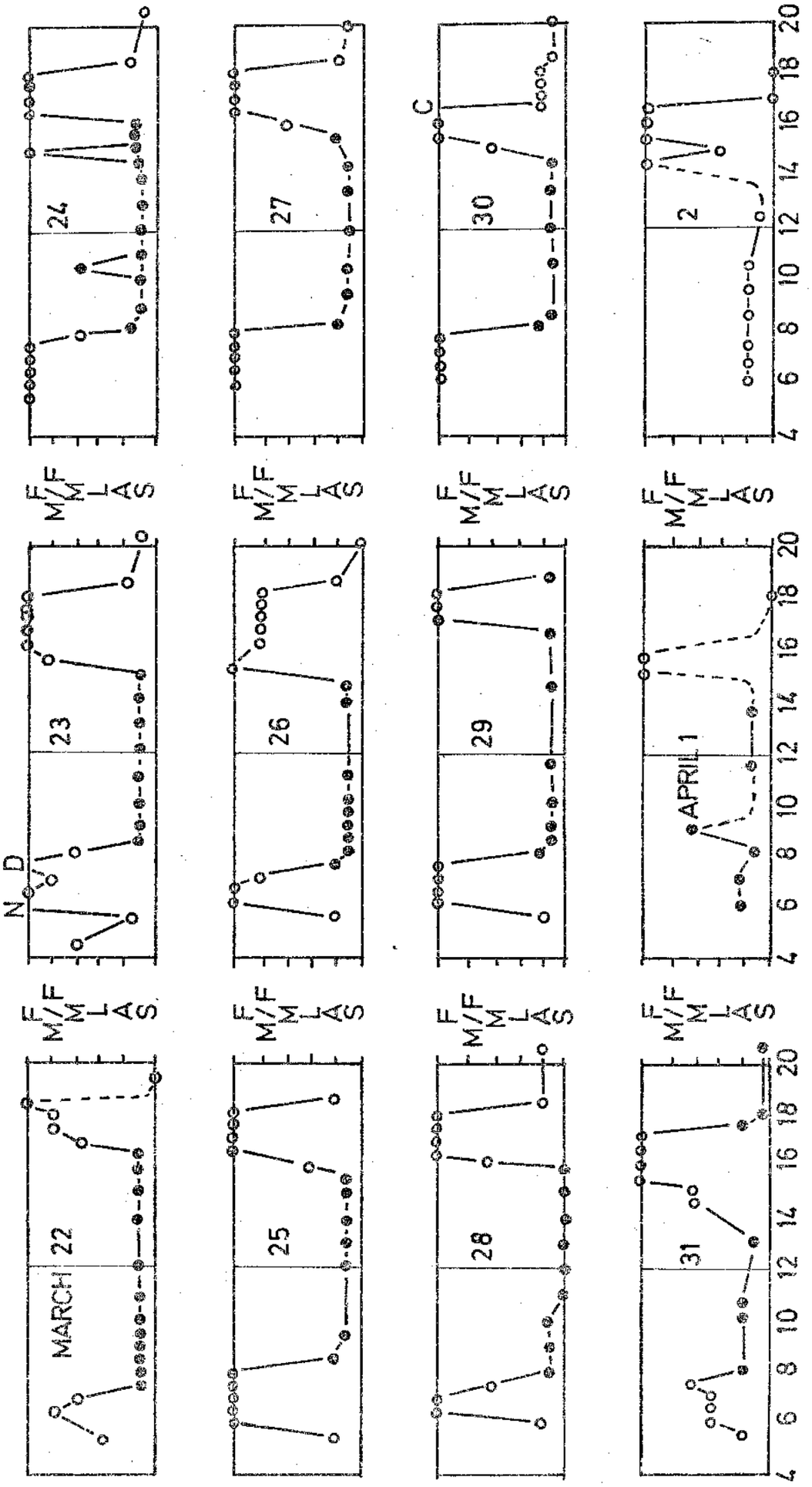
TORTOISE 99

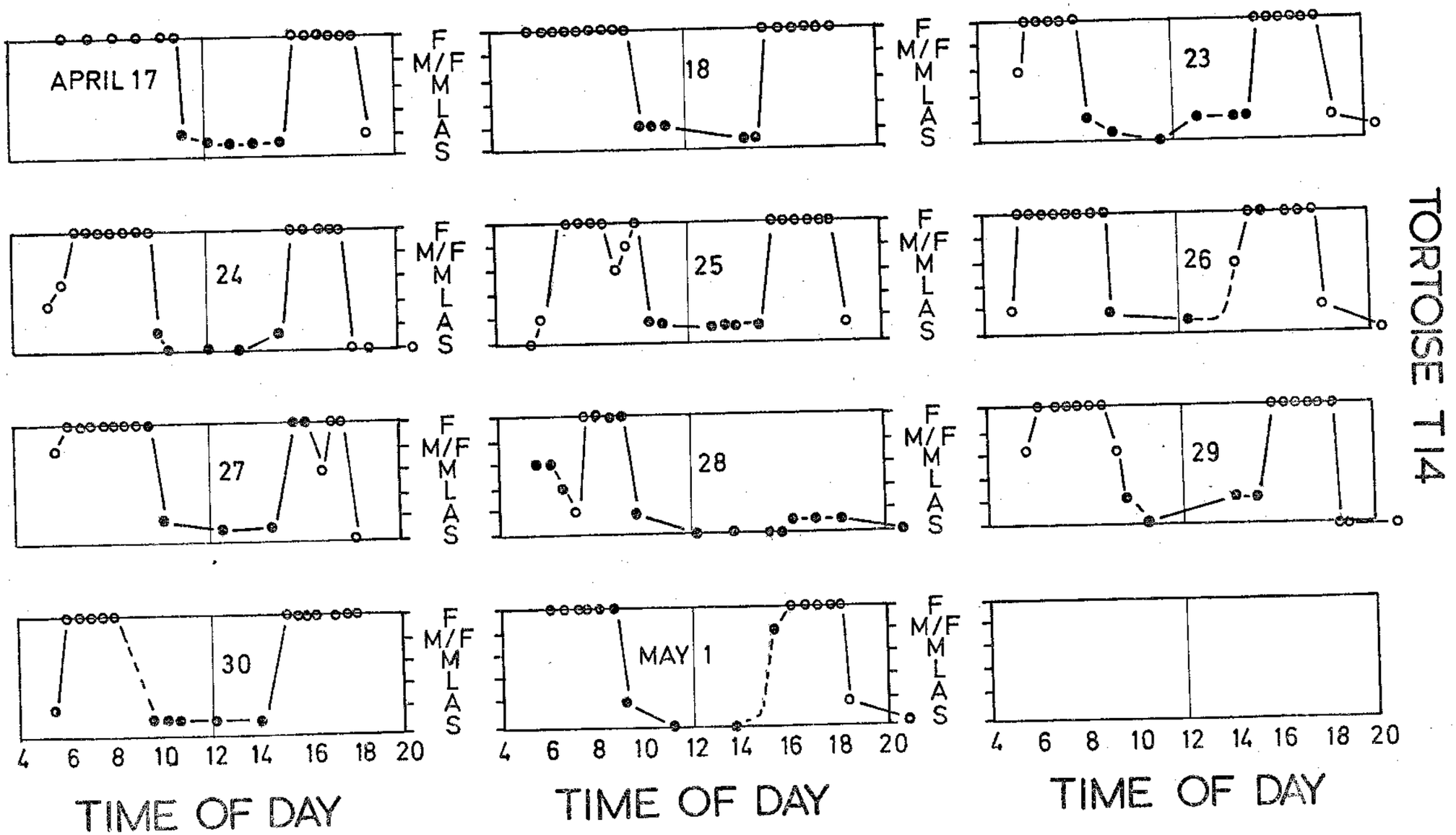

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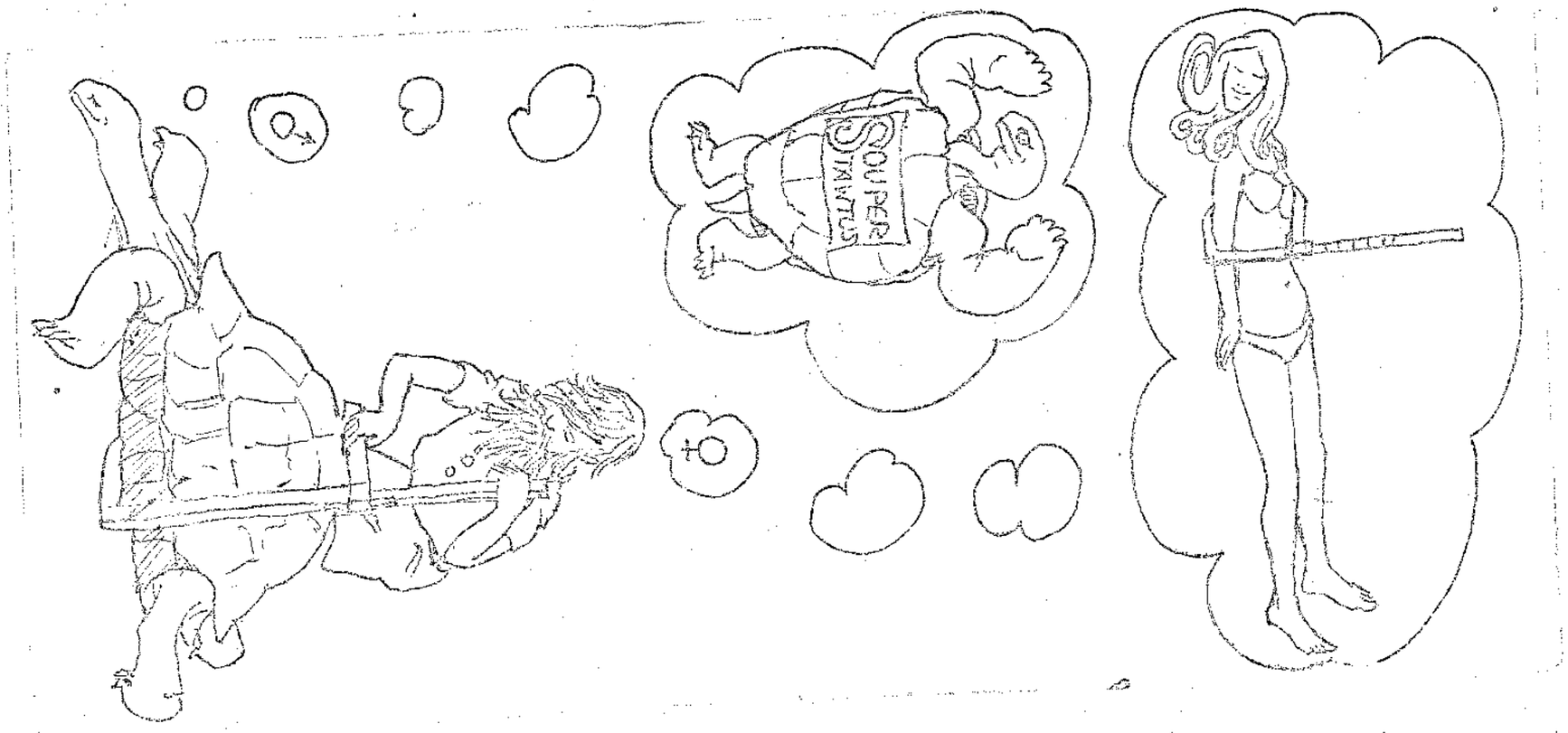
TORTOISE 244



TORTOISE 45


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