PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Biomass, Production and Carrying Capacity of Giant Tortoises on Aldabra

M. J. Coe, D. Bourn and I. R. Swingland

Phil. Trans. R. Soc. Lond. B 1979 **286**, 163-176
doi: 10.1098/rstb.1979.0024

Phil. Trans. R. Soc. Lond. B. **286**, 163–176 (1979) [163]
Printed in Great Britain

The biomass, production and carrying capacity of giant tortoises on Aldabra

By M. J. Coe, D. Bourn and I. R. Swingland
Animal Ecology Research Group, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

The giant tortoise (*Geochelone gigantea* (Schweigger)) population of Aldabra has varied greatly in numbers since the beginning of the present century. Recent estimates have shown that the population is composed of 150466 ± s.e. 16441 animals. Of this total, 60% are located in an area of 33.6 km^2 at the eastern end of Grande Terre.

Animals composing the small population of 2000 tortoises on Malabar grow continuously, while those on Grande Terre only grow seasonally and are much smaller than their less numerous counterparts on Malabar. It is suggested that shade factors limit the time available for feeding in Grande Terre.

Records of movement show that while some animals do move large distances 56% of the population are not relocated more than 500 m from their initial marking point.

A mean annual rainfall of 941 mm would be expected to yield 1887 g m^{-2} a^{-1} (dry mass) of primary production, with a range of from 2337 to 4037 g m^{-2} a^{-1}. Tortoises of average mass (20–30 kg) consume 79 kg a^{-1}. Estimates of total consumption for areas with differing tortoise densities suggest that they would consume 11.3% at the eastern end of Grande Terre and 0.7% in the *Pemphis* scrub.

Defecation records suggest that the gross assimilation efficiency of giant tortoises is about 50%.

The mean mass of tortoises on Aldabra are 21.7 kg on Grande Terre, 49.9 kg on Malabar and 51.3 kg on Picard. Standing crop biomasses derived from these weights are 35387 kg km^{-2} on Grande Terre, 35084 kg km^{-2} on Malabar and 25342 kg km^{-2} on Picard. These biomass data are significantly higher than those achieved by large herbivores on mainland African wildlife ecosystems.

By using data available on biomass mortality, P/B ratios (turnover times) of 0.042 for Grande Terre and 0.034 for Malabar are obtained. Annual production calculated from these ratios are 1486 kg km^{-2} a^{-1} for Grande Terre and 1193 kg km^{-2} a^{-1} for Malabar.

The production efficiency of the giant tortoise population is about 2.1% which is in close agreement with figures obtained for other long-lived poikilotherms.

Potential production for Grande Terre predicted from the mean rainfall only differs by 2.6% from that estimated. The eastern end of Grande Terre, however, exceeds this predicted figure by 61% and it is suggested that this is due to increased primary production induced by water available from the freshwater lens raised by spring tides. This phenomenon is similar to mainland African wildlife ecosystems fed by abundant ground water.

1. Introduction

Fossil evidence suggests that Aldabra has been inundated and subsequently recolonized by Giant tortoises three or four times in the last 170000 years (Braithwaite, Taylor & Kennedy 1973; Taylor, Braithwaite, Peake & Arnold 1979, this volume). These discoveries illustrate the fact that these large cold-blooded vertebrates must be able to stand long periods floating in sea water without access to either food or fresh water. Indeed it was their ability to stand long periods without food that made them a prime target for early seafaring people who visited Aldabra and other Islands in the Indian Ocean and who removed large numbers of tortoises as a food source which could provide fresh meat on extended sea voyages. To a large degree it must be presumed that man is largely, if not wholly, responsible for the extinction of tortoises on all of the islands that they previously occupied in the Indian Ocean. The difficult terrain of Aldabra and its comparative isolation have probably been prime factors in their survival on this their last remaining stronghold.

A number of authors (Grubb 1971; Stoddart & Peake 1979, this volume) have drawn attention to the fact that the numbers of tortoises on Aldabra have varied greatly during the present century from an apparent increase at its beginning, falling to very low numbers in the late 1930s and then rising again to their very high numbers at the present time.

Evidence of actual numbers of tortoises present on Aldabra is lacking in these earlier anecdotal accounts of casual visitors, the first contemporary estimate being that of Palombelli (1954) who concluded that the population size was about 80000 animals. In 1964 Gaymer (1968) visited Aldabra as a member of the Bristol University Seychelles Expedition and marked animals with red and yellow cellulose paint marks on the carapace. He revisited Aldabra (Gaymer 1968, 1973) and provided tortoises with permanent marks with the use of numbered titanium disks. These operations were carried out at several points on Grande Terre and in the vicinity of Passe Houareau on Malabar. These disks were embedded in a shallow hole drilled in the third vertebral scute with a hand drill and secured with Devcon resin. From the ratio of marked to unmarked animals in the areas he censused he concluded that the tortoise population of Aldabra was about 33000 animals.

Grubb (1971), working with the early phases of the Royal Society Expedition to Aldabra (Phases I–III) in 1967–8, carried out a detailed study of the tortoise population in the southeast of Grande Terre and concluded that an area of 10.6 km^2 contained up to 40830 tortoises. He further extrapolated this data to the whole of the Platin area of Grande Terre (30.7 km^2) and suggested that the total population was 98240 animals.

Frazier (1971) studying the thermoregulation and behaviour of the Aldabran giant tortoise estimated the total population of the atoll as 120000 animals, but his calculations were based on restricted census data although it does agree with later estimates.

Since Aldabra probably represents the only terrestrial environment in the world where a cold blooded vertebrate is the only significant primary consumer, the Aldabra Research Committee encouraged Coe to devise and coordinate a more detailed study of the tortoise's ecology. This programme was designed to be conducted in three phases. The first of these was conducted by Bourne who studied animal numbers, their distribution and population structure (1973–4), while the second, recently completed by Swingland, studied reproduction and recruitment (1975–6). The last phase, yet to be initiated, will investigate feeding in relation to tortoise production and vegetation–tortoise interactions.

The marking technique used by Gaymer (1973) was improved by Bourn (1976) who used an electric drill and a specially designed counter-sinking bit. Numbered titanium disks were embedded in the fourth central scute with Devcon resin. During this first phase of the population study, 6014 animals were given permanent marks on Grande Terre, and 168 on Malabar. Including those animals marked by Gaymer, a total of 6882 tortoises have been provided with permanent marks on the atoll. As a result of these operations and subsequent transect censuses, preliminary analysis indicated a total population of 140019 animals (Bourn 1976) but more detailed study (Bourn & Coe 1978) has raised this estimate to 150466 (95% confidence limits 134020–166907) animals. A study of marked–release–recapture data for the main census area (Morgan 1976; Morgan & Bourn 1978) has confirmed that these estimates are acceptable.

In the light of this information, which has revealed especially high densities on Grande Terre, the object of the present paper is to examine these data in relation to biomass and secondary production of the giant tortoise population and to compare this information with data available for large herbivore dominated communities on the African mainland.

The tortoise population

(*a*) *Animal numbers and their distribution*

The most recent estimate of tortoise numbers on Aldabra (Bourn & Coe 1978) has demonstrated that 97.7% of the total population of 150466 animals occurs on Grande Terre, with 60.2% occupying an area of 33.6 km^2 in the eastern census area and 20.5% along the south coast. Thus of a total land area of 138 km^2 80.7% of the total population occupy little more than 37% of this area. This striking feature of the tortoises' distribution is in large part related to the geology of Aldabra, where large areas of broken and fissured 'champignon' limestone render the *Pemphis* scrub carried virtually unavailable to tortoises.

In addition to the large number of animals occupying Grande Terre (146912) 2250 are located in an area of 3.2 km^2 on Malabar (out of a total land area of 29.56 km^2), 1235 animals live on Picard and up to 70 live on the small lagoon islands.

The phenomena of ultra high densities and biomass are therefore only of real importance on Grande Terre. Since, however, it has been shown that recruitment to Malabar and Grande Terre populations is regulated by density (Swingland & Coe 1979, this volume), it is important to examine whether biomass and production data may be used to assess their respective relations to the potential carrying capacities of the two main islands.

While densities on Grande Terre vary between 27.0 (±1.8) in the eastern census area and 1.6 (±0.6) in the *Pemphis* scrub, such figures do not take into account patterns of micro-distribution within the area censused. Areas with local densities as high as 70 animals per hectare in the southeast of Grande Terre are characterized by scattered trees and abundant *Sporobolus* grassland, in coastal areas and 'tortoise turf', a complex mixture of apparently genetically dwarfed species (Merton, Bourn & Hnatiuk 1976) inland. Gibson (1977, personal communication has recently pointed out that these high densities are to a large degree concentrated on these preferred vegetation types even when they only compose a small percentage of the total area examined.

Bourn & Coe (1978) have analysed the distribution of tortoise density in relation to their habitat type and have demonstrated that the highest numbers occur in association with low vegetation and a percentage tree cover (available shade) of 10%. Clearly these two factors demonstrate the importance of a vegetation layer that is all potentially available as tortoise food on the one hand and strict thermoregulatory requirements on the other.

The transect data obtained by Swingland have yet to be analysed but preliminary studies (Bourn & Coe 1978) have failed to show a significant association between areas of differing tortoise density and factors related to geomorphology, freshwater pools, rain, time of day or season. We are, however, well aware of the importance of local seasonal migrations between inland scrub area and coastal grassland.

If we examine the available data on tortoise distribution (Grubb 1971; Bourn & Coe 1978), we note that the animals may be potentially limited by the nature of the terrain, food availability, shade and water. Tortoises are virtually excluded from areas of deeply dissected and fissured limestone. Additionally, however, we are also aware that large areas of open grassland which provide abundant potential food are also not visited by tortoises due to the absence of adequate shade. This fact is well illustrated by the differences in the standing crop biomass of grazed and ungrazed *Sporobolus* grassland measured on the south coast between Cinq Cases and Takamaka which differed by a factor of 7.5 (230 and 1725 g dry mass m^{-2} respectively) despite the fact that the two sites measured were only a few metres apart. A distinct graze line is evident at a point where the tortoise's movement is limited by its distance from shade. Swingland (1976) has demonstrated that this grazing cut-off distance occurs at about 300 m from the nearest shade.

On Malabar where tortoises are limited to a small area of suitable terrain and their numbers are low there is abundant tree cover but the tortoises are able to feed for much longer periods of the day than they can on Grande Terre without needing to seek shade. Additionally, studies of growth (Swingland 1976) have demonstrated that tortoises on Malabar grow virtually continuously while their abundant counterparts on Grande Terre only grow seasonally. Indeed these differences are exemplified by the fact that tortoises of the same age are much heavier on Malabar than their neighbours on Grande Terre. Thus through problems associated with the effect of limited shade on feeding time the Grande Terre population would seem to be food limited.

While tortoises do require access to water, the Grande Terre animals have abundant semi-permanent pools and temporary pools associated with fresh water lenses that are made available at high spring tides when they are elevated to the surface. By contrast, the animals of Malabar have little permanent fresh water available to them although evaporative losses are less due to the increased shade. The water that they may obtain from a predominantly browse dominated vegetation may well be a factor that renders the Malabar animals less dependent on free standing water.

(*b*) *Movement*

Frazier (1970) reported tortoises moving up to 47 km from the point at which they were marked. Recent analysis of recapture data (Bourn & Coe 1978) has indicated that such long-distance movement is exceptional and that 56% of the animals recaptured during transect censuses on Grande Terre had moved less than 500 m from the hectare in which they were initially marked. Of the remainder only 8% had moved more than 2 km and of these ten marked individuals had moved between 5.7 and 25.5 km (straight line distance). Clearly, therefore, in terms of studying density and biomass density, these long distance movements are unimportant although they do clearly illustrate that the whole population of Grande Terre may be considered as one population both from an ecological and a genetic standpoint.

(*c*) *Tortoise numbers and food supply*

Walter (1954) and Whittaker (1970) have demonstrated that over a wide geographical area rainfall may be used to predict primary production. Rosenzweig (1968) has established a similar log–linear relation between actual evapotranspiration (E_A) and net above-ground primary production (p_{nap}) in grams dry mass per square metre per year.

Rainfall data for Aldabra (Stoddart & Mole 1977) indicate that between 1958 and 1974 the mean annual rainfall was 940.6 mm with wide year to year variation from 547 mm (1968) to 1473 mm (1974). More recently, Stoddart & Walsh (1979, this volume) have examined data from other areas in the Indian Ocean and have suggested that by using 10 and 20 year running means it is possible to detect a cycle of high and low rainfall with a periodicity of about 35 years. This information is of considerable interest, for it closely coincides with the periodicity proposed by Phillipson (1975) and Cobb (1977) who have studied rainfall records for the Tsavo National Park in eastern Kenya. It is therefore possible that the short-term mean (1070 mm) derived from the Royal Society weather station on Picard indicates that we are at present in or entering a period of higher rainfall. In terms of considering the influence of rainfall on the food supply of tortoises the long-term mean (941 mm) has been used.

Table 1. Food consumption

season	number of observations	average dry mass/(g d^{-1})	observer
wet season (Jan.)	5	380 ± 64.8	Swingland
dry season (June)	4	160 ± 116.7	Swingland
late dry season (Sept.)	2	110 ± 77.9	Bourne & Coe

mean food intake = 217 g dry mass d^{-1}.

In order to apply the formulation of Rosenzweig (1968) it is necessary to know the potential evapotranspiration, but in semi-arid environments where potential evapotranspiration is greater than actual precipitation (P_{A}), $E_{\mathrm{A}} = P_{\mathrm{A}}$. Coe, Cumming & Phillipson (1976) have considered them to be equal up to 700 mm. In the absence of suitable evaporation data for Aldabra the long-term mean rainfall of 194 mm is not likely to deviate far from this presumed relation.

Thus we may calculate p_{nap} for Aldabra by using Rosenzweig's predictive equation:

$$\log_{10} p_{\mathrm{nap}} = \log_{10} E_{\mathrm{A}}(1.66 \pm 0.27) - (1.66 \pm 0.07),$$

from which we observe that p_{nap} is 1887 g m^{-2} a^{-1} (dry mass). We should, however, note here that on the same basis the calculated p_{nap} for the short-term mean (1070 mm) would be 2337 g m^{-2} a^{-1} and a range from 768 g m^{-2} a^{-1} in 1968 to 4037 g m^{-2} a^{-1} in 1974. Clearly these differences in available food could have a profound effect on year to year recruitment (Swingland & Coe 1979, this volume), on short-term food shortage and nutritive stress, or even be responsible for catastrophic mortality of adults as Phillipson (1975) has postulated for elephants in the Tsavo National Park (Kenya).

Detailed studies of food consumption by tortoises on Aldabra have yet to be carried out but preliminary measurements give a first approximation (table 1). It will be noted that by using animals of average size on Grande Terre, the amount of food consumed varies from 380 g d^{-1} (dry mass) in the wet season to 110 g d^{-1} at the height of the dry season in September. If we assume that the three rates of feeding described are each representative of consumption for 4 months of the year, we may estimate that these animals will eat 217 g d^{-1} or 79 kg a^{-1}. The most striking feature of these measurements is the very small amount of food being eaten by these cold-blooded herbivores in relation to their mass (20–30 kg) and also the great annual variation which must to a large degree be related to the restricted time available for feeding during the dry months of the year. This reduction in feeding time would certainly account for the absence of any sign of active growth for animals on Grande Terre over much of the year, and from which we might predict that the production efficiency of these creatures would be very low.

During the course of culling operations, animals were fed coloured paper markers 1–3 days before being killed and dissected as part of the reproductive study. These investigations yielded data on the amount consumed and the throughput times for animals in the medium size range. Throughput times obtained during this study are shown in table 2. It will be noted that there is again considerable seasonal variation in this parameter. With this preliminary sample it is not possible to establish a relation between the size of the animal and either food consumed or the throughput time. The mean throughput time for an animal in the 20–30 kg size class is 27 days.

TABLE 2. FOOD PASSAGE THROUGH GUT

season	number of observations	average throughput time (+s.e.)/d	observer
wet season (Jan.)	5	6 ± 2.8	Swingland
dry season (June)	4	30 ± 10.7	Swingland
late dry season (Sept.)	2	49.4 ± 38.5	Bourn & Coe
not specified	8	23.5 ± 11.9	Frazier (1971)

Mean throughput time = 27.2 days.

Using the mean tortoise densities for the four census localities on Grande Terre (Bourn & Coe 1978) and the estimated p_{nap} calculated for the mean annual rainfall (P_{A}), we may estimate the percentage of the primary production consumed. These figures (table 3) vary from 11.3% in the eastern census area to 0.7% in the *Pemphis* scrub. The mean figure of 7.2% represents considerable pressure on the available food resource, bearing in mind that much of the browse is unavailable until leaves, flowers or fruits fall, when they are also eaten by tortoises. Indeed, virtually all litter produced in the areas of high tortoise density comprise an important item of diet for this broad-spectrum opportunistic herbivore.

TABLE 3. RELATIONSHIP OF FOOD CONSUMED TO ESTIMATED p_{nap}

Grande Terre	tortoise density / ha^{-1}	vegetation consumed (C) / g m^{-2} a^{-1}	estimated p_{nap} / g m^{-2} a^{-1}	100 C/p_{nap}
E census area	26.95	212.47	1887.3	11.3
S coast census area	20.17	159.02	1887.3	8.4
other suitable areas	20.00	157.68	1887.3	8.4
other *Pemphis* areas	1.64	12.93	1887.3	0.7
mean	17.19	135.53	1887.3	7.2

Daily defecation rates were measured for tortoises in the Cinq Cases area of Grande Terre in the late dry season of 1974. Ten animals in the 20–30 kg size class were followed from 05h 30–08h 00. The mean mass of dung produced per individual was 34.8 g dry mass d^{-1} (s.e. ± 17.03). Since Frazier (1971) has shown that 68% of all defecations occur in the early morning the total amount of dung produced per animal would be 51.2 g dry mass d^{-1}. Observations on defecation and food consumption were carried out on animals of the same size range in 1974 so we may calculate that the gross assimilation efficiency for the giant tortoise in the late dry season would be about 50%. It should be noted that this figure approximates that of wild ruminants which perhaps suggests that more detailed studies on the giant tortoise may show that this figure is too high. The virtually intact leaves recovered from dung boli suggest that the assimilation efficiency is more likely to approximate that of the non-ruminant African elephant (*Loxodonta africana* Blumenbach) which has recently been measured as 22% (Rees 1977).

(*d*) *Biomass*

The very high densities recorded on Grande Terre represent animals of a wide size range and tell us little about the actual standing crop of animals present or more realistically the proportion of that standing crop that can be attributed to annual production. If we calculate mean masses for the large sample of animals measured on Aldabra we obtain figures of 21.65 ± 0.15 kg for Grande Terre, 49.9 ± 4.2 kg for Malabar, and 51.3 ± 6.9 kg for Picard. It is immediately apparent that the mean mass for the less dense populations of Malabar and Picard are respectively 130 and 137% greater than animals on Grande Terre, a difference which cannot be solely accounted for in terms of the age structure of the different populations.

TABLE 4. TORTOISE DENSITY AND BIOMASS

	area/(km^2)	tortoise density km^{-2}	total no. of tortoises	biomass kg km^{-2}	production kg km^{-2} a^{-1}
Grande Terre (mean mass 21.65 + 0.15 kg)					
E census area	33.60	2695.2	90 560	58 352	2450.8
S coast census area	18.40	1678.9	30 891	36 347	1526.6
other suitable areas	9.60	2000.0	19 200	43 300	1818.6
other *Pemphis* areas	38.17	163.9	6 260	3 548	149.0
		$\bar{x}$ = 1634.5		$\bar{x}$ = 35 387	1486.3
Malabar (mean mass 49.9 ± 4.2 kg)					
census area	3.20	703.1	2 250	35 084	1192.8
whole area	27.96	80.5	2 250	4 017	136.6
Picard (West Island) (mean mass 51.3 ± 6.9 kg)					
non-*Pemphis*	2.47	494.0	1 235	25 342	861.6
whole area	7.47	163.3	1 235	8 480	288.3
other islands	0.11	636.0	70	—	—

Production = biomass × (0.034) kg km^{-2} a^{-1} (Malabar);
= biomass × (0.042) kg km^{-2} s^{-1} (Grande Terre).

The standing crop biomass derived for the three main island populations (table 4) range from 58352 to 3548 kg km^{-2} on Grande Terre (mean 35387 kg km^{-2}), 35084 on Malabar and 25342 kg km^{-2} on Picard. The biomass data for Grande Terre are calculated for the whole land area since even though they occur at low density (164 km^{-2}), in *Pemphis* scrub it is difficult to assess accurately the area from which they are totally excluded. The figures for Malabar and Picard, however, refer to the area over which the tortoises are known to range. If we express the biomass for the whole area of Malabar and Picard that is potentially, if not actually, available we see that the biomasses are reduced to 4017 and 8480 kg km^{-2} respectively.

The mean biomass of Grande Terre (35387 kg km^{-2}) is higher than any wildlife area of the African mainland dominated by large herbivorous mammals. The closest figures to these Aldabra biomasses are those recorded for the Rwindi Plain, Zaire (17448 kg km^{-2}), Bunyoro North, Uganda (13261), Rwenzori National Park, Uganda (19928) and Manyara National Park, Tanzania (19189) (Coe *et al.* 1976). It is of interest, however, to note that the mean annual rainfall of all these four areas (863–1150 mm) closely approximates that of Aldabra.

Very few comparable figures are available for reptile biomasses recorded elsewhere in the world, and more particularly where they comprise a dominant element in the fauna. Lizard biomasses range from 26.7 kg km for Texas (Tinkle 1967) to 376 kg km^{-2} for Kansas (Fitch 1967). Harris (1964) has recorded a biomass of 240 kg km^{-2} for the *Agama* lizard (*Agama agama*) in Nigeria, and Western (1974) a mean biomass of 102 kg km^{-2} for several species of lizard in South Turkana, Kenya. It must, however, be remembered that all these measurements refer to ecosystems in which reptiles compose a very small part of a very complex community. Graham (1968) studying the Nile crocodile (*Crocodylus niloticus*) in Lake Rudolf, Kenya, has recorded biomasses ranging from 3475 to 13900 kg km^{-2}, but these figures do not take into account the fact that a large part of the material required to sustain this biomass is derived from a very much larger area than that used to estimate these biomass densities. Ruibal & Philibosian (1974) have reported a biomass of between 1300 and 2300 kg km^{-2} for an arboreal new world lizard (*Anolis acutus*).

TABLE 5. COMPARATIVE TISSUE COMPOSITION OF AFRICAN ELEPHANT AND ALDABRAN TORTOISE

(Results expressed as a percentage of total mass.)

component	*Loxodonta africana* (Coe 1977)	*Geochelone gigantea*
bone	18.6	42.9
skin	11.6	—
soft tissues	51.5	21.8
intestines and organs		16.7
gut contents	16.3	12.0
liquid	2.0	6.6

Measurements of biomass provide a good indication of the standing crop supported by an ecosystem but they do not take into account such important factors as the turnover time (expressed as the ratio production: biomass) which will largely be determined by the generation time of the dominant species composing that community. The giant tortoises of Aldabra represent an almost single-species herbivore community whose generation time approximates that of the African elephant.

In addition to living for up to 65 years, the giant tortoise's body contains relatively little soft tissue. Dissections conducted by Swingland during the study of reproduction on Aldabra have indicated that 43% of the tortoise's body mass is composed of bone while only 38% is represented by soft tissue. If we compare these figures with those of the African elephant (Coe 1978) we note that only 18.6% (or 30% including the skin) is bone while 51.5% makes up the contribution of soft tissues (table 5). Thus we might expect that the amount of annual production going into soft tissue and bone replacement would be much less in the tortoise than it is in the equally long-lived elephant, apart from obvious differences in their metabolism.

(*e*) *Production*

Coe *et al.* (1976) have examined the relation between rainfall and biomass, energy expenditure and secondary production for 24 wildlife ecosystems in Africa. Using production and biomass data in the literature, they have shown that the production: biomass ratio (P/B) for herbivores grouped into large (over 800 kg), intermediate (110–750 kg), and small (5–90 kg) size categories were respectively 0.05, 0.20, and 0.35. When data for the large herbivore biomasses were converted to production by using the above ratios they established that a linear relation existed between this parameter and rainfall (regression coefficient = 0.832; probability = <0.001).

Calculation of a P/B ratio for the Aldabra tortoise requires that annual production can be measured directly, or estimated indirectly. By using accurate data available on the age distribution of the Malabar and Grande Terre populations it is possible to calculate a mean survival time and from this to estimate the percentage of the population that can be presumed to be turned over or replaced each year. Age distributions given by Grubb (1971) and Bourn & Coe (1978) yield P/B ratios of 0.074 (7.4% a^{-1}) for Grande Terre and 0.064 (6.4% a^{-1}) for Malabar. Since, however, the age distribution data available only refer to those animals up to 30 years old which can be aged directly from scute rings, these P/B ratios do not take into account those animals in the population that are older than 30 years. It is therefore to be expected that the actual rate of turnover will be 1–2% below the 6.4–7.4% estimated above.

An alternative approach is to estimate the animal biomass lost by mortality and assuming that the population is relatively stable (Bourn & Coe 1978; Swingland & Coe 1979, this volume) at present, this figure can be taken to be equivalent to the amount of material being added each year in secondary production.

Bourn & Coe (1978) have calculated that the annual mortality rates for the Malabar and Grande Terre population are respectively 2.7 and 2.9% for animals over 60 cm curved length. We may therefore estimate that on Malabar 19 animals per square kilometre die each year compared with 44 on Grande Terre. The mortality of animals on Grande Terre has been estimated by 5 year age classes from 15–65 years (Bourn & Coe 1978). If the mean individual tortoise mass is calculated for each of these age classes it is possible to derive the biomass lost each year to the population owing to mortality. Thus for the Grande Terre animals we may obtain a P/B ratio of 0.04. Since, however, this figure does not take into account those animals lost each year from the 0.15 year age classes, a correction has been calculated based on the percentage of animals which falls in these three 5 year age classes, from which we obtain a corrected P/B ratio of 0.042.

The low population size on Malabar presents difficulties in estimating mortality in individual age classes. If, however, the mean mass per 5 year age class is calculated and a figure of 2.71% mortality per annum is used in the same proportions that animals are observed to die on Grande Terre we obtain a P/B ratio of 0.033 for the 15–65 year age classes and 0.034 for the whole age range of 0–65 years.

Table 4 shows the estimated annual tortoise production in relation to biomass and density from the above ratios. It is immediately apparent that in spite of the high densities and biomasses recorded on Grande Terre the annual production ranges from only 149 kg km^{-2} a^{-1} in the *Pemphis* areas to 2450.8 in the densely populated areas of the southeast, the mean production for the whole land area being 1486 kg km^{-2} a^{-1}. Similarly for Malabar the annual secondary production for the census area occupied by tortoises is 1193 and 137 kg km^{-2} a^{-1} for the whole island. By using the same P/B ratio as Malabar for Picard in the absence of adequate mortality data to calculate the ratio separately, annual productions of 862 km kg^{-2} a^{-2} are obtained for the tortoise area and 288 for the whole island.

The production figures for Malabar are close (–26%) to that of Grande Terre indicating that although the population of the former is so much less dense, the larger body size (+130%) of these animals allows them to achieve similar production, suggesting that we are observing two strategies for operating within the available food resources. Swingland (1976) has suggested that the greater shade cover on Malabar allows these animals to achieve greater size by spending longer periods feeding.

We have calculated that the tortoises of Grande Terre eat 0.136 kg m^{-2} a^{-1} or 136000 kg km^{-2} a^{-1}. If we therefore use a gross assimilation efficiency of 50%, the population should assimilate 72050 kg km^{-2} a^{-1}. The population has, however, only been calculated to produce 1486 kg km^{-2} a^{-1} in secondary production, which only represents 2.1% of the material assimilated.

McNeill & Lawton (1970) have examined the relation between annual production and respiration and have demonstrated that they can distinguish regressions for homeotherms and poikilotherms. Additionally, though, they have also shown that they can distinguish data for long-lived poikilotherms (animals in which a proportion of the population exceeds 2 years of age) from short-lived poikilotherms (animals in which all individuals live less than 2 years). Although they do not include data for reptiles they have presented data for five species of fish which are comparatively long lived. The percentage of energy going to production is here expressed as a percentage of that being available from assimilation (production + respiration). These figures vary from 7.7% for the roach (*Rutilus rutilus* L.) to 6.0% for the dace (*Leuciscus leuciscus* L.), which are very low compared with those obtained for short-lived poikilotherms which may achieve production efficiencies as high as 62%. McNeill & Lawton (1970) explain the low production efficiencies of long-lived poikilotherms in terms of the high respiratory cost, and extended non-productive periods experienced by animals that live for more than 2 years. Clearly, for an animal like the giant tortoise of Aldabra, we not only know that these creatures are very long lived but also that they experience long dry periods when their production must be virtually nil. Thus in terms of the tentative production efficiency calculated above (2.1%) this figure would appear to be of the right order of magnitude. In the event, however, that further work on feeding may well reveal a lower gross assimilation efficiency (*ca.* 30%), the production efficiency will still only be raised to 3.6%. Heatwole (1976) has presented data for the Australian Scincid Lizard (*Egernia cunninghami*) taken from Shine (1971) where the production efficiency for growth is less than 1%.

3. Discussion

We have shown that the high biomass of giant tortoises on Aldabra tells us very little about the manner in which the resources of this Indian Ocean island can sustain such a large herbivore standing crop. When, however, we calculated the P/B ratio for this long-lived reptile we found that the secondary production represents only 3–4% of the standing crop biomass. It is now necessary for us to examine the relations of the annual production data to factors which may potentially limit production and through it the standing crop biomass. Clearly, shade is an important factor which may drastically limit the time available for feeding in a cold-blooded vertebrate, which may account for the difference in mean mass between animals on Grande Terre and Malabar. Here it is argued that the availability of food both in terms of quantity and quality is liable to influence animal size, their numbers and recruitment.

Coe *et al.* (1976) have produced a predictive equation by which production and biomass may be calculated from the mean annual rainfall. This relation is valid up to 700 mm and is not expected to deviate significantly up to the mean rainfall for Aldabra (941 mm a^{-1}). These expressions may therefore be used to predict the herbivore production and biomass for comparison with that estimated for Aldabra. Table 6 compares the relation between the estimated production with that predicted from the expression

$$(1.649 \pm 0.486)\ x - (1.720 \pm 1.357) \quad [x = 2.973].$$

It will be observed that while estimated production for the whole atoll deviates by up to 60% from that of predicted production (1525 kg km^{-2} a^{-1}), that for the area occupied by tortoises only differs by 23%. Additionally, and most notably, there is the fact that the production estimated for Grande Terre (where 98% of the tortoise population is located) only differs by 2.6% from that predicted from the mean rainfall. This would suggest that if we accept that the level of primary production is dependent on available precipitation, the present tortoise population of Grande Terre closely approximates the 'carrying capacity'.

Table 6. Estimated and predicted production

	mean biomass kg km^{-2}	estimated production† kg km^{-2}	predicted production‡ kg km^{-2}	% difference between estimated and predicted productions
Grande Terre	35 387	1486	1525	−2.6
Malabar				
whole area	4 017	137	1525	−91.0
tortoise area	35 084	1193	1525	−21.8
Picard				
whole area	8 480	288	1525	−81.1
tortoise area	25 342	862	1525	−43.5
mean				
whole area	15 961	637	1525	−58.2
tortoise area	31 937	1180	1525	−22.6

† Estimated production for Grande Terre = biomass (0.042) kg km^{-2} a^{-1}; estimated production for Malabar and Picard = biomass (0.034) kg km^{-2} a^{-1}.

‡ Predicted production = $(1.649 \pm 0.486)\ 2.973 - (1.720 \pm 1.357)$ (formula after Coe *et al.* 1976).

Semi-arid environments on the African mainland are characterized by large annual variations in rainfall, so that while the mean rainfall may indicate the general level of primary production available to herbivores it does not take into account short-term and perhaps periodic fluctuations in climate. If we assume that there are periodic climate fluctuations, we can predict that the potential 'carrying capacity' of Aldabra in terms of available food resources may vary with the same period. Although the mean annual precipitation on Aldabra is 941 mm, measurements during the operation of the Royal Society meteorological station suggest that since 1968 the mean rainfall has been 1070 mm, which would sustain an annual tortoise production of 1886 kg km^{-2}. The highest and lowest rainfalls recorded by the station have been 547 mm (1968) and 1487 mm (1974) which would sustain annual productions of respectively 624 and 3245 kg km^{-2} a^{-1}. Thus it would appear that the present observed biomass on Grande Terre is closely related to the mean annual rainfall in terms of the annual production achieved by the tortoise population.

On the African mainland, large herbivores with relatively long generation times are incapable of taking advantage of short-term variation in rainfall. Indeed Phillipson (1975) has shown that low rainfall and concomitant low primary production can be related to catastrophic death in the elephant populations of the Tsabo National Park, Keyna. In contrast with this situation, the tortoises of Aldabra simply stop growing during drought and provided these periods are comparatively short they can maintain a high biomass but reduce their annual production. The manner in which the tortoises can respond to sudden increases in rainfall and food is exemplified by the study of their reproduction (Swingland & Coe 1978), which has shown that during a period of increased and unseasonal rain in 1975 the animals of Grande Terre increased the number of eggs per nest and mean egg mass in an almost immediate response to increased food availability. Hence although the tortoises of Aldabra have a similar generation time and P/B ratio to that of the African elephant (0.05) their response to temporal variations in climate and food supply is more reminiscent of that of insects, small mammals and birds which may respond immediately to sudden rain and produce large numbers of young.

The production data we have examined above refer only to the mean recorded on the whole of Grande Terre and do not take into account the high densities and biomass observed in the southeast of this island. Here a biomass of 58352 kg km^{-2} would be estimated to sustain an annual production of 2451 kg km^{-2} a^{-1} which is 61 % higher than that predicted from its rainfall.

TABLE 7. COMPARATIVE BIOMASS AND PRODUCTION DATA FOR AFRICAN WILDLIFE ECOSYSTEMS AND ALDABRA

locality	rainfall	estimated production kg km^{-2}	biomass kg km^{-2}	predicted biomass† kg km^{-2}	predicted production† kg km^{-2}	% difference between estimated and predicted production
Amboseli (Kenya)	350	934	4848	1555	299	+68
Rwidindi (Zaire)	863	1936	17448	7115	1323	+31
Manyara (Tanzania)	915	2405	19189	7852	1457	+39
Rwenzori (Uganda)	1010	2554	19928	9274	1714	+33
Aldabra (SE Grande Terre)	941	2450	58352	8231	1525	+61

† Predicted biomass = $(1.685 \pm 0.238)x - (1.095 \pm 0.661)$; predicted production = $(1.649 \pm 0.486)x - (1.720 \pm 1.357)$, where x = mean annual precipitation. (Both after Coe *et al.* 1976).

Coe *et al.* (1976) noted that of the 24 wildlife systems examined for the African mainland, four of them exceeded the potential large herbivore 'carrying capacity'. On examining the data for these four areas, they concluded that four of them were supplied with abundant ground water while the fourth was located on a fertile volcanic soil. Under these circumstances we might expect that the available primary production might exceed that predicted from measures of mean rainfall. Table 7 compares the biomass and production data for these four areas and demonstrates that their estimated production exceeds that estimated from standing crop biomass by between 30 and 68 %. The large production observed in Amboseli being in large part accounted for by the presence of a large swamp area fed by abundant spring water from Kilimanjaro. Southeast Grande Terre on Aldabra seems to fall into the same category as Amboseli, for its estimated production exceeds that predicted from rainfall by 61 %. While there are clearly few direct similarities between these two areas the availability of ground water may well be a significant factor. In most arid regions of the world, rainwater is rapidly lost by percolation and runoff, but in the east and southeast of Grande Terre a large lens of fresh water is raised close to the surface by high spring tides which would make much of the precipitation potentially available for plant growth even in the absence of appreciable rain. Additionally but of probably minor significance, is the presence of guano-based soils (Piggott 1968) in this area. It is perhaps no coincidence that the genetically dwarfed 'tortoise turf' (Merton *et al.* 1976) which is so abundant on Grande Terre and of great importance as tortoise food may also be related to the availability of this periodically abundant ground water and perhaps also to the pockets of fertile soil on which it occurs.

The authors would like to thank the Royal Society who provided logistical support for this work on Aldabra. During the preparation of this manuscript we have had the benefit of discussions with Professor George Dunnett and Dr John Phillipson. The population dynamics and reproductive phases of the tortoise programme have been supported by generous grants from the Natural Environment Research Council. Last but by no means least we would like to thank the Seychellois of Aldabra without whose technical help and field skills this work would never have been completed.

REFERENCES (Coe *et al.*)

Bourn, D. 1976 The giant tortoise population of Aldabra (Cryptodira: Testudinidae). Part 1. Preliminary results. *Zool. afr.* **11**, 275–284.

Bourn, D. & Coe, M. 1978 The size, structure and distribution of the giant tortoise population of Aldabra. *Phil. Trans. R. Soc. Lond.* B **282**, 139–175.

Braithwaite, C. J. R., Taylor, J. D. & Kennedy, W. J. 1973 The evolution of an atoll: the depositional and erosional history of Aldabra. *Phil. Trans. R. Soc. Lond.* B **266**, 307–340.

Cobb, S. 1977 The distribution and abundance of the large herbivore community of Tsavo National Park, Kenya. D.Phil. thesis, University of Oxford.

Coe, M. J., Cumming, D. H. & Phillipson, J. 1976 Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* **22**, 341–354.

Coe, M. J. 1977 The decomposition of elephant carcases in the Tsavo (East) National Park, Kenya. *J. arid. Envir.* **1**, 71–86.

Fitch, H. S. 1967 Ecological studies of lizards on the University of Kansas Natural History Reservation. In *Lizard ecology: a symposium.* Columbia: University of Missouri Press.

Frazier, J. G. 1971 Behavioural and ecological observations on Giant tortoises on Aldabra Atoll. D.Phil. thesis, Oxford University.

Gaymer, R. 1968 The Indian Ocean Giant tortoise *Testudo gigantea* on Aldabra. *J. Zool., Lond.* **154**, 341–363.

Gaymer, R. 1973 A marking method for giant tortoises and field trials on Aldabra. *J. Zool., Lond.* **169**, 393–401.

Graham, A. 1968 The Lake Rudolf crocodile (*Crocodylus niloticus* Laurentis) population. M.Sc. thesis, University of Nairobi.

Grubb, P. 1971 The growth, ecology and population structure of giant tortoises on Aldabra. *Phil. Trans. R. Soc. Lond. B.* **260**, 327–372.

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

Heatwole, H. 1976 *Reptile ecology.* Brisbane: University of Queensland Press.

McNeill, S. & Lawton, J. H. 1970 Animal production and respiration in animal populations. *Nature, Lond.* **255**, 472–474.

Merton, L. F. H., Bourn, D. M. & Hnatiuk, R. J. 1976 Giant tortoise and vegetation interactions on Aldabra Atoll. Part 1: inland. *Biol. Conserv.* **9**, 292–304.

Morgan, D. D. V. 1976 A statistical study of data on Giant tortoises on Aldabra. M.Sc. thesis, University of Oxford.

Morgan, D. D. V. & Bourn, D. M. 1978 A comparison of two methods of estimating the size of a population of giant tortoise on Aldabra. Manuscript.

Palombelli, F. 1954 L'isola della tartorughe. *Epoca* **7**, March issue.

Phillipson. J. 1975 Rainfall, primary production and 'carrying capacity' of Tsavo National Park (East), Kenya. *E. Afr. Wildl. J.* **13**, 171–201.

Piggott, C. J. 1968 *Soil survey of Seychelles. Tech. Bull.* no. **2**, Ministry of Overseas Development, Directorate of Overseas Surveys, London.

Rees, P. A. 1977 Some aspects of the feeding ecology of the African elephant (*Loxodonta africana africana* Blumenbach 1797) in captivity. Honours thesis, University of Liverpool.

Rosenzweig, M. L. 1968 Net primary productivity of terrestrial communities: production from climatological data. *Am. Nat.* **102**, 67–74.

Ruibal, R. & Philibosian, R. 1974 The population ecology of the lizard *Anolis acutus*. *Ecology* **55**, 525–37.

Shine, R. 1971 The ecological energetics of the scincid lizard *Egernia cunninghami* (Gray 1832). Unpublished Hons. thesis, Australian National University, Canberra.

Stoddart, D. R. & Mole, L. V. 1977 Climate of Aldabra. *Atoll Res. Bull.* **202**, 1–21.

Stoddart, D. R. & Peake, J. F. 1979 Historical records of Indian Ocean giant tortoise populations. *Phil. Trans. R. Soc. Lond.* B **286**, 147–161 (this volume).

Stoddart, D. R. & Walsh, R. P. D. 1979 Long-term climatic change in the western Indian Ocean. *Phil. Trans. R. Soc. Lond.* B, **286**, 11–23 (this volume).

Swingland, I. R. 1976 Ecological studies of the giant land tortoise *Geochelone gigantea* on Aldabra Island. Report to Aldabra Research Committee, April 1976, pp. 1–14.

Swingland, I. R. & Coe, M. J. 1979 The natural regulation of giant tortoise populations on Aldabra Atoll: recruitment. *Phil. Trans. R. Soc. Lond.* B **286**, 177–188 (this volume).

Taylor, J. D., Braithwaite, C. J. R., Peake, J. F. & Arnold, E. N. 1979 Terrestrial faunas and habitats of Aldabra during the late Pleistocene. *Phil. Trans. R. Soc. Lond.* B **286**, 47–66 (this volume).

Tinkle, D. W. 1967 Home range, density, dynamics and structure of a Texas population of the lizard *Uta stansburiana*. In *Lizard ecology: a symposium*. Columbia: University of Missouri Press.

Walter, H. 1954 Le facteur eau dans les régions arides et sa signification pour l'organisation de la végetation dans les contrées sub-tropicales. In *Les divisions ecologiques du monde*. Paris: C.N.R.S.

Western, D. 1974 The distribution, density and biomass density of lizards in a semi-arid environment in Northern Kenya. *E. Afr. Wildl. J.* **12**, 49–62.

Whittaker, R. H. 1970 *Communities and ecosystems*. London: Collier-Macmillan.