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Feeding Ecology and Seasonal Movements of Giant Tortoises on Aldabra Atoll

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Summary. We investigated seasonal changes in diet and distribution of giant tortoises (*Geochelone gigantea* (Schweigger)) on Aldabra atoll in the Indian Ocean. Animals were counted and their activity and feeding behaviour recorded on transects where vegetation composition and primary production had been studied (Gibson and Phillipson in press *a, b*).

There were striking seasonal shifts in tortoise distribution, and male, female, and juvenile tortoises were found in different proportions in different vegetation types.

Tortoises are selective grazers, feeding on a wide range of foodstuffs of which the most important (61% of feeding observations) was tortoise turf. Diet varied seasonally, with shrub leaves (mostly litter) overtaking tortoise turf in importance in the late dry season; diet broadened as the dry season progressed. Male and female diets were not significantly different but juveniles fed on herbs and mosaic rock vegetation more often than adults.

Seasonal shifts in distribution are due to movements in response to changes in food availability, measured by the foods' cover abundances and production phenologies. Tortoises concentrate on preferred foods when available, but become less selective as production falls. Some differences in size and sex class distribution between habitats can also be explained by food availability.

In the late dry season density peaks on the coastal *Sporobolus virginicus* (L.) Kunth sward. A detailed study showed that, while at least 20% of the population uses the sward each year, visit times are short and turnover of tortoises high, as would be expected on a non-preferred food.

The giant tortoise interacts with its food supply similarly to other large herbivores, except that the low maintenance needs of this large poikilotherm allow it to develop unusually high population densities.

Introduction

Many herbivores are limited by their food supply, an effect to which nutritional and other constraints on the type of food eaten by a particular species contribute. Large herbivores in the semi-arid tropics encompass a range of feeding types from generalist grazers to highly selective forms (Sinclair and Norton-Griffiths 1979). In large heterogeneous areas such as the Serengeti this selectivity interacts with vegetation phenology to generate large-scale seasonal migrations of mammal herbivores (Jarman and Sinclair 1979).

This type of system has usually been observed where the dominant herbivores are large mammals – which are homeothermic, have few young at once, and often have highly developed social behaviour. By contrast, the giant tortoise is poikilothermic, lays many eggs at once, has weak social interactions and a longer life span than most large mammals. On Aldabra it is the only large herbivore, occurring at high density (27 individuals ha^{-1} on Grande Terre) and limited by food (Coe et al. 1979; Hamilton and Coe in press). The animals make striking seasonal movements (Swingland and Lessells 1979) and their diet includes a wide variety of plant species (Grubb 1971). It is of interest to compare this system with herbivore-plant systems dominated by large mammals elsewhere.

In this paper we document the seasonal patterns of movement and feeding behaviour of the giant tortoises and compare these patterns with seasonal and spatial differences in food availability. The generation of diet choice and seasonal movements in giant tortoises is then compared with current knowledge about other large herbivores.

Methods

Study Area

Aldabra is a large (156 km^2) raised atoll 1,000 km southwest of the central Seychelles (Fig. 1 a). The climate is semiarid with a wet season from December to April and a dry season from May to November. The indigenous population of some 150,000 giant tortoises is split into five sub-populations between which there is less than 1% exchange per year (Gibson and Hamilton in prep.). We studied the densest sub-population, in the Cinq Cases area (Fig. 1 b).

Tortoise Observations

1) Transect Observations. Tortoises were observed systematically on seven transects where the vegetation had been recorded in detail (Gibson and Phillipson in press *b*), each month from November 1977 to January 1979. Observations were made each month between dawn and 0900 h, the period of peak feeding activity (Results). Every four months observations were made at other times of day to investigate daily activity patterns.

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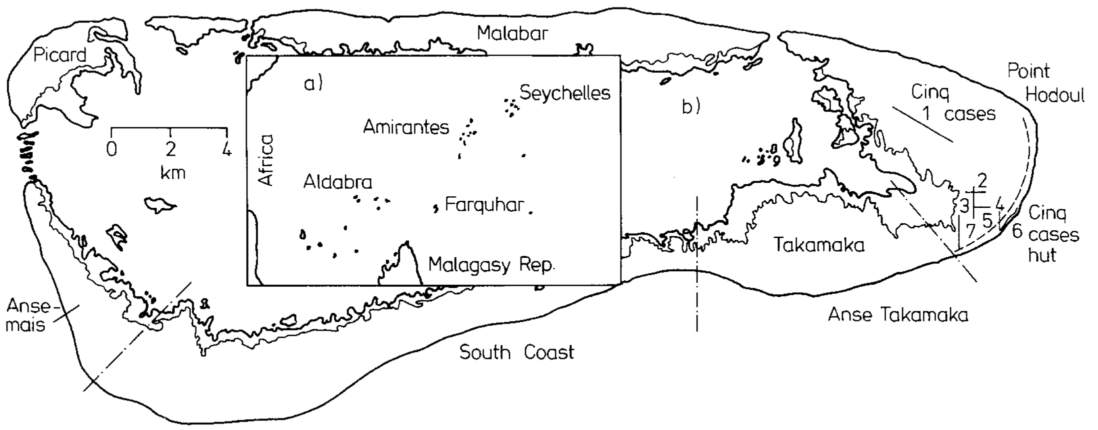

Fig. 1 a, b. The location of Aldabra island **a** and study areas on Aldabra **b**. Dash-dot lines: boundaries between the major sub-populations of giant tortoises on the atoll. Dashed line: approximate location of the 8-m ridge and "pinnacle zone" barrier to tortoise movement in the Cinq Cases region. Numbers in the Cinq Cases region refer to transects

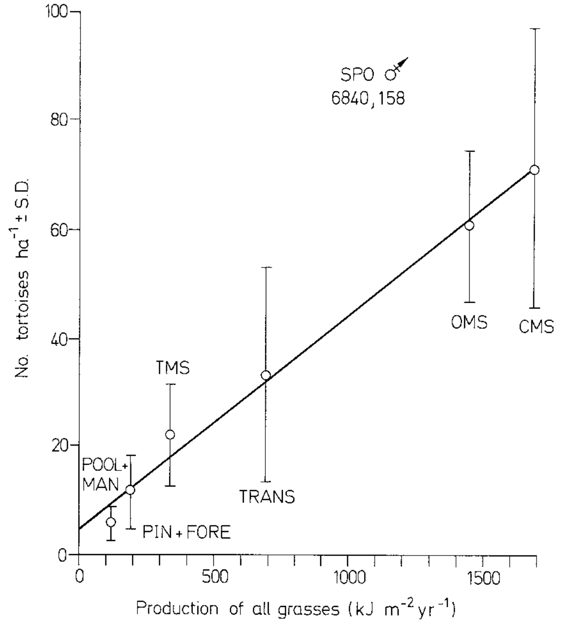

Fig. 2. The relationship between grass production and density of giant tortoises in the Cinq Cases region (line is fitted by eye). Production data from Gibson and Phillipson (in press *a*) and tortoise density from the census hectares of Bourn (1978). Vegetation types: *POOL* and *MAN* pool vegetation and mangroves, *PIN* pinnacle zone, *FORE* foreslope of 8 m ridge, *TMS* mixed scrub, *OMS* open mixed scrub, *TRANS* census hectares containing both mixed scrub and open mixed scrub, *CMS* coastal mixed scrub and *SPO S. virginicus* coastal sward (after Gibson and Phillipson (in press *b*)).

Transects were divided into 50 m sections. All tortoises within 5 m (thick vegetation) or 10 m (open vegetation) of the transect line were counted. For each tortoise we recorded:

a) Size. Tortoises were grouped into size classes by width of the third dorsal scute: size class 1 was ≤ 5.9 cm, size class 2 6.0–10.9 cm, and so on (5 cm intervals). Disc-marked animals (Gaymer 1973) were measured with a steel tape to the nearest 0.1 mm.

b) Sex. Male, female, or juvenile.

c) Activity. Type of behaviour at first sighting; recorded as 'unknown' if the animal was disturbed by the observer.

d) Food type. If the animal was feeding we recorded food species, plant part, whether attached to plant, whether dead or living, and the height above ground from which food was taken.

2. Coastal Observations. At the end of the dry season (November/December) there is a dramatic peak in tortoise density on the coastal *Sporobolus virginicus* sward (Voeltzkow 1897; Swingland and Lessells 1979). At this season all tortoises seek shade over midday (Swingland and Frazier 1979; Results), and for those using the coast *Guettarda speciosa* thickets near Cinq Cases hut provided the only available shade. Tortoises could only leave or reach the coast here via gaps in the 8-m ridge directly inland of Cinq Cases, so that by counting the animals sheltering under the thickets between 1200 and 1400 h we could monitor individual movement patterns and estimate the total number of animals using the sward. Each day from 22 October to 29 November 1978, from 13 to 19 December 1978, and from 3 to 23 January 1979 we made a count, and for marked tortoises recorded size, sex and position. We regularly searched the coastal mixed scrub behind the 8-m ridge for marked animals. On 24 November 1978 and 23 January 1979 we searched the *S. virginicus* sward from 1 km west of Anse Takamaka to 1.5 km west of Point Hodoul (Fig. 1) before 0900 h, and counted all animals on the sward. Combining these counts with individual turnover rates calculated from movements of marked animals, we estimated the total number of animals using the sward during the activity peak on the coast.

Analysis

1) Pooling of Transect Data. There was a good relationship between grass productivity in each vegetation type (Gibson and Phillipson in press a) and tortoise density (Fig 2; reanalysis of data from Bourn and Coe 1978). We therefore analysed our data by vegetation type rather than locality (transect). We calculated the size and sex class distributions of activity of tortoises using each vegetation type each month by combining the transect observations with estimates of the area of each vegetation type taken from the

Table 1. Estimated total number of tortoises in the Cinq Cases area

Month	Number	Variance/mean ratio between habitats[a]
November 1977	57115	27.7
December	58538	13.5
January 1978	65809	15.4
February	83224	38.0
March	74055	39.3
April	74945	33.0
May	66395	21.0
June	73540	15.7
July	66154	10.7
August	62429	15.2
September	65308	18.0
October	48618	17.3
November	55817	30.9
December	54728	13.9
January 1979	58683	23.4
12 month mean	66352±S.E. 2681	

Area of different vegetation types involved in estimates: open mixed scrub, 356.5 ha; mixed scrub 1,367.5 ha; coastal mixed scrub 138 ha; *S. virginicus* and ridge foreslope 82.5 ha; pool vegetation 90 ha

[a] Variance/mean ratio of tortoise density between vegetation types; this provides an index of the degree to which tortoises were concentrated in particular vegetation types

Aldabra vegetation map (Gibson and Phillipson in press b). Errors were calculated taking each segment falling in a given vegetation type as a single number/density estimate for that vegetation type.

2) Total Population Estimate. To check the accuracy of our population density estimates and ensure that our transect observations had not omitted an important part of the population, we calculated the total population in the Cinq Cases area for each month (Table 1). This estimate varied seasonally, which could mean that a large fraction of the total population had occupied vegetation types omitted from the transects; however further analysis suggests that it is due to sampling error.

Mangrove swamps and *Pemphis acidula* Forst. scrubs cover large areas of the Cinq Cases region but were omitted from the transects. Densities are low in these vegetation types at all seasons (Fig. 2; Bourn 1976; personal observations) and there are no density changes of the order required to explain the seasonal range in the total population estimate.

The mixed scrub covers a large area and so makes a large contribution to the total population estimate, but because of its area was sampled less intensively than other vegetation types, and density estimates were based on smaller areas due to the thick vegetation. The total population estimate was lowest in the dry season when density peaks in the mixed scrub. Also, density estimates in the open and coastal mixed scrubs had larger errors at the peaks. An unfavourable combination of these errors could lead to overestimation of total numbers in the wet season and underestimation in the dry season. The true figure probably lies between these extremes, and the variation is likely to be due to sampling errors rather than to omission of an important fraction of the tortoise population.

Table 2. The proportions of different items in the diet of tortoises from coastal mixed scrub by feeding frequency and faecal composition. Feeding frequencies are percentages based on tortoises which were feeding only

	a) Tortoise turf +mosaic		b) Litter	
	Feeding frequency	Faecal composition	Feeding frequency	Faecal composition
January 1978	76.3	72.05	7.9	16.0
February	84.1	83.5	3.2	13.9
March	77.3	84.0	6.8	7.6
June	71.4	60.4	8.6	37.7
August	73.3	85.2	13.3	13.0
October	84.6	74.0	10.3	21.9
January 1979	93.5	94.1	0	4.06

3) Diet Composition. The frequencies of observations of feeding on different items were taken to indicate diet composition. As a check we compared feeding frequencies with the proportion of common plant species in faeces of tortoises collected from one vegetation type (Table 2). The proportion of tortoise turf in the diet of tortoises in coastal mixed scrub by feeding frequency was similar to that in the faeces, but for shrub leaves feeding frequency gave a lower result. This could be due to either a lower assimilation efficiency or a shorter handling time per unit weight of shrub leaves. Most shrub species were taken as fallen leaves, and the short sward of tortoise turf meant that bite sizes were small, so both factors may be involved. We consider that while feeding frequencies may slightly underestimate the proportion of shrub leaves in the diet, they provide an adequate description of tortoise feeding patterns.

Results and Discussion

Tortoise Distribution

Tortoise density varied widely between vegetation types (Figs. 2, 3) reaching a maximum of > 100 ha^{-1} in the coastal mixed scrub (wet season); in general densities were highest in the coastal and open mixed scrubs. Taking the area of each vegetation type into account we see that in terms of absolute numbers one- to two-thirds of the population is in the mixed scrub throughout the year and the remainder mostly in coastal and open mixed scrubs.

There were clear seasonal changes in tortoise density in all vegetation types studied (Fig. 3) except pool vegetation where density was always low. Tortoise density peaked on the *Sporobolus virginicus* sward in the late dry/early wet season, in coastal and open mixed scrubs later in the wet season, and in the mixed scrub in the dry season.

Male, female, and juvenile tortoises occurred in different proportions in different vegetation types (Fig. 4). Females were overrepresented in mixed scrub but underrepresented in coastal mixed scrub and *S. virginicus* sward. Juveniles were overrepresented in coastal mixed scrub and mixed scrub.

Feeding Patterns

The proportion of animals feeding varied systematically with time of day. Most tortoises were feeding in the early

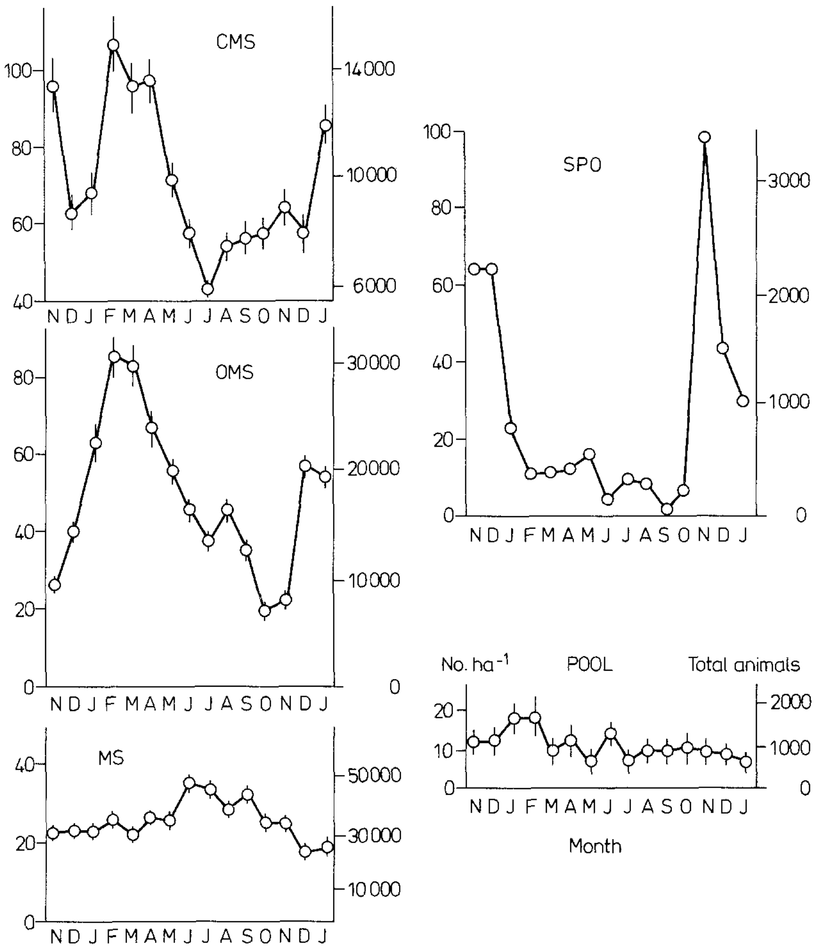

Fig. 3. The seasonal distribution patterns of giant tortoises in five vegetation types. Left-hand y axes show tortoise density in numbers ha^{-1}; the right-hand ones show the estimated total number of animals; based on the area of different vegetation types in the Cinq Cases region. Bars show ±1 S.E. (Errors not given for *S. virginicus* turf because of systematic variation in density along the coastal transect where it occurs)

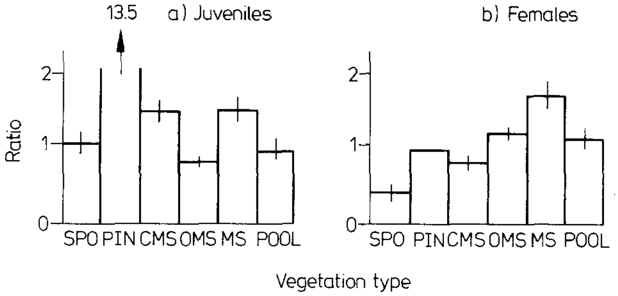

Fig. 4a, b. The sex ratios of tortoises in each vegetation type. Bars are ±1 S.E. calculated using tan^{-1} transformation of the data for each month of the study; males taken as 1.0. Only 27 juveniles, 2 males and 2 females were seen in the pinnacle zone during the study. Vegetation types as for Fig. 2

morning. After 0900 h fewer animals fed and by 1200 h nearly all were resting in shade. Feeding started again in the afternoon but the proportion never reached that of the morning peak. Except where feeding observations were based on very few animals at midday, diet composition did not vary over the day, so we used only early morning observations for the analysis. Feeding frequency also varied seasonally, with a lower proportion of animals feeding at any given time as the dry season progressed.

Giant tortoises have been seen feeding on most Aldabran plant species, and on other material such as carrion (including tortoise), goat faeces, and camp debris (Frazier 1971; Grubb 1971; Merton et al. 1976). Our data confirmed these observations, but most feeding was on a narrow range of plant materials (Fig. 5). Tortoise turf (Grubb 1971) was the commonest item, followed by shrub leaves, especially *Terminalia boivinii* Tul., most of which (504/531 observations) were taken from the ground as fresh litter. Leaves of sedges such as *Fimbristylis cymosa* R.Br. and *Cyperus* spp. were rarely taken; most sedge feeding was on flowers or developing seeds. Dicotyledonous herbs, long (>10 cm) grasses, *S. virginicus*, and plants growing in holes <10 cm across in 'mosaic rock' (Gibson and Phillipson in press *a*) each also made up >0.5% of feeding observations. All other materials accounted for <0.5% of observations each and were pooled as 'other'.

Diet composition changed considerably over the year (Fig. 5). The major feature is the alternation between tortoise turf (>60% of wet season observations) and shrub leaves, which overtake tortoise turf in importance in the late dry season; together these make up over half the diet at all seasons. No other material accounted for >15% of observations in any month, but most showed strong seasonal use patterns. In general the diet became more varied as the dry season progressed, while in the wet season the animals concentrated on tortoise turf.

Male and female diets were not significantly different ($X^2 = 4.39$, 4*df*, $P < 0.25$) but juveniles more often fed on herbs and mosaic rock vegetation than adults ($X^2 = 124.17$, 6*df*, $P < 0.001$).

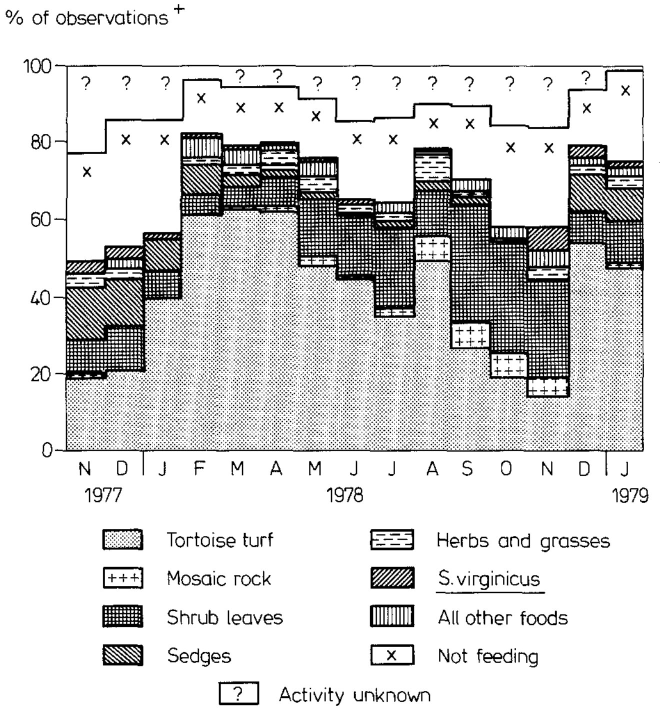

Fig. 5. The proportion of Cinq Cases tortoises feeding on different materials in each month of the study. Monthly figures for each vegetation type (Table 3) have been combined and corrected for the area covered by each vegetation type (Table 1) to generate this Fig. + 'Observations' include all observations made on transects

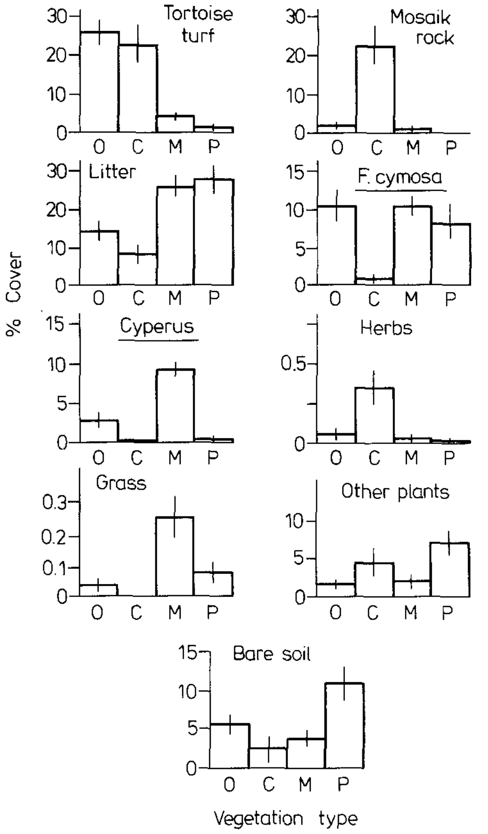

Fig. 6. The composition of vegetation types along the transects. All Figs. are given as % of total ground cover ±1 S.E., calculated using $\sin^{-1}$ transformation of the percentage cover on each transect segment. The abundance of *T. boivinii* in the litter is shown at the base of Fig. 6c. Data are from Gibson and Phillipson (in press *b*). 'Other vegetation' was mostly the sedge *Fimbristylis ferruginea* in 'P' and the fern *Acrostichum aureum* in 'C'. Vegetation types: *O* open mixed scrub, *C* coastal mixed scrub, *M* mixed scrub and *P* pool vegetation

Table 3. The overall abundance of different foods in the diet and in the environment

Food	% in environment[a]	D/E[b] total	D/E juveniles
Tortoise turf	15.3	3.99	3.35
Mosaic rock	3.75	0.803	3.66
Shrub litter	38.5	0.532	0.320
Sedges	29.0	0.267	0.090
Herbs	0.06	18.3	91.9
Long grasses	0.36	8.28	5.96
S. virginicus	1.76	0.789	–

[a] Percentage of vegetation i.e. excluding rock

[b] Percentage in diet/percentage in environment

Diet Selection, Food Availability, and Seasonal Movement

The Cinq Cases tortoise population is food-limited (Coe et al. 1979; Hamilton and Coe in press), so variation in food availability is likely to explain much of the change in tortoise distribution. The standing crop and production phenologies of different species (Gibson and Phillipson in press *a*) and the distribution of potential food types between vegetation types (Fig. 6) both vary, so that relative availability of food in different habitats changes seasonally. In this section we compare changes in tortoise diet and distribution with variation in habitat quality in time and space.

Diet Selection. Tortoises may be: a) *non-selective feeders*, taking food in proportion to environmental availability and showing little selection among common food types; food types rare in all environments would not affect tortoise diet on a population scale; seasonal changes in diet proportion of environmentally common foods would correlate well with their production or standing crop phenology; or: b) *selective feeders*, preferring particular foods, but when these are not available taking less-preferred foods in proportion to their abundance; rare food types would appear in the population diet; proportion of preferred foods in the diet would correlate with production or standing crop phenology but that of non-preferred foods would not.

Our evidence indicates that the latter is the case. Comparison of the proportion of items in the diet (whole year, all habitats) with their environmental abundance (ground cover) shows that the tortoise population as a whole 'preferred' only tortoise turf, herbs, long grasses, and *Terminalia boivinii* leaf litter (Table 3). Mosaic rock was 'preferred' by juveniles, but if the rock component is removed all tortoises 'preferred' it in the dry season, when it was mainly eaten. Herbs and long grasses were extremely rare (<0.5%) in all vegetation types yet were highly overrepresented in the diet.

Standing crop was not significantly correlated with the proportion of any item in the diet. The production of tortoise turf and of *T. boivinii* leaf litter (both 'preferred') was

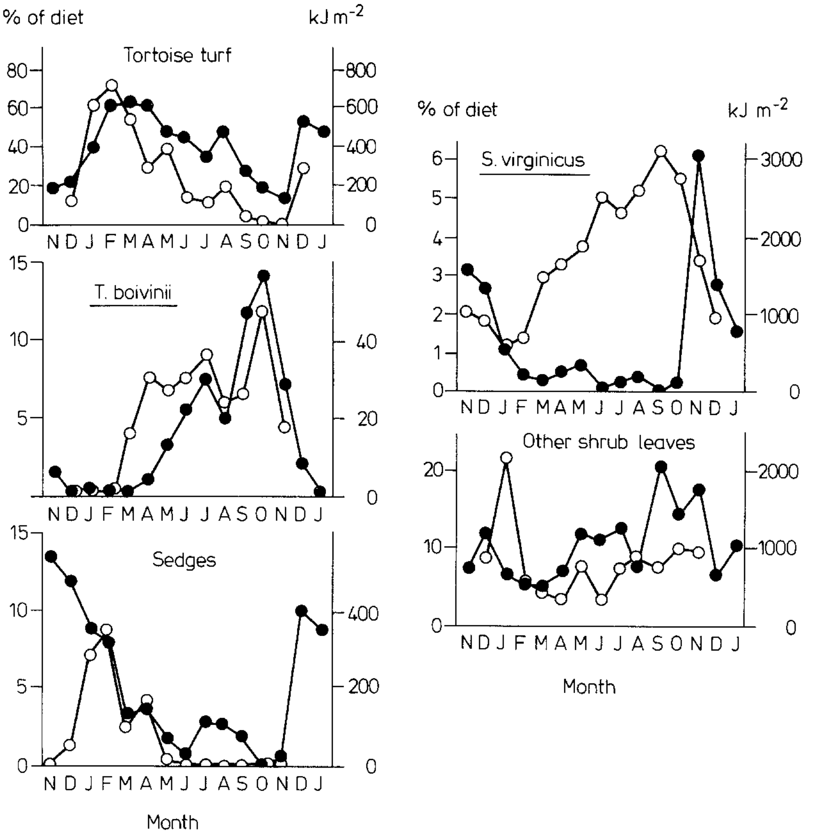

Fig. 7. The relationship between standing crop or production phenology and the proportion of food items in the diet. *S. virginicus* standing crop is shown and the production phenology of other items is given. For tortoise turf $r^2 = 0.541$, $n = 13$; for *T. boivinii* leaves $r^2 = 0.545$, $n = 12$; for sedge flowers $r^2 = 0.146$, $n = 14$ (negative relationship). The regressions for tortoise turf and *T. boivinii* leaves were significant at the 0.01 level. Production and standing crop data from Gibson and Phillipson (in press *a*)

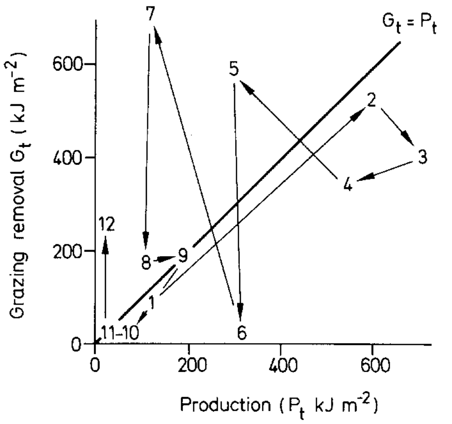

Fig. 8. Grazing removal and the production of tortoise turf in open mixed scrub. Arrows connect consecutive months' data. The solid line represents removal of exactly a month's production; points lying above the line show 'overgrazing' (eating into the standing crop capital), and points below the line indicate that less than a month's production has been removed. Month 1 is January 1978. Plant data from Gibson and Phillipson (in press). Production was measured by clipping plots protected from grazing, and grazing removal was calculated by comparing production figures with the change in standing crop on plots exposed to grazing

correlated with their proportions in the diet, but that of other items was not (Fig. 7). (Herbs and long grasses were too rare for the analysis.) Shrub litter, the second most important food type but non-'preferred', shows no correlation between diet proportion and availability: peak feeding occurred well after the early dry season leaf fall and ceased before the December litter fall peak.

Selectivity changes were related to changes in food availability. Tortoise turf was the major diet component and the only common 'preferred' food. There was little time lag between the start of tortoise turf production in the open mixed scrub and the peak in tortoise density there, and during the wet season tortoises were removing all or more of a month's production (Fig. 8). Tortoise grazing accounted for 98% of tortoise turf annual production, a very high figure for any herbivore on its major foodplant (Scott et al. 1979). For much of the late wet and early dry seasons tortoises alternated between removal of less than a month's production and eating into the standing crop capital. By October-November, when tortoise turf production was 0–3 g m^{-2} $month^{-1}$, an average (20 kg) Cinq Cases tortoise would need to crop 360–500 m^2 of tortoise turf to obtain 60% of its daily intake (Hamilton and Coe in press). It would clearly be impossible for a tortoise to sustain itself on a high tortoise turf diet at this season.

In the wet season 'preferred' foods made up about 16% of the environment; in the dry season tortoise turf production was very low, and the only other foods taken in greater proportion than their environmental occurrence were *T. boivinii* litter ($< 1\%$ of environment) and possibly mosaic rock vegetation (about 3%). Tortoises were clearly forced to turn to available but non-'preferred' foods such as the fallen leaves of other shrubs, sedge leaves, and *Sporobolus virginicus*.

Food Availability and Tortoise Distribution. Potential food types are distributed differentially between vegetation types (Fig. 6), and together with seasonal variation in standing crop and production this generates large temporal and spatial differences in food availability between habitats.

Table 4. Changes in diet composition in different vegetation types. Figures are proportions of all tortoises of measured activity eating a particular item. *OMS* open mixed scrub, *MS* mixed scrub, *CMS* coastal mixed scrub, *POOL* pool vegetation

	1977		1978												1979
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Tortoise turf															
OMS	28.2	28.6	56.7	87.7	81.8	82.6	72.5	63.4	62.4	62.2	49.0	40.0	29.8	63.3	73.3
MS	6.25	10.3	17.5	30.8	41.5	46.9	30.3	34.1	27.2	44.8	19.2	11.9	12.0	46.5	17.6
CMS	47.0	56.8	79.5	84.5	74.5	69.0	66.0	66.2	40.4	50.0	41.2	32.4	55.8	71.4	72.1
POOL	10.7	6.1	20.0	51.1	34.6	31.25	10.0	17.7	11.1	28.6	12.0	8.0	5.9	17.4	20.0
Mosaic															
OMS	0	0	0	0	0	0.5	0.7	0	5.4	1.8	4.0	0	7.0	0	0
MS	0	0	0	0	0	0	1.6	0	0	4.5	3.85	0	2.0	0	0
CMS	3.5	0	0	0	1.8	6.0	7.2	10.3	11.5	21.9	25.0	35.1	15.6	0	7.7
POOL	0	0	0	0	0	3.1	5.0	0	0	0	4.0	8.0	5.9	0	0
Shrub leaves except *T. boivinii*															
OMS	15.5	10.7	5.8	0.4	0.9	3.1	4.0	7.9	9.7	8.1	14.0	7.3	5.3	7.8	5.1
MS	8.3	15.5	8.8	7.7	9.4	9.4	15.2	14.1	14.8	7.5	25.6	16.9	25.5	4.65	19.6
CMS	2.6	4.1	2.6	3.9	5.5	7.8	15.5	2.0	7.7	6.25	4.4	9.5	10.4	10.0	3.85
POOL	14.3	12.1	6.0	4.4	0	15.6	15.0	2.9	11.1	14.3	16.0	20.0	5.9	4.35	0
T. boivinii leaves															
OMS	0	0.9	1.0	0	0	0	2.7	3.0	3.2	5.4	6.0	12.7	8.8	1.8	0
MS	2.1	0	0	0	0	1.6	4.5	7.1	9.9	6.0	15.4	18.6	9.8	2.3	0
CMS	0	0	0	0	0	0	0	1.5	0	0	0	0	0	2.9	0
POOL	3.6	0	0	0	0	0	0	5.9	5.6	0	16.0	4.0	5.9	4.35	0
Sedges															
OMS	7.0	3.6	9.1	4.5	0.9	1.5	0.7	2.0	1.1	0	1.0	0	3.5	6.0	7.0
MS	22.9	20.6	10.6	13.9	5.7	6.2	3.0	1.2	3.7	4.5	2.6	0	0	1.6	13.8
CMS	0	1.35	2.6	0.8	2.7	0.9	0	0	0	0	0	0	0	2.9	1.0
POOL	7.1	18.2	14.0	13.3	15.4	6.25	10.0	2.9	5.6	4.8	0	0	0	21.8	20.0
Herbs and long grasses															
OMS	2.8	2.7	0.5	0.4	0.4	0.5	2.6	1.0	3.3	5.4	3.0	0	0	1.8	1.3
MS	2.1	3.4	0	4.6	5.7	7.85	7.7	2.4	1.2	7.5	1.3	0	3.9	2.3	5.9
CMS	1.7	0	0	0	0	1.8	0	1.5	7.7	9.35	1.5	1.4	3.9	2.9	0
POOL	0	3.0	0	0	7.7	6.25	5.0	2.9	0	14.3	0	8.0	0	4.35	6.7

Shifts in tortoise distribution appear to reflect these changes. Tortoise density is correlated with grass (mainly tortoise turf) production available in different habitats (Fig. 2): the wide error bars in this graph reflect seasonal changes in tortoise density. In the wet season densities are highest in the open and coastal mixed scrubs where tortoise turf is commonest; as the proportion of shrub leaf litter in the diet rises so does tortoise density in the thicker mixed scrub (but note that the population is much more dispersed: Table 1), and *S. virginicus* is important in the diet only during the density peak on the coast, when two-thirds of the standing crop is removed (Fig. 7).

Can we show that the selectivity changes and seasonal movements are in fact responses to changes in food availability? An alternative hypothesis would be that animals moved for other reasons, and took the best available food in whatever habitat they found themselves in. In this case seasonal use patterns for a particular item should be strong only where it was common, whereas if food choice was a true generator of movement, seasonal use patterns should be independent of abundance. Table 4 shows that the latter was the case: for instance, tortoise turf showed a strong seasonal diet pattern even in pool vegetation where it made up only 1.2% of the environment. All other items except the rarest, for which analysis is difficult, show the same. For the population as a whole, then, food constraints are probably a major factor in movement.

Not all components of the population were similarly distributed: there was an excess of juveniles in mixed scrub and coastal mixed scrub, and an excess of females (or deficiency of males) in mixed scrub while they were relatively rare in coastal mixed scrub and *S. virginicus* sward. We can explain the concentration of juveniles in coastal mixed scrub in terms of food supply: they concentrate more than adults on herbs and mosaic rock vegetation (Table 3) which are commonest here (Fig. 6). Both these food sources occur in small patches (mosaic rock vegetation is defined as occurring in patches <10 cm in diameter; herbs occur in smaller patches than tortoise turf, $X^2=75.7$, $df=1$, $P<0.001$). Small tortoises would gain a higher reward from small patches than larger animals, and the shape and depth of the holes would make much of this vegetation inaccessible to large tortoises. These food sources provide a refuge for small animals which may put them at an advantage over large animals in habitats where they are common.

However we cannot explain the excess of juveniles and females in mixed scrub in terms of food supply. There is no comparable refuge food source for juveniles, and male and female diets do not differ (p. 4), so that other factors such as mortality risks or reproductive goals must operate.

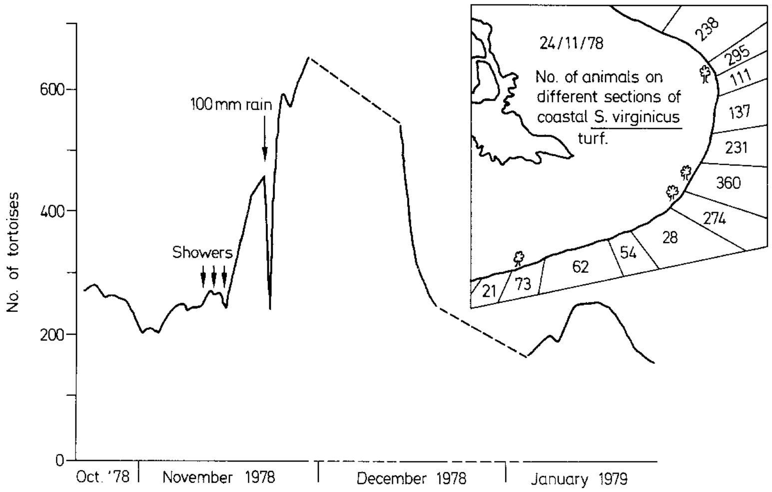

Fig. 9. The number of tortoises at noon under the Cinq Cases shade trees from October 1978 to January 1979. Solid lines are periods of observation; broken lines denote gaps between observations. Arrows indicate the first occasions of rain in the 1978–9 wet season. When 100 mm of rain fell, most tortoises remained feeding on the sward and did not seek shade. The inset shows the location of shade trees on the coast and the number of tortoises found in topographically separated sections of the coastal sward on 24th November 1978

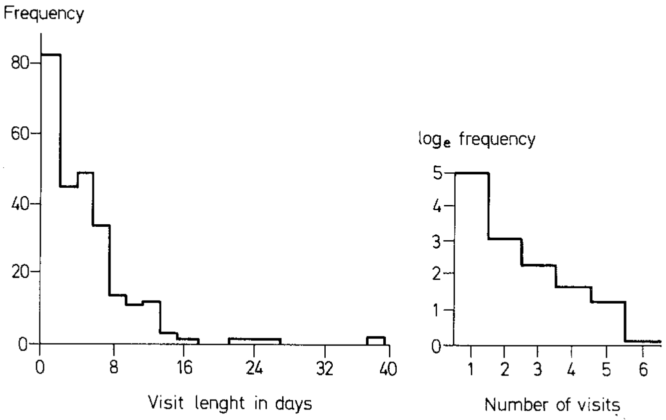

Fig. 10. The patterns of visits by individual tortoises to the *S. virginicus* sward at Cinq Cases in October–November 1978. 'Visits' were separated by at least two occasions when an animal was not seen under any tree on the coast; if an animal reappeared after only one day it was assumed to have been overlooked. The time of animals' arrival was unrelated to visit length

There is little or no predation on tortoises over 5 years old (Swingland and Coe 1979). Potential predators such as the sacred ibis *Threskiornis aethiopicum abbotti* (Lath.) and robber crab *Birgus latro* L. were abundant throughout, so differential mortality is unlikely to explain juvenile distribution. Adults mainly die from lack of shade and trapping in holes (Merton et al. 1976), but lack of shade only becomes important when shrub cover is below 10% (Bourn and Coe 1978), i.e. only on *S. virginicus* sward and in the pinnacle zone. Tortoises may avoid the coast for these reasons, but the lack of females is only explained if for some reason males are more likely to risk feeding there.

Nest site distribution may explain the concentration of females and juveniles in mixed scrub. The combination of deep soil and patchy shade where most nests are sited (Swingland and Coe 1978, personal observations) is commonest here, and no nests have been found in the raised beach sands in the Cinq Cases area despite extensive search. Possibly females tend to stay in suitable nesting areas and the excess of juveniles is due to the large numbers hatching there; but this needs confirmation from a detailed study of nest site distribution and movement and survival of small tortoises.

Movement Patterns. We would expect individual behaviour to reflect the population response to changes in food availability. Animals feeding on a preferred (presumably profitable) food should remain feeding on it so long as it remained profitable, but animals feeding on less profitable food supplies should be more erratic in their use of them. We cannot examine the first part of this proposition, but we can examine the individual behaviour of animals using the *S. virginicus* sward in the late dry season.

The density peak built up very rapidly after the season's first rainfall (Fig. 9). *S. virginicus* is non-'preferred' (Table 3) and indeed tortoises in pens were reluctant to eat it (Hamilton and Coe in press), but when the salt accumulated over the dry season is washed off a relatively high standing crop becomes available before other food types increase production (Fig. 7). We would predict that the peak is generated by many animals using the sward for a short time rather than fewer animals arriving as soon as the sward becomes suitable and staying till it is relatively unprofitable for any animal.

Most animals visited the coastal sward for only a few days (Fig. 10). Many returned for subsequent visits. Of these, many were seen in the coastal mixed scrub between visits, and a few were seen further inland. Only one was found on *S. virginicus* sward in an area not covered by the main study.

The high turnover rate on the sward means that the density peak represented a large number of animals. Using the proportion of marked animals in the population (5.93%) and assuming that we saw all of those, we estimate 12,900 using the sward from October to January; taking the turnover rates into account for the periods missed, we estimate 16,250. The second estimate is probably more realistic, but in either case at least 20% of the Cinq Cases tortoises were using the sward in 1978–79, if only for a few days each.

Two factors are probably involved in the tortoise population leaving the coastal sward. The animals graze the sward to a very low standing crop (Fig. 7) and this intense grazing progresses out from the shade trees (unpublished data). The risk of death from heat stress (the major mortality on the coast: Swingland and Lessells 1979) increases as the animals must graze further from shade. Also, by late December–early January, the tortoise turf inland has started producing (Fig. 7). Tortoises were continually moving inland after short coastal visits and should have found this preferred food as soon as it became available.

The Giant Tortoise as a Herbivore

The giant tortoise diet includes many plant species, nearly all taken from the ground, but most are only taken at particular seasons or in small quantities. This pattern could be considered typical of a 'large generalist herbivore'. However, neither tortoise feeding nor that of other 'large generalist herbivores' is at random. The terms 'generalist' and 'specialist' have been used primarily in insect work to describe diet breadth expressed taxonomically or through secondary plant chemistry (e.g. Rosenthal and Janzen 1979), and the patterning of tortoise and large mammal diets is very different from the restrictions on 'specialist' insect diets (e.g. Feeny 1976). Restrictions on diet breadth due to nutrients, water, toughness or structural 'quality' parameters have been emphasised in work on taxonomically polyphagous insects and large herbivores. Jarman and Sinclair (1979) use 'selectivity' to describe these latter types of diet restriction. We do so here, finding it a useful approach for describing food choice in a 'generalist' (taxonomically polyphagous) herbivore like the tortoise; indeed most 'specialists' are also selective as to plant part and or condition (examples in Rosenthal and Janzen 1979).

Tortoise turf, the most highly selected food in the diet, is taxonomically diverse (Grubb 1971, Merton et al. 1976) but all component species are maintained as new growth <1 cm high by intense grazing (Gibson and Phillipson in press *a*). Besides the possible advantages of high nutrient value and low toughness, the consequent small particle size may be important: there is little mixing or physical breakdown in the tortoise gut, and the animals rely on long throughput times (upwards of a week) to achieve an energy assimilation efficiency of around 35% on tortoise turf (Hamilton and Coe in press). Other preferred items in the diet such as flowers, fruits and fresh growth would probably share the same general characters of high nutrient content and low toughness. The exception was *T. boivinii* leaves. These were conspicuous when freshly fallen; possibly they are simply easy to pick out against the background.

Selectivity declined after the peak of tortoise turf feeding in the wet season and diet broadened as the dry season progressed. The pattern of seasonal species and/or plant part selectivity change has been demonstrated in African antelopes (e.g. the impala: Jarman and Sinclair 1979).

Differences between the giant tortoise and other large herbivores thus seem to be of degree only. As a reptile, its low metabolic requirements allow it to build up very high population and biomass densities (Hamilton and Coe in press) but otherwise it behaves like a typical large grazing herbivore. The Cinq Cases system is unusual however in the extent to which its herbivores are food limited. Growth (Gibson and Hamilton in prep.) and reproduction (Swingland and Coe 1979) are tightly restricted by food supply and the seasonal movements are determined by the changing patterns of plant production and distribution. The seasonal movements also take place within a closely bounded area and involve only one common herbivore species, which makes the Aldabran system unusually useful for examining the dynamics of a large herbivore's interactions with its food supply.

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