Food Consumption and Energy Budgets of the Giraffe

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SUMMARY

(1) To estimate the efficiency of the foraging strategy described in Pellew (1984), the rates of food intake of adult giraffe in the Serengeti National Park are assessed. Daily energy intakes derived from the diet are compared with estimates of the energy requirements for year-round reproduction. The reproductive performance of giraffe in the Serengeti is discussed in the light of such energy budgets.

(2) Giraffe are exerting a major impact upon the development of the *Acacia* regeneration, removing up to 85% of the new shoot production. The browsing impact varies throughout the year, being greatest in the dry-season when production rates decline. Such high offtake rates are the result of a disequilibrium in the browse production–consumption system caused by the double perturbations of elephant impact and the reduction of fire. There is no short-term evidence that the giraffe impact is curtailing plant productivity, and it is suggested that *Acacia* species have evolved a high resilience to browsing as a result of the positive selection for tolerant genotypes.

(3) The daily rates of food consumption, 1·6% and 2·1% of the live-weights of adult male and female giraffe, are similar to other ruminants. However, the quality of the diet, assessed in terms of crude protein levels, is consistently higher than that of African grazing ungulates, particularly in the dry-season, when the protein levels of the browse diets show only a marginal decline.

(4) The energy budgets suggest that giraffe can maintain a positive energy balance throughout the year and during most stages of the female reproductive cycle. Any possible energy deficit during the post-partum lactation phase is avoided by the selection for browse of high energy content, especially in the dry-season. The foraging strategy adopted by giraffe enables the animal to attain the metabolic threshold for year-round breeding.

INTRODUCTION

Unlike many African ungulates, giraffe (*Giraffa camelopardalis tippelskirchi* Matschie) in the Serengeti calve throughout the year. Analysis of the monthly calving frequencies shows a bimodal distribution of births, with a minor peak in December–January during the early wet-season, followed by a major peak in May–August during the first half of the dry-season, but with births recorded in every month of the year (Pellew 1983a). This aseasonal pattern of parturition suggests that adult giraffe are able to obtain the necessary nutrient and energy requirements to achieve the metabolic threshold for reproduction at all times of the year.

Theories of optimal foraging have received considerable attention in the recent literature of animal ecology (see review by Pyke, Pulliam & Charnov 1977). The basic principle common to these theories is that the fitness of a foraging animal is a function of the efficiency of its foraging, and that natural selection operates so as to maximize this

fitness in that the more efficient individual will show an enhanced reproductive success. Development of the theory began with the modelling of foraging behaviour in relatively simple systems, typically involving predator–prey interactions, in which each feeding activity is a singular event and in which the cost–benefit functions of a range of possible foraging strategies can be relatively easily assessed. Attempts to model the foraging strategies of generalist herbivores, particularly large ungulates (e.g. Westoby 1974; Belovsky 1978; Owen-Smith & Novellie 1982) have all to some extent been frustrated by the extreme variability of the food resource and the behavioural response of the consumer to this variation. Temporal and spatial differences in nutrient content and digestibility within and between plant parts and plant species; the spatial heterogeneity of food items within the plant community; the problem of resource depletion resulting from consumption; the presence of chemical deterrents to herbivory within the plant; variations in bite size and ingestion rates with different food types—all these variables are difficult to incorporate in ungulate foraging models, but are of elementary importance to the herbivore in determining its feeding strategy. As stressed by Owen-Smith & Novellie (1982), the value of their model lies not in predicting how an ungulate might optimize its foraging, but rather in identifying the critical determinants of the feeding strategy that warrant further research.

   This paper does not attempt to model a theoretical strategy to optimize the feeding of giraffe. Instead, it assesses the efficiency of the foraging strategy described in Pellew (1984), i.e. the quantity and quality of the food consumed daily by adult giraffe in relation to their daily energy requirements. The daily rate of energy intake is accepted as the unit of 'currency' to assess foraging efficiency. As suggested by Schoener (1971), most animals have a limited amount of time in which to forage because of the demands of other activities, and their fitness will be improved by increasing their energy intakes in their allotted foraging time. Owen-Smith & Novellie (1982) show that the proportion of the foraging time spent feeding by greater kudu (*Tragelaphus strepsiceros*) varies very little throughout the year despite a four-fold seasonal difference in food density, and that this feeding time is close to the maximum potential limit imposed by the relative rates of food ingestion and food digestion in the rumen. This implies that the animal has adopted a tactic of nutrient maximization, and the authors conclude that the target nutrient is probably energy rather than protein content.

   Energy budgets for giraffe are presented, based on the estimates of the daily rate of energy intake and the energy requirements for maintenance and reproduction. In the light of such energy balances, the natality data are discussed and the reproductive performance of giraffe in the Serengeti is assessed. An efficient foraging strategy in a favourable environment results in a high rate of nutrient intake, which in turn promotes an enhanced reproductive performance.

METHODS

Rate of food consumption

   Two fundamentally different approaches have been used in previous studies to determine the consumption rates of browse by ungulates, these being plant-based and animal-based techniques (Rutherford 1979).

Plant-based technique

   Consumption can be estimated without reference to the herbivore by the simultaneous measurements of the rates of browse production of adjacent browsed and unbrowsed trees.

Assuming that all environmental factors influencing production, except for the presence or absence of the consumer, apply equally, comparisons of production rates provide estimates of the total production consumed. When the percentage utilization of a particular species is required, mass units (kg ha^{-1}) can be replaced by measurements of linear shoot increments (mm shoot^{-1}) (Rutherford 1979). Absolute consumption rates (kg ha^{-1} day^{-1}) can then be calculated for those species for which the rates of unconsumed browse production are already known. The Index of Consumption of a browse species is defined as the percentage of the unbrowsed production that is consumed by giraffe.

The technique for estimating the rate of browse production, using fenced enclosures and tagged sample shoots, is described in Pellew (1983b). A random sample of control trees from outside each enclosure was taken for the measurement of browsed shoot increments with the same number of browsed and unbrowsed sample trees. The stratification of canopies into leader, high, medium and low strata and the allocation of sample shoots to strata were exactly replicated inside and outside each enclosure. Sample shoots within each stratum were selected for tagging so as to duplicate as exactly as possible the unbrowsed sample shoots in terms of shoot length and diameter, general shoot vigour, position within the stratum, and aspect within the canopy. Differences in length increments were thus assumed to be attributable to giraffe browsing. Linear growth increments of sample shoots were measured at quarterly increments. Browsed shoots were tagged with inconspicuous brown string, which did not influence the feeding behaviour of giraffe.

Calculation of the consumption index enables the browsing impact upon a particular species to be quantified. But such impact assessments cannot be extrapolated to determine the daily rate of food intake unless production estimates are made separately for each species important in the daily diet. Such data are available for only three *Acacia* species: *A. tortilis* and *A. hockii* of the ridge-top woodland type, and *A. xanthophloea* of the riverine woodland type (Pellew 1983b). To convert consumption rates ha^{-1} into intake rates giraffe^{-1}, data of the local giraffe densities within each woodland type would also be necessary.

Animal-based technique

Daily intake rates giraffe^{-1} were estimated by a simulated animal-based technique involving the clipping of food items to mimic giraffe browsing, with these simulations corrected by the results of limited feeding trials with captive animals. The stages in the technique are shown schematically in Fig. 1. The mean daily consumption rates (kg giraffe^{-1} day^{-1}) were assessed separately for each of the more important browse species in the diet (dietary representation > 1%, $n = 12$). Secondary species (dietary representation < 1%, $n = 33$) were amalgamated, and their daily consumption rates were approximated using the mean values of the primary species. Adult male and female giraffe were assessed separately. The mean rate of food intake of each primary species was calculated from

$$\text{Mean rate of food intake} = \text{mean bite rate} \times \text{mean bite mass}$$
$$\text{(g min}^{-1}) \qquad \text{(bites min}^{-1}) \qquad \text{(g bite}^{-1})$$

The mean bite rate was measured by direct observation of feeding giraffe, with bite counts recorded during timed feeding bouts (Dunham 1980). The problem with the technique lies in the accurate determination of the mean bite mass, which is particularly difficult with a wild animal that cannot be handled (e.g. for oesophageal fistulation). The bite mass was first estimated by hand clipping to simulate the browsing behaviour of giraffe. The clipped

Food consumption by giraffe

Mean Bite Rate
(bites min^{-1}) for each
browse species in diet

Direct observations of
feeding giraffe (♂♂ or ♀♀)
with bite counts over
measured feeding periods

Clipping to simulate giraffe
browsing with each clipping
representing one bite:
clippings oven-dried and
weighed: estimation of Mean
Sample Weight (g sample^{-1})
(analogous to Mean Bite
Mass) for each browse
species in diet

Mean Food Intake Rate
(g min^{-1}) for each browse
species in diet

Food intake rates derived
from simulated clippings
corrected by Correction
Factor determined from
feeding trials with captive
animals (Table 1)

Corrected Mean Food
Intake Rate (g min^{-1}) for
each browse species in
diet

Total Feeding Time day^{-1}
determined from 24-hour
Activity Studies (Pellew
1984): from percentage
Total Daily Diet (Pellew
1984) the Feeding Time
day^{-1} for each species can
be calculated separately for
♂♂ and ♀♀ giraffe

Mean Daily Consumption
Rate (kg giraffe^{-1} day^{-1})
for each browse species in
diet

Sum of daily consumption
rates of each browse species
in diet

Total Daily Food Intake
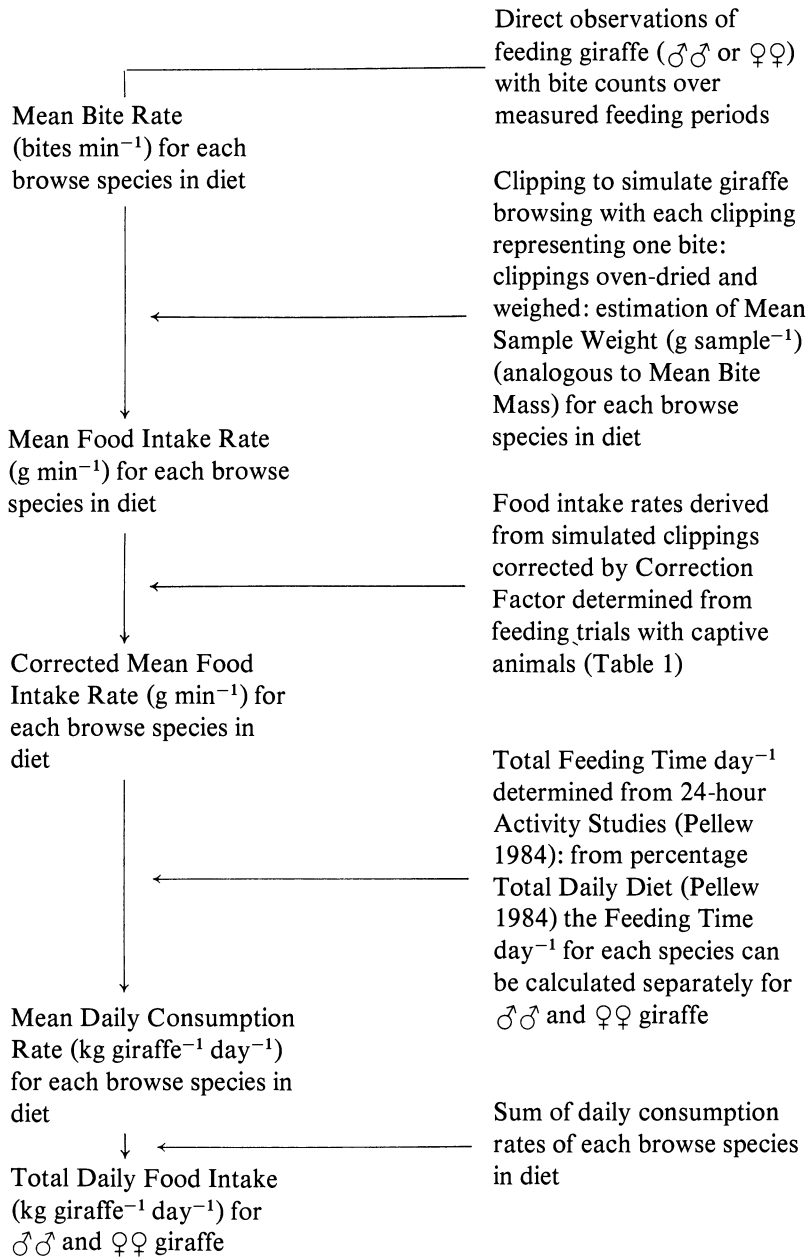(kg giraffe^{-1} day^{-1}) for
♂♂ and ♀♀ giraffe

FIG. 1. Stages in the determination of the total rates of daily food intake by adult male and female giraffe.

samples, analogous to bites, were oven-dried and weighed to determine the mean sample weight (g sample^{-1}), which was then used to calculate the uncorrected mean rate of food intake for each primary species. Later in the study and after the clipping simulations had been completed, the accuracy of these simulated bites was checked against a direct measure of the mean bite mass determined with captive animals. By supplying measured

quantities of freshly-cut browse of a single species over timed feeding periods, the mean bite mass of that species was determined, where

$$\text{Mean bite mass} = \frac{\text{dry mass of browse consumed}}{\text{number of bites taken}}$$
$$(\text{g bite}^{-1})$$

The dry mass consumed was measured by the technique described by Dunham (1980).

From comparisons of food intake rates estimated by clipping and from the feeding trials, correction factors were calculated. These were applied to the clipped samples to produce corrected rates of food intake min^{-1} (Table 1). Because of the limited variety of freshly-cut material available in the vicinity of the corral in which the captive giraffe were kept, correction factors could be determined for only three of the twelve primary species (*Acacia tortilis*, *A. xanthophloea*, and *Grewia bicolor*).

The results of these feeding trials suggest that the simulation clipping consistently over-estimated the mean bite mass (Table 1). The intake rates of the other nine primary species were therefore reduced by the mean correction factor of the three checked species ($\times$ 0·876 for adult bulls and $\times$ 0·808 for adult cows).

The problems associated with the extrapolation of feeding behaviour data from pen-fed animals to wild giraffe are appreciated. Considerable effort was taken to fully habituate the trial animals to cut browse, and to present this material in a way that simulated the natural vegetation. The methods and controls employed in the feeding trials are described in Pellew (1981). The mean bite rates recorded during the trials are not significantly different to those of wild giraffe (Table 1), suggesting that the feeding behaviour during the trials was representative of the wild behaviour.

Mean daily consumption rates of each primary species were then calculated, where

$$\begin{array}{lcll}\text{Mean daily consumption rate} & = & \text{corrected mean rate of} & \times & \text{feeding time/day} \\ (\text{kg giraffe}^{-1}\,\text{day}^{-1}) & & \text{food intake (g min}^{-1}) & & (\text{min 24-h}^{-1})\end{array}$$

and where

$$\begin{array}{lcll}\text{Feeding time/day} & = & \text{total time spent} & \times & \text{\% seasonal dietary representation} \\ \text{for a given species} & & \text{feeding day}^{-1} & & \text{of that species}\end{array}$$

The total time spent feeding day^{-1} was determined from the monthly 24-hour activity studies throughout the year: these data, together with the seasonal diets of adult bulls and cows, are presented in Pellew (1984).

Energy budgets

The metabolizable energy (ME) contents of the seasonal diets of adult male and female giraffe are presented in Pellew (1984). From the estimates of total daily dry-matter intake, the seasonal ME (Mcal 24-h^{-1}) derived from the diet can be calculated.

Estimates of a herbivore's daily energy expenditure for maintenance and reproduction can be presented as multiples of the animal's basal metabolic rate (BMR) (Moen 1973; Belovsky 1977), which can be calculated from Kleiber's (1961) formula

$$E = 70\,W^{0\cdot75}\,(\text{Mj day}^{-1})$$

where E is the energy expenditure for basal metabolism and W is the body weight of the animal in kilograms. For adult male and female giraffe with estimated live-weights of 1200

TABLE 1. Bite rates, bite sizes, and food intake rates of adult male and female giraffe determined from feeding trials with captive animals and from clipping to simulate browsing

Browse species	Determined from feeding trials			By direct observation	Determined from simulated clippings		Correction factor applied to clipped mean food intake rate	Corrected mean sample weight (g sample⁻¹)
	Mean bite rate (bites min⁻¹)	Mean bite mass (g bite⁻¹)	Mean food intake rate (g min⁻¹)	Mean bite rate (bites min⁻¹)	Mean sample weight (g sample⁻¹)	Mean food intake rate (g min⁻¹)		
Adult males								
Acacia tortilis	16·9	1·71	28·89	16·4	1·86	30·50	0·947	1·76
A. xanthophloea	17·6	1·76	30·98	16·5	2·12	34·98	0·886	1·88
Grewia bicolor	10·2	3·27	33·37	9·7	4·09	39·67	0·841	3·44
Mean	14·9	2·25	33·47	14·2	2·69	38·20	0·876	2·36
Adult females								
Acacia tortilis	16·3	1·17	19·19	16·4	1·46	23·94	0·801	1·17
A. xanthophloea	17·4	1·51	26·27	16·5	1·92	31·68	0·829	1·59
Grewia bicolor	10·2	2·20	22·46	9·9	2·81	27·82	0·807	2·27
Mean	14·6	1·63	23·79	14·3	2·06	29·46	0·808	1·62

kg and 800 kg (Dagg & Foster 1976), the energy expenditures for basal metabolism are 14·27 and 10·53 Mcals 24-h^{-1} respectively.

The BMR multiples adopted for giraffe are presented in Table 6. These estimates are based upon the figures for deer used by Moen (1973), Gasaway & Coady (1974), and Belovsky (1978), and particularly by Sinclair (1977) for buffalo (*Syncerus caffer*) and wildebeest (*Connochaetes taurinus*) with extrapolation at the rate of body weight$^{0·75}$. The multiple of 1·33 adopted for maintenance behaviour by non-lactating cows was suggested by Moen (1973) as a gross approximation of the energy requirement of a ruminant for normal foraging activity. Seasonal activity data of giraffe (Pellew 1984) show a dry-season increase in mobile activities, including feeding and walking, so the BMR multiples are increased proportionately. Bull giraffe are more active than cows, showing greater mobility in their search of oestrous females. The energy cost of gestation is relatively small until the last quarter when foetal development accelerates (Abrams 1968). Lactation in giraffe continues for up to 1 year (Pellew, unpublished), and it is assumed that after the immediate post-partum period, the energy cost declines at a constant rate. The diagrammatic representations of the monthly energy balances of giraffe (Fig. 3) are similar in design to those of buffalo and wildebeest produced by Sinclair (1977).

RESULTS

The index of consumption

Annual consumption rates

The mean annual increments of browsed and unbrowsed shoots of the three *Acacia* species are shown in Table 2. The 95% confidence limits of the browsed increments are large due to the occasional shoots that escape browsing by growing inwards towards the canopy centre. Because of the wide range of possible consumption rates, the consumption estimates are referred to as 'indices' and not as absolute rates. Also presented in Table 2 are the mean annual rates of shoot production of the unbrowsed trees (from Pellew 1983b), from which are calculated the rates of production of the trees after browsing by giraffe using the index of consumption.

In each species, shoots at the top of the canopy in the leader stratum (leading shoots to a canopy depth of 15 cms; Pellew 1983b) show the greatest mean annual increments, although they are also subject to the heaviest browsing impact. As shown in Table 3, the percentage consumption decreases lower down the canopy with the impact on the shoots of the lowest stratum (bottom one-third of the canopy) being relatively light. The reduced consumption of these low shoots compensates for their smaller production rates, so inter-stratum differences in the mean shoot increments of browsed trees are relatively small and non-significant.

Seasonal consumption rates

Quarterly indices of consumption of the three *Acacia* species are presented in Table 4. The cumulative mean quarterly increments of the browsed and unbrowsed sample shoots (all strata combined) over 1 year are graphed in Fig. 2.

The browsing impact varies considerably throughout the year, increasing during the dry-season quarter (July–September): differences between quarters are not significant because of the large variances in the mean quarterly shoot increments. The dry-season production of shoots is relatively low, and what little forage is produced is largely

TABLE 2. Mean annual rates of browse consumption by giraffe determined from comparisons of browsed and unbrowsed mean annual shoot increments

| Browse species | Total number of sample shoots (all strata) | Mean annual shoot increment | | | Mean annual shoot production | | Mean daily consumption rate (calculated from the index of consumption) (kg ha⁻¹ day⁻¹) ± 95% C.L. |
		Browsed by giraffe (mm shoot⁻¹ year⁻¹) ± 95% C.L.	Unbrowsed (mm shoot⁻¹ year⁻¹) ± 95% C.L.	Index of consumption 95% C.L. range	Browsed (calculated from the index of consumption) (kg ha⁻¹ year⁻¹) ± 95% C.L.	Unbrowsed Pellew (1983b) (kg ha⁻¹ year⁻¹) ± 95% C.L.	
A. xanthophloea	112	511 ± 223	3360 ± 793	85% 71%–93%	757 ± 506	4975 ± 1987	11·6 ± 9·8
A. tortilis	168	695 ± 301	2181 ± 647	68% 35%–86%	288 ± 218	904 ± 434	1·7 ± 1·8
A. hockii	128	674 ± 294	1738 ± 510	61% 21%–83%	23 ± 19	58 ± 32	0·1 ± 0·1

TABLE 3. Indices of consumption at different heights within the canopy of *Acacia* regeneration

| Browse species | Canopy stratum | Number of sample shoots | Mean annual shoot increment | | Index of consumption |
			Browsed (mm year⁻¹) ± 95% C.L.	Unbrowsed (clipped) (mm year⁻¹) ± 95% C.L.	
Acacia xanthophloea	Leader	25	660 ± 340	5742 ± 1230	89%
	High	31	459 ± 193	3685 ± 863	87%
	Medium	29	438 ± 172	2096 ± 580	79%
	Low	27	531 ± 171	1536 ± 461	65%
	Total	112	511 ± 223	3360 ± 793	85%
Acacia tortilis	Leader	36	799 ± 362	2998 ± 971	73%
	High	48	683 ± 342	2239 ± 589	69%
	Medium	45	656 ± 280	1585 ± 514	59%
	Low	39	749 ± 241	1235 ± 480	39%
	Total	168	695 ± 301	2181 ± 647	68%
Acacia hockii	Leader	28	794 ± 412	2507 ± 785	68%
	High	36	722 ± 333	1952 ± 559	63%
	Medium	33	717 ± 292	1486 ± 402	52%
	Low	31	548 ± 181	952 ± 276	42%
	Total	128	674 ± 294	1738 ± 510	61%

TABLE 4. Mean quarterly rates of browse consumption by giraffe determined from comparisons of browsed and unbrowsed mean quarterly shoot increments

Quarter	Season	Mean quarterly shoot increment (mm) ± 95% confidence limits		Quarterly increment as % of mean annual increment		Quarterly index of consumption
		Browsed	Unbrowsed	Browsed	Unbrowsed	
Acacia xanthophloea						
Jan–March	Wet	683 ± 109	1239 ± 263	133·6%	36·9%	45%
April–June	Wet/(Dry)	96 ± 20	801 ± 211	18·8	23·8	88
July–Sept	Dry	−320 ± 77	541 ± 119	−62·6	16·1	159
Oct–Dec	Dry/Wet	52 ± 17	779 ± 200	10·2	23·2	93
Total annual		511 ± 223	3360 ± 793	100·0%	100·0%	85%
Acacia tortilis						
Jan–March	Wet	443 ± 192	855 ± 217	63·8%	39·2%	48%
April–June	Wet/(Dry)	131 ± 49	584 ± 208	18·8	26·8	78
July–Sept	Dry	−12 ± 6	94 ± 25	−1·7	4·3	113
Oct–Dec	Dry/Wet	133 ± 54	648 ± 197	19·1	29·7	79
Total annual		695 ± 301	2181 ± 647	100·0%	100·0%	68%
Acacia hockii						
Jan–March	Wet	289 ± 107	593 ± 164	42·9%	34·1%	51%
April–June	Wet/(Dry)	224 ± 96	543 ± 141	33·2	31·2	59
July–Sept	Dry	15 ± 8	93 ± 33	2·2	5·4	84
Oct–Dec	Dry/Wet	146 ± 83	509 ± 172	21·7	29·3	71
Total annual		674 ± 294	1738 ± 510	100·0%	100·0%	61%

consumed. The very high indices of consumption during the dry quarter for *A. xanthophloea* and *A. tortilis* (>100%) suggest that all that quarter's production of new shoots is consumed, together with some older material produced the previous wet-season. This is well demonstrated in Fig. 2, where the dry-season decline in the cumulative mean increment of browsed shoots can be seen, particularly in *A. xanthophloea*.

Total daily food intake

The daily consumption rates by adult male and female giraffe, presented in Table 5, are estimated at 19·0 kg dry-matter day^{-1} and 16·6 kg day^{-1} respectively, equivalent to 30·8 g min^{-1} and 22·2 g min^{-1} of actual feeding time. Assuming average live-weights of 1200 kg and 800 kg (Dagg & Foster 1976), these daily intake rates represent 1·6% and 2·1% respectively of their body-weights.

Energy budgets

The estimated energy costs of adult giraffe for maintenance and varying reproductive conditions are presented in Table 6. These estimates of energy requirements are then graphed on a monthly basis in Fig. 3, assuming that subsequent parturitions occur in both wet- and dry-seasons. The mean gestation period for Serengeti giraffe is 15·0 months with an inter-calving interval of 18·8 months and a mean post-partum anoestrus of 3·8 months (Pellew 1983a). Because of the aseasonal incidence of oestrus in the cows, the sexual activity of the bulls is assumed to be constant throughout the year.

The seasonal energy supplies derived from the diet are also shown in Fig. 3. The efficiency with which ruminants utilize ingested metabolizable energy for maintenance purposes is about 80% (Blaxter 1967). Rogerson (1968) reported utilization efficiencies of
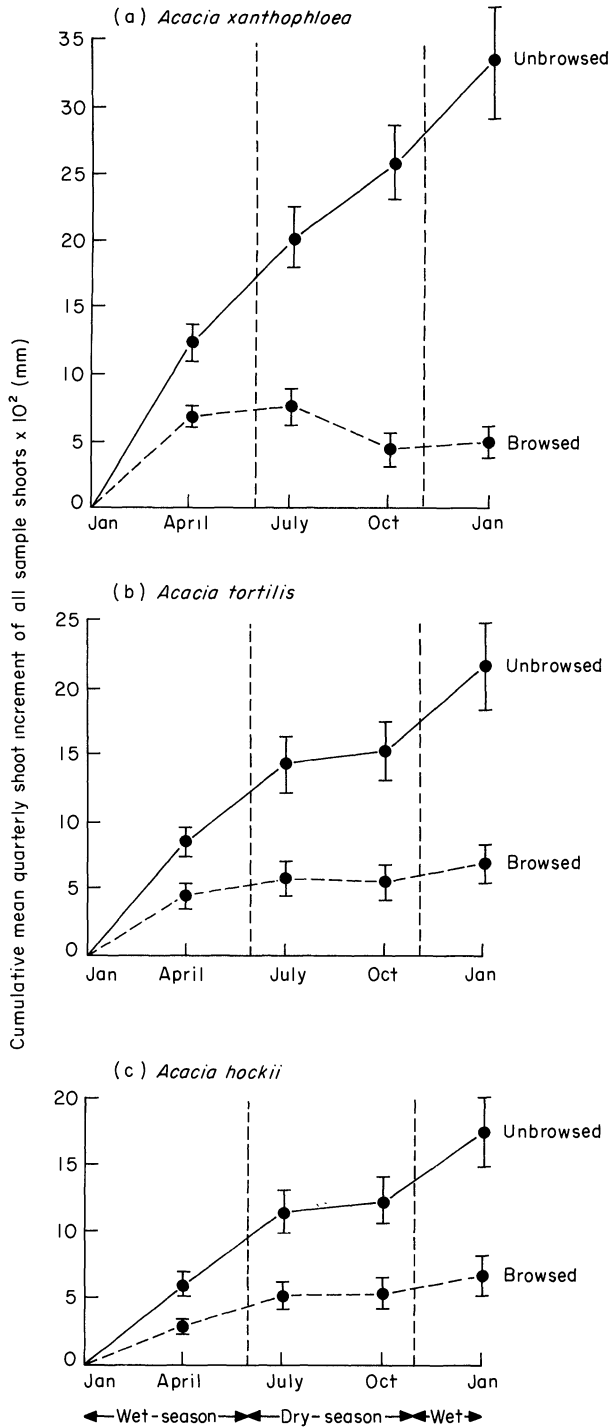
FIG. 2. Cumulative mean quarterly linear increments of browsed and unbrowsed sample shoots, with standard errors.

TABLE 5. Browse consumption rates of adult male and female giraffe determined from simulated clippings corrected by the results of feeding trials with captive giraffe

Browse species	Mean bite rate from direct observations (bites min⁻¹)	Corrected mean sample weight (g sample⁻¹)	Corrected mean food intake rate (g min⁻¹)	% Annual† total diet	Total feeding† time 24-h⁻¹ (min)	Mean daily consumption rate (kg day⁻¹)	% Daily consumption
Adult males							
Acacia tortilis	16·4	1·76	28·89	33·3%	205·4	5·94	31·2%
Grewia bicolor	9·7	3·44	33·37	14·8	91·6	3·06	16·1
Grewia fallax	7·7	4·48	34·50	11·2	69·4	2·39	12·6
Balanites aegyptiaca	14·9	2·30	34·27	8·2	50·8	1·74	9·1
Acacia xanthophloea	16·5	1·88	30·98	8·0	49·5	1·54	8·1
Acacia senegal	25·3	0·93	23·53	7·4	45·8	1·08	5·7
Acacia hockii	20·4	1·42	28·97	2·5	15·4	0·45	2·4
Cordia ovalis	8·6	4·11	35·35	2·3	14·0	0·50	2·6
Commiphora trothae	15·9	1·94	30·85	2·1	12·7	0·39	2·0
Acacia gerrardii	15·3	1·76	26·93	1·4	8·6	0·23	1·2
Albizia species	15·3	2·16	33·05	1·2	7·2	0·24	1·3
Acacia robusta	16·4	1·97	32·30	0·9	5·7	0·18	0·9
Other species (n = 30)			31·08*	6·7	41·7	1·30	6·8
Total				100·0%	617·8	19·04	100·0%
Adult females							
Acacia tortilis	16·4	1·17	19·19	27·1%	202·4	3·88	23·4%
Grewia bicolor	9·9	2·27	22·47	16·6	124·3	2·79	16·8
Grewia fallax	7·3	3·68	26·86	11·8	88·5	2·38	14·3
Acacia xanthophloea	16·5	1·59	26·27	6·9	51·6	1·36	8·2
Acacia hockii	16·6	1·15	19·09	4·8	35·9	0·68	4·1
Acacia senegal	22·3	0·70	15·59	4·8	35·8	0·56	3·4
Cordia ovalis	8·9	2·77	24·62	4·3	31·9	0·78	4·7
Balanites aegyptiaca	15·7	1·51	23·66	3·8	28·2	0·67	4·0
Acacia gerrardii	18·6	1·34	24·95	3·0	22·5	0·56	3·4
Commiphora trothae	16·3	1·37	22·36	1·8	13·7	0·31	1·9
Acacia robusta	17·1	1·42	24·28	1·1	8·5	0·21	1·3
Albizia species	14·1	1·75	24·68	1·0	7·2	0·18	1·1
Other species (n = 32)			22·83*	13·0	98·2	2·24	13·5
Total				100·0%	748·7	16·60	100·0%

* Mean food intake rate of the twelve species applied to other species.
† From Pellew (1983b).

TABLE 6. Estimated energy costs of adult giraffe in varying reproductive conditions,
expressed as multiples of basal metabolic rate

Giraffe sex	Body weight (kg)	Reproductive status	Estimated energy expenditure			
			Wet-season		Dry-season	
			Multiple of BMR	Energy expenditure (Mcals 24-h⁻¹)	Multiple of BMR	Energy expenditure (Mcals 24-h⁻¹)
Adult male	1200	Maintenance: sexual activity constant throughout the year	1·40	20·0	1·55	21·4
Adult female	800	Maintenance	1·33	14·0	1·50	15·8
		Non-lactating, late-term pregnant	1·75	18·4	1·90	20·0
		Post-partum, lactating, non-pregnant	2·15	22·6	2·30	24·2
		6-months post-partum, lactating, ±pregnant	1·80	19·0	1·95	20·5
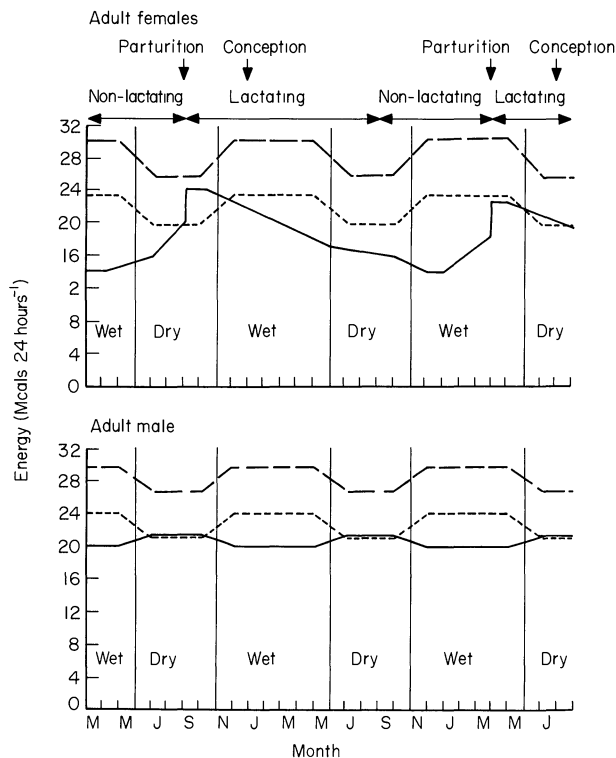
FIG. 3. Diagrammatic representation of the monthly energy balances of adult giraffe: (———)
energy requirements (Table 6); (———) Gross Metabolizable Energy from the diet; (-----)
Utilizable Energy assuming 80% utilization efficiency.

82% for wildebeest and 80% for eland, which coincide with the range of 80–85% for sheep
and cattle. Even allowing for 80% efficiency, the energy available from the diet appears to
exceed the animal's requirements throughout most of the female reproductive cycle.
Breeding females may experience a small deficit during the immediate post-partum
lactation phase, particularly during the dry-season, but as the energy expenditure incurred
in lactation declines, supply and requirements are balanced. Adult bulls appear just able to
meet their energy requirements throughout the year.

DISCUSSION

Browsing impact and Acacia *resilience*

The indices of consumption presented in Table 2 suggest that giraffe are removing a substantial proportion of the new shoot production, possibly as much as 85% in the case of *A. xanthophloea*. The lack of any comparable data for *Acacia* savannas elsewhere in Africa make it difficult to assess the significance of this intensity of browsing. As stressed by Lamprey *et al.* (1980), tolerance levels to varying degrees of browse impact are virtually unknown in East African browse species; yet such information is of fundamental importance for determining carrying capacities of ungulate browsers, particularly where the browse resource has potential value for livestock management schemes.

In temperate deciduous forest, consumption rates by deer lie typically in the range of 10–30% of the available browse biomass (for a review of browse utilization, see Rutherford 1979). Bobek, Weiner & Zielinski (1972) estimated the winter consumption rate by deer at 26% of the available browse in young plantations, with some 81% of the available shoots of *Populus tremula* being consumed. The authors reported that such severe utilization may cause the complete elimination of this species from the habitat. By selecting for the longest shoots protruding from the canopy, horses in the New Forest, England, feeding on gorse (*Ulex europaeus*) during winter may remove up to 45% of the annual shoot production (R. J. Putman; pers. comm.). Such comparisons may be misleading in that the giraffe consumption data refers specifically to new shoot production only, whereas the data of other workers generally includes shoot and leaf material. But consumption rates in the order of 60–85% of new shoot production are considerably greater than have been previously recorded in the literature.

Two aspects of the Serengeti data are pertinent: is the browse production–consumption system stable or are these high offtake rates the manifestation of a disequilibrium? For how long can these *Acacia* species tolerate such high consumption rates?

Stability of the browse production–consumption system

The Serengeti giraffe population is expanding at a rate of some 5–6% per annum in response to a substantial increase in the biomass of available browse (Pellew 1983a). The perturbations causing this increase are the elimination of much of the mature woodland canopy by elephants, combined with the steady decline in fire following the eruption of the ruminant herbivore populations (Norton-Griffiths 1979). The Serengeti is currently undergoing a process of major readjustment to these perturbations, and it is in this perspective that the giraffe impact must be assessed.

The effect of a change in resource availability in plant–herbivore systems has been modelled by Caughley (1976). The response of the giraffe population has been very rapid (extensive regeneration development dates back only to the late 1960s). At the time of the production–consumption measurements (1977), the system may have already reached the 'over-shoot' stage, with offtake exceeding the sustainable browse yield.

However, critical but unquantified examination of the tagged shoots up to May 1981 showed a continued high level of offtake, but no evidence of any decline in plant vigour. Browsing stunts growth, producing unusual topiary shapes, but there is no implication of 'over-browsing' (a term here defined as a reduction of plant productivity caused by unsustainable offtake). Pellew (1983b) demonstrated that the giraffe impact actually stimulated shoot production, which soon declined when the browsing stimulus was withdrawn. The dynamics of the giraffe population show no significant manifestation of

the operation of homeostatic feedback mechanisms activated by resource limitation (Pellew 1983a). If the giraffe population is still within the initial up-swing phase of its response, then the browsing impact will increase. The delay in the activation of the homeostatic response within the giraffe population is the result of the extreme tolerance of the acacias to browsing.

Tolerance of the acacias to consumption

How can an 85% consumption rate be described as not over-browsing? *Acacia* species appear able to tolerate, at least in the short-term, levels of offtake that would quickly kill temperate species. Tolerance to herbivory necessitates an enhanced photosynthetic efficiency so that a positive metabolic balance can be maintained after defoliation. In *Acacia* species, a significant proportion of the total plant chlorophyll is present in the epidermal layers of older shoots that are not consumed by giraffe. Thus, following even severe defoliation, such as the removal of the leaf-flush at the end of the dry-season (Pellew 1983b), the plant may remain photosynthetically active. The relative efficiency of shoot chlorophyll compared to leaf chlorophyll is unknown, but may be limited by restricted gas exchange, reduced light penetration through bark tissues, and the accumulation of starch.

McNaughton (1979) demonstrated that one reason for the ability of the Serengeti grasslands to support such a high ungulate biomass was the co-evolutionary adaptation of the vegetation to grazing. It is suggested that the resilience of *Acacia* species to browsing is the result of the positive selection for tolerant genotypes. Owen & Wiegert (1976) hypothesize that consumers maximize fitness in sexually-reproducing terrestrial plants, especially those that are long-lived, such as trees.

Seasonal consumption rates

The quarterly production and consumption estimates, shown in Table 4, suggest that the browsing impact varies markedly during the year with a build up in impact during the dry-season when production rates are at their lowest. *A. tortilis* dominates the regeneration thickets of the drier ridge-top and upper slope areas, where *A. hockii* also occurs as a minor ingredient (Pellew 1983b). Both species show very low production rates during the driest quarter, with almost total consumption of the few shoots produced. Occupance by giraffe of the ridge-top woodland type shows a significant decline in the dry-season (Pellew 1984) and this avoidance is the result of food limitation. In the wet-season, production accelerates resulting in the accumulation of browse biomass (Fig. 2). Although occupance levels increase to exploit this resource, the proportion consumed is relatively low. Wet-season occupance of the ridge-top areas is not food limited.

A similar pattern of production–consumption is apparent in the *A. xanthophloea* riverine woodland. In the wet-season, the woodland type is significantly avoided by both bulls and cows (Pellew 1984) so biomass accumulates. But as food limitation becomes manifest in the ridge-top areas in the early dry-season, occupance of the riverine woodland increases significantly. Although shoot production of *A. xanthophloea* persists at a relatively high rate (16·1% of the total annual production), this material is insufficient to support the locally high giraffe densities, which must also exploit the older browse that accumulated in the wet-season (Fig. 2). Approximately 41% of the shoot biomass that built up during the wet-season period January–June (and mainly derived from the low consumption period January–March) is removed during the high occupance dry-season quarter. Giraffe are attracted into the riverine woodland during the dry-season by the sustained production of new shoots of high protein content (mean crude protein content of

new *A. xanthophloea* shoots = 18·2%, Pellew 1984), although a major proportion of their diet comprises older shoots from the previous wet-season (mean crude protein content = 10·0%).

Total daily food intake

The quality of the giraffe's diet in the Serengeti remains high throughout the year as a result of the seasonal selection of woodland types within which to feed (Pellew 1984). The crude protein content of the diet of adult females shows a non-significant decline from the high wet-season level of 18·8% to 14·6% in the dry-season: in adult males from 14·2% to 11·7%. Such browse diets are of substantially greater nutritive value to a ruminant than are the diets of grazing ungulates where the crude protein content may regularly fall below the threshold of maintenance metabolism (Pratt & Gwynne 1977).

But the quantity ingested by giraffe is not significantly different to that of grazers. The minimum daily maintenance intakes for cattle have been variously estimated at between 1·5 and 3·0% of body weight (Agricultural Research Council 1965); at 2·7% for young dairy cattle, falling to 1·7% for older animals (Hafez & Schein 1969); and at approximately 2% for a 500 kg adult female buffalo (Sinclair 1977). A daily intake by adult giraffe of some 1·6–2·1% of body weight, comprising such highly digestible and protein-rich material, is certainly in excess of the minimum maintenance requirements.

From the nutritional analyses of the seasonal diets (Pellew 1984) estimates can also be made of the daily intake of individual chemical components. These are presented in Table 7. Despite their smaller total consumption, cows ingest per day more protein and soluble carbohydrate than bulls. The quality of the daily food ration decreases in the dry-season with more fibre ingested. Digestible nutrients comprise some 55% of the bulls' intake, and some 60% of that of the cows.

TABLE 7. Daily rates of intake (kg day^{-1}) of individual nutritional components in the seasonal diets of adult male and female giraffe

Nutritional component	Adult males		Adult females	
	Wet-season	Dry-season	Wet-season	Dry-season
Crude protein	2·70	2·22	3·12	2·42
Ether extract	0·67	0·97	0·53	0·61
Nitrogen-free extract	7·01	5·48	7·73	6·37
Acid detergent fibre	7·44	8·63	4·33	5·93
Total digestible nutrients	11·02	10·39	10·62	9·66

Time/weight measurements of food intake

In most foraging studies of wild ungulates, dietary data are recorded on a time basis with the implicit assumption that inter-specific differences in the duration of feeding realistically reflect similar differences in the quantity (dry weight) of food actually ingested. Hladik (1977) has shown that, for generalist primates that feed upon animal matter as well as fruits and leaves, data of feeding duration on different food types must be extensively corrected for comparisons of rates of nutrient intakes. In Fig. 4, the daily rates of food intake (kg day^{-1}) for each of the twelve principal browse species are plotted against their percentage representation (min day^{-1}) in the daily diet of adult female giraffe (data from Pellew 1984). The strong positive correlation suggests that feeding duration is a satisfactory measure of consumption for comparisons between browse species.

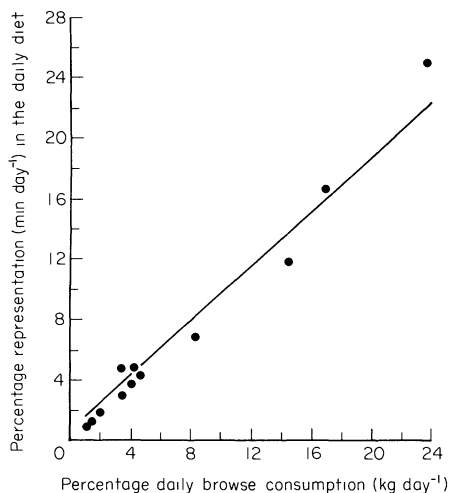Giraffe have two techniques of food ingestion: stripping leaves off thornless

FIG. 4. Correlation of percentage daily consumption with percentage representation in the daily diet for the twelve principal browse species in the diet of adult female giraffe. $y = 0.64 + 0.91x$; $r = +0.98$; $P < 0.001$.
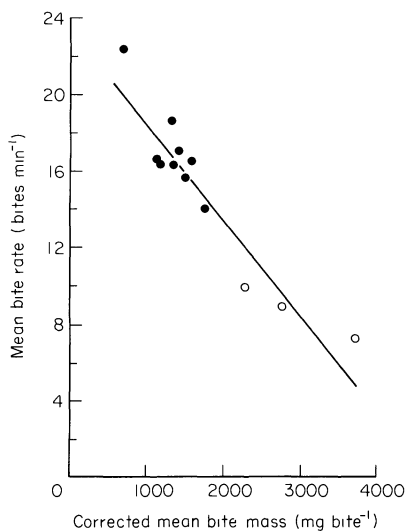

FIG. 5. The relationship between bite rate and bite size shown by adult female giraffe feeding upon the twelve principal browse species in the diet. $y = 23.51 - 0.005x$; $r = -0.94$; $P < 0.001$; (●) browse with thorns; (○) browse without thorns.

broad-leaf shrubs by pulling the shoot through the mouth, and biting off individual shoots and leaf-whorls of thorned Mimosaceae species. To assess the significance of these two techniques upon the rates of food ingestion, the mean bite rate was plotted against the mean bite mass (i.e. the corrected mean sample weight) for the twelve principle browse species in the daily diet of adult female giraffe. The results are shown in Fig. 5.

When feeding upon the thornless shrubs, the mean bite mass is significantly larger than when feeding upon the thorned *Acacia* species (mean bite mass $= 2.91$ g bite^{-1} and 1.3 g

bite^{-1} respectively; $t = 3.38$, $P < 0.01$). However, the mean bite rate is significantly slower (8.7 bites min^{-1} compared with 17.9 bites min^{-1} respectively; $t = 4.26$, $P < 0.01$), so the resulting mean rates of food intake are not significantly different (24.6 g min^{-1} compared with 21.6 g min^{-1} respectively; $t = 1.71$, $P > 0.10$). Differences in the technique of food gathering do not exert any significant influence upon the inter-specific rates of food ingestion.

Energy budgets and reproductive performance

It is clear from Fig. 3 that adult female giraffe are able to obtain sufficient energy from their diet for year-round breeding. Assessed in terms of energy intake and reproductive performance, the foraging strategy is obviously efficient, this efficiency being achieved by the manipulation of the behavioural factors involved in feeding (Pellew 1984). These factors include the choice of habitat in which to feed, the selection criteria by which individual food items are selected or rejected, and the allocation of time to foraging or to other energy consuming activities. Each factor is manipulated to maintain a positive energy balance.

The dry-season movement across the catena to exploit the accumulated biomass and sustained production of the riverine woodland enables the giraffe to maintain a high rate of nutrient and energy intake at the most critical time of the year. The energy budgets suggest that the time of probable energy deficit is the period of post-partum lactation in the dry-season, and at this time the breeding females show a significant selection for browse of high energy content (Pellew 1984). If the female diet was of the same nutritional quality as that of the males, which show no significant selection for energy content, then they would be energy limited in the dry-season.

Adult females forage for a relatively constant proportion of each 24 hours throughout the year (approximately 53%; Pellew 1984) with no significant seasonal difference, despite substantial changes in the food availability. It is suggested that females have adopted the strategy of 'energy maximizers' (Schoener 1971) in that their fitness is increased by maximizing their net rate of energy intake in the allotted foraging time. However, adult males show a significant decline in foraging time (48% in the dry-season and 39% in the wet-season, $P < 0.01$, Pellew 1984) as the quantity of food increases. Males have adopted the strategy of 'time minimizers' in that their fitness is increased by minimizing their foraging time, provided they achieve the metabolic threshold for reproduction, leaving more time to seek out oestrous females.

The reproductive performance of the Serengeti giraffe is superior to other recorded giraffe populations, with a shorter mean calving interval (18.8 months) and an earlier mean age of first conception (50.3 months) (Pellew 1983a). By influencing fecundity, both these parameters are sensitive indicators of the demographic vigour of a population (Hanks 1981). Most African grazing ruminants show seasonal parturition, calving in the mid- and late wet-season when the grass quality is at its maximum (Spinage 1973). The energy budgets of wildebeest and buffalo, produced by Sinclair (1977), show considerable deficits in the dry-season as the energy content of the grass falls to about half its wet-season level. Seasonal parturition, correlated with rainfall and its effect upon the protein content of the herbage, has also been demonstrated in hippopotamus (*Hippopotamus amphibius*) by Laws & Clough (1966) and in buffalo by Field (1976). Conception in seasonal calvers occurs during the period of energy deficit, but as demonstrated by Wiltbank *et al.* (1962), a high level of energy intake resulting in good body condition before parturition has more influence upon the post-partum anoestrus than the level of energy intake at the time of oestrus.

Seasonal breeding in ungulates has evolved so that parturition occurs at the time when environmental conditions are optimal for the survival of both the mother and calf (Sadleir 1969; Skinner, Van Zyl & Oates 1974). The high year-round quality of their diet enables the giraffe to extend their breeding period beyond the normal seasonal constraint experienced by most grazing ruminants. Other browsing (or dry-season browsing) ungulates which in East Africa breed throughout the year include impala (*Aepyceros melampus*), gerenuk (*Litocranius walleri*), and lesser kudu (*Tragelaphus imberbis*) (Leuthold & Leuthold 1975). However, under the more extreme conditions of seasonality in southern Africa, impala revert to being seasonal breeders as they are unable to achieve the metabolic thresholds for reproduction, despite the selectivity of their feeding (Dunham & Murray 1982). In Equatorial Africa, browsers are able to breed throughout the year, whilst outside this area year-round breeding is confined to the larger mammals with gestation periods exceeding 1 year, and not exclusively to browsers (N. Owen-Smith, personal communication).

Hall-Martin *et al.* (1975) suggest that the nutritionally important stage of the reproductive cycle of giraffe (and presumably other year-round breeders) is the time of conception, and that any selective disadvantage which might be exercized upon the young would be mitigated by the long lactation period in this species. This study shows that the energy balance remains positive for dry-season births, so no selective nutritional disadvantage will operate. The survival rates of Serengeti giraffe calves born in the wet- and dry-seasons are not significantly different (Pellew, unpubl. data).

The reproductive performance of female giraffe in the Serengeti is not nutritionally limited, for the manipulation of the behavioural factors involved in feeding results in a foraging strategy that optimizes the combination of the quantity and quality of the food ingested. The metabolic thresholds for gestation, parturition and lactation can therefore be attained at all times of the year.

ACKNOWLEDGMENTS

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