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Sex differences in giraffe foraging behavior at two spatial scales

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Abstract We test predictions about differences in the foraging behaviors of male and female giraffes (*Giraffa camelopardalis tippelskirchi* Matchie) that derive from a hypothesis linking sexual size dimorphism to foraging behavior. This body-size hypothesis predicts that males will exhibit specific behaviors that increase their dry-matter intake rate relative to females. Foraging behavior was examined at two hierarchical levels corresponding to two spatial and temporal scales, within patches and within habitats. Patches are defined as individual trees or shrubs and habitats are defined as collections of patches within plant communities. Males were predicted to increase dry-matter intake rate within patches by taking larger bites, cropping bites more quickly, chewing less, and chewing faster. Within habitats, males were expected to increase intake rate by increasing the proportion of foraging time devoted to food ingestion as opposed to inter-patch travel time and vigilance. The predictions were tested in a free-ranging population of giraffes in Mikumi National Park, Tanzania. Males spent less total time foraging than females but allocated a greater proportion of their foraging time to forage ingestion as opposed to travel between patches. There was no sex difference in rumination time but males spent more time in activities other than foraging and rumination, such as walking. Within patches, males took larger bites than females, but females cropped bites more quickly and chewed faster. Males had longer per-bite handling times than females but had shorter handling times per gram of intake. Within habitats, males had longer average patch residence times but there was no significant sex difference in inter-patch travel times. There was no overall difference between sexes in vigilance while foraging, although there were significant sex by habitat and sex by season interactions. Although not all the predictions were confirmed, overall the results agree qualitatively with the body-size hypothesis. Sex-related differences in foraging behavior led to greater estimated intake rates for males at the within-patch and within-habitat scales.

Key words Giraffe · Herbivore · Foraging behavior · Ruminant · Sexual dimorphism

Introduction

Most ruminant species with females larger than 25 kg exhibit pronounced sexual body size dimorphism in which males are much larger than females (Owen-Smith 1988). This dimorphism has profound nutritional and energetic consequences such that males and females of the same species may be more ecologically dissimilar than are different species from each other (e.g., Demment 1983). Specifically, because total basal metabolism increases as a fractional exponent of body mass, larger animals require more total energy per unit time whereas smaller animals require more energy per unit body mass per unit time, and this relationship holds interspecifically (Kleiber 1975), intraspecifically (Thonney et al. 1976), and under field conditions when activity costs are included in estimates of metabolism (Nagy 1987). However, gut capacity in herbivores is a linear function of body mass (Parra 1978; Demment 1982). The result of these two relationships is that larger herbivores have a higher ratio of gut volume to metabolic requirement (i.e., greater "food-processing capacity", Demment 1983; Demment and Van Soest 1985) and retain food in the gut for longer periods. This increases a large ruminant's efficiency of nutrient extraction per unit of intake relative to that of smaller ruminants (Foose 1982; Van Soest 1996; Illius and Gordon 1991, 1992). Based solely on these body-size considerations males

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and females can be expected to differ in digestive efficiency such that males can tolerate a lower-quality diet than females.

Reproductive concerns may also affect any potential nutritional and energetic differences between the sexes. Female ruminants often have the additional metabolic loads of gestation and lactation, which also depress their "food-processing capacity" relative to males even further. Males, on the other hand, must spend time maintaining dominance status, competing against other males for mates, and consorting with females. Males of many ungulate species do little or no eating during rutting periods (Miquelle 1990) when their condition may decline (e.g., Jarman and Jarman 1973). Males that can meet their energetic needs in shorter time by increasing intake rate could increase fitness by spending more time vying for mating opportunities. Male and female herbivores can therefore be seen to have widely diverging foraging concerns that should be reflected in each sex's foraging behavior and habitat selection (Demment 1983; Pellew 1984a,b; Clutton-Brock et al. 1987; Main and Coblentz 1990; Main et al. 1996; Miquelle et al. 1992).

Based on the above considerations we predict that female herbivores will be more selective, will spend more time searching for quality forage, and will forage in areas where higher quality vegetation is more abundant. Because males can better exploit lower quality forages, we expect males to forage in areas with greater forage biomass that offer potentially higher intake rates, exhibit a more generalized diet with respect to quality than females, spend less time searching for food items, and adjust ingestion behavior to increase intake rate (Gross 1990).

We tested some of these predictions by conducting a field study of free-ranging Masai giraffes (*Giraffa camelopardalis tippelskirchi* Matchie). Male giraffes are larger than females; the mean adult body masses are approximately 1200 kg for males and 800 kg for females (Dagg and Foster 1982; Owen-Smith 1988). Males consume greater amounts of forage dry matter per day than do females and females consume more forage per unit body mass per day than males (Pellew 1984a; Prins and Domhof 1984). Because giraffe breeding is aseasonal, male giraffes must partition time daily between feeding and reproductive activities such as locating and consorting with receptive females, and maintaining dominance status among other males (Pratt and Anderson 1985). Given these considerations, Pellew (1984a) has suggested that male giraffes could increase fitness by following a time-minimizing foraging strategy that potentially provides them with increased mating opportunities, whereas female giraffes could increase fitness by pursuing an energy or nutrient-maximizing strategy that directly benefits the condition of offspring and also ensures adequate energy for lactation (see also Schoener 1969, 1971). In support of this, male giraffes are already known to spend less time per day foraging than females (Leuthold and Leuthold 1978; Pellew 1984b) apparently by achieving greater forage ingestion rates (Pellew 1984a). The present study is designed to test hypotheses about the mechanisms underlying these observed differences in intake rates and foraging time. We apply a hierarchical conceptualization of the foraging process as described in the following section.

Foraging in large herbivores can be viewed as a hierarchical process (Johnson 1980; Senft et al. 1987). The following arguments are appropriate for a browser such as the giraffe but are easily adapted to grazing species as well. Within small patches of forage (i.e., an individual tree or shrub) a herbivore selects, crops, and masticates bites. Within habitats (i.e., collections of patches) the animal chooses among patches of various types and travels between them. Within the landscape, the animal decides how to allocate foraging time among the available habitats. In this paper we examine the mechanisms governing intake rate at the within-patch and within-habitat levels.

Within a patch, bites are in close proximity so that there is no search time that is exclusive of handling (Spalinger and Hobbs 1992). The average within-patch dry-matter intake rate (IWP) is an increasing asymptotic function of bite mass (S) as in Eq. 1 (Spalinger et al. 1988; Spalinger and Hobbs 1992; Ginnett and Demment 1995).

$$\mathrm{IWP} = \frac{S}{F + IS} \qquad (1)$$

The symbols F and I are parameters that represent the average fixed (per bite) and incremental (per gram) time costs of handling each bite, respectively (Ginnett and Demment 1995). The value of $1/I$ sets the asymptotic maximum intake rate. The fixed and incremental handling costs may be composed of three quantities: h, the time need to form and sever a bite from the plant; c, the average time of a single chewing motion; and E, the average number of chews allocated to 1 g of ingested material. Several recent studies (Spalinger and Hobbs 1992; Gross et al. 1993) assume that $F = h$ and $I = cE$, but Ginnett and Demment (1995) show that this may not be true for giraffes. In any case, increases in the value of any of h, c, or E will always lower IWP, which makes them useful quantities for comparing intake behavior.

Within habitats, patches may vary in IWP. The animal also incurs a time cost due to travel between patches that is exclusive of any travel during which handling (i.e., mastication) occurs. Because foraging exposes the animal to predation risk, some amount of time must be spent in vigilance, which lowers foraging efficiency (e.g., Bertram 1980; Siegfried 1980; Underwood 1982; Lima 1987). The average intake rate at the within habitat level (IWH) can therefore be expressed as in Eq. 2.

$$\mathrm{IWH}_j = \frac{\sum_{i=1}^{n} IWP_i T\mathrm{p}_i}{n(T\mathrm{te}_j + T\mathrm{s}_j) + \sum_{i=1}^{n} T\mathrm{p}_i} \qquad (2)$$

In this formulation, $T\mathrm{p}_i$ is the time spent handling forage from patch i and includes any travel time between patches during which the animal masticates, n is the number of patches visited, T_{te} is the mean inter-patch travel time exclusive of travel during which mastication occurs, and T_s is the average time spent scanning for predators during a foraging bout consisting of a single instance of patch residence followed by travel to the next patch. Because these quantities may be habitat specific, they are indexed for each of the j available habitats. If the travel and scanning costs are small relative to handling costs then IWH converges to the weighted mean IWP, taking into account the proportion of time spent foraging within each of the n different patches. Note that because it is possible for the animal to process food by masticating while traveling between patches, an alternate expression for the denominator of Eq. 2 replaces T_{te} by T_t, which is simply the mean travel time inclusive of travel while masticating, and Tp_i by Tr_i, which is the time actually spent resident at patch i.

The body-size hypothesis, combined with our conceptualization of the foraging process, suggests a number of predictions regarding differences in the foraging behaviors of males and females. In general, we expect males to exhibit behaviors that increase intake rate relative to females. Within patches, behaviors that increase intake rate include taking larger bites and reducing the fixed and incremental time costs of handling. These two costs can be reduced by cropping bites more rapidly, chewing faster, and allocating fewer chews per gram of forage. At the within-habitat level, males are expected to allocate a greater proportion of foraging time to ingestion as opposed to travel and vigilance. Table 1 contains a summary of behavioral variables used in our comparisons, their definitions, and dimensions.

Table 1 Summary of within-patch and within-habitat behavioral variables, their units, and definitions

Variable	Units	Definition
IWP	g time^{-1}	Average dry-matter intake rate within a patch
S	g	Average bite mass taken from a patch
F	time bite^{-1}	Fixed time cost of handling a bite from a patch
I	time g^{-1}	Incremental time cost of handling a bite
h	time bite^{-1}	Time needed to form and sever a bite from a patch
c	time chew^{-1}	Time needed for one chewing motion
E	chews g^{-1}	Chewing effort per gram of intake
IWH	g time^{-1}	Average dry-matter intake rate within a habitat
T_p	time	Total time spent handling bites from a patch. May include travel while masticating
T_{te}	time	Average inter-patch travel time exclusive of travel while masticating
T_r	time	Total time spent actually resident in a patch
T_t	time	Average inter-patch travel time inclusive of travel while masticating
T_s	time	Average time spent scanning for predators during a single bout of patch residence and travel

Methods

Study area

The study area was located in a 50-km^2 area surrounding the park headquarters village in Mikumi National Park, Tanzania (7°20′S, 37°07′E). This is a favored area for giraffes within the park and good roads facilitate access to the animals. From north to south the vegetation can be classified into three broad habitat types along an elevational gradient from 480 to 600 m: flood plain grasslands with low shrubs, a mixed-shrub savannah at slightly higher elevations, and an open woodland community at the southernmost and highest elevation sites. *Harrissonia abbyssinica* is the dominant shrub and forage species in the flood plain. The mixed-shrub communities are dominated by *Diospyros usambarensis* , *Combretum hereroense,* and *Lonchocarpus capassa*, while in the open woodlands the most common forage species are *C. zeyheri* and *C. collinum*. These three communities are transversed by riverine communities in which the dominant forage species are *Haplocoelum inopleum*, *Gardenia* spp., and *Spirostachys africana*. The study area was subdivided by a 500 m by 500 m grid system to facilitate recording animal locations. The wet or green season typically runs from January to June, and the dry or brown season from June to December.

Activity budgets

On each of six dates during 1989, a mixed-sex group of giraffes was located early in the morning and followed until dark. Activity data were collected by instantaneous recording of group scans (Altmann 1974; Martin and Bateson 1986) at 5-min intervals for the 12-h period between 0630 and 1830 hours. Difficulty in following the animals after dark at a non-disturbing distance precluded nighttime observations.

Three major behavioral categories were recognized: foraging, ruminating, and other. Foraging was subdivided into feeding (standing at a tree or shrub ingesting forage) and travel (all walking between individual forage plants). Rumination and other were subdivided into standing, walking, or lying. Other included all other activities such as resting, social interactions, and sexual behavior that occurred exclusive of rumination and foraging. Walking is further categorized as trekking (Pellew 1984b), which includes all walking done exclusive of foraging, and as total walking (trekking + travel).

Ingestive behavior

During 1989 we collected 1,884 observations of giraffe foraging behavior by using focal animal sampling with continuous recording (Altmann 1974; Martin and Bateson 1986) by laptop computer and an event-recording program. Giraffes have unique and permanent spot patterns that allow individuals to be easily identified (Dagg and Foster 1982) and a file was kept of either left-side photographs or drawings of identifiable spot patterns to aid in recognition. A recognizable adult animal was chosen from a group of actively foraging giraffes and its identity and grid location, as well as the date and time of day, were recorded. Animals were not chosen randomly from the group. Instead, we attempted to obtain foraging records from as many different individuals in the group as was possible. A foraging record began when the giraffe approached a patch (individual tree or shrub) and lowered its head to feed. The timings of all biting and chewing motions while the animal was processing forage were recorded by pressing coded keys on the laptop computer. After the animal left the patch, travel time was recorded until the animal began to feed from the subsequent patch, which ended the record. Occasionally a giraffe would temporarily cease foraging and look around, a behavior that we define as vigilance. Each patch visited was classified by species and by its height in relation to the animal. We recognized six relative height classes: 0, below the knees; 1, between the knees and belly; 2, between the belly and base of the neck; 3, base of the neck to mid-neck; 4, midneck to eye level; and 5, above eye level. All observations were made from inside a Land Rover at distances of 15–100 m, through binoculars if necessary.

Estimating bite mass

Bite mass was estimated by both direct and indirect means. Direct bite mass estimates were made by clipping vegetation from patches in a manner that simulated the feeding style of the animal (Pellew 1984a). These samples were only collected after very close observations (< 20 m), during which the animals had either removed entire shoots, or had stripped the leaves from shoots to lengths that could be measured. An additional stipulation was that the tree or shrub not be seriously depleted so that a sample of 10–15 shoot clippings or hand strips could be collected. Immediately prior to clipping the bite size estimates, we recorded the biting rate of the animal that was feeding from that particular tree or shrub. Clipped bite mass samples were returned to the lab, dried to constant weight at 105°C and weighed to the nearest 0.01 g. All bite masses are expressed on a dry-matter basis.

Because these direct bite mass estimates were difficult to obtain and because exiting the vehicle to make clippings disturbed the animals, we made indirect bite mass estimates by establishing a statistical relationship between the direct bite mass estimates and the observed time per bite (TPB, the inverse of bite rate). This was accomplished by fitting a simple linear regression model (TPB = $F + IS$) using the direct bite size estimates and the observed biting rates. We supplemented this analysis by including in the regression published data on giraffe bite weights and biting rates of Pellew (1984a). Given the resulting regression equation we then used inverse prediction to estimate bite mass from an independent data set of observed bite rates. Based on these indirect bite mass estimates we then estimated within-patch intake rates (IWP) from observed bite counts and handling times.

Data analysis

Activity budgets were analyzed as follows. Data from the 12 scans taken during each hour were pooled by sex. The frequencies of animals in each behavioral category during each hour then were converted to percentages and subjected to arc sin square root transformation prior to analysis. Three-way analysis of variance (ANOVA) was performed on the transformed data with sex, date, and time of day as factors. No males were observed on one date (27 February) so those data are excluded from the ANOVA analyses but are included in Table 2 for comparison. In these analyses, time of day is not considered to be a repeated measure. Giraffe groups were extremely plastic and often changed composition throughout the day so that the individuals being monitored in the evening were often different from those monitored in the morning. Secondly, the repeated-measures model assumes no interaction between subjects (in this case the same-sex group on a particular date) and the repeated measure. As will be seen, this assumption is not met by these data. Multiple comparisons between dates were performed using the Ryan-Einot-Gabriel-Welsh multiple range test (SAS Institute 1988) which controls the experiment-wise error rate.

The within-patch variables h, S, and IWP were analyzed by three-way ANOVA models of full-rank with sex, season, and species as factors. We restricted this analysis to the seven most eaten forage species, which accounted for approximately 90% of all observed foraging bouts. The estimated bite sizes were transformed to their natural log to normalize the data. The within-habitat variables T_P, T_r, T_t, and T_{te} were log-transformed and analyzed by a similar ANOVA model with sex, season, and habitat as factors. Because these designs were unbalanced, hypothesis tests were based on type III sums of squares (SAS Institute 1988; Shaw and Mitchell-Olds 1993) and multiple comparisons between species or habitats were performed using the Turkey-Kramer method which accounts for unequal cell sizes (SAS Institute 1988). Prior to analysis, all replicate observations on identifiable individuals were averaged to provide a single value per individual and avoid pseudoreplication (Hurlbert 1984).

Results

Activity budgets

Males spent less time foraging, feeding, and traveling between forage plants than females, but spent more time engaged in other activities (Table 2, all Ps ≤ 0.002). Although males spent less time feeding, they consistently spent a greater proportion of their diurnal foraging time ingesting forage than did females (Fig. 1). Females spent more total time walking than males ($P = 0.02$), but male giraffes spent more time trekking ($P = 0.001$). No significant effects of sex on rumination time were evident ($P = 0.97$). The time of day effect was significant for all behavioral categories tested (all Ps < 0.05). Only male giraffes were observed lying down, and this only on rare occasions, so no ANOVA was performed on this variable.

There were no significant time of day by sex interactions indicating that males and females tended to engage in the same activities at the same time of day. Nor were any significant sex by date interactions evident – i.e. seasonal changes in behavior of males and females roughly paralleled each other (Table 2). In contrast, the date by time of day interaction was significant for all

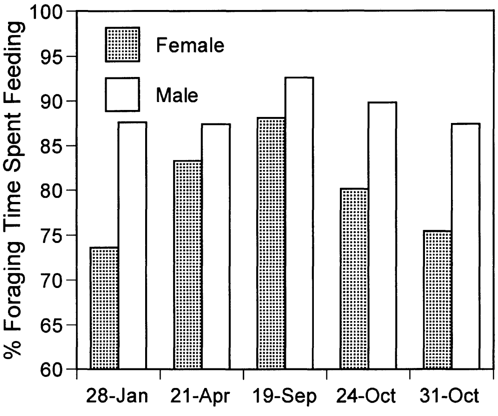

Fig. 1 Percent of foraging time spent ingesting forage by male and female giraffes on five different dates. The difference between sexes is significant based on arc sin transformed data (paired t, $P < 0.01$)

Table 2 Summary of giraffe activity budgets during 1989 classified by sex and date. Behavioral categories are not mutually exclusive and are defined in the Methods section. The table contains percentages of time spent in each activity. Dates *1–6* refer to 28 Jan, 27 Feb, 21 Apr, 19 Sep, 24 and 31 Oct respectively. Data for 27 Feb were not used in ANOVA but are included here for comparison. Date means followed by the same letter are not significantly different ($P > 0.05$). *Asterisks* indicate a significant sex difference

		Date						
		1	2	3	4	5	6	Mean
Foraging	Female	5.83	52.4	53.2	57.9	79.1	63.4	61.4^{**}
	Male	41.1		41.9	40.7	56.1	55.6	47.1
	Mean	47.4_{b}		47.6_{b}	49.3_{b}	67.6_{a}	59.5_{a}	
Feeding	Female	39.6	46.6	44.3	51.0	64.0	47.8	49.3^{**}
	Male	36.0		36.6	37.7	50.4	48.6	41.9
	Mean	37.8_{b}		40.4_{b}	44.4_{b}	57.2_{a}	48.2_{b}	
Travel	Female	12.1	5.8	8.9	6.9	15.1	15.6	11.7^{**}
	Male	5.1		5.3	3.0	5.6	6.9	5.2
	Mean	8.6_{ab}		7.1_{ab}	4.9_{b}	10.3_{a}	11.3_{a}	
Ruminate	Female	17.7	12.6	28.2	20.8	10.3	18.2	$19.0^{\text{n.s.}}$
	Male	24.8		29.6	20.1	13.9	19.4	21.6
	Mean	21.2_{ab}		28.9_{a}	20.4_{abc}	12.1_{c}	18.8_{bc}	
Other	Female	28.6	35.0	18.6	21.4	10.7	18.4	18.6^{**}
	Male	34.1		28.6	39.2	30.1	25.0	31.4
	Mean	31.4_{a}		23.6_{abc}	30.3_{ab}	20.4_{c}	21.2_{bc}	
Walking	Female	18.7	7.1	13.8	10.3	17.8	21.3	16.4^{*}
	Male	15.8		13.0	11.6	16.8	13.2	14.1
	Mean	17.2_{a}		13.4_{ab}	10.4_{b}	17.3_{a}	17.3_{ab}	
Trekking	Female	7.7	1.3	4.9	3.4	2.7	5.7	4.9^{**}
	Male	10.7		7.7	8.7	11.2	6.3	8.9
	Mean	9.2_{a}		6.3_{b}	6.0_{b}	7.0_{ab}	6.0_{b}	

$^{*}0.05 > P > 0.01$, ** $P < 0.01$, $^{\text{n.s.}}$ not significant, $P > 0.05$

variables tested (all $P_s < 0.001$). This was due to the fact that giraffes began foraging earlier in the day during the dry season corresponding with the somewhat earlier time of sunrise. Rumination was concentrated in the early mornings and late afternoons during the wet season while during the dry season most animals ruminated in the mid-afternoon. Activity times between or within dates were not obviously related to either temperature or cloud cover.

Within-patch behavior

Comparison of regression equations (Fig. 2) used to estimate F and I from the clipped bite size samples shows that males had significantly smaller per gram processing costs than females (ANCOVA, $P = 0.01$). Males tended to have larger fixed handling costs than females but the difference was not significant (ANCOVA, $P = 0.23$).

To compare the average time of a chewing motion, c, the data were averaged within known individuals and a reciprocal transformation (to chewing rate) applied to normalize the data. The chewing rate of females was 66 chews min^{-1} compared to 63 chews min^{-1} for males (Student's $t = 3.22$, $df = 112$, $P = 0.002$). A similar difference was noted in the chewing rates of ruminating giraffes (Student's $t = 2.15$, $df = 20$, $P = 0.04$).

ANOVA results for all within-patch analyses are summarized in Table 3. Male bite formation times averaged 1.84 s bite^{-1} and were significantly longer than those of females, which averaged 1.66 s bite^{-1}. There was no significant effect of species or season on bite formation time. On average, males took larger bites than females (Fig. 3). This tendency was greater during the wet season as evidenced by a significant season by sex interaction. There was a consistent overall trend for bite size to decline from the wet to the dry season as well as significant variation across forage species. Estimated within-patch intake rates followed a similar pattern of variation (Fig. 3).

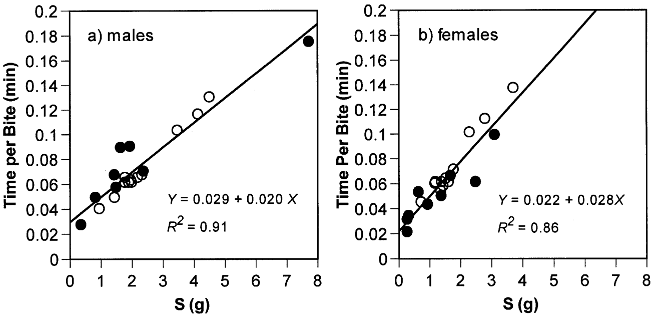

Fig. 2a,b Regression analysis of the clipped bite mass estimates versus time per bite. The slope (I) is equivalent to the average per-gram time cost of processing forage. The intercept (F) represents a constant time cost of processing a bite that is independent of its mass. **a** For males $F = 0.029$ min bite^{-1} and $I = 0.020$ min g^{-1}. **b** For females, $F = 0.022$ min bite^{-1} and $I = 0.028$ min^{-1}. *Closed circles* are the clipped bite mass estimates from this study, *open circles* represent data of Pellew (1984a). The two regressions differ in slope (ANCOVA, $P = 0.01$) but not in intercept (ANCOVA, $P = 0.23$)

Table 3 Summary of ANOVA results for within patch and within-habitat variables. Values indicate significance levels for the appropriate F-tests. Values of zero indicate probabilities less than 0.0005 (acronym definitions: h mean bite-formation time in min, S mean bite mass in g, *IWP* mean within-patch intake rate in g min^{-1}, T_p average patch processing time in sec including travel while masticating, T_{te} average inter-patch travel time in sec exclusive of travel while masticating, T_r mean inter-patch travel time in s inclusive of travel while masticating, *IWH* mean within-habitat intake rate in g min^{-1}

Within-patch source of variation	*df*	h	S	IWP
Sex	1	0.000	0.000	0.000
Season	1	0.106	0.000	0.000
Species	6	0.092	0.000	0.000
Sex × Season	6	0.520	0.023	0.000
Sex × Species	6	0.146	0.050	0.121
Season × Species	6	0.130	0.006	0.001
Sex × Season × Species	6	0.394	0.295	0.167
Error	399			

Within-habitat source of variation	*df*	T_p	T_{te}	T_r	T_t	IWH
Sex	1	0.004	0.057	0.005	0.187	0.000
Season	1	0.404	0.174	0.398	0.123	0.029
Habitat	3	0.270	0.569	0.208	0.602	0.045
Sex × Season	3	0.883	0.804	0.850	0.834	0.756
Sex × Habitat	3	0.332	0.660	0.428	0.521	0.896
Season × Habitat	3	0.224	0.212	0.260	0.058	0.001
Sex × Season × Habitat	3	0.232	0.009	0.298	0.004	0.013
Error	262					

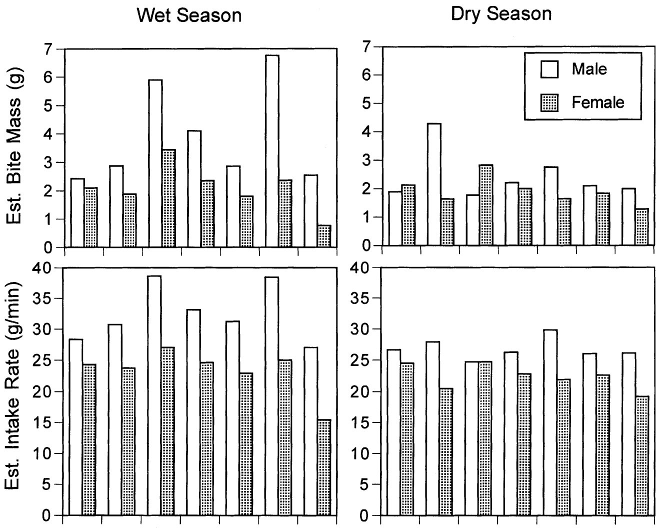

Fig. 3 Estimated bite masses and intake rates for the seven most common forage species of giraffe in Mikumi National Park, Tanzania, during 1989. Species abbreviations are as follows: *CASSABB Cassia abbreviata, COMHER Combretum hereroense, COMZEY C. zeyheri, DIOUSA Diospyros Usambarensis, HARABY Harrisonia abyssinica, LONCAP Loncocarpus capassa, SPIAFR Spirostachys africana.* The effects of season, sex, and species are significant for both variables (see Table 3 for significance levels)

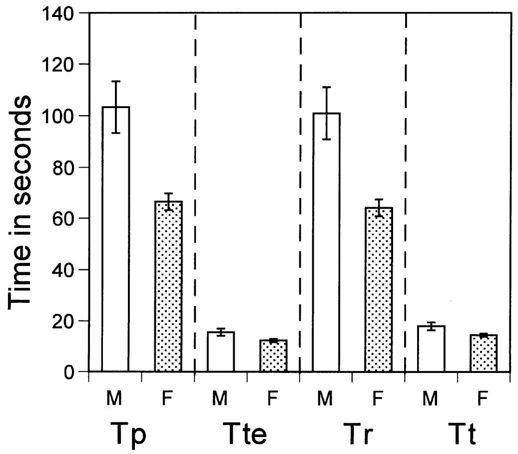

Fig. 4 Comparison of male and female handling and travel times corresponding to two different methods of describing foraging. Males had longer patch processing times (T_p) and longer patch residence times (T_r) than females. The sex differences in travel time were not significant either when chewing time was excluded from travel (T_{te}), or included in travel time (T_t)

Within-habitat behavior

Males had significantly longer patch processing times (T_p) and patch residence times (T_r) than females (Table 3, Fig. 4). There were no significant differences in T_p and T_r between habitats or seasons, nor were there any significant interaction effects. Giraffes generally did a small amount of mastication while traveling between patches and this is reflected in the shorter residence times relative to processing times. There were no significant effects of sex, season, or habitat on either travel time variable. Interestingly, when residence times are classified by feeding height, T_r is greater in taller patches and is similar for both sexes (Fig. 5a). Processing times followed a similar pattern of variation. The overall sex difference in T_r and T_p is due to differential selection of patches on the basis of height. Males consistently did more feeding in taller patches than females (Fig. 5b).

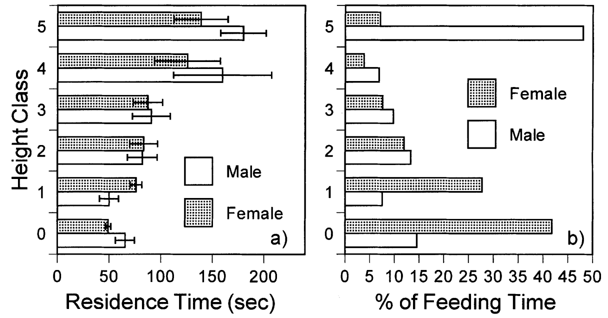

Fig. 5 **a** Mean patch residence times for males and females as a function of patch height. Patch height classes were determined relative to the height of each animal and are explained in the text. Horizontal lines represent ± 1 SE. **b** Percent of total feeding time allocated to patches of various heights by male and female giraffes. Patch height classes were determined relative to each animals height and are explained in the text

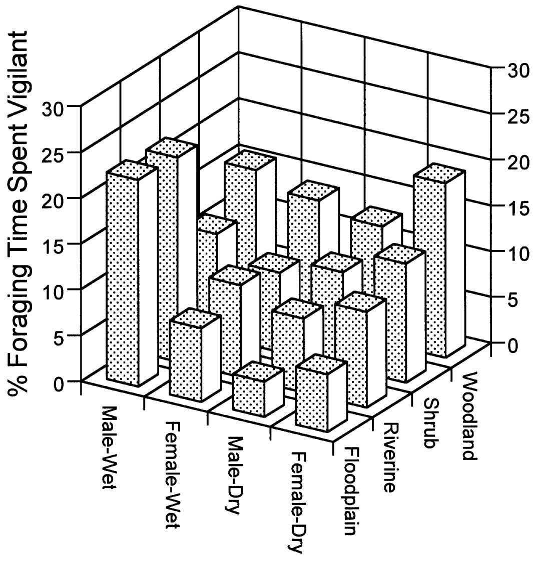

Fig. 6 Percent of foraging time spent vigilant classified by sex, season and habitat. Males were more vigilant than females during the wet season in all habitats but females were more vigilant during the dry season

Table 4 Estimated within-habitat intake rates (*IWH*) classified by sex and season. Values are dry-matter intake rates expressed in g min^{-1}. Effects of sex, season and habitat are all statistically significant (see Table 3 for P-values)

	Wet season		Dry season		
Habitat	Male	Female	Male	Female	Mean
Flood plain	22.7	16.6	17.8	15.8	18.3
Mixed shrub	25.1	19.1	17.7	15.9	19.4
Open woodland	19.3	19.3	22.0	14.9	18.9
Riverine	17.8	14.4	21.2	14.6	17.0
Mean[a]	21.2	17.4	19.7	15.3	

[a] Least-square means

The percent of foraging time spent scanning did not show any significant overall effect of sex, season, or habitat ($P_s > 0.05$). There was, however, a significant interaction between sex and season ($P = 0.03$). Males spent more time scanning than females during the wet season but this difference was reversed during the dry season (Fig. 6).

Males maintained greater within-habitat intake rates than females (Table 4). Consistent with the seasonal drop in bite mass, IWH declined from the wet to the dry season and also varied significantly across habitats.

Discussion

In general, the results are consistent with predictions based on the body-size hypothesis . Males, although they are larger and require more forage than females, spent less time in daily foraging and this is consistent with other studies of giraffes (Leuthold and Leuthold 1978; Pellew 1984b) as well as with studies of other herbivores such as blue wildebeest and red hartebeest (Ben-Shahar and Fairall 1987), waterbuck (Spinage 1968), and gerenuk (Leuthold and Leuthold 1978). The analysis of activity budgets indicates that the sexual difference in foraging time was due to two factors. First, males maintained higher forage intake rates as evidenced by their devoting less daily time to forage ingestion (feeding) than females even though their absolute daily energy and food requirements are greater (Pellew 1984a). Second, male giraffes allocated a greater proportion of foraging time to food ingestion rather than inter-patch travel. Direct comparison of this study with previous ones, however, is problematic. Leuthold and Leuthold (1978), in their study of giraffe activities in Tsavo National Park, do not clearly define their behavioral categories and it is unclear whether their category "feeding" includes any travel time or simply represents food ingestion as in the present study. Pellew's category "feeding" (Pellew 1984a) is strictly food ingestion and so is comparable, but travel time (walking while feeding) is not distinguished from any other walking so a comparison of total foraging effort between Serengeti and Mikumi giraffes is not possible.

The within-patch functional response model (Eq. 1), see also Spalinger and Hobbs 1992; Laca and Demment 1992; Ginnett and Demment 1995), as well as empirical studies (e.g., Allden and Whittaker 1970; Wickstrom et al. 1984; Hudson and Watkins 1986; Spalinger et al. 1988), suggest four mechanisms that could account for higher male intake rates within small patches: (1) increased bite size, (2) reduced chewing effort, (3) increased chewing rate, and (4) shortened bite formation time. We discuss each of these in turn.

Increased bite size

Because IWP is positively related to bite mass, males could increase IWP and thereby shorten feeding times by taking larger bites than females. This study as well as that of Pellew (1984a) supports this hypothesis. The sex difference in bite size was the greatest during the wet season, when new plant shoots were growing rapidly and there was greater opportunity for selection of bite size (Fig. 3). Shipley et al. (1994) showed that across 34 species of browsing herbivores, maximal bite mass scales to the 0.63 power of body mass. If this held true intraspecifically, and assuming mean body masses of 1200 kg and 800 kg for males and females respectively, we would expect a ratio of male:female maximal bite masses of approximately 1.29. The mean ratio of male to female bite sizes was much greater than this during the wet season (1.87) when there was greater scope for bite size selection, but approaches this ratio during the dry season (1.28) when the potential for bite size selection is more limited by plant morphology. This seasonal shift in bite size ratios is due to the fact that female bite mass changed very little with season whereas male bite mass increased dramatically during the wet season. This strongly suggests that females did not take maximal bite sizes during the wet season. Given a generally inverse relationship between bite size and bite quality, this is consistent with our suggestion of an energy or nutrient-maximizing bite selection policy for females and a time-minimizing strategy for males.

Reduced chewing effort

Males could elevate intake rate relative to females by chewing less. We could not make a strong test for a sex difference in chewing effort with our field data but in another experiment a captive male giraffe was shown to chew less per gram of intake than a captive female (Ginnett and Demment 1995). Our regression analysis, however, indicates that males have lower per-gram handling costs than females, which strongly suggests that a difference in chewing effort exists. Other sexually dimorphic ruminants such as ibex exhibit a sex difference in chewing effort in which females apply more chews per gram than males (Gross et al. 1995).

Increased chewing rate

Increased chewing rates can also elevate intake rate. Contrary to our prediction males chewed more slowly than females. Given equal bite sizes this small difference in chewing rates would slightly elevate female intake rates relative to males, particularly at larger bite sizes (Ginnett and Demment 1995). This difference was greatly outweighed, however, by the general tendency for males to take larger bites than females.

Shortened bite formation time

Finally, intake rate can be elevated by shortening bite formation time. Females consistently had shorter bite formation times than males. Interestingly, the only exception to this was for *H. abyssinica*, the only species in the analysis possessing true spines. Although the spines of *H. abyssinica* are of the small, recurved variety that Cooper and Owen-Smith (1986) found to be the most effective at retarding bite rates in smaller herbivores, they did not seem effective against giraffes (see also Pellew 1984a). Given equal bite sizes, shorter bite formation times would allow females would obtain higher intake rates, particularly at small bite sizes although this difference would become negligible at large bite sizes (Spalinger and Hobbs 1992; Ginnett and Demment 1995). This is in apparent contradiction to our predictions. However, there is a strong tendency for bite formation time of giraffes to scale positively with bite mass (Ginnett and Demment 1995). Therefore the shorter bite formation times of females can be explained by their selection of smaller bite sizes.

At the within-habitat level, males increased foraging efficiency by allocating a greater proportion of foraging time to food ingestion (Figs. 1 and 4). This occurred because males, on a per-bout basis, had much longer average residence times within patches, while males and females had roughly equal travel times between patches. The sexes therefore do not appear to differ in search strategy but rather in that males remain in patches for longer periods than females. This occurred because males preferentially chose taller patches that contained potentially greater numbers of bites than the shorter patches preferred by females. Although residence times of both males and females increased similarly with patch height, males fed more often on the taller patches thus elevating foraging efficiency via patch selection as suggested by Eq. 2.

Males were more vigilant than females during the wet season. In the field it was not generally possible to distinguish between vigilance associated with predation risk and that associated with social behavior. Giraffe group sizes are larger during the wet season (T. Ginnett, unpublished data) and it is possible that the larger congregations of females during this period resulted in a greater degree of socially-related vigilance by males. Alternatively, it is possible that this result was due to a seasonal shift in prey preference by lions, which are the major predator of giraffes. More work on giraffe social and anti-predator behavior is necessary to address this question. We suggest that because of the higher within-patch intake rates achieved during this season, males could afford to allocate more time to predator avoidance and social activities.

We do not explicitly consider nutritional quality in this paper. However, rumination time may be an indirect indicator of diet quality. Previous studies of giraffe have found that males spend more time ruminating than do females (Leuthold and Leuthold 1978; Pellew 1984b), a difference that we failed to detect. In the Serengeti, the longer rumination times by males were coincident with higher fiber contents in the diets selected by males

(Pellew 1984b). Whether or not the lack of difference in rumination times of male and female giraffes in Mikumi represents a lack of difference in dietary quality between sexes is as yet unknown. Our lack of nighttime observations makes this difficult to interpret as rumination is an important component of nighttime activities (Pellew 1984b). Pellew (1984b) found, however, that sexual similarities and differences in activity budgets were reflected at night as well as during the day.

Recent work by Young and Isbell (1991) suggests the interesting possibility that foraging behavior of both male and female giraffes within groups may be influenced by the sexual composition of those groups. If the social environment does, in fact, influence ingestive behavior and therefore intake rate, activity budgets are likely to be affected as well. The activity budgets reported here were estimated from mixed-sex groups in which females always outnumbered males. In general, however, the sex composition of giraffe groups varies with habitat type (Innis 1958; Foster 1966; Leuthold 1979; Pellew 1984b; Pratt and Anderson 1982; Young and Isbell 1991). The extent to which habitat structure and social milieu affect activity budgets and foraging behavior is virtually undocumented in ungulates (but see Jarman and Jarman 1973) and seems an important subject for future investigations.

Our test of the body size hypothesis is necessarily qualitative in that it examines the direction of differences in male and female behaviors. Quantitative test are premature because current theory does not allow us to make predictions concerning the degree of any such differences, only that such differences should exist. In summary, the body size hypothesis coupled with a mechanistic conceptualization of the foraging process successfully predicts the direction of differences in male and female foraging behaviors at multiple spatial and temporal scales. Because most herbivores exhibit some degree of sexual body-size dimorphism, these types of behavioral differences may be a general phenomenon. Our view is that a mechanistic understanding of such intraspecific variation in behavior is critical to the development of new theory and may have relevance for management and conservation efforts as well. Most management efforts rarely take differences in male and female ecology into account and we feel judicious management programs should consider these aspects of a species ecology.

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