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Sex Differences in Giraffe Feeding Ecology:
Energetic and Social Constraints

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Abstract

Sex ratios of giraffe groups differ in different habitats, with open vegetation having female-biased groups, and tall, thick vegetation having male-biased groups. On a ranch in south-central Kenya, we quantified habitat differences of male and female giraffe groups and showed that the preference for open habitats by female groups was limited to groups with young. We suggest that this difference is due to the avoidance of predators of young giraffes. We also showed that rates of giraffe feeding peaked at intermediate feeding heights equal to approximately 60 % of adult giraffe height. In the dense habitats with a variety of tree heights used by male groups and female groups without young, both male and female giraffes fed most at heights where they could feed fastest. However, in the open habitats used by female groups with young, females fed mostly at heights below optimum because these habitats are dominated by short food plants. On the other hand, the dominant males accompanying these female groups fed at heights above optimum on rare tall trees, possibly to increase intrasexual vigilance. Apparently, both male and female giraffes sometimes forfeit feeding efficiency for short-term reproductive gains.

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Introduction

The giraffe (*Giraffa camelopardalis*) is an ideal animal for examining questions in feeding ecology. First, because its long neck allows it to reach foliage unavailable to most other herbivores (OWEN-SMITH 1985; DU TOIT 1990), interspecific competition for food is minimal. Second, unlike that of other ungulate species that feed close to the ground, the feeding behavior of giraffes is easy to observe. Although many studies have examined the foods eaten by giraffes (HARRISON 1936; INNIS 1958; WYATT 1969; HALL-MARTIN 1974; NGOG-NJE 1984; PELLEW 1984a; HANSON et al. 1985), studies of the feeding ecology of giraffes have only rarely examined giraffe feeding height quantitatively (WYATT 1969; DU TOIT 1990).

Studies of giraffe social behavior have revealed two patterns that may be related to their patterns of feeding. First, the sex ratio of giraffe groups varies with habitat. Males are more common in forest and in taller, thicker vegetation, and females are more common in open habitats (FOSTER 1966; FOSTER & DAGG 1972; PRATT & ANDERSON 1982; PELLEW 1984 b). Several explanations have been suggested for this sex difference in habitat use: 1) males may feed in habitats with taller trees because males are ~ 20 % taller (PELLEW 1984 b); 2) habitat differences may have evolved to reduce intersexual competition for food (PELLEW 1984 c); 3) males may exclude females from favorable habitats by virtue of their greater size; 4) females with young may prefer more open habitats because those habitats provide particularly nutritious foods (PELLEW 1984 b), and; 5) females with young may prefer to feed in open areas because they provide better views of potential predators of their young. However, these habitat differences have not been quantified nor adequately explained.

Second, giraffe mothers spend considerable time away from their offspring (INNIS 1958; DAGG & FOSTER 1976), and 'creches' or 'calving pools' are sometimes formed where young suckling giraffes aggregate in groups unaccompanied by adult females or with only a few adult females that do not include all of the mothers (LEUTHOLD 1979; LANGMAN 1977; PRATT & ANDERSON 1985). This is a rare behavior among mammals (T. CARO, pers. comm.).

Here we report the results of a study on the feeding ecology of giraffes in Kenya. We present data on habitat preferences and feeding heights of females and males and discuss how constraints act differentially on females and males to influence their choice of habitats.

Methods

Study Site and Subjects

This research was carried out from June through August 1987 at Wildlife Ranching and Research on the Athi Plains 40 km southeast of Nairobi, Kenya. At an elevation of 1800 m, the ranch is covered by a mixture of savanna grassland and acacia woodland in a semi-arid environment. Cattle and game animals (giraffes, Grant's gazelles, Thomson's gazelles, hartebeests, wildebeests, impalas) are managed on the ranch, and harvested for meat. No giraffes were shot during this study or in the previous six months. Only a few immature males (isolated from others) had been shot over the previous five years.

The main food plants of giraffes on the ranch are *Acacia xanthophloea*, *A. seyal*, *A. drepanolobium*, and *Balanites glabra*. *Acacia xanthophloea* and *A. seyal* ssp. *seyal* (Mimosaceae) are thorny savanna trees up to 20 m tall that comprise the woodlands at the lower (moister) end of soil catenas. These two acacia species were difficult to distinguish in the field (hybrids do occur), and are not distinguished here. *Acacia drepanolobium* occurs on impeded drainage ('black cotton') soils at the upper end of the soil catenas. Although it can grow to several m, giraffe browsing usually keeps individuals below 2 m tall. In addition to simple woody thorns it produces swollen thorns that house aggressive ants. *Balanites glabra* (Simaroubaceae) is an evergreen tree to 10 m tall with stout green thorns that occurs at low densities in *A. drepanolobium* savanna grassland.

During the study period, 8 adult males, 27 adult females, three juvenile and subadult males, three juvenile and subadult females, and 12 calves lived on the ranch, for a total of 53 giraffes. All giraffes were individually identified through photographic files that showed each individual's unique neck pattern. All were habituated to the presence of humans and vehicles, and could be easily approached. Giraffes typically live in temporary and fluid groups that vary in composition, ranging from single individuals to groups of over 20 (DAGG & FOSTER 1976; LEUTHOLD 1979).

Data Collection

The study was conducted in two parts. The first was detailed observations of giraffe feeding behavior and a general description of age/sex classes in associations. 39 15-min focal samples (after ALTMANN 1974) were conducted on 35 different giraffes as they fed. Sampling was concentrated on the morning and late afternoon periods when giraffes fed most actively. Sampling was stratified to ensure that different sexes, ages, and individuals were sampled. No individual was sampled more than twice. After a focal animal was selected, it was approached in a vehicle to 30—100 m and identified. All others associating with the focal animal were also identified. Focal animals were observed through binoculars to count individual bites.

The same four observers conducted each focal sample. During each focal sample, the following data were recorded: 1) the species of each food plant, 2) the height above the ground at which each feeding bout occurred, 3) the number of bites taken during each feeding bout, and 4) the time in s of each feeding bout. Feeding bouts were defined as beginning when the first bite was taken and ending when the giraffe pulled its head away from the plant. Feeding heights were estimated following WYATT (1969). Females and males were considered to be 1.0 m at the knee, 2.0—2.5 m at the point of the shoulder, and 4.5—5.5 m at the head, respectively. Estimates of feeding heights were determined by the same personnel for all focal samples and checked regularly with meter sticks in the field.

Feeding rate was defined as the number of bites per s. To exclude the effect of different handling times on species that differed in mean height, feeding rates relative to feeding height were calculated only on combined data for *Acacia seyal* and *A. xanthophloea*, for which there were sufficient observations at all feeding heights. Data from *Acacia drepanolobium* were limited to feeding heights near the ground, and sample sizes from *Balanites glabra* were too small to estimate feeding rates.

Groups of giraffes were classified as "predominantly male groups" if the number of adult males equalled or exceeded the number of adult females, and "predominantly female groups" if the number of adult females exceeded the number of adult males. In the second part of the study, when it became clear that female groups with and without young differed in their use of habitats, female groups were further distinguished by the age of the youngest giraffe in the group. Thus, groups of "females with juveniles" included immatures no younger than 6—10 months and groups of "females with calves" included immatures up to three months old. All female groups surveyed in the first part of the study were accompanied by calves or juveniles.

The second part of the study involved running transects of the habitats where giraffes were observed feeding to quantify habitat preferences among different giraffe groups. 13 transects were run. Groups were observed at a distance for 30—60 m while the individuals were identified. A 300-m transect was then run along the previously observed line of feeding giraffes. The accurate placement of the transect was continually confirmed with evidence of fresh giraffe feeding. Every 15 m, a point-center quadrat was established and the distance to the nearest tree over 0.75 m tall was measured and identified to species, and its height measured to the nearest 0.5 m. Every fifth transect, the distance to the nearest tree over 3.0 m was measured, the species identified, and height measured. In each transect, twenty points were surveyed for smaller trees, and five points surveyed for taller trees.

Throughout the study, data on male dominance behavior were collected. Male dominance hierarchies were determined on the basis of fighting and approach-retreat interactions between recognizable males, and the outcomes of these interactions were recorded whenever they were observed. The dominance hierarchy was linear, with higher-ranking males associating mainly with predominantly female groups.

Results

Habitat Preferences

Although individuals did not consistently stay in the same giraffe groups, certain types of groups were consistent in their preferences for particular habitats (Figs. 1, 2). Female groups with young (n = 7) were found in habitats with significantly shorter trees (t = 6.80, p < .001) and a significantly lower log density of tall trees (t = 3.95, p < .01) than habitats where female groups

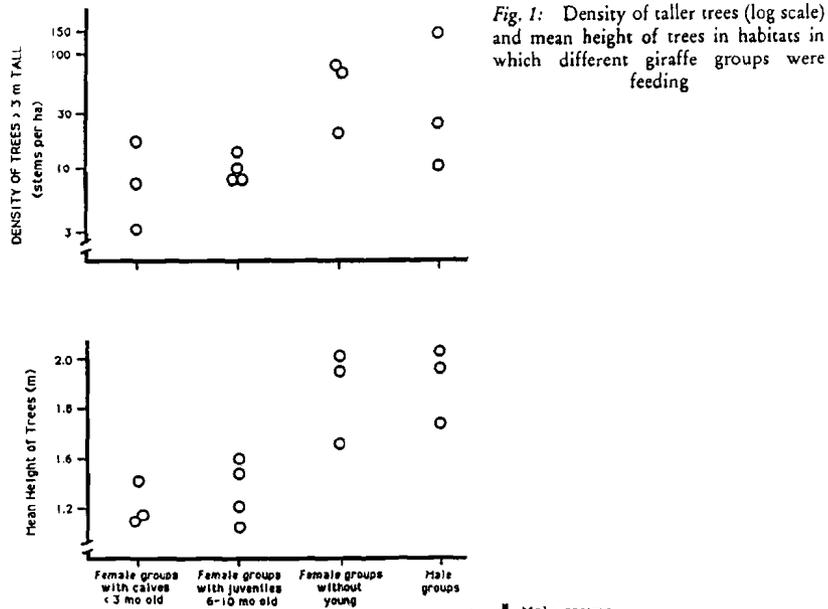Fig. 1: Density of taller trees (log scale) and mean height of trees in habitats in which different giraffe groups were feeding
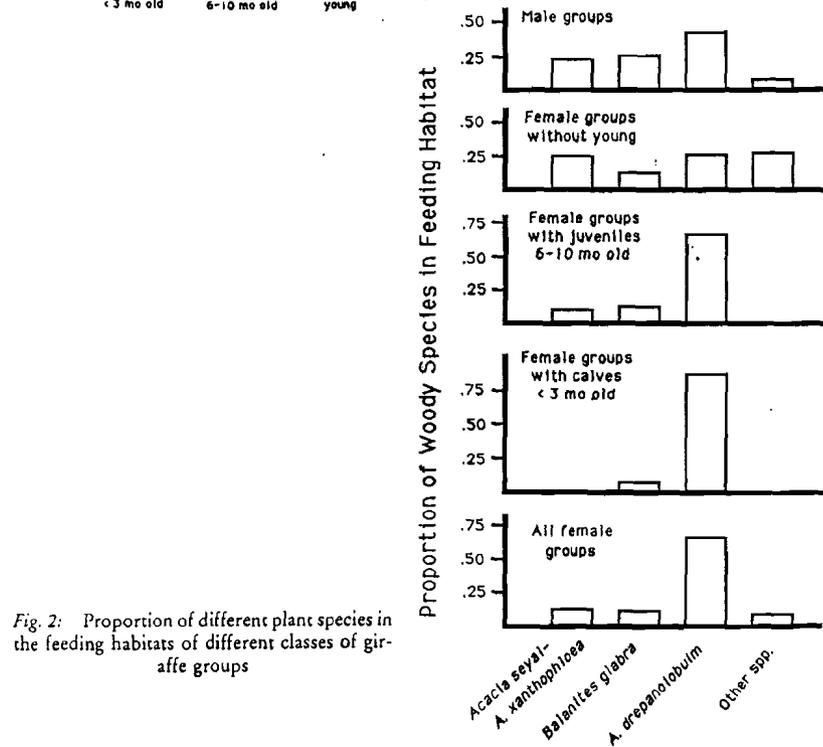
without young (n = 3) and predominantly male groups (n = 3) were found (Fig. 1). Female groups with young were found in habitats dominated by the short tree *Acacia drepanolobium*, whereas individuals that formed male and female groups without young were found in habitats with a more even mixture of tree species (Fig. 2).

Diets

Females in female groups (with young) fed significantly more on shorter *Acacia drepanolobium* (t = 4.86, p < .001) and significantly less on *A. xanthophloea* and *A. seyal* (t = 3.64, p < .01) than did females in predominantly male groups. Males also fed mostly on the taller *Acacia xanthophloea* and *A. seyal* (Fig. 3). Overall, adult males fed significantly more on *A. xanthophloea* and *A. seyal* (arcsine-transformed data, t = 3.23, p < .01) and significantly less on *A. drepanolobium* (t = 3.35, p < .01) than did adult females. Because females and males did not differ significantly in diet when they formed predominantly male groups, these intersexual differences in diet are related primarily to differences in habitat preferences of these groups rather than sex differences per se. However, despite the difference in habitat use of groups of females with young and predominantly male groups, the diet of adult males that joined female groups did not differ from that of adult males that formed predominantly male groups.
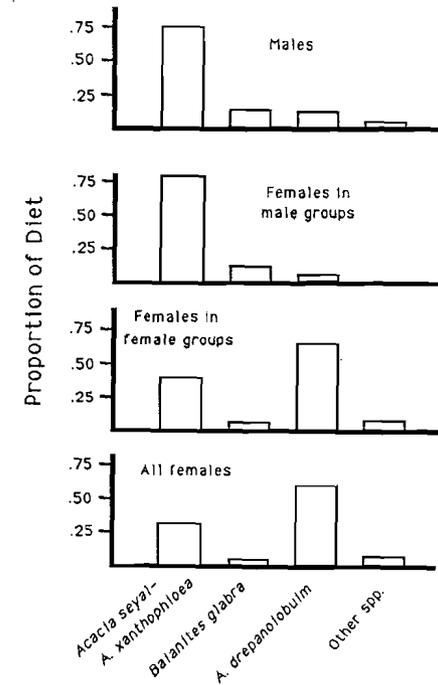

Fig. 2: Proportion of different plant species in the feeding habitats of different classes of giraffe groups

Fig. 3: Proportion of various plant species in the diets of different classes of giraffes, based on number of bites during focal samples

Sex and Habitat Differences in Feeding Rates

The rate at which giraffes fed varied with feeding height. For all giraffes, feeding rates were low near the ground and near the upper limit of giraffe feeding height. Feeding rates were greatest at the intermediate heights of 3.0 m for adult males and 2.5 m for adult females (Fig. 4). These peaks represent approximately 60 % of adult height for the two sexes. Giraffes that fed at extremely high and low heights appeared awkward to observers. Possibly, the movement of the giraffe's head, which facilitates the stripping of young branches, is most free at intermediate heights.

In predominantly male groups, both adult males and adult females exhibited patterns of feeding at different heights that paralleled patterns of feeding rates, with most feeding occurring at heights where giraffes could feed most quickly (Figs. 5a, 6a). This is in accordance with optimal foraging theory (Pyke et al. 1977). However, females in female groups with young fed significantly lower than females in predominantly male groups (1.65 ± 0.09 m vs. 2.56 ± 0.44 m, t = 2.03, p < .05; Fig. 5b). This is likely to reflect their differential use of habitats. On the other hand, males in predominantly female groups fed significantly higher than males in male groups (4.63 ± 0.49 m vs. 3.37 ± 0.36 m, t = 2.10, p < .05; Fig. 6b) despite the relative scarcity of taller trees in the open habitat used by female groups.
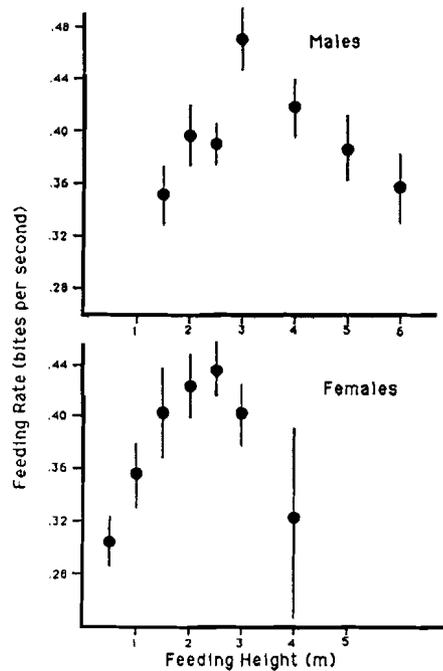

Fig. 4: Feeding rates (no. bites/s) at different feeding heights for adult male and female giraffes on *Acacia seyal* and *A. xanthophloea.* Bars: ± SE

Fig. 5: Proportion of feeding at different heights across all food plant species for female giraffes in a: predominantly male groups and b: predominately female groups. Open circles: values of feeding rate (from Fig. 4)
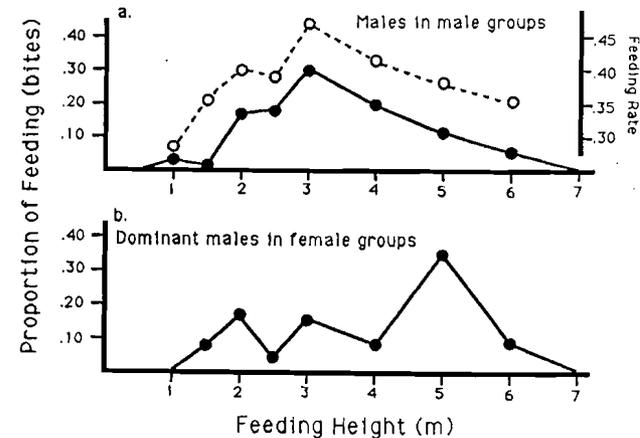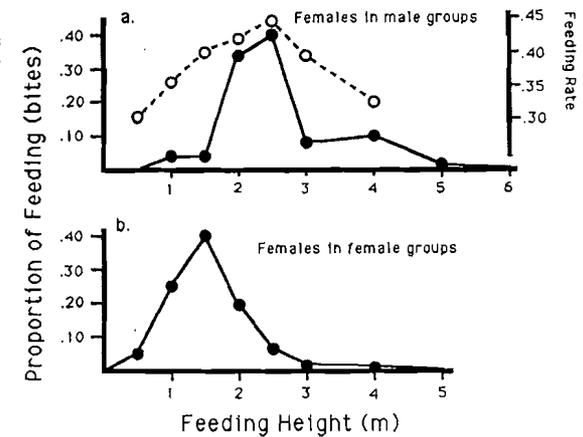

Fig. 6: Proportion of feeding at different heights across all food plant species for male giraffes in a: predominately male groups, b: predominately female groups. Open circles: values of feeding rate (from Fig. 4)

Discussion

Several explanations have been given for observed sex differences in habitat preferences among giraffes. First, males may feed in habitats with taller trees because males are taller (Pellew 1984b). This seems unlikely, however, because the average height of trees in the *Acacia drepanolobium* savanna is well below the optimal feeding height of females. Second, habitat differences may have evolved to reduce intersexual competition for food (Pellew 1984c). While the habitat

differences shown here do result in significant differences in diet, and therefore in niche separation, it would be difficult to test whether this niche separation was the result of selection to reduce intersexual competition (SHANK 1982). Third, males may exclude females from favorable habitats by virtue of their greater size. Strong dominance hierarchies exist among males based primarily on size, and males are larger than females. However, it seems unlikely that males exclude females from preferred habitats because several females were found in virtually every male group and males were never seen to interact agonistically with females. The results presented here suggest instead that sex-biased use of different habitats may be largely the result of constraints on females with young.

Habitat Preferences of Females with and without Young

The results above show that females without young used denser habitats whereas females with young used more open habitats with shorter trees. However, this preference of females with young for more open habitats appears to have a cost. In such habitats, females fed most often at heights that are lower than that at which feeding rate is greatest. In contrast, females in denser habitats have available a greater variety of food-plant species which vary in height. In such woodland habitats, females did feed at the heights of peak feeding rate.

Two possible benefits might outweigh the cost females with young incur in reduced feeding rate. First, females with young may prefer more open habitats because those habitats provide particularly nutritious foods (PELLEW 1984b). Among female mammals in general, nutritional needs increase through pregnancy and lactation (MILLAR 1977). However, this explanation seems unlikely because although the preference for open habitats was limited to females with young, females whose offspring were in those groups were often not present. LEUTHOLD (1979) has described the formation of creches, or nursery groups, of juveniles up to 6—8 months old, whose mothers leave them to enter denser, taller vegetation. It is likely that in this study mothers also left their young in order to feed in the woodlands. This unusual behavior of mothers regularly leaving their young to feed may be a response in part to the higher energetic cost of feeding in open habitats. That the single pregnant female near term during this study fed almost exclusively in the woodlands also suggests that the woodlands, with their greater diversity of food-plant species, are not lower in nutritional quality than the more open habitats.

The alternative explanation is that females with young may feed in open areas because they provide better views of potential predators of their young. Juvenile mortality rates in giraffes are high; only 30—50 % of giraffes survive their first year (FOSTER & DAGG 1972; LEUTHOLD & LEUTHOLD 1972, 1978; PELLEW 1983). We suggest that the females' choice of shorter, more open vegetation is a response to the high risk of predation for their offspring. The tendency of mothers to leave their offspring to feed elsewhere might be considered an argument against this. On the other hand, although mothers regularly left

their young to feed elsewhere, they never left their calves alone. Theoretical and empirical evidence suggests that animals are less vulnerable to predators when they are with others than when they are alone (POWELL 1974; KENWARD 1978; PULLIAM & CARACO 1984). It is also possible that young giraffes are able to detect and elude predators at an early age, and so are not put at much greater risk by their mothers' absence. The formation of creches may therefore be a solution to the conflicts produced by the high risk of predation for younger giraffes and the nutritional needs of mothers.

Differences in Feeding Rates among Males

Males were most often found in woodland habitats. In these habitats males fed at optimal heights. However, some males were found with female groups in more open habitats and fed at greater heights than the optimum. This is particularly striking given that the mean height of trees in these habitats was low, and taller trees occurred at a much lower density than in woodland habitats. Du TOIT (1990) has also documented the greater tendency for males to hold their heads higher (at steeper neck angles) than female giraffes and suggested that this is the result of competition for rich food resources. However, our data indicate that this extreme feeding height occurs only among high-ranking males accompanying female groups; males and females in predominantly male groups in woodlands fed at similar heights for their body sizes.

Two explanations are possible for the greater feeding height of high-ranking males. First, a high-ranking male may be more vigilant against predators than subordinate males if his offspring can benefit from such vigilance. However, because giraffe groups are fluid and change regularly in composition, the likelihood that a given male will be related to the young in any particular group is low. It is unlikely that protection of unrelated immatures is worth the cost in feeding efficiency.

We suggest an alternative explanation that is based on male-male competition for mates. Between feeding bouts, giraffes do not lower their heads. By feeding at greater heights, high-ranking males may both increase their vigilance for competing males and advertise their presence or status to such males. This may function to discourage competitors from approaching to mate with receptive females.

In summary, sex differences in feeding behavior of giraffes appear to be related to selective pressures operating separately on males and females to increase their reproductive success. Females without young appear to feed in more optimal habitats than females with young. Although females with young appear to suffer a cost in feeding efficiency by feeding in more open habitats, they may increase their offspring's chance of avoiding predators by using such habitats. This cost may be minimized further by the formation of creches where mothers leave their offspring to feed in denser habitats. Males, on the other hand, appear to feed optimally unless they are high-ranking males. Such high-ranking males probably incur a feeding cost by being with females in open habitats. However, they may offset this feeding cost by the reproductive advantage of maintaining exclusive access to receptive females and mating with them.

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