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Foraging in a 3-D world: The Influence of Body Size and Sex on Vertical and horizontal foraging Behaviour of Yellow Baboons

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ABSTRACT

Foraging is among complex animal behaviours, which involve making decisions on what and where to forage, so as to maximize nutritional gain and reduce predation risk. In ungulates, it is known to also be influenced by sexual size dimorphism, however, this is not clear in sexually size dimorphic yellow baboon. Using focal animal sampling techniques, we collected data from habituated troops of yellow baboons to test whether body size and/or sex has influence on their use of vertical and horizontal strata when foraging. Results showed that, yellow baboons foraged more frequently on the ground up to 1 m than beyond this height. However, adult females foraged on the ground significantly more frequently than adult and subadult males. While, adult and subadult males used higher canopy beyond 2 m, more frequently than adult females. Moreover, adult females and subadult males foraged more frequently at the troop centre than adult males. This study concludes that sex and to some extent body size significantly influence foraging decisions of yellow baboon in the use of vertical and horizontal strata. Detailed understanding of spacing behaviour of baboons is recommended as it is important towards better understanding of their complex social life.

Keywords: terrestrial behaviour - feeding behaviour - yellow baboons - feeding concentric theory - 3-D foraging.

INTRODUCTION

Foraging behaviour of animals in a landscape is mostly determined by some factors including food availability, habitat types, and predation risk (Druce *et al*. Emer 2009, Willems and Hill 2009). According to optimal foraging theory (McNamara *et al*. 2005) when foraging, animals not only maximize their nutritional gain, but also reduce the risk of being predated by making decision on where to forage. For most animals, predation risk may have greater impact on foraging decisions than other factors (Eccard and Liesenjohann 2008, Makin *et al*. 2012). Because in a uniform landscape, predation risk in relatively equally distributed in all food patches, thus animals will generally avoid areas of high predator density. This suggests that animals do not utilize uniform landscape equally (Abu Baker and Brown 2010).

In sexually size dimorphic ungulates in addition to predation risk, foraging decision is similarly influenced by animal's differences in nutritional and energy demand in relation to body size (Smith *et al*. 2004,

Heymann 2011). Hence for them foraging decision in a landscape becomes a matter of trade-off between food quality, quantity and safety (Ruckstuhl and Neuhaus 2002, Hay *et al*. 2008). In respect to forage selection hypothesis (Ruckstuhl and Neuhaus 2000, Post *et al*, 2001, Ruckstuhl 2007), large bodied animals have lower passage rate, hence more efficient in digestion of even lower quality forage, so they will trade-off food quality for quantity. While small bodied animals have higher passage rate, hence less efficient in digestion of low-quality forage, so to them the quality of forage is important than its quantity.

Most non-human primates, including yellow baboons (*Papio cynocephalus*), vervet monkeys (*Chlorocebus aethiops*), macaques (rhesus-*Macaca mulatta* and Barbary-*Macaca sylvanus*) and some guenons (*Cercopithecus*) have complex foraging behaviour whereby during the day, they forage on both ground (including below ground-ditches/Korongos) and above ground, but sleep above the ground in the night (Emerson *et al*. 2011). Because of this, they are said to be foraging across a 3-dimensional landscape (3-D foraging). Arboreal foraging behaviour in primates is believed to highly being influenced by avoidance of ground predators (Smith et al. 2004) while the need for quality diet encourages ground feeding behaviour (Xiang *et al*. 2009).

There is considerable body of knowledge on the influence of sexual body size dimorphism on foraging decision of ungulates, particularly on where to forage (predation risk hypothesis) and what to forage (forage selection hypothesis) (Ruckstuhl and Neuhaus 2000, Post *et al*. 2001, Ruckstuhl 2007, Hay *et al*. 2008). Few studies have documented the impact of body size and sex differences on terrestrial behaviour of primates especially horizontal and vertical foraging behaviour (3-D foraging), yet presenting contradictory findings on the subject. For instance, study on terrestrial behaviour of black- and white snob nosed monkeys (*Rhinopithecus bieti*) by Kirkpatrick and others (1998), indicated that adult females and juveniles used the ground more than adult males. However, another study by Xiang and others (2009), on the same species indicated that adult males and juveniles used the ground more than adult female.

Similarly, a study by Smith and others (2004) indicated that because of their role in community, large bodied male primates are more arboreal than females; while Houle and others (2014) indicated that the reproductive investment of female may influence them to use higher canopy trees than males. Knowledge of spacing behaviour between individuals especially related to foraging behaviour is important in understanding group cohesion in animals as it is directly relating to costs and benefits of group living.

Yellow baboons are social animals with differing sexual body sizes, but coexist at local scale without displaying vivid intraspecific food competition, and spend considerable amount of time both on ground and above ground. This is uncommon to most social animals with differing body sizes, because of their different nutritional requirements (Cowlishaw 1999, Grassi 2000). In that regard, yellow baboons make a good candidate for studying the influence of age/sex class and body size on the use of terrestrial habitat for foraging decision. Therefore, we put forward three hypotheses related to the vertical and horizontal foraging behaviour of yellow baboons. Firstly, we hypothesized that, because of their protective role, adult males foraged at the canopy, behind and in front of the troop more frequently for easy detection of predators. Secondly, because of safety and higher nutritional demands, small bodied adult female and subadult males foraged at the canopy and center of the troop more frequently for easy access to high quality food and avoidance of ground predators. Thirdly, because of large body size hence large body mass, adult males foraged at the

ground more frequently for easy access of abundant and diverse food.

MATERIALS AND METHODS

Study site and study animals

We conducted this study within the home range of habituated troops of yellow baboons, known as the Viramba troops between the central floodplain and the easterly hills in Mikumi National Park (MINAPA) across two ecological years (i.e., four wet and dry seasons) in different vegetation types covering an area of about 135 km^2 (Fig. 1). The area roughly extends from the Mgoda River to the park main gate in north-south direction, and 2 km east of the power line to Mkata River in the East-West direction. The area is mostly composed of grassland, wooded grassland and woodland mainly dominated by *Brachystegia Combretum*. The combination of this vegetation and riverine forests, creates an important feeding and foraging zone for yellow baboons (Norton *et al*. 1987, Rhine *et al*. 1989).

This research work complied with ethical protocol for conducting research on wild animals approved by Tanzania Wildlife Research Institute, and adhered to the legal requirements for conducting research in National parks, as provided by Tanzania National Parks Authorities (TANAPA).

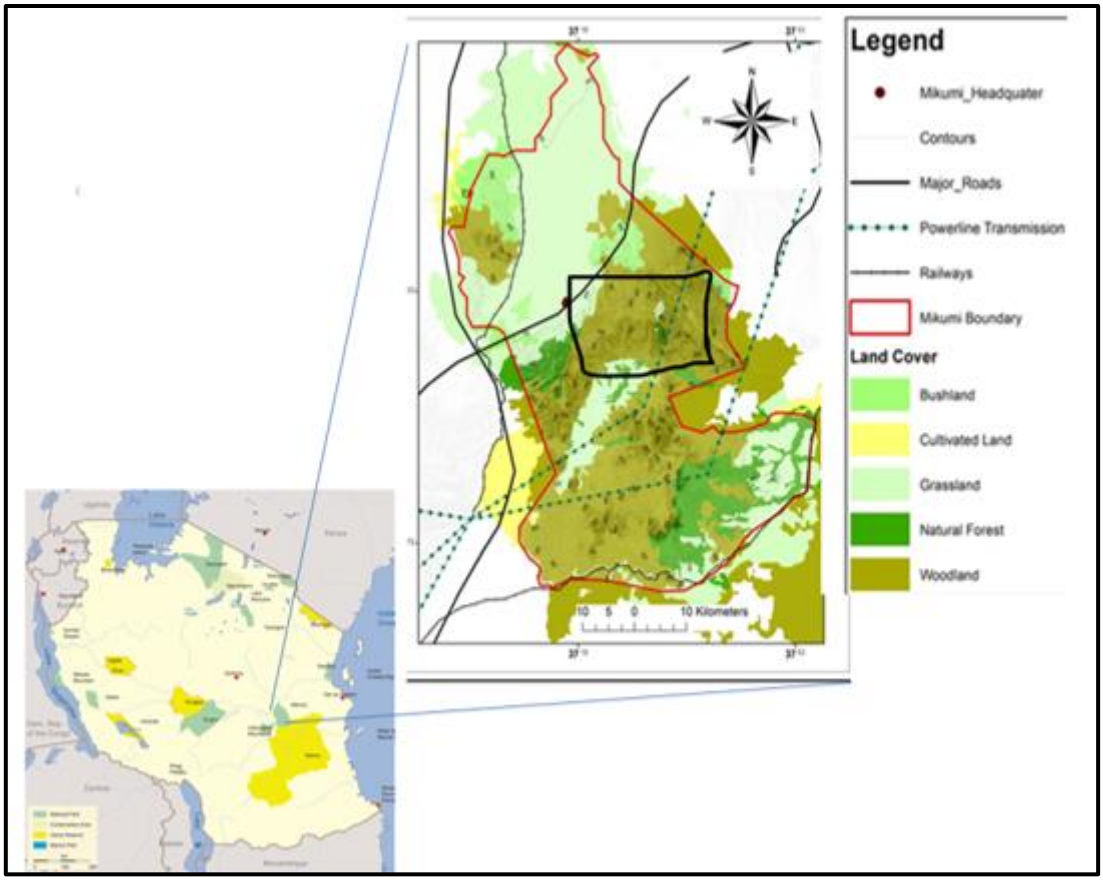

Figure 1. Map of study area, Mikumi National Park indicating the location of the study site, the Viramba troop range (black rectangle).

Data reported in this study were collected as part of the long-term study on feeding behaviour of yellow baboons. The data were collected from a total of 79 habituated individuals in two troops, which were originally a single troop (Viramba troop). There were 37 individuals in the first troop, consisting of 9 adult females, 4 adult males, 6 sub adult males and 18 juveniles and infants; and 42 individuals in the second troop composing 17 adult females, 7 adult males, 5 subadult males and 13 juveniles and

infants. Because the study was interested in the influence of body size and age/sex classes, data were collected from adult males and females and sub adult males only. Sub adult males were selected because, they have relatively similar body size as adult female, so their selection was to control for the influence of body size over sex. Females were defined as adults after first menstruation cycle whereas males were defined as adults after transfer to another troop and/or start consorting. When males reached five (5) years of age were defined as subadult.

Data collection

Focal animal sampling technique was used for data collection from study subjects. A day was divided into four periods of 150 mins each. In each period, a single subject was followed for 16 mins, divided into eight bouts of 2 mins intervals each. Focal animals were randomly selected by picking up a single name from a container. The chosen name was listed for focal animal follow in one of the 4 periods of the day. A maximum of 6 subjects were followed in each given period of a day. Animal follows were conducted daily from about 07:00 h when troops descend from sleeping site to 17:00 h when they retire to sleeping site. A single troop was followed for 4 continuous days in a week, and then observations were switched to the other troop. Activity of focal animal at any given height (vertical or horizontal) was recorded using one-zero technique after every 2 mins intervals. Vertical strata were categorised as: Korongo (ditch), ground, lower canopy (intermediate) and upper canopy (canopy) while horizontal strata were categorised as; centre, periphery, behind and in front (Table 1). Age and sex classes of focal subject, date (in Julian calendar), seasonal quarter, time of day, location (GPS), habitat type and weather condition were recorded prior to focal animal follows.

Table 1 Definitions of vertical and horizontal strata occupied by focal individuals in relation to the feeding and foraging behaviour

CATEGORY	DESCRIPTION
Vertical strata	
Below ground /Korongo	A height below ground level, in a watercourse or natural ditch/trench (Korongo in Swahili)
Up to 1m (Ground)	A vertical height up to 1 m from ground level
Up to 2m (Intermediate)	A vertical height up to 2 m from ground level
Beyond 2m (Canopy)	A vertical height above 2 m from ground level
Horizontal strata	
Centre	This is Centre of Mass as defined by Altmann (1979) and Montanari et al (2021). The point where most members of the troop are found.
Periphery	Individual's position with no neighbours within 5 m and other troop members do not occur on all sides of that position. To leave the periphery, an individual can only move in limited directions to move towards other troop members.
Behind	Defined when troop direction can be assigned (due to troop moving or directional orientation) as a position away from troop centre opposite to troop direction. An individual has no neighbours within 5 m but is visible to other troop members.
In front	Defined when troop direction can be assigned (due to troop moving or directional orientation) as a position away from troop centre in same direction as troop direction. An individual has no neighbours within 5 m but is visible to other troop members.

Data analysis

Focal animal follow was used as the basic unit of analyses; therefore, baboon feeding/ foraging at different strata were analysed as total number of follows baboons were recorded feeding and/or foraging at a particular stratum at least in one interval (feeding follows). Data were treated at two different levels. The first level was on the use of the strata at least once for feeding/ foraging (number of feeding follows per stratum). The second level was on the

proportion of use of the strata by different age/sex classes in a feeding follow (number of intervals within feeding follows). In both cases, Generalized Estimating Equation (GEE) was performed for the significance impact of age/sex classes in their utilization. Foraging stratum was used as response variable, age-sex class was treated as a fixed categorical explanatory variable, whereas Subject ID was treated as random explanatory variable. For the first level of data treatment (i.e., whether the stratum was used or not during feeding and/or foraging), the response variable was assumed to be a binomial distribution with trial size of 1. For the second level of treatment (proportion of strata use), response variable was assumed to be a binomial distribution with trial size of 8. In both cases, binary logistic model was used as a logit link function.

Time spent feeding/foraging at different stratum by study subjects was deduced from the number of intervals per feeding follow. Proportion of feeding intervals in a single feeding follow (i.e., number of intervals the subject was feeding out of eight intervals, multiplied by 100) were summed up for the entire study period. Its average for each stratum per study subject were calculated and presented as time spent feeding in a respective stratum by study subjects. "Test of Model Effects" from GEE analyses were used to assess overall significance of body size and/sex on foraging behaviour. When overall significance was found, "Parameter Estimates" from GEE analyses were used to assess where the differences occur. Error bars represent the standard error of the mean, unless explained otherwise.

RESULTS

A total of 3838 animal follows were conducted in 270 observational days, over which adult males were followed in a total of 756 follows, adult females in 2307 follows and sub adult males in a total of 775 follows. Of the 3838 follows, baboons were recorded as feeding at least once in a total of 3074 follows, which is over 80% of all follows. Generally, yellow baboons were recorded feeding and/or foraging more on the ground up to 1m above, and less in the Korongo (ditch) (Table 2). However, despite of less overall feeding records in the Korongo, proportion of baboons' feeding at this stratum was higher compared with when they were on the canopy beyond 2 m above (feeding proportion at specific strata - Table 2). On horizontal strata, generally baboons were feeding and/or foraging more at the centre of the troop, and less behind the troop (Table 2). However, proportions of baboons feeding when they were in front and behind the troop were higher than when they were at the centre of the troop (feeding proportion at specific stratum-Table 2).

Table 2. Yellow baboons' use of different vertical and horizontal positions for feeding

Follows	**Vertical strata**				**Horizontal strata**			
	Korongo	Up to 1m above ground (ground)	Up to 2m above ground (lower canopy)	Beyond 2 m above (canopy)	entre	eriphery	Front	Behind
Number of all animal follows	175	3022	436	1211	1430	492	305	268
Number of feeding follows	146	2680	363	810	1101	383	284	246
Overall feeding proportion **%** (stratum feeding follows /overall feeding follows (N)	4.7	87.2	11.8	26.4	52.3	18.2	13.5	11.7
Feeding proportion at specific stratum**%**	83.4	88.7	83.3	66.9	77	77.8	93.1	91.8

Note: N for vertical strata = 3074; N for horizontal strata=2107. N for horizontal strata were few because horizontal positions could only be assessed in relation to directionality, and were recorded at the start and end of any particular follow.

Feeding occurrence in the vertical strata

Generally, number of feeding records varied between age-sex classes, adult females had higher records of feeding follows (1862), while adult males had lower records of feeding follows (557) (Table 3). Proportion of feeding/foraging at different strata show that, adult females had slightly higher feeding proportion at the height up to 1 m (ground level), while adult males and subadult males had relatively similar feeding proportion at this stratum (Table 3). Subadult males fed/foraged less often in the Korongo, but most frequently at the height beyond 2 m above the ground (canopy). Adult males fed/foraged less at the height up to 2 m above the ground (lower canopy), while adult females and subadult males had relatively similar feeding and foraging proportions at this stratum (Table 3).

Table 3 Number of yellow baboons' feeding follows by vertical strata and age-sex categories (in the brackets are the proportion/percentage of feeding at specific vertical height)

Age-sex class	Feeding follows	Height Categories			
		Korongo	Up to 1m	Up to 2m	Beyond 2m
Adult Males	557	29 (5.2%)	473 (84.9%)	52 (9.3%)	144 (25.9%)
Adult Females	1862	94 (5.0%)	1666 (89.5%)	228 (12.2%)	431 (23.1%)
Subadult Males	655	23 (3.5%)	541 (82.6%)	83 (12.7%)	235 (35.9%)
Total	3074	146	2980	363	810

Additional analysis (Table 4) indicated that, age-sex class had significant contribution in the variation of vertical feeding and foraging behaviour of study subjects on the ground up to 1 m above (Wald X^2_1 = 16.851, DF=2, N= 3074, P = 0.000), and at the height beyond 2 m (Wald X^2_1 = 24.749, DF=2, N= 3074, P = 0.000), but not in other vertical strata (Table 4, test of model effects). For the feeding on the ground up to 1 m above, the significant difference was between adult males and adult females (P-value = 0.002), where adult males fed and foraged at this height less frequently than adult females (B-coefficient = -0.046). Similarly, significant difference existed between subadult males and adult females (P-value =0.001), where subadult males fed and foraged at this height less frequently (B-coefficient = -0.069). However, adult males and subadult males did not differ significantly in foraging at ground up to 1m above (P-value =0.296), although subadult males fed and foraged at this height less frequently than adult males (B-coefficient = -0.023) (Table 4). At height beyond 2 m, the significant difference was between subadult males and adult females (P-value= 0.000), where subadult males feed and foraged more at this height than adult females (B-coefficient = 0.127). The significance difference at this stratum was also between subadult males and adult males (P-value= 0.001), where subadult males feed and forage more at this height than adult females (B-coefficient = 0.100) (Table 4). While overall there was no variation between study subjects in feeding and foraging on the ground up to 2 m, adult females and subadult males fed more at this height compared with adult males (B-coefficient values) (Table 4).

Table 4 Result of Generalized Estimating Equation (GEE): analysis on variation in use of height levels by number of yellow baboons' feeding follows and age-sex classes.

Response variable	Test of Model Effects				Parameter Estimates					
					B-coefficient			P-value		
	Wald Chi-Square	DF	N	P-value	AM vs AF	SAM vs AF	SAM vs AM	AM vs AF	SAM vs AF	SAM vs AM
Korongo	1.847	2	3074	0.397	0.002	-0.015	-0.017	0.880	0.215	0.211
Up to 1m	16.851	2	3074	**0.000**	-0.046	-0.069	-0.023	**0.002**	**0.001**	0.296
Up to 2m	5.062	2	3074	0.080	-0.029	0.004	0.033	**0.045**	0.792	0.058
Beyond 2m	24.749	2	3074	**0.000**	0.027	0.127	0.100	0.324	**0.000**	**0.001**

AM= Adult Males; **AF**=Adult Females and **SAM**- Subadult Males.

Time spent at vertical strata

Time spent feeding by study subjects at different vertical stratum reflect the pattern of feeding occurrence at these strata observed in Table 3 above. Generally, all three age classes spent more time feeding and foraging on the ground up to 1 m above than in other strata. However, on average adult females spent relatively more time,78% of intervals (equivalent to about 13 mins out of 16 mins of a single animal follow) feeding at this stratum than adult and sub adult males (Fig. 2). All age-sex classes spent little time feeding in Korongos, an average of about 2% of intervals in a single feeding follow, equivalent to less than one minute (0.32 minutes) (Fig. 2). While subadult males, spent little time foraging and feeding in Korongos, they spent relatively more time feeding and foraging beyond 2 m, an average of 22% of intervals in a single feeding follow, equivalent to 3.5 mins out of 16 mins of a single follow feeding at this stratum compared with about 2.8 mins spent by adult males and females (Fig. 2).

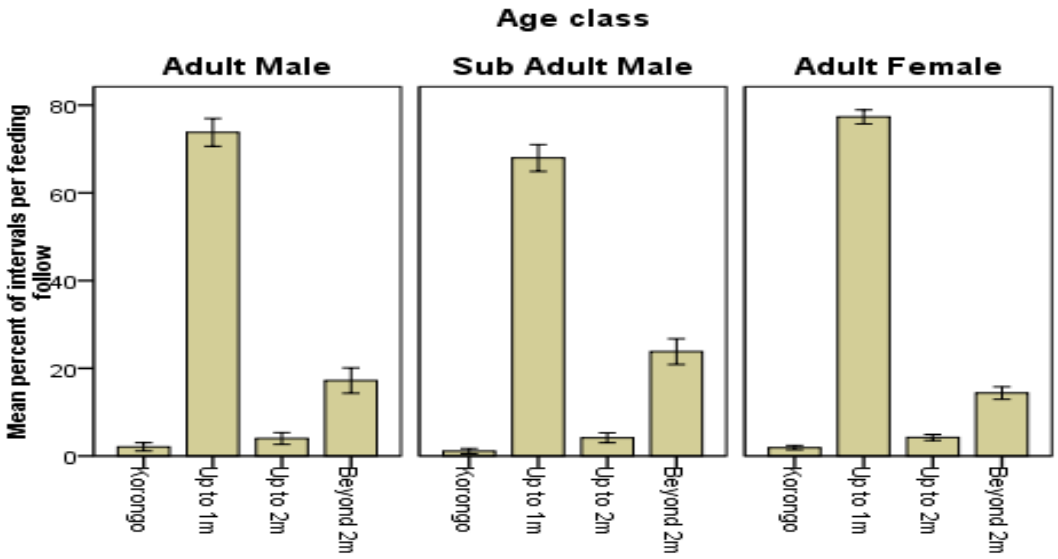

Figure 2 Use of height category: Mean percent of intervals per feeding follow by age-sex classes: Adult Males [N=557], Adult Females [N= 1862] and Sub Adult Males [N= 655]; Error bar= standard error of mean.

Analysis also showed that, overall age-sex classes had significantly affected variance in time spent by yellow baboons feeding on the ground (Wald X^2_1 = 16.7321, DF=2, N= 3074, P = 0.000), and at the canopy (beyond 2 m) (Wald X^2_1 = 19.9741, DF=2, N= 3074, P = 0.000), (Table 5, test of model effects). The significant difference in time spent feeding on the ground up to 1 m, was between subadult males and adult females (P-value= 0.000), where subadult males spent little time feeding at this height than adult females (B-coefficient= -0.462). Similarly, the significant difference was also between subadult males and adult males (P-value= 0. 015), where subadult males spent little time feeding at this height than adult males (B-coefficient= -0.277). Time spent feeding beyond 2 m was significantly different between subadult males and both adult females and males (P- values), and in both cases, subadult males spent more time feeding and foraging at this height than both adult males and females (B-coefficients) (Table 5).

Table 5: Results of Generalized Estimating Equation (GEE): analysis for number of intervals per yellow baboons' feeding follow at different height levels by age-sex classes.

Response variable	Test of Model Effects				Parameter Estimates					
					B-coefficient			P-value		
	Wald Chi-Square	DF	N	P-value	AM vs AF	SAM vs AF	SAM vs AM	AM vs AF	SAM vs AF	SAM vs AM
Korongo	2.055	2	3074	0.358	0.089	-0.538	-0.627	0.668	0.214	0.152
Up to 1m	16.731	2	3074	**0.000**	-0.185	-0.462	-0.277	0.078	**0.000**	**0.015**
Up to 2m	0.494	2	3074	0.781	-0.117	0.009	0.126	0.502	0.970	0.617
Beyond 2m	19.974	2	3074	**0.000**	-0.220	0.595	0.375	0.068	**0.000**	**0.006**

AM= Adult Males; **AF**=Adult Females and **SAM**- Subadult Males.

Feeding occurrence on horizontal position/strata

Horizontal position was defined by position of focal study subject relative to the centre of the troop. The centre of the troop was measured by position occupied by majority of troop members (Table 1). Horizontal position was recorded at the start and end of each follow and could not always be estimated especially when troop was not moving or showing directional orientation. Thus, there are fewer feeding follows with recorded positions and data on feeding intervals on positions on the horizontal plane.

Proportionally, subadult males and adult females fed at the centre of the troop more frequently than adult males; whereas adult males fed behind the troop relatively more frequently than adult females and subadult males (Table 6). Feeding and foraging at the periphery of the troop, was proportionally similar between adult males and adult females, whereas adult and subadult males fed at similar proportion in front of the troop (Table 6).

Table 6 Number of yellow baboons' feeding follows by horizontal position and age-sex categories (with proportion of position specific feeding follows in brackets).

Age-sex class	Feeding follows	Horizontal position categories			
		Centre	Periphery	Behind	In front
Adult Males	378	178 (47.1%)	68 (18.0%)	75 (19.8%)	30 (7.9%)
Adult Females	1278	667 (52.2%)	245 (19.2%)	138 (10.8%)	176 (13.8%)
Sub Adult Males	451	256 (54.4%)	70 (14.9%)	71 (15.1%)	41 (8.7%)
Total	2107	1101	383	284	247

Additional analysis indicated that, age-sex classes have significant contribution in the variation of feeding occurrence in horizontal positions between the study subjects. The significant differences in the feeding were observed at the centre of the troop (Wald X^2_1 = 7.032, DF=2, N= 2107, P = 0.030); behind the troop (Wald X^2_1 = 18.128, DF=2, N= 2107, P = 0.000) and in front of the troop (Wald X^2_1 = 14.740, DF=2, N= 2107, P = 0.001) (Table 7, test of model effects). At the centre of the troop, significant difference in feeding was between subadult males and adult males (P-value = 0.008), where subadult males fed more frequently at this position than adult males (B-coefficient =0.097). The significance difference in feeding behind the troop was between adult females and males, both adults and subadults (P-values= 0.000 and 0.008 respectively), at this position both adult males and subadult males feed more frequent as compared to adult females (B-coefficients, Table 7, parameter estimates). Similarly, significant difference in feeding in front of the troop was between adult females and both adults and subadults males (P-values= 0.001 and 0.028 respectively), at this position both adult males and subadult males feed less frequent as compared to adult females (B-coefficients, Table 7, parameter estimates).

Table 7 Result of Generalized Estimating Equation GEE analysis: variation in number of yellow baboons' feeding follows at different horizontal positions by age-sex classes.

Response variable	Test of Model Effects				Parameter Estimates					
					B-coefficient			P-value		
	Wald Chi-Square	DF	N	P-value	AM vs AF	SAM vs AF	SAM vs AM	AM vs AF	SAM vs AF	SAM vs AM
Centre	7.032	2	2107	**0.030**	-0.051	0.046	0.097	0.143	0.189	**0.008**
Periphery	3.080	2	2107	0.214	-0.011	-0.036	-0.025	0.585	0.081	0.261
Behind	18.128	2	2107	**0.000**	-0.058	-0.047	0.012	**0.000**	**0.008**	0.450
In front	14.740	2	2107	**0.001**	0.090	0.049	-0.041	**0.001**	**0.028**	0.211

AM= Adult Males; **AF**=Adult Females and **SAM**- Subadult Males.

DISCUSSION

The focus of this paper was to assess whether body size (age class) or sex (gender) have influence on the use of vertical height and horizontal plane by yellow baboons on feeding and foraging behaviour. We expected differences in spatial position that would support the three hypotheses put forward indicating the influence of body size and/or sex. Similarity between adult females and subadult males in the use of both vertical and horizontal plane would indicate the influence of body size, while similarity between adult males and subadult males would indicate the influence of sex/gender.

Generally, baboons fed and foraged most frequently from the ground up to 1m high. This could be due to the fact that baboons are predominantly terrestrial primate that move and feed frequently on the ground (Stacey1986, Barton, 1993), which is not unique behaviour to baboons among primates. The behaviour has also been reported in white-faced capuchins (Gould *et al*. 1997), Sichuan snub-nosed monkeys (Li 2007) and spider monkeys (Youlatos 2002, Campbell *et al*. 2005). This behaviour is associated with different factors including predation risk (Campbell *et al*. 2005), resources distribution (Cowlishaw 1999, Youlatos 2002), and morphological difference (Dunbar and Badam 2000).

The higher frequency of feeding and foraging on ground up to 1 m by baboons observed in this study is associated with resource distribution in their home range. Habitat structure (vegetation cover) in the home range of study troops is largely dominated by grassland and wooded grassland comprised more with grasses, shrubs and forbs. Shrubs, grasses and herbs, which usually grow less than 1 meter above ground provided baboons with more abundant and protein rich food like leaves and seeds from herbs and forbs. Leaves of herbs and forbs are preferred because they contain higher proportion of protein than leaves of most tree species (Li 2007). Moreover, feeding on the ground enables baboons to use larger patches, and to space out when seeking new food patches hence reduce intra-group specific competition, compared to feeding within trees where individuals will be crowded into a limited canopy space and a limited number of branches increase competition (Cowlishaw 1999).

The frequent use (large number of follows) of tree canopy (height beyond 2 m) by baboons observed in this study is largely associated with vigilance behaviour of baboons rather than feeding. This is supported by the fact that baboons were recorded to use the height beyond 2 m in more than 1200 follows, of which they only fed in 810 follows (66%). Grassland and wooded grassland domination of baboons' home range increased presumed risk of predation due to tall grasses and closed understory. For baboons to safely move around in such environment need to increase their level of vigilance through scanning the area from higher canopies to increase visibility. This is because vigilance more often serves as a good technique of detecting

predator before attack (Smith *et al*. 2004). Moreover, higher canopies of most tree species in Mikumi had larger branches, thus provide good support for baboons when vigilanting, unlike lower heights which had fewer branches and trunks. Frequent use of higher canopies for vigilance by primates has been also reported in spider monkeys (Youlatos 2002 and Campbell *et al*. 2005) and black-and –white snub-nosed monkeys (Xiang *et al*. 2009).

It was further observed that, while feeding on the ground, baboons fed more frequently at the centre of the troop. The centre of the troop was defined in reference to Altmann (1979) i.e., "the point where most members of the troop are found". This position could be clearly defined when the troop is resting and/or feeding on the ground rather than when the troop is moving or in the canopy. Finding on the use of centre position more frequently for feeding and foraging is consistent with the "feeding concentric ring hypothesis" observed on feeding behaviour of Japanese macaques (*Macaca fuscata*). In this species, feeding was more at the centre of the troop, with fewer individuals mainly subdominant and subordinate males at the periphery (Itani 1954 cited in Altmann 1979). The observed higher number of feeding records at the centre in this study is associated with overriding number of females over males. Females will always trade off safety over quality, so will choose to feed on safer environment (predation risk hypothesis). Similar observation that, females feed more at the centre than males was made by Itani (1954) as cited in Altmann, 1979 in describing the feeding concentric ring hypothesis.

Difference in the use of vertical position

Much as baboons were generally observed to use the ground and higher canopy more frequently than other vertical strata, the use of the two height categories during feeding and foraging behaviour varied significantly between age and sex classes. Sex variation in spacing behaviour by baboons has been also reported by Cowlishaw (1999) on the spacing behaviour of desert baboon (*Papio cynocephalus ursinus*). The slight less frequent use of ground by males (adult and sub adults) for feeding and foraging than adult female observed in this study is associated with anatomy, nutritional demand and reduction of intra specific food competition, which is better explained by scramble competition hypothesis (Main *et al*. 1996). Because of anatomy and body requirement, large bodied animals usually feed and forage in more abundant food, hence are usually associated with living on the ground (Xiang 2009).

In this study, because large part of baboons' home range was covered by grassland, large bodied adult males were expected to feed and forage more on ground to supplement their fruit diet with more abundant grass leaves. However, because of their selective omnivorous nature, edible grass leaves were scarce. Anatomically, males are less tolerant to lower forage biomass because of allometric relationship of bite-size to body-size ratio (Ruckstuhl and Neuhaus 2002), and because of this, they became less competent than females (scramble competition hypothesis), hence use the ground slightly less frequent than adult females. This is because when variation in energy and nutritional requirements is sufficiently large, males and females use different strategies to detect and acquire food (Breed *et al*. 2006). As for subadult males, the slightly less frequent use of ground for feeding and foraging despite of their small body size, is associated with their tendency to bond with adult males so as to learn sex specific skills (social preference hypothesis) (Bon *et al*. 2001, Pérez- Barbería *et al*. 2005). In addition to that, higher socializing behaviour of subadult males when on the ground is also associated with less feeding and foraging occurrence when at this level. Moreover, the slightly higher feeding occurrence by adult males at the ground than subadult males is associated with consorting behaviour and friendship with adult females to increase their mating success. In several occasions, when consorting adult males had

been observed feeding when adult female feeds, and feed on the same food as adult females. Similar behaviour has also been reported on chacma baboons (Palombit 2000).

The frequent use of higher vertical heights (height beyond 2 m) by adult males and sub adult males observed in this study is associated with their social role and energy requirements of their bodies. Higher nutritional demand influenced by their smaller body size is also associated with the frequent feeding and foraging at higher canopy by sub-adult males. As reported, fruits which are higher in carbohydrates and rich in readily available energy for primates (Milton 1993) are more abundant and at high density in upper canopies (Houle *et al*. 2014), moreover fruits at higher canopies are less toxic with little fibres (Milton 1993, Houle *et al*. 2014). In addition to access for fruits, sub-adult males used higher canopies to supplement their fruit diet with plant exudates because it is rich in carbohydrates and some minerals (Porter *et al*. 2009). Thus, the use of higher canopy provides subadult males with much needed energy for growth.

For adult male, their slightly more frequent use of higher canopies than adult female has been also reported by Houle et al. (2014), who reported that, larger bodied and dominant individuals usually monopolize higher canopies because of higher fruit density at this height, leaving smaller bodied individuals and subordinate occupying lower canopies. In this study, the use of higher canopies by adult males is more associated with their social role of vigilance, protecting the troop and reduction of predation risks. The chief predator of baboons are leopard, cheetah and lion, all these are ground predator that can be easily be seen from tree canopies (Cowlishaw 1994, Diego 2003, pers. Obs). Adult males use higher canopy for increasing visibility towards potential invading males and predators, and they become more vigilant and may reduce their feeding rate (van Schaik *et al*. 1983). Similar situation has been reported on feeding behaviour of white-faced capuchin (Rose and Fedigan 1995), in tamarins (Smith *et al*. 2004) and in desert baboon (Cowlishaw 1999).

Moreover, as it was for the feeding on the ground, the difference in the feeding occurrence between adult males and adult females at higher canopy was slight and insignificant. Again, as it was for ground feeding and foraging, consorting behaviour and friendship between adult males and adult females is associated with this finding. The fact that there was significant difference in the use of ground between adult males and adult females, as well as between adult females and sub-adult males while there was no significant difference between males (adult and sub-adult, Table 4, Parameter estimates, P-values) indicates that sex rather than body size (age) influences the use of ground by baboon during feeding and foraging. Lack of significant difference between adult males and adult females in their use of higher canopies indicates that social bond and role influence the use of canopies by baboons during feeding and foraging. Moreover, lack of clear pattern (insignificant difference) on sex differences in the use of other vertical height categories may indicate the means of baboons for reducing intraspecific competition. For that reason, different sexes of the same species may feed at different height levels and/or occupy different horizontal position particularly during feeding as it has been observed in rain forest primates (Gartlan and Struhsaker 1972), desert baboons (Cowlishaw 1999) and grey bamboo lemur (Grassi 2000).

Differences in the use of horizontal position

Much as baboons can exhibit differences in the use of vertical strata, they can similarly differ in their use of horizontal position within and away from vicinity of other troop members during feeding. This form of spatial positioning can only be measured when troops are showing some form of directional behaviour, which can be defined as front and

rear to overall troop positions. Because of this, there were fewer follows and no interval data. Generally, the difference in use of horizontal position between age-sex classes is mainly associated with social roles. Adult females and sub-adult males feeding and foraging relatively more frequent at the centre (nuclear) of the troop than adult males is highly associated with reduction of predation risks influenced by their body size. Both adult females and sub-adult males because of their small body size are vulnerable to predation as they are easier target to predators, but adult males would usually retaliate to predator attack (Cowlishaw 1994). In that regard, as the strategy to reduce predation risk especially in daytime, smaller bodied individuals especially adult females and young juvenile will tend to feed and/or move in areas safe from predators (centre of the troop) (predation risk hypothesis) (Hay *et al*. 2008, Ruckstuhl and Neuhaus 2002); with protection of adult males in front of the troop. Moreover, frequently feeding at the troop centre by adult females, is further associated with their reproduction investments. Adult female invests more in post-reproductive activities hence will tend to feed and move in areas safe from predator (Trivers 1972, Palombit 1997). The role of males to protect the troop from predators and potential invaders is much associated with the significant difference between males and females feeding behind the troop. This has been well described in the progression order of yellow baboons, that when moving and/or feeding baboon move in an order of protective ring whereby large bold adult males tend to provide outer protective ring to centrally located vulnerable individuals, young juveniles and lactating females. This is also consistent with description by Altmann (1979), that "when the troop moves out onto the open plains, a clear order of progression appears. Out in front of the troop move the boldest troop members-the less dominant adult males and the older juvenile males, following them at the troop's periphery are; pregnant and oestrus adult females and juveniles. The rear of the troop is a mirror image of its front".

The protective role of males explains the relatively more feeding frequency of adult females when in front of the troop compared to males. The presence of sub-adult males/older juvenile in front of the troop with less dominant bolder males is associated with the intention of sub-adult males to learn the role of protecting the troop (Social preference hypothesis- Bon *et al*. 2001). In addition to that, although sub-adult males are more or less similar in size as adult females, they are considered to have less fear intensity compared to adult female, hence less nervous, therefore can retaliate to predator attack as do adult males (Schmitt and Di Fiore 2015). The non-significant different results between males (adult and sub-adult) on feeding behind and in front of the troop, indicates that sex has influence on the horizontal positioning of yellow baboons during feeding. Moreover, the lack of difference in feeding at the troop centre between adult males and adult females, and the less feeding occurrence of males in front of the troop indicates that the influence of sex on the horizontal position is due to the protective role of males.

Differences in time spent in the spacing behaviour during feeding

In addition to differences in feeding and foraging occurrence, and in spacing behaviour of yellow baboons, difference was also observed in the time spent feeding at different heights. Sub-adult males spent little time feeding on the ground up to 1 m than both adult females and adult males. The similarity in time spent feeding between adult males and adult females was not expected, because of their differences in body sizes, they were instead expected to have different activity budget with adult males expected to spent little time feeding on ground than adult females because of high retention rate (Michelena *et al*. 2004). However, because of their reproductive investment in access to mating partner, adult males will tend to forge friendship with

prospective female partner (Trivers 1972, Palombit 1997), hence adult males will be found together with females at the same place most of the time as long as the place is safe for adult females and infants. The smaller body, hence lower body weight and lack of reproductive role is associated with sub-adult males spending more time feeding at higher canopies than both adult females and adult males.

CONCLUSION

This study set three hypotheses and a number of predictions to scrutinize the influence of body size and sex on the use of vertical and horizontal strata by yellow baboons during their feeding and foraging behaviour. This was done based on the fact that, baboon are sexually body size dimorphic animals with differed nutritional and energy requirement, because of this, they may choose to use the same feeding area/habitat differently. Findings of this study provide empirical evidence that during feeding and foraging at different vertical and horizontal strata, baboons do not occupy these strata randomly rather with specific pattern largely influenced by sex, and to some extent body size/age. Regardless of age and/or sex class, feeding on the ground is highly influenced by nutritional and energy demand of body size while feeding and foraging at vertical heights is much influenced by social role of sexes.

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