



Sexual segregation in foraging giraffe



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ABSTRACT

Sexual segregation in giraffe is known to vary between savannas. In this study, we compared sexual segregation in giraffe in one nutrient-rich savanna, the Serengeti National Park, one nutrient-poor, Mikumi National Park, and one medium rich savanna, Arusha National Park, (from here on referred to just by name) based on effects of sexual size dimorphism and related hypotheses. Data were collected in the wet and dry seasons, by driving road transects and making visual observations of browsing giraffe. Additional data were collected from literature (plant chemistry; mammal communities). There was a noticeable difference in browsing by females and males and in browsing between the three savannas. Females browsed a higher diversity of tree species in Serengeti whereas males browsed a higher diversity in Arusha, while the diversity of species browsed in Mikumi was high and about the same in both sexes. Females selected for high concentrations of nitrogen and low concentrations of tannins and phenolics compared to males in Serengeti but selection in Mikumi was more complex. Males browsed higher in the canopy than females in all sites, but the browsing height was generally higher in Serengeti than Mikumi and Arusha. Season had an effect on the browsing height independent of sex in Mikumi, where giraffes browsed higher in the dry season compared to the wet season. Males spent more time browsing per tree compared to females in all three sites; however, browsing time in Mikumi was also affected by season, where giraffes had longer browsing bouts in the wet season compared to the dry season. We suggest that sexual differences in forage requirement and in foraging interacts with differences in tree chemistry and in competing herbivore communities between nutrient rich and nutrient poor savanna in shaping the sexual segregation.

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1. Introduction

Sexual segregation is a behaviour where males and females of polygynous ungulates use different forage or foraging habitats or live in separate groups outside the mating season (Ginnett and Demment, 1999; Shannon et al., 2006; Ruckstuhl and Neuhaus, 2000, 2002; Clutton-Brock et al., 1982). Most ungulate species with females weighing more than about 25 kg exhibit sexual body size dimorphism in which males are larger than females (Owen-Smith, 1992; Ginnett and Demment, 1997; Jarman, 1974). This divergent morphology is favored by selection as large males are likely to win over small ones in the competition for receptive females (Badyaev, 2002). Dimorphism in size between sexes leads to

differences in energy requirements and hence in food and foraging habitat selection (Stokke and Du Toit, 2014; Ginnett and Demment, 1997; 1999; Young and Isbell, 1991; Shannon et al., 2006).

Most hypotheses proposed to explain sexual segregation in polygynous, sexually dimorphic ungulates (Main et al., 1996; Loe et al., 2006) are based on the Jarman - Bell principle (Bell, 1970; 1971; Jarman, 1974; Geist, 1974). The principle predicts that large herbivores, in contrast to small herbivores, can feed on poor quality forage (high concentration of fiber, low digestibility), because they have low metabolic requirement/gut capacity ratio and long retention time (Demment and Van Soest, 1985; Van Soest, 1996). Interspecific allometric studies show that metabolic rate scales to body mass raised to a power of about 0.75 (metabolic mass) while gut capacity scales isometrically with body mass (Demment and Van Soest, 1985; Du Toit et al., 2014). Originally presented to explain differences between species, the principle has been widely

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applied to explain sexual segregation within species where mass differences is often large (Pérez-barbería and Gordon, 1999; Gross et al., 1996; Main et al., 1996; Mysterud, 2000b; Ruckstuhl and Neuhaus, 2000; Perez-Barberia et al., 2008). Giraffes exhibit sexual dimorphism where males are about 5.0 m and females 4.5 m tall, weighing 1200 kg and 800 kg, respectively (Skinner and Chimimba, 2005). They are the largest extant ruminants and browsers, feeding on leaves, shoots, flowers and seed pods (Dagg, 2014; Du Toit, 2003). Giraffes live in arid to sub-humid savannas, forming loose groups of 2 to about 35 animals; males may be solitary (Dagg, 2014; Leuthold, 1979). According to the Jarman-Bell principle (Jarman, 1974; Bell, 1971), giraffes do well in nutrient-poor savannas, taking advantage of their ability to process large quantities of relatively poor quality forage. Giraffes are, however, generally considered to be *Acacia* specialists (Dagg, 2014; Parker and Bernard, 2005; Pellew, 1980) but their diet depends on the availability of preferred plant species (Kingdon et al., 2013; Berry and Bercovitch, 2016). *Acacias* grow predominantly in relatively nutrient-rich environments, and have relatively high concentrations of nitrogen and low concentrations of phenolics and tannins (Caister et al., 2003).

The relatively small female giraffes select for high nitrogen concentration and against tannins and fiber (Caister et al., 2003), whereas the large males can tolerate more plant defences, and often select for large bite mass (Ginnett and Demment, 1997). In nutrient rich savannas, many trees fulfill the requirements for the females, and the diversity of tree species eaten by females can be relatively high compared to that eaten by the males, who feed longer on one tree. In nutrient-poor savannas, trees have higher concentrations of tannins and phenolics (Stamp, 2003; Coley et al., 1985), and particularly female giraffes may concentrate the foraging to one or a few tree species that have high nutrient concentration and low defence concentrations. If, such high nutrient tree species are lacking giraffes have to divert foraging to many species in order to 'dilute' any particular type of chemical occurring in one tree species (Freeland and Janzen, 1974; Singer et al., 2002).

Male and female giraffes often segregate into foraging on different plant parts or in different habitats (Ruckstuhl and Neuhaus, 2002; Main et al., 1996; Mysterud, 2000b; Illius and Gordon, 1987). The small females feeding on small bite sizes of high quality might force the big males to feed higher in the canopy in order to get bites of adequate size and quality (Du Toit, 1990; Woolnough and Du Toit, 2001; Ginnett and Demment, 1999). As males can feed above the reach of females, they can do this without moving to another feeding habitat (Du Toit, 1990; Cameron and Du Toit, 2007; Ginnett and Demment, 1999). In addition, female giraffes may compete with smaller species of browsers, which particularly in the dry season, when resources are most limited, might force female giraffes to feed higher in the canopy and thus concentrate feeding within a narrow height interval between small browsers and the giraffe males (Woolnough and Du Toit, 2001; Makhabu, 2005; Cameron and Du Toit, 2007; O'kane et al., 2011; O'connor et al., 2015). This process is often called scramble competition (Du Toit, 2005; Stokke and Du Toit, 2014).

Conradt (1998), Ruckstuhl (1998) and Ruckstuhl and Neuhaus (2002) suggest that the activity budget might differ between sexes, and that the fibrous food of males needs longer ruminating time. In addition, males spend more time on forage ingestion compared to females, and thus might have longer feeding bouts on one tree, reducing the synchrony between sexes (Ginnett and Demment, 1997; Conradt and Roper, 2000). According to Ginnett and Demment (1997) males take larger bites, have reduced chewing effort but increased chewing rate and have larger bite formation time compared to females. These differences need, however, not lead to habitat segregation, as the food resource largely consists of

the same species for both sexes (Bleich et al., 1997; Ruckstuhl and Neuhaus, 2002; Main and Coblenz, 1990).

In the present study we compared the sexual segregation in giraffe between a rich (Serengeti), a poor (Mikumi) and a medium rich (Arusha) savanna. We predicted that (1) female giraffes should consume plant species with higher concentration of nitrogen and lower concentration of tannins than males; (2) female giraffes should browse a higher diversity of plant species than males in the rich savanna, but both sexes should browse a high diversity in the poor; (3) male browsing height should be higher than females, but browsing height for both sexes should be higher in rich savanna than in poor; and (4) males should have longer browsing bouts per plant than females.

2. Materials and methods

2.1. Study areas

Serengeti is located in northern Tanzania, between latitudes 1° and 3°30' S and longitudes 34° and 36° E. Arusha is located on the eastern slopes of Mt. Meru between latitude 3°15' S and longitude 36°45' E. Mikumi is located in eastern Tanzania between 7°00' and 7°50' S, and 37°00' and 37°30' E (Fig. 1).

Serengeti is characterized by grasslands, wooded grasslands and shrublands (Jager, 1982; Anderson et al., 2008). The soils are influenced by the nutrient rich ash deposits of the volcanoes on the Ngorongoro Highlands (Anderson et al., 2008). Arusha contains both fertile volcanic soils in the lower slopes of Mt Meru, resulting from volcanic activities of the mountain, and sandy soils at the higher elevations (Galanti & Loibooki, 2003). Mikumi consists of flood plains which have black cotton soils while the eastern hills have leached, sandy soils poor in nutrients (Lyaru, 1997; Maige, 1990; Backéus et al., 2006).

Rainfall in Serengeti is seasonal and bimodal, with long rains falling from March to May and short rains from November to December. The southern plains receive less than 500 mm rain a year while the northwestern region receives about 1200 mm although most areas receive 600–800 mm (Norton-Griffiths et al., 1975; Sinclair et al., 2007). Arusha receives short rains in November and December and long rains from March to May. The higher south-western slopes of Mt Meru receive up to 2000 mm of rainfall per year, while the northern slopes receive 500–600 mm per year. The lower zone, where this study was conducted, receives an annual rainfall of about 1000 mm (Galanti & Loibooki, 2003). Mikumi has one long rainy season, from November to May, peaking around April with annual rainfall geographically ranging from 750 to 850 mm per year (Vedeld et al., 2012).

In Serengeti, *Acacia* woodlands (we follow the old taxonomy of *Acacia*; Palgrave, 2002) occur in the central and western parts of the park, where the study was conducted (Sinclair et al., 2007). There is a rich community of medium sized grazers dominated by the blue wildebeest, *Connochaetes taurinus* and browsers such as impala, *Aepyceros melampus* (Campbell and Borner, 1995; Jarman and Sinclair, 1979). In Arusha the vegetation in the lower areas of the park is dominated by *Acacia xanthophloea*, *Dodonea viscosa* and *Euclea divinorum* (Galanti & Loibooki, 2003; Mahenya et al., 2016). The park has little wildlife, and, for example, lacks impala entirely (Mahenya, oral information). The flood plains of Mikumi has scattered trees and shrubs (Lyaru, 1997). The vegetation becomes gradually denser from the plains to open *Combretum* woodland, mixed wood land and finally culminates into *Brachystegia* stands (Lyaru, 1997; Maige, 1990). The fauna is dominated by elephant *Loxodonta africana* and buffalo, *Syncerus caffer* (Bell, 1982).

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