



Research article

Grouping behaviour and activity patterns of impala (*Aepyceros melampus*) in a nutrient –rich and a nutrient-poor savanna in Tanzania

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ABSTRACT

African savannas are broadly categorised into nutrient-rich and nutrient-poor according to soil nutrient availability and precipitation. Soil nutrients limit plant growth in the nutrient-rich savannas, leading to little plant biomass of high nutrient concentrations. In the nutrient-poor savannas soil nutrients are depleted before plant growth ceases, resulting in large production of nutrient-poor plant biomass. Impala (*Aepyceros melampus*), are medium-sized antelopes occurring in both savannas, but they face feeding challenges in the nutrient-poor savannas because of high energy requirements. Activity patterns of impala are well studied, but few studies compared savannas with differing soil nutrients and animal communities. I used the scanning methods to study impala activities in a nutrient-rich savanna, the Serengeti National Park, and a nutrient-poor savanna, the Mikumi National Park in Tanzania, during the wet and dry seasons. Impala are gregarious and mixed feeders, utilising grasses during the wet season, switching to browsing during the dry season, making them good candidates for comparing savannas and seasons. The impala formed bigger groups in Mikumi during the wet season splitting during the dry season. Grazing time was higher in the wet season than in the dry season in Serengeti, but did not differ between the seasons in Mikumi. Browsing time was longer in Mikumi than Serengeti during the dry season, and longer in Serengeti than Mikumi during the wet season. Resting time was longer in Serengeti than Mikumi during the wet season, while walking time was longer in Mikumi than Serengeti during the dry season. Family groups spent longer time resting than bachelor groups in both sites. The study shows obvious differences in grouping and activity patterns of impala between the sites and the seasons. Further studies are recommended to explore the influence of savanna and season on grouping behaviour and activity patterns of herbivores.

1. Introduction

African savannas are broadly categorised into arid-eutrophic (dry, nutrient-rich) and moist-dystrophic (moist, nutrient-poor) (Huntley, 1982; Scholes, 1990; Aarrestad et al., 2011). They differ in phytomass nutrient concentrations (Aarrestad et al., 2011; Wigley et al., 2018). Soil nutrients limit plant growth in the arid-eutrophic savannas, leading to little biomass of high nutrient concentrations (Bell, 1982; Scholes, 1990; Charles-Dominique et al., 2016). Heavy rainfall in moist dystrophic savannas leads to the leaching of nutrients over years, resulting in the production of comparatively much plant biomass of low nutritive quality (Bell, 1982; Olf et al., 2002). Nutrient hotspots in dystrophic savannas, such as around termite mounds and riverine areas show higher plant productivity and nutrient content (Jouquet et al., 2016; Mayengo et al., 2020b). These hotspots are important habitat for ungulates (Stähli, 2012; Mayengo et al., 2020b).

The high-quality vegetation of the arid-eutrophic savannas tends to support a large biomass and diverse mammalian herbivores, especially small and medium size ruminants (Olf et al., 2002). In contrast, the poor quality vegetation of the moist-dystrophic savannas supports a low biomass of large-bodied mammalian herbivores (Fritz et al., 2002; Olf et al., 2002). Large carnivore biomass normally correlates with total prey biomass, thus their density tends to be higher in the eutrophic savannas (East, 1984; Sinclair et al., 2003). Impala (*Aepyceros melampus*) occur in both savanna types. Grouping behaviour and activity patterns of herbivores tend to vary in relation to differing food quality and availability (Fryxell, 1991; Smith and Cain, 2009; Koenig et al., 2013). Forage quality had shown to reduce impala movement (Pays et al., 2021) time spent vigilant (Pays et al., 2012), and influence feeding behaviour (Blanchard and Fritz, 2008). Furthermore, group size tends to differ between habitats (Szemán et al., 2021). Thus, different forage quality between

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savannas may have profound effects on behaviour and activity patterns of herbivore species occurring in these savannas.

Impala are gregarious herbivores that forage in either male bachelor groups or female/young family groups, the latter including one mature male (Muposhi et al., 2013). They are seasonal breeders that mate during the rainy season from April to June, and birth six months later at the end of the dry season (Ogutu et al., 2008; Hunnink et al., 2020). Territorial male impala leave the bachelor groups during the breeding season to establish and defend territories (Oliver et al., 2007; Hunnink et al., 2020). Resources of the territories such as food and water attract females (Hunnink et al., 2020). The territorial males have mating rights to females in their territory (Hunnink et al., 2020). The territorial behaviour tends to vary between areas due to variations in quantity, quality and distribution of food resources (Maher and Lott, 2000; Bowyer et al., 2020; Hunnink et al., 2020).

Impala utilise mainly grasses in the wet season when they are plentiful and nutritious, and browse in the dry season when grasses mature (Kos et al., 2012). Grasses are considerably more palatable than browse, thus impala prefer grasses when available (Codron et al., 2007; Hunnink et al., 2020). Impala optimise their diet to maintain high protein content, avoiding browsing on defended trees (Sponheimer et al., 2003). The dietary flexibility of impala tend to differ between sites and seasons due to the variation in grass-browse availability and quality (Sponheimer et al., 2003; Kos et al., 2012). Activity patterns are normally influenced by food supply and quality, and nutrient requirements that vary between males and females (Leuthold, 2012; Szemán et al., 2021). The reproductive roles of females and males and a difference in body size (females are smaller) affect how they spend time on different activities. Females normally spend more time feeding, and feed more selectively due to relatively higher nutrient requirements (Szemán et al., 2021), while males spend more time on walking (Shrestha et al., 2014). In addition, family groups with young tend to spend more time resting and being vigilant than males to protect the young animals from strong solar radiation and predators (Matson et al., 2005).

Grazers tend to aggregate and forage in groups, thought to be a predator avoidance strategy (Shorrocks and Cokayne, 2005; Szemán et al., 2021). There is, however, a trade-off in group size between predator avoidance and intraspecific forage competition within the group, which tends to vary with forage quality and availability (Dalerum et al., 2008; Stears et al., 2014). Grazing in groups is also a range management method, as the cropping allows regrowth of nutrient rich, highly productive lawns (Fryxell, 1991; Stähli, 2012). This advantage is most obvious for medium-sized grazers in dystrophic savannas with tall and unpalatable grasses when matured (Stähli, 2012). Seasonally, grazing mammals tend to form large groups when forage is plentiful, as in the wet season, and decrease the size of their groups when forage decline in the dry season (Koenig et al., 2013; Stears et al., 2014).

Grouping is also a strategy to reduce predation risks (Creel et al., 2014; Szemán et al., 2021). However, there is a negative relationship between group size and time spent vigilant, either due to the reduced need to be vigilant in a big groups (i.e. many eyes hypothesis) or increased need of time for foraging following competition with group members (Dalerum et al., 2008; Creel et al., 2014). Impala are the prey of many predators such as leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycan pictus*) (Sinclair et al., 2003; Hayward and Kerley, 2008). While the impala face higher predation pressure in eutrophic savanna (Sinclair et al., 2003), nutrient availability limit grouping in dystrophic savannas. However, the groups may be big in Mikumi during the wet season to create palatable grazing lawn through intense grazing (Stähli, 2012).

Activity patterns vary between the wet and the dry season due to variation in quality and quantity of forage and water (Codron et al., 2007). Generally, food quality and availability decline during the dry season than in the wet, increasing the energy-demanding walking to search for food and water (Muposhi et al., 2013). Thus, energy-saving resting should be most common in the dry season (Muposhi et al.,

2013). Availability of surface water reduces energy costs associated with travel to and from water points and exposure to predators (Veldhuis et al., 2019). The effect of seasons on activity patterns is expected to vary between the savannas due to differences in herbivore abundance and diversity, which determine feeding competition and facilitation. For example, migrating herbivore in Serengeti increase competition for grasses during the wet season, but promote new grass flushes during the dry season which are utilised by the smaller herbivores (Arsenault and Owen-Smith, 2002; Holdo et al., 2011). In addition, quantity and quality of grass and browse resources which vary between savanna influence the dietary switch of impala during dry season (Codron et al., 2006).

Impala behaviour is well known, however few studies have compared behaviour in eutrophic and dystrophic savannas. The study compared the grouping behaviour and activity patterns of impala in Serengeti National Park, an eutrophic savanna, and Mikumi National Park, a dystrophic savanna in Tanzania. The parks differ in soil nutrients and plants, and animal communities (Backéus et al., 2006; Anderson et al., 2008). The Serengeti soils are made up of nutrient-rich ash deposits of the volcanoes on the Ngorongoro Highlands (Anderson et al., 2008), while Mikumi soils are sandy, leached and poor in nutrients (Backéus et al., 2006). The vegetation of Serengeti consists of largely palatable *Vachellia* and *Senegalia* species and nitrogen rich grasses and sedges, utilised by diverse and abundant small and medium-size mammalian herbivores (Anderson et al., 2007). In contrast, the vegetation of Mikumi consists of miombo species which are utilised by large-bodied and medium-sized herbivores (TAWIRI, 2019). The high nutrient requirements of impala are expected to influence their activities and grouping behaviour in these parks. I hypothesised the following: 1) groups to be larger in Mikumi than in Serengeti during the wet season to keep the grasses immature, 2) groups to be larger in the wet season compared to the dry season in both sites, 3) more time devoted grazing in Mikumi in both seasons due to the unpalatable miombo species, 4) more time devoted grazing in the wet season and browsing in the dry season in Serengeti, 5) more time devoted resting in Serengeti in both seasons due to availability of nutritious forage, 6) more time devoted walking in Mikumi during the dry season searching for nutrient-rich patches, 7) males spend more time walking in both sites and seasons while females spend more time resting in Mikumi to save energy, and 8) family groups spend more time vigilant in Serengeti than Mikumi due to higher predation risks in Serengeti.

2. Materials and methods

2.1. Study areas

Serengeti National Park (14,763 km²) is located in northern Tanzania between latitudes 1° and 3° 30' S and longitudes 34° and 36° E. Mikumi National Park (3230 km²) is located in southern Tanzania between latitudes 7° 00' and 7° 50' S, and longitudes 37° 00' and 37° 30' E (Figure 1).

Serengeti is characterised by various habitats from open grasslands, wooded grasslands and closed woodlands (Anderson et al., 2008). Rainfall is seasonal and bimodal, with long rains from March to May and short rains from November to December. Rainfall varies geographically, but the central region of the park, where this study was conducted, receives about 600–800 mm per year (Kilungu et al., 2017). Mean monthly temperatures during the year are 15–25 °C (Kilungu et al., 2017). Serengeti National Park is drained by three major rivers flowing westward towards Lake Victoria, namely, Mara, Mbalageti, and Grumeti. The herbivore fauna of Serengeti is diverse, dominated by blue wildebeest, *Connochaetes taurinus*, plains zebra, *Equus quagga*, impala, and gazelles *Eudorcas thomsonii*, and *Nanger granti*. Density of carnivores per km² in the parks was estimated to 1.1 (Durant et al., 2011).

Mikumi soils are nutrient-poor except the Mkata flood plain, which contains black cotton soils (Backéus et al., 2006). The plain is a nutrient hotspot, where most of the wildlife are found (TAWIRI, 2019). The park has one rainy season, from November to May, peaking around April, with an annual rainfall ranging geographically from 750 to 850 mm per year.

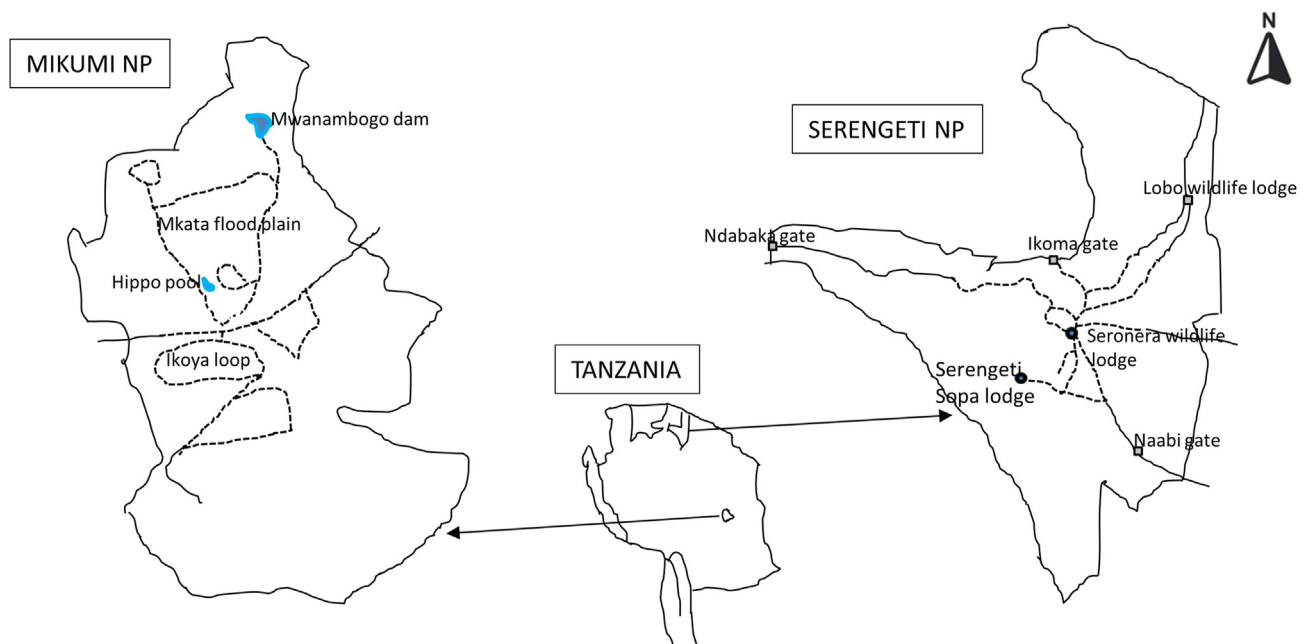


Figure 1. A map of Serengeti and Mikumi National Parks showing the study transects (dotted lines).

The mean monthly temperatures are 16–28 °C (Nyahinga et al., 2016). Mikumi is drained by the Mkata river during the rainy season. During the dry season, animals drink from dams within the park. The flood plains comprises scattered trees and long grasses. The vegetation gradually becomes denser with distance from the plains to *Brachystegia* and *Julbernardia* stands (Backéus et al., 2006). The fauna of Mikumi is dominated by large-bodied species such as elephants, *Loxodonta africana*, and buffalo, *Syncerus caffer*. Impala are dominant small herbivores that occur mostly in the flood plain (TAWIRI, 2019). Mikumi has fewer predators densities and species, dominated by lions and leopards (Crosmary et al., 2018).

2.2. Data collection

Activities of impala were classified into five categories as shown in Table 1. Observations were done during the wet season (April – mid-June) and dry season (August – mid-October) in 2014. I used the scan sampling technique to study impala activities. I drove along all accessible park roads (Figure 1), and when impala were sighted within about 50 m, the car was stopped for observation. The data were collected after the impala resumed its original behaviour, not actively looking at the observer. The whole group was scanned every 3 min for 15 min by using a stopwatch, and the activities of individual animals were recorded. Other information recorded was group size and group type (bachelor or family). Observations were done during the day, from 0700 to 1600 h. Transects were alternated every day to reduce the possibility of recording

Table 1. Definition of behavioural activities of impala used in the study.

Activity	Definition
Grazing	Actively feeding on grasses and graminoids either stationary or moving
Browsing	Actively feeding on leaves, shoots or fruits of trees, shrubs and forbs
Resting	Standing or laying, with eyes open or closed, ruminating or not, but not scanning the surroundings
Walking	Active movement from one point to another
Vigilant	Scanning the surroundings with the head raised above the shoulder

the same individuals more than once, however, animals were not identified individually. The study was approved by Tanzania Commission for Science and Technology and Tanzania Wildlife Research Institute (TAWIRI).

2.3. Data analysis

The impala group were compared between the sites, seasons, and group type. I ran a linear model with the explanatory variables and their interactions, and group size as a dependent variable. The group size was log-transformed to fulfil the assumptions of normality. In addition, I calculated the proportion of time the animals spent grazing, browsing, resting, walking, and being vigilant as response variables, to determine its relationship with the site, group type, season, and group size. The impala groups were used as a random variable in the analysis due to repeated observations (5 replicates) for each group. The response variables had the value zero where no individual in a group was engaged in a particular activity and one where all individuals in a group were engaged in the same activity. Some activities were minimal (Figure 2), thus zero-one inflated models were needed. Thus, I used GAMLSS (generalized additive models for location, scale, and shape) with beta inflated distribution (BEINF), which accommodates both 0 and 1 values and take control of the many zeros (Ospina and Ferrari, 2012). All the analyses were done in R version 4.0.3.

3. Results

A total of 146 impala groups in Mikumi (75 in the dry season and 71 in the wet season) and 137 in Serengeti (67 in the dry season and 70 in the wet season) were sampled. Grazing, resting, and walking were the main activities performed by the impala in both sites and seasons (Figure 2).

3.1. Comparison of group size between sites, seasons and group type

The bachelor and the family groups were bigger in Mikumi compared to Serengeti ($p < 0.001$, Figure 3a). The size (mean \pm SD) of the family groups was 58 ± 4 in Mikumi and 28 ± 1.6 in Serengeti, while the size of the bachelor groups was 21 ± 5 animals in Mikumi and 12 ± 1 animals in Serengeti. However, there was a significant interaction effect between

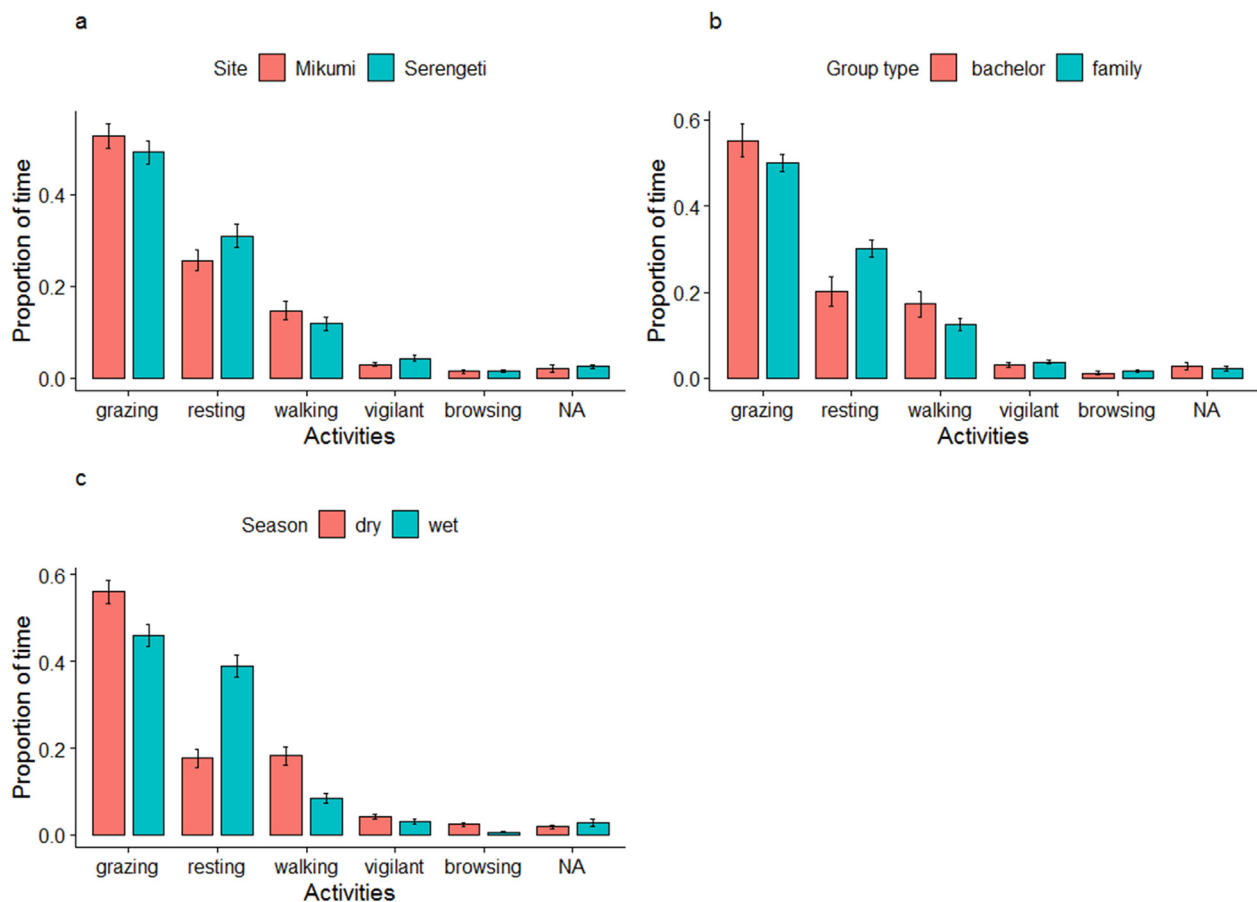


Figure 2. Comparison of the impala activities between: (a) sites (b) seasons (c) group type. The error bars above and below the mean show 95% confidence intervals.

the sites, seasons, and group type on the group size (Table 2). Regardless of the group type, group size did not differ between the sites during the dry season, but was significantly bigger in Mikumi compared to Serengeti during the wet season (Table 2, Figure 2b). The effect of season on group size differed between the bachelor and family groups, where the size of the bachelor groups did not differ between the seasons, but the family groups were bigger during the wet season compared to the dry season (Table 2, Figure 3c).

3.2. Grazing and browsing

The grazing time did not differ between the sites and the seasons (Table 3). However, there was a significant interaction effect between the sites and seasons on the proportion of time spent grazing (Table 3). The animals spent more time grazing in Serengeti during the dry season, while there was no variation between the seasons in Mikumi (Figure 4a). In addition, the impala spent more time browsing during the wet season in Serengeti compared to Mikumi and more time browsing during the dry season in Mikumi compared to Serengeti (Table 3, Figure 4b).

3.3. Resting and walking

The resting time did not differ between the sites and seasons, but the interaction effect between the sites and seasons was significant (Table 3). The resting time did not differ between the sites during the dry season, but was longer in Serengeti compared to Mikumi during the wet season (Table 3, Figure 4c). In addition, the proportion of time spent walking was longer in the dry season in Mikumi and in the wet season in Serengeti (Table 3, Figure 4d).

The proportion of time spent resting differed between the bachelor and family groups, but the proportion of time spent walking was similar

(Table 3). The family group spent longer time resting than the bachelor group (mean \pm SD = 3.10 \pm 0.3 min for the family groups and 0.19 \pm 0.06 min for the bachelor groups).

3.4. Vigilance behaviour

The proportion of time spent vigilant did not differ between the sites, seasons, family and bachelor groups. In all sites, seasons and groups, the proportion of time spent vigilant decreased with group size (Table 3).

4. Discussion

Impala groups were larger in Mikumi than in Serengeti during the wet season probably to keep the grasses immature and palatable through grazing. However, the difference between the sites was not significant during the dry season because resources are scarce, thus, the groups were smaller to avoid competitions. The proportion of time spent grazing and browsing differed between Serengeti and Mikumi and between the wet and the dry season due to variations in quality of grasses and browse between the sites and the seasons. In addition, the family groups spent more time resting than the bachelor groups in both sites perhaps to protect young animals from strong solar radiation and predators.

4.1. Comparison of grouping behaviour between Serengeti and Mikumi during the wet and the dry season

The variations in grouping behaviour between Serengeti and Mikumi depended on the season, because availability and quality of food resources and water differ between seasons in all sites. Grazing ungulates normally live in open habitats and form large groups (Szemán et al.,

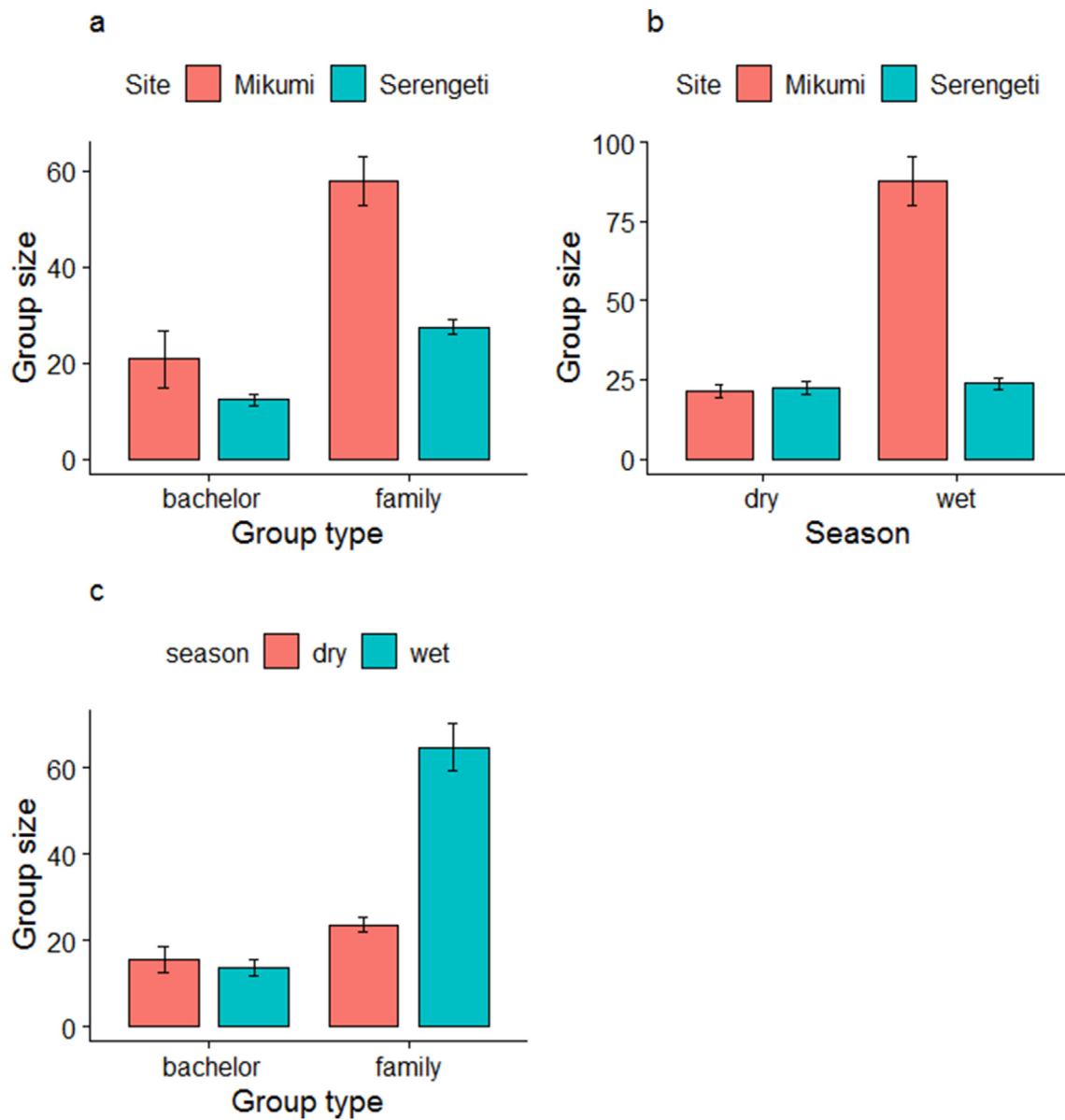


Figure 3. Comparison of the group size of impala between: (a) group type and sites (b) season and sites (c) group type and season. The error bars above and below the mean show 95% confidence intervals.

2021). In Mikumi, the impala formed large groups in the Mkata flood plain, utilising grasses that are dominated by *Hyparrhenia spp.* The aggregation of grazers normally create and maintain nutrient-rich grazing lawns during the rainy season through intense grazing (Stähli, 2012). The lawns form an important forage for small and medium sized grazers in

dystrophic savannas (Verweij et al., 2006). Stähli (2012) and Mayengo et al. (2020b) found comparable results, where grazers selected nutrient rich patches in dystrophic savannas in Tanzania. In addition, large herds of herbivores increase soil nutrient availability through the deposition of urine and dung, increasing the quality of the lawns (Veldhuis et al., 2018;

Table 2. Parameter estimates of the factors that determined the size of impala groups. Coefficients of the levels of the categorical variables that do not appear in the table i.e. Mikumi National Park, bachelor groups and dry season are part of the intercept.

Response variable	Predictors	Coefficients	Std. error	t-values	p-values
Group size	Intercept	2.922	0.214	13.631	<0.001
	Serengeti	-0.808	0.268	-3.010	0.002
	Wet season	-0.977	0.425	-2.292	0.022
	Family groups	-0.099	0.233	-0.425	0.671
	Serengeti * wet season	1.482	0.483	3.064	0.002
	Wet season * family group	2.452	0.443	5.529	<0.001
	Serengeti * family group	1.134	0.302	3.746	0.0002
	Serengeti * wet season * family group	-2.916	0.522	-5.586	<0.001

Table 3. Parameter estimates of the factors that determined the activity patterns of the impala. Coefficients of the levels of the categorical variables that do not appear in the table i.e. Mikumi National Park, bachelor groups and dry season are part of the intercept.

Response variable	Predictors	Coefficients	St. error	t-values	p-values
Proportion time spent grazing	Intercept	0.557	0.195	2.857	0.004
	Wet season	-0.168	0.182	-0.925	0.355
	Serengeti	0.011	0.187	0.061	0.951
	Family groups	-0.268	0.166	-1.607	0.109
	Wet season * Serengeti	-0.656	0.256	-2.561	0.011
Proportion time spent browsing	Intercept	-2.550	0.259	-9.833	<0.001
	Wet season	-1.078	0.315	-3.417	0.0007
	Serengeti	-0.354	0.219	-1.611	0.108
	Family groups	0.033	0.241	0.139	0.889
	Wet season * Serengeti	0.781	0.396	1.970	0.049
Proportion time spent resting	Intercept	-1.200	0.229	-5.232	<0.001
	Wet season	0.287	0.206	1.393	0.164
	Serengeti	-0.084	0.217	-0.388	0.698
	Family groups	0.414	0.184	2.242	0.025
	Wet season * Serengeti	0.507	0.284	1.785	0.007
Proportion time spent walking	Intercept	-0.781	0.199	-3.918	0.0001
	Wet season	-0.877	0.195	-4.492	<0.001
	Serengeti	-0.272	0.206	-1.320	0.187
	Family groups	-0.211	0.179	-1.175	0.241
	Wet season * Serengeti	0.513	0.281	1.822	0.045
Proportion time spent vigilant	Intercept	-1.050	0.287	-3.650	0.0003
	Wet season	0.190	0.133	1.428	0.154
	Serengeti	-0.296	0.294	-1.006	0.315
	Family groups	0.146	0.267	0.550	0.582
	Log (group size)	-0.606	0.079	-7.599	<0.001

Mayengo et al., 2020a). Mikumi has a low abundance of medium size grazers compared to Serengeti (TAWIRI, 2019). The medium size grazers such as wildebeest and zebra, which are abundant in Serengeti utilise mature grasses, forming nutritious low-lying grass sward, which is picked by smaller grazers (Anderson et al., 2007; Hempson et al., 2015).

The impala groups were comparable between the sites during the dry season. Grouping behaviour tend to have negative impacts on animals, especially when resources are limited (Fritz and De Garine-Wichatitsky, 1996; Szemán et al., 2021). Thus, the aggregations split in the dry season when food resources are scarce to reduce competition within the group (Favreau et al., 2018). Browsing in big groups do not have the same advantage of improving forage quality as grazing, and because the impala browse in the dry season, the groups split in both sites. Bigger groups during the rainy season are also related to breeding, where territorial males establish and defend an area to attract females for mating (Oliver et al., 2007; Hunnink et al., 2020). However, territorial behaviour is influenced by availability and quality of resources (Bowyer et al., 2020). The tendency to form larger groups in the rainy season and spitting in the dry season supports results from other studies (Averbeck et al., 2010; Favreau et al., 2018).

4.2. Grazing and browsing

Grazing was the main activity performed by the impala in Serengeti and Mikumi, during the wet and the dry season, and by the family and the bachelor groups. Impala normally graze during the wet season and browse during the dry season (Sponheimer et al., 2003; Kos et al., 2012). However, the effect of season on grazing time differed between the sites, being longer during the dry season compared to the wet season in Serengeti, but did not differ between the seasons in Mikumi. The low grazing activity in Serengeti during the wet season might be a response to competition from migrating herbivores, coming from the southern Serengeti (Dobson, 2009; Holdo et al., 2011). The migrating herbivores take the mature grasses, stimulating regrowth afterwards (Arsenault and

Owen-Smith, 2002). Impala prefer the grass flushes that are nutrient rich (Wilsey, 1996; Wronski, 2003), thus switched to grazing in the dry season. Grazing was maintained in Mikumi in both seasons because the miombo species are relatively unpalatable, thus not preferred by impala (Codron et al., 2006; Mandinyanya et al., 2018). In contrast, the impala utilised the *Vachellia* and *Senegalia* species of Serengeti that largely lack chemical defences (Agrawal, 2007).

4.3. Resting and walking

The animals tended to spend more time resting during the wet season in both sites, and these results agree with (Muposhi et al., 2013). Resting time did not differ between the sites during the dry season, but was longer in Serengeti than Mikumi during the wet season. Resting is an energy serving activity, however, animals tend to walk a long distance to search for resources when they are in short supply (Martin et al., 2015). The dry season is characterised by limited food resources and water in both sites, but the severity may vary between the sites. Mikumi lacks a permanent source of water, thus dry season walking might indicate searching for water. In contrast, Serengeti has a permanent source of water from Mara river and its tributaries (Wolanski and Gereta, 2001; Kihwele et al., 2021). Resting during the wet season is a sign of feeding satisfaction and protection of animals from extreme temperatures in both sites (Owen-Smith et al., 2010; Shrestha et al., 2014).

The family groups spent more time resting than the bachelor groups in both sites, which agrees with Muposhi et al. (2013). Family groups with juveniles tend to reduce exposure to temperature extremes by staying under shade (Shrestha et al., 2014) and to avoid predators (Shukla et al., 2021). Females with young offspring select sub-optimal forage habitats to reduce predation risks and to save energy (Ahmad et al., 2016; Pays et al., 2021). In addition, females have higher energy requirements than males due to their small body size and reproduction demands (Szemán et al., 2021). Thus, females face a trade-off between moving to search for food and water and resting to save energy and

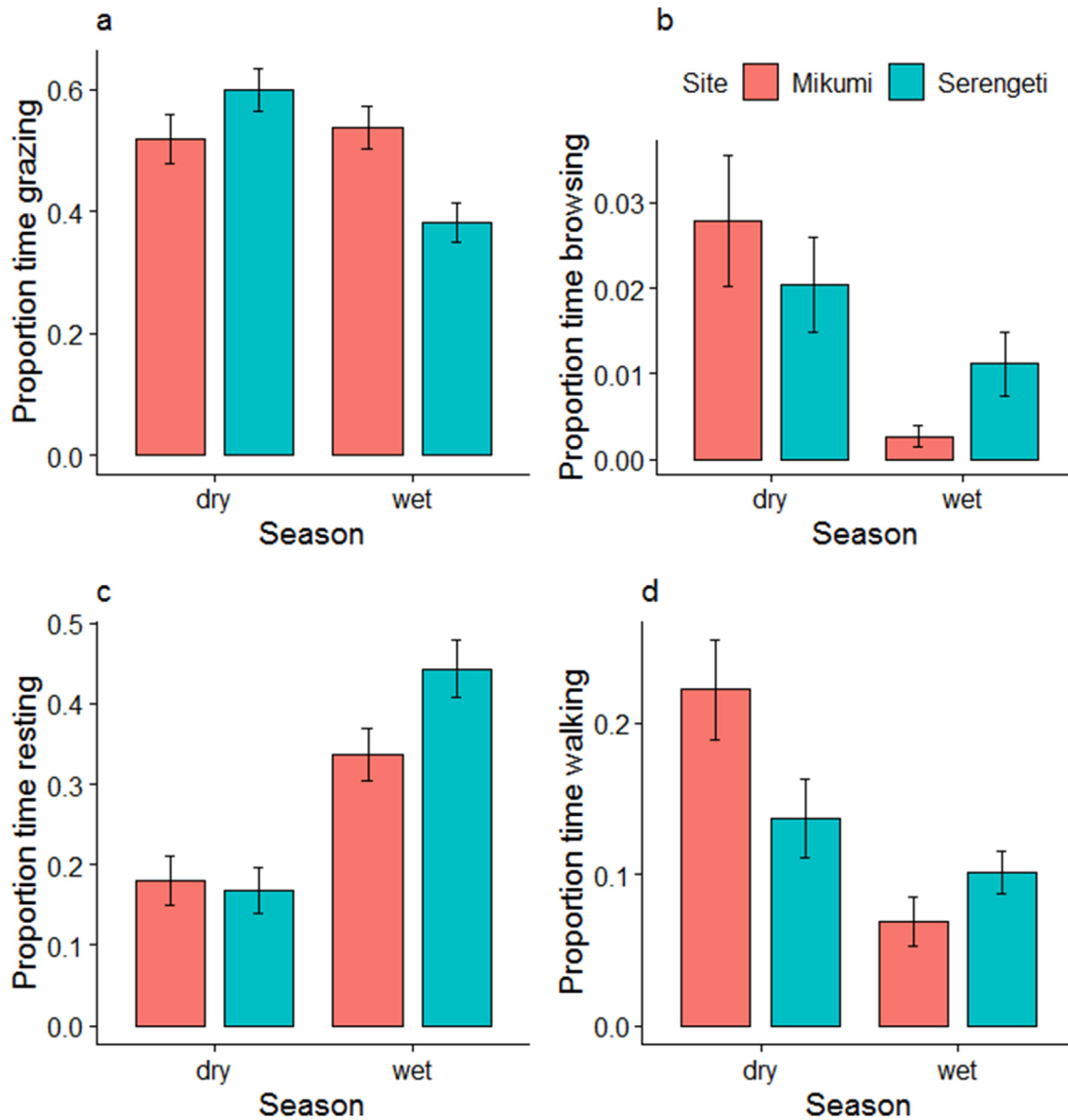


Figure 4. Comparison of the proportion of time spent grazing (a) browsing (b) resting (c) and walking (d) between the two sites during the rainy and dry seasons.

protect offspring from high temperatures, and, equally, between using the best forage habitats and protect offspring from predation (Hamel and Côté, 2007). Males, on the other hand, are mobile to guard their territory or trying to obtain one (Wronski et al., 2006; Muposhi et al., 2013).

4.4. Vigilance behaviour

The vigilance time did not differ between the sites and seasons, but decreased with group size, perhaps because predation risks tend to decrease with group size due to the dilution effect and the presence of many watching eyes in the group (Shorrocks and Cokayne, 2005; Dale-urum et al., 2008; Beauchamp et al., 2021). Normally, animals gain more energy by decreasing their vigilance effort and increasing their feeding time when groups are big (Michelena and Deneubourg, 2011). The vigilance behaviour was expected to be more pronounced in the family groups because of the presence of juveniles, which are prone to predation. The family groups benefit from the communal watching of predators. The vigilance behaviour tends to differ between savannas due to differences in carnivore densities (Périquet et al., 2012). However, it did not differ between the sites in this study despite the higher carnivores densities in Serengeti (Sinclair et al., 2003; Crosmary et al., 2018). The

abundance and diversity of small herbivores in Serengeti might reduce predation pressure on impala (Sinclair et al., 2003).

4.5. Limitations of the study

The study compared grouping behaviour and activity patterns of impala in Serengeti National Park, an eutrophic savanna and Mikumi National Park, a dystrophic savanna. Due to limited resources, I studied only one eutrophic and dystrophic savanna. As a result, some features of the parks that are not directly related to the savanna types, such as surface water availability and rain distribution might have affected the results. In addition, the study was conducted for 2 months in each park within a single year. Thus, factors specific to the year of the study such as the amount and distribution of rainfall and solar radiation might have also affected the results.

5. Conclusion

The study showed differences in grouping behaviour and activity patterns between Serengeti and Mikumi and between the wet and the dry season. The impala formed larger groups in Mikumi than Serengeti

during the wet season, but the group size did not differ between the sites during the dry season. Grazing did not differ between the seasons in Mikumi, but was higher in the wet season in Serengeti compared to the dry season. The time spent resting was higher in Serengeti during the wet season, but did not differ between the sites during the dry season. Continuous behavioural monitoring of impala activities and grouping behaviour in the contrasting environments will provide information that can be used for adaptive management.

Declarations

Author contribution statement

Rosemary Peter Mramba: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

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Data availability statement

Data will be made available on request.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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