

Full Length Research Paper

Glade use by common warthog, African buffalo, mountain reedbuck and bushbuck in Mount Meru Game Reserve, Tanzania

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Glade use by common warthog (*Phacochoerus africanus*), African buffalo (*Syncerus caffer*), mountain reedbuck (*Redunca fulvorufula*) and bushbuck (*Tragelaphus scriptus*) was studied in five man-made, five upper natural and 15 lower natural glades in Mount Meru Game Reserve, Tanzania. Direct observations were made on glade use by each species on four different days; 200 and 300 observation periods for warthogs (mornings and afternoons), and buffalo, reedbuck and bushbuck (mornings, afternoons and nights), respectively. Warthogs spent more time (54%) in glades, than reedbuck (38%), bushbuck (30%) and buffalo (26%). Warthogs used man-made and lower natural glades more than expected due to food availability and lower altitude. Buffalo used upper natural glades more than lower and man-made glades because of food availability and the presence of water within or near glades. Bushbuck used man-made and upper natural glades more than lower natural glades due to food availability, water availability and cover. Reedbuck used upper natural glades more than lower and man-made glades because of cooler temperatures, water availability, cover and minimal disturbance from humans. Thus, results show that glade uses by ungulates were influenced by presence of glade water and food, as well as glade ambient temperature and cover, and the amount of human disturbance.

Key words: Glades, Glade edge, forest edge, glade interiors, African buffalo, bushbuck, mountain reedbuck, common warthog.

INTRODUCTION

Glades are open grassland patches in a continuous forest that hold unique ecological roles and associated species (Young et al., 1995). Glades located in the forest matrix differ in plant communities and hence, influence the pattern of resource use by animal species using the glades, the surrounding forests or both (Gaston, 2003; Fuller et al., 2007). Ungulates are more attracted to certain habitats because of plant composition and structure (Matlack and Litvaitis, 1999; Fink et al., 2006).

Herbivores prefer habitat edges because of higher structural complexity, more varied plant composition and therefore, greater availability of food (Matlack and Litvaitis, 1999). Glades edges provide an abundant amount and wide variety of shrubs and trees for browsers, shelter for ungulates against predators, and ungulates may use the glades for locating water and mates (Pratt and Gwynne, 1977; Shaw, 1985). Glade interiors are important because they provide a dense

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Abbreviations: MMGR, Mount Meru Game Reserve; MRPP, Multiple response permutation procedure.

supply of grasses and forbs for ungulate foraging.

In the Mount Meru Game Reserve (MMGR), glades and their edges provide suitable habitat for a diversity of ungulates (Vesey-Fitzgerald, 1974; Kingdon, 1982). Glades serve as important feeding sites for several species of ungulates due to the abundance of grasses and herbs in relatively small areas in continuous forest (Kingdon, 1982; Estes, 1991). The vegetation attributes of natural and man-made glade communities are similar to each other, in that both glade types harbour grasses such as *Asplenium bugoiense*, *Cyperus rotundus*, *Pennisetum mezianum* and *Adropogon gayana* and the forb, *Coccinia trilobata*. However, differences may exist in the frequency of glade edge and interior use by the different species of ungulates, and in the resilience of vegetation in natural and man-made glades to grazing and browsing pressures (Brawn et al., 2001; Fink et al., 2006).

This study was aimed at investigating the conservation value of forest glades for Warthog, Buffalo, Mountain Reedbuck and Bushbuck in MMGR. It was first hypothesized that these ungulate species use the three glade types (man-made, upper natural and lower natural) differently. The second objective was to determine if altitude influence the ungulates behavioural activities (comfort, anti-predator and feeding) and third objective was to provide management recommendations as to whether man-made glades should be actively managed (*status quo*) or be allowed to revert back to forest.

MATERIALS AND METHODS

Study site

The study was conducted at Mount Meru Game Reserve (MMGR), located at (03° 16' to 03°20' S; 36° 45' to 36° 53' E) on the eastern slopes of Mount Meru, 350 km south of the Equator, 25 km from Mount Kilimanjaro and 35 km northeast of Arusha town. The reserve is 66 km² in size and is mountainous with elevations ranging from 1,473 to 4,566 m.a.s.l. The habitats of the reserve include evergreen forest, secondary forest, shrub land, wetlands and glades (Mangubuli and Lyamuya, 1988). MMGR has 33 glades: six man-made, six upper natural and 21 lower natural glades (Figure 1). The research design followed a three-way comparison of the ungulates of 25 glades: five man-made, five upper natural and 15 lower natural glades, located between 1,400- 2,000 m.a.s.l.

Ungulate surveys

Ungulate surveys were conducted between September 2005 and May 2006. The ungulates studied were the common warthog (*Phacochoerus africanus*), African buffalo (*Syncerus caffer*), mountain reedbuck (*Redunca fulvorufula*) and bushbuck (*Tragelaphus scriptus*). These species were selected because they are common species found in MMGR and use the glades for various behavioral activities (Asaad, College of African Wildlife Management Mweka, Post Graduate Diploma Dissertation, 1987). Other species found in the reserve include; elephant (*Loxodonta africana*), common Duiker (*Sylvicapra grimmia*), leopard (*Panthera*

pardus), giraffe (*Giraffa Camelopardalis*), waterbuck (*Kobus ellipsiprymnus*), and hyena (*Crocuta crocuta*). Diurnal observations of ungulates were made from a hide at the forest edge with binoculars. Nocturnal observations were made from a vehicle hidden in the glade edge, using night vision binoculars. Observation periods were as follows: morning (07h00 - 10h00), afternoon (15h00 - 18h00), and night (19h00 - 22h00).

The 25 glades (five man-made, five upper natural and 15 lower natural) were surveyed on four different days; the order of visits followed a randomized design pattern within and between glade types. For African Buffalo, Mountain Reedbuck and Bushbuck, a total of 300 observation periods were conducted (25 glades surveyed on four different days with three observation periods (morning, afternoon and night) per day during the dry and rain season (that is 25 glades x 4 days x 3 observation periods). For Warthogs, a total of 200 observation periods were conducted as follows: 25 glades surveyed on four days with two observation periods (morning and afternoon) per day (i.e. 25 glades x 4 days x 2 observation periods). Only two observation periods per day were done because warthogs are strictly diurnal (Estes, 1991; Skinner and Chimimba, 2005).

During each observation period, species present, the number of individuals for each species and their behavioral activities were recorded. The activities were categorized into three major categories: (1) comfort - a state of physical ease and freedom from pain or constraints, including behaviors such as wallowing, urinating, and walking, (2) anti-predator - an alert posture with the head up, fleeing or frozen near cover, and (3) feeding - the acquisition and ingestion of food items (Estes, 1991).

Statistical analysis

Chi-squared tests were performed to examine the association between species and their presence in the three glade types. The same tests were used to examine associations between species and morning, afternoon and night observation periods. To examine if a given species preferred one or more of the glade types, a chi-square goodness-of-fit value was calculated to measure the disagreement between observed and expected glade-type use frequency for each of the observation periods when the species was present in the glade type (Zar, 1984; Statsoft, 1995). For all of the species, the expected glade-type use frequency was 1:1:3 (or 100% of the observation periods conducted in five man-made, five upper natural and 15 lower natural glades), with the ratio for the total number of observations being 40:40:120 for Warthogs and 60:60:180 for the other ungulates.

Kruskal-Wallis ANOVAs test was used to compare the ungulate behavioral indices and glade-type use for each species, when present during each of the observation periods. Regression analysis was performed for each species to examine the relationship between altitude, and the average group size, average group size per visit to the glade and average time spent by a group in the glade.

RESULTS

There was significant variation between a species presence and absence in the glades for all four ungulate species (Table 1). For warthog, the observed frequency of glade-type use deviated significantly from the expected frequency ($\chi^2_2 = 6.57$, $p < 0.05$); upper natural glades were used less than expected and man-made and lower

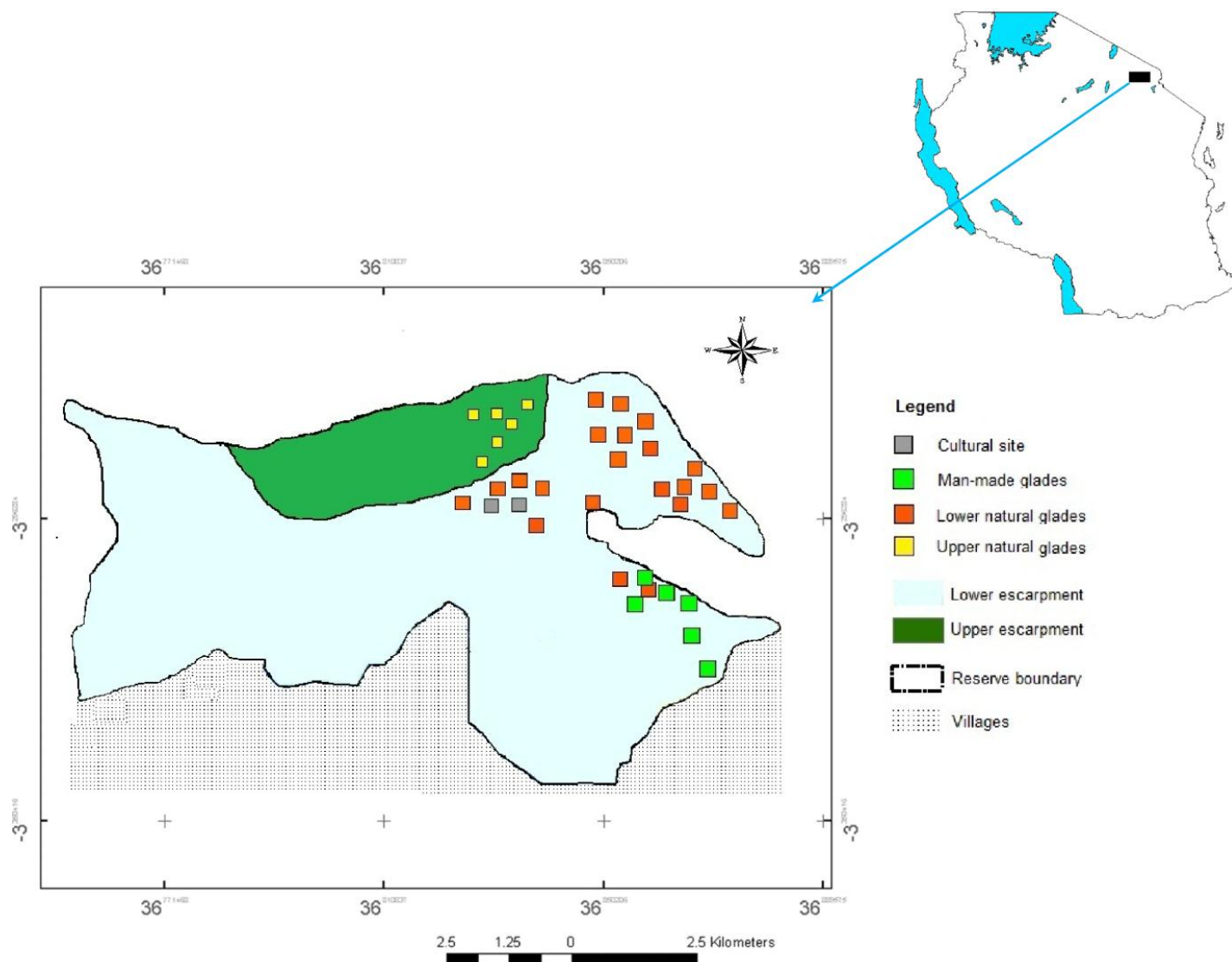


Figure 1. Map of Mount Meru Game Reserve in Tanzania, showing the location of the study area and the distribution of the 33 glades in the Reserve.

Table 1. The frequency of presence or absence in the three glade types for each ungulate species varied significantly, as determined by Chi-square analysis.

Species	Presence (P)/ absence (A)	Number of observation periods by glade type			Total (%)	Chi-square value
		Man-made (%)	Upper natural (%)	Lower natural (%)		
Common warthog	P	26 (65)	11 (27)	70 (58)	107 (54)	14.12 ^a
	A	14 (35)	29 (73)	50 (42)	93 (46)	
	Total	40	40	120	200	
African buffalo	P	15 (25)	30 (50)	33 (18)	78 (26)	23.49 ^a
	A	45 (75)	30 (50)	147 (82)	222 (74)	
	Total	60	60	180	300	

Table 1. Contd.

Mountain Reedbuck	P	36 (60)	29 (48)	50 (28)	115 (38)	22.94 ^a
	A	24 (40)	31 (52)	130 (72)	185 (62)	
	Total	60	60	180	300	
Bushbuck	P	26 (43)	25 (42)	38 (21)	89 (30)	15.83 ^a
	A	34 (57)	35 (58)	142 (79)	211 (70)	
	Total	60	60	180	300	

^a $p < 0.001$

natural glades more than expected. For buffalo, the observed frequency of glade-type use deviated significantly from the expected frequency ($\chi^2_2 = 17.39$, $p < 0.001$); upper natural glades were used more than expected and lower natural glades less than expected. For mountain reedbuck, the observed frequency of glade-type use deviated significantly from the expected frequency ($\chi^2_2 = 14.15$, $p < 0.001$); lower natural glades were used less than expected and man-made glades more than expected. For bushbuck, the observed frequency of glade-type use deviated significantly from the expected frequency ($\chi^2_2 = 11.13$, $p < 0.01$); lower natural glades were used less than expected, and man-made and upper natural glades more than expected.

Significant differences were found in the frequency of species present and absent during the different observation periods in the different glade types (Table 2). The frequency at which the man-made, upper natural and lower natural glades were used for comfort, anti-predator and feeding behavioural activities did not differ significantly ($p > 0.05$) between warthog, buffalo and bushbuck. Significant differences were found for mountain reedbuck in the areas of comfort, anti-predator and feeding parameters (Table 3). For warthog, comfort, anti-predator and feeding behaviours did not change with altitude (all $R^2 > 0.05$). However, for buffalo, mountain reedbuck and bushbuck, some of the behavioural parameters did change significantly with altitude (Table 4).

DISCUSSION

Studies by Irby (1982), Bailey (1984), Howard (1986b), Dunbar and Robert (1992), Barton et al. (1992), Britta and Eduard (2008) who asserted in general, the habitat use by ungulates is dependent on food availability, water, cover, space, topography, and ambient temperatures, which is similar to our findings.

In this study, Common Warthog was the ungulate found in the glades most often. They were present in more than half of the observation periods. More of their time was

spent in man-made and lower natural glades than expected. They were also observed in upper natural, although not as often. Thus, these open grassy areas are particularly important for warthogs. This is no surprise as they are commonly associated with open shorter grassland areas within a continuous forest, especially when water is available within or nearby the grassy areas (Estes, 1991; Skinner and Chimimba, 2005).

Warthog were probably using the glades to graze on the short grasses, sedges, and herbs. The plant species found in man-made and lower natural glades at MMGR that Warthog are known to feed on are the grasses: Couch grass (*Cynodon dactylon*), Smooth flatsedge (*Cyperus laevigatus*), Blue-couch (*Digitaria scalarum*), *Pennisetum mezianum*, African bristlegrass (*Setaria sphacelata*), *Sporobolus africanus*; and the forbs, *Caucalis incognita*, *Conyza floribunda*, *Justicia flava*, *Oxalis cardifolia* and *Oxalis latifolia* (Kahana, Tshwane University, Ph.D. Dissertation, 2013). These plants species attract Common Warthog to graze and root in the interior of these glade-types, and thus, may have influenced their use of man-made and lower natural glades to be more than expected. These results agree with findings of Mason (1982) who reported that warthogs in South Africa graze on grass species, Couch grass (*Cynodon dactylon*), Crab grass (*Digitaria spp.*), and Smut grass (*Sporobolus spp.*).

Although common warthog were not selective regarding altitude, and preferred damp areas as reported earlier by Mason (1982), Estes (1991), Skinner and Chimimba (2005), they avoided upper natural glades. The first reason for this avoidance may be that the ambient temperatures are lower in the upper natural glades and warthogs are intolerant of lower temperatures (Krebs, 1994; Sinclair et al., 2006). The second reason may be that warthogs display predator-sensitive behaviour, as in the upper natural glades the denser closed forest provides adequate cover for leopards (*Panthera pardus*) and other predators to hunt them (Sinclair and Arces 1995a; Peacor, 2002; Nelson et al., 2004).

Thus, man-made and lower natural glades were found to be more useful to common warthog, whereby these

Table 1. Ungulate presence and absence during (morning, afternoon and night) observation periods.

Species/glade types		Observation periods			Total (%)	Chi-square value
		Presence (P)/absence (A)	Morning (%)	Afternoon (%)		
Common Warthog						
Man-made	P	13 (65)	13(65)	None	26(65)	0.00
	A	7 (35)	7 (35)	None	14(35)	
	Total	20	20	None	40	
Upper natural	P	8 (40)	3 (15)	None	11 (28)	3.14
	A	12(60)	17 (85)	None	29 (72)	
	Total	20	20	None	40	
Lower natural	P	28 (37)	42 (47)	None	70 (58)	6.72 ^a
	A	32 (63)	18 (53)	None	50 (42)	
	Total	60	60	None	120	
African Buffalo						
Man-made	P	5 (10)	5(5)	5 (20)	15 (25)	0.00
	A	15 (90)	15 (95)	15 (80)	45 (75)	
	Total	20	20	20	60	
Upper natural	P	14 (70)	9 (45)	7 (35)	30 (50)	5.20
	A	6 (30)	11 (55)	13 (65)	30 (50)	
	Total	20	20	20	60	
Lower natural	P	9 (15)	4 (7)	20 (33)	33 (18)	14.92 ^b
	A	51 (85)	56 (93)	40 (67)	147 (82)	
	Total	60	60	60	180	
Mountain Reedbuck						
Man-made	P	15 (75)	15 (75)	6 (15)	36 (60)	11.25 ^a
	A	5 (25)	5(25)	14 (75)	24 (40)	
	Total	20	20	20	60 (100)	
Upper natural	P	13 (75)	14 (85)	2 (5)	29 (48)	17.75 ^b
	A	7 (25)	6 (15)	18 (95)	31 (52)	
	Total	20	20	20	60	
Lower natural	P	21 (35)	28 (47)	1 (2)	50 (28)	16.46 ^b
	A	39 (65)	32 (5)	59 (98)	130 (72)	
	Total	60	60	60	180	
Bushbuck						
Man-made	P	3 (15)	16(80)	7 (35)	26 (43)	18.05 ^b
	A	17 (85)	4 (20)	13 (65)	34 (57)	
	Total	20	20	20	60	
Upper natural	P	12 (60)	11 (55)	2 (10)	25 (42)	12.48 ^{b*}
	A	8 (40)	9 (45)	18 (90)	35 (58)	
	Total	20	20	20	60	
Lower natural	P	9 (15)	13 (22)	16 (27)	38 (21)	2.47
	A	51 (85)	47 (78)	44 (73)	142 (79)	
	Total	60	60	60	180	

^a p < 0.01; ^b p < 0.001.

glade types provided for their behavioural requirements. It is not clear as to why they were found predominantly in

lower natural glades during the afternoon observation periods. Warthogs may use these glades specifically for

Table 3. Comparison of glade use parameters for three behaviours (comfort, anti-predator and feeding) between the three glade types for Mountain Reedbuck.

Glade use parameter (n = 115)	Glade type			Kruskal Wallis ANOVA =
	Upper natural (n = 29)	Lower natural (n = 50)	Man-made (n = 36)	
Comfort parameters				H _(1,15)
Average number of visits to glade	1.0 ± 0.2	0.6 ± 0.5	2.0 ± 0.4	7.08 ^a
Average group size	2.1 ± 0.3	0.7 ± 0.5	2.3 ± 0.3	10.89 ^b
Average group size per visit	1.6 ± 0.4	0.6 ± 0.4	0.9 ± 1.2	8.87 ^b
Average time (minutes) spent by a group in glade	5.5 ± 1.9	3.3 ± 2.7	11.6 ± 0.5	6.94 ^b
Average time (minutes) spent by a group per visit ^c	4.3 ± 1.9	2.7 ± 1.8	5.0 ± 0.3	2.81
Average time (minutes) spent by individual in glades ^d	2.2 ± 1.3	2.5 ± 1.6	4.4 ± 0.0	5.27
Anti-predator parameters				H _(1,15)
Average number of visits to glade	0.1 ± 0.2	0.5 ± 0.2	0.6 ± 0.3	4.81
Average group size	2.3 ± 0.7	0.5 ± 0.2	1.3 ± 0.6	7.02 ^a
Average group size per visit	2.3 ± 0.7	0.4 ± 0.1	0.9 ± 0.3	7.05 ^a
Average time (minutes) spent by a group in glade	1.3 ± 0.0	2.5 ± 1.1	3.3 ± 1.4	5.24
Average time (minutes) spent by a group per visit ^c	1.3 ± 0.0	1.9 ± 0.7	2.8 ± 1.0	6.02 ^a
Average time (minutes) spent by individual in glades ^d	0.2 ± 0.0	1.8 ± 0.8	1.5 ± 1.0	4.86
Feeding parameters				H _(1,15)
Average number of visits to glade	1.4 ± 0.3	0.8 ± 0.5	2.0 ± 1.6	6.12 ^a
Average group size	3.0 ± 1.4	0.8 ± 0.4	2.5 ± 2.5	6.77 ^a
Average group size per visit	1.7 ± 0.7	0.5 ± 0.2	0.9 ± 0.7	8.22 ^b
Average time (minutes) spent by a group in glade	23.3 ± 13.4	9.5 ± 8.7	23.7 ± 27.0	6.08 ^a
Average time (minutes) spent by a group per visit ^c	16.9 ± 12.4	4.6 ± 3.1	8.1 ± 7.9	5.53
Average time (minutes) spent by individual in glades ^d	8.3 ± 5.8	4.7 ± 3.5	7.2 ± 5.2	5.16

^ap < 0.05; ^bp < 0.01; ^cAverage time spent by a group per visit (in minutes) was calculated by taking the average time spent in the glade by the group divided by the total number of visits by groups to the glade; ^dAverage time spent (in minutes) by an individual reedbuck in the glades was calculated by taking the average time that individuals spent in the glade divided by the total number of animals visiting the glade.

Table 4. Significant relationships were found between altitude, and the average group size, average group size per visit to the glade and average time (minutes) spent by a group in the glade for three of the ungulate species.

Ungulate behavioural parameters	Comfort	Anti-predator	Feeding
	R ²	R ²	R ²
Average group size			
African Buffalo	0.35 ^a	0.02	0.17
Mountain Reedbuck	0.43 ^b	0.03	0.26
Bushbuck	0.02	0.35 ^a	0.39 ^a
Average group size per visit			
Mountain Reedbuck	0.65 ^c	0.04	0.54 ^b

^ap < 0.05; ^bp < 0.01; ^cp < 0.001.

feeding during this period, or they may linger there before returning to their burrows for the night.

African buffalo are grass and roughage feeders who

can digest fibrous food more efficiently than other ungulates (Kingdon, 1982; Estes, 1991). They were observed in glades during 26% of the observation periods,

the least of all of the ungulate species; their primary activity there was foraging. As reported by Kingdon (1982), in the forest, buffalo are commonly found in small groups of up to 12 animals of bulls, cows and their offspring. On this reserve, buffalo were observed in the glades to be in small groups. They used upper natural glades more than expected and group size increased at the higher altitudes of upper natural glades.

Grasses preferred buffalo, such as *Cynodon dactylon*, *Cyperus spp* *Panicum* and *Digitaria* were grazed in all three glade types at MMGR (Kahana, Tshwane University, Ph.D. Dissertation, 2013); similar to earlier findings reported by Vesey-Fitzgerald (1974) for buffalo in Arusha National Park, Tanzania. The upper slopes of MMGR may better suit this species as they were observed using the glades in the upper slopes for water and food more frequently than the glades in the lower slopes (Kingdon, 1982; Estes, 1991, 1993; Skinner and Chimimba, 2005). The interior of upper natural glade had the highest total density of plant stem per hectare, which favours bulk feeders, such as buffalo (Kahana, Tshwane University, Ph.D. Dissertation, 2013). The continuous plant growth supported by the humid forest climate more on the upper slopes attracts buffalo to use these upper glades throughout the year. Given their body size, the lower ambient temperatures in higher altitudes may allow buffalo to feed during the day and, also in the process, expend less energy (Krebs 1994; Sinclair et al., 2006).

African buffalo used lower natural glades less than expected and were present at higher frequencies during the night. They may do so to avoid the higher daytime temperatures associated with the lower glades (Krebs, 1994; Sinclair et al., 2006). Also, buffalo were observed moving up the mountain slope after foraging in the late evening to optimize their physiology and benefit from resource availability (Skinner and Chimimba, 2005; Sinclair et al., 2006).

African buffalo used the man-made glades less often than upper natural and more than lower natural glades; and during all observation periods (morning, afternoon and night), but also mostly at night. They may have been drawn to these glades because of, the presence of forage material and water in or near the glade attracted buffalo to use man-made glades (Skinner and Chimimba, 2005; Fuller et al., 2007), and do so as part of their rotational grazing strategy (Vesey-Fitzgerald, 1974).

Mountain Reedbucks are exclusively grazers and are commonly found in grassy mountain ridges from 1,500 m upwards (Estes, 1991; Skinner and Chimimba, 2005). They were observed during 38% of the total observation periods, with a preference for man-made and upper natural glades, particularly in the morning and afternoon. They also were observed more often in the morning and afternoon in the lower natural glades, although at lower frequencies than during the morning and afternoon in man-made and upper natural glades. Their presence in

all three glades was likely influenced by food availability, the presence of water in or near the glades, and the cover of the forest. Sinclair et al. (2006) and Ndibalema (2007) reported food supply and habitat suitability influence habitat use by animals. Disturbances from humans may be an important reason why mountain reedbuck used lower natural glades less than expected, given their shy nature. Five of the 15 lower natural glades studied were located between 5 and 10 m away from trail routes running through the reserve to villages bordering the reserve and causing disturbances to animals using the glades. Geist (1971) reported that disturbance imposes physiological stress and causes local range shifts in habitat use and hence, reduce carrying capacity. These trail routes have since been closed to reduce human traffic in MMGR (Tanzania National Parks, personal communication).

On this reserve, mountain reedbuck used upper natural glades more than expected and group size and group size per visit increased at these higher altitudes. The reason could be that upper natural glades had the highest plant total density stems per hectare compared to lower natural and man-made glades (Kahana, Tshwane University, Ph.D. Dissertation, 2013). The highest species richness of grasses and forbs and grass total abundance at the forest-glade edge attracted Mountain Reedbuck; the high plant total abundance at the forest-glade edges served as effective cover (Kahana, Tshwane University, Ph.D. Dissertation, 2013). Being an edge user species, the abundant food resources at the edge attracted these animals to use upper natural glades.

Mountain reedbuck were the only ungulate species with significant glade-use behavioural parameters (comfort, anti-predator and feeding) and these were more often observed in man-made glades (during all periods of the day and night), than in upper and lower natural glades. Behavioural parameters included the average number of visits, group size, group size per visit, time spent by a group in a glade, time spent by a group per visit and average time spent in the glades by individuals within the group. As they tend to avoid open areas, the dense vegetation resulting from the management action of clearing of forest-glade edges of man-made glades provided good cover. This attracted mountain reedbuck to perform behavioural activities in man-made glades rather than in upper and lower natural glades. Similar to findings by Irby (1977), plants, such as *Eragrostis tennifolia*, *Pennisetum spp*, *Setaria spp*, *Themeda triandra*, and *Heteropogon contortus* were present and attracted them to feed in all three glade-types (Kahana, Tshwane University, Ph.D. Dissertation, 2013).

In man-made glades, the presence of mountain reedbuck varied with observation period. Their presence was highest in the afternoon, followed by morning and lowest at night. The reason reedbuck were predominantly found in man-made glades in the afternoon is not clear; these glades may be specifically used for feeding during

this period.

Bushbucks are browsers, water dependent and secretive, preferring areas with sufficient cover to conceal them (Kingdon, 1982; Estes, 1991; Estes, 1993). They were only observed during 30% of the observation periods and were more frequently found in man-made glades in the late afternoon and upper natural glades in the morning and afternoon. Bushbuck avoid mid day heat as a strategy for reducing heat stress (Sinclair et al., 2006), during the hotter part of the day, there is a tendency for animals to lie in dense vegetation, whereas in cooler temperatures they are active during the day.

Bushbuck used man-made and upper natural glades more than lower natural glades, similar to mountain reedbuck because of their dependence on cover. The thick vegetation from the management action of clearing forest edges of the man-made glades also provided cover and food for the bushbuck. Thus, these glades also provided the required habitat cover to conceal bushbuck while using glades. The lower natural glades were used less than expected because of disturbance from human activities as previously noted for the mountain reedbuck.

There was a positive correlation between altitude and the average group size of bushbuck feeding in upper natural glades. The reason for this could be due to the availability of water and cover, and minimal disturbance from human activities in upper natural glades. Risk from predators is highest when an animal is actively searching for food (Lima and Dill, 1990; Sutherland, 1996; Whittingham et al. 2004; Whittingham and Evans, 2004; Whittingham et al., 2006). Therefore, they were displaying a predation sensitive foraging behaviour in the upper natural glades by foraging in larger groups (Sinclair and Arces, 1995a; Peacor, 2002; Nelson et al., 2004).

In conclusion, of the four study species, warthog, mountain reedbuck and bushbuck used man-made and lower natural glades more than expected because of the plant quantity and richness and the presence of preferred food and water within or nearby the glades. Man-made glades were particularly important for mountain reedbuck to perform their behavioural activities (comfort, anti-predator and feeding). The use of man-made glades by mountain reedbuck at different times of the day, during different seasons and at different life cycle stages (Jennings et al., 2003) increases the conservation value of these glades. Therefore, the conservation values for man-made glades are deemed to be high due to behavioural uses by mountain reedbuck and also, the presence of buffalo, warthog and bushbuck in these glades. However, allowing the forest to re-invade the glade will lead to a reduction in the size of the area with open grassland, as well as a reduction in the size of the forest-glade edge. This would have significant impacts on interior and edge user species. Thus, the present practice of clearing the forest-glade edges of man-made glades should continue. Otherwise, ungulate species will be forced to use only natural glades or search for similar

habitat types in areas adjacent to MMGR. In addition, our findings support the formation of open grassland areas within continuous forest. New grassland areas should be strategically placed and well-planned. A commitment to continued clearing should be a requirement. Further studies on vegetation changes in relation to grazing intensity and seasonal differences in ungulate usage are required.

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