diversity

Article

Mammal Species Richness at a Catena and Nearby Waterholes during a Drought, Kruger National Park, South Africa

Beanélri B. Janecke

Animal, Wildlife & Grassland Sciences, University of the Free State, 205 Nelson Mandela Road, Park West, Bloemfontein 9301, South Africa; janeckbb@ufs.ac.za; Tel.: +27-51-401-9030

Abstract: Catenas are undulating hillslopes on a granite geology characterised by different soil types that create an environmental gradient from crest to bottom. The main aim was to determine mammal species (>mongoose) present on one catenal slope and its waterholes and group them by feeding guild and body size. Species richness was highest at waterholes (21 species), followed by midslope (19) and sodic patch (16) on the catena. Small differences observed in species presence between zones and waterholes and between survey periods were not significant (p = 0.5267 and p = 0.9139). In total, 33 species were observed with camera traps: 18 herbivore species, 10 carnivores, two insectivores and three omnivores. Eight small mammal species, two dwarf antelopes, 11 medium, six large and six mega-sized mammals were observed. Some species might not have been recorded because of drought, seasonal movement or because they travelled outside the view of cameras. Mammal presence is determined by food availability and accessibility, space, competition, distance to water, habitat preferences, predators, body size, social behaviour, bound to territories, etc. The variety in body size and feeding guilds possibly indicates a functioning catenal ecosystem. This knowledge can be beneficial in monitoring and conservation of species in the park.

Keywords: catena ecosystem; ephemeral mud wallows; habitat use; mammal variety; Skukuza area; species presence; Stevenson-Hamilton supersite

check for updates

Citation: Janecke, B.B. Mammal Species Richness at a Catena and Nearby Waterholes during a Drought, Kruger National Park, South Africa. *Diversity* **2021**, *13*, 387. https://doi.org/10.3390/d13080387

Academic Editor: Michael Wink

Received: 10 July 2021
Accepted: 31 July 2021
Published: 18 August 2021

1. Introduction

The habitat of many species is often distributed in patches across the landscape. Species may occupy several patches or only a few [1]. The number of patches available will influence the type of species and total number of individuals (population sizes) of a species present in a particular landscape. This is related to the distribution and abundance of the species [1]. A landscape is defined by Gertenbach [2] (p. 9) as, "an area with a specific geomorphology, climate, soil and vegetation pattern together with the associated fauna". Animals use certain habitat patches in a landscape based on several factors, such as spatial distribution of resources, ability of animals to use the resources and habitat requirements [3]. Species that are widespread are in general more abundant than species with a restricted occurrence [4,5]. Abundance information can give an indication of the number of individual animals of a certain species that occur in a population. This can provide a basis when making decisions for practical conservation [6]. It can be quite expensive or difficult to obtain abundance information of species at a local scale, depending on the landscape and type of species studied. Usually, being able to predict abundances on a fine-scale from the presence-absence data on a larger scale (that is generally more readily available) can have a considerable application in conservation biology [6]. This current study focussed on small, local scale presence of mammal species at specific habitat patches that can be used as a basis for large scale predictions on the distribution and abundance of mammals in similar areas in the landscape.

The Kruger National Park (KNP) is a savanna ecosystem where heterogeneity and complexity are studied, acknowledged and applied in management practices [7]. Mammal herbivores heavier than 5 kg represent 30 species in KNP, and that is excluding the smaller herbivores, rodents, bats, carnivores, primates, etc. [8]. A defining characteristic of savannas is the continuous herbaceous layer and a discontinuous tree and shrub stratum in the same landscape [7]. Heterogeneity in the landscape influences vegetation patterns and thus also community assemblages, densities of herbivores and predators at different spatial scales [8]. Different scales and factors exist to determine the heterogeneity of savannas, such as variation in soil conditions and properties, topography, rainfall, fire regimes and distribution of surface water [9]. Some abiotic factors, such as distance to water and steep slopes, can limit grazing and browsing in certain areas, while wind and presence of shade will affect where animals can rest and where they will graze [10]. This will impact on mammal presence in a specific area. Biotic factors such as plant productivity, phenology, species composition and forage quality have an impact on the distribution of forage. The time spent by large herbivores in different habitats is usually based on resource levels and its accessibility in that area [10]. This heterogeneity, expressed as for example diversity of habitat types created by differing abiotic and biotic components, is important for the distribution and utilisation of habitat patches by large mammals [9], which will ultimately affect their presence or absence in a local area.

The landscape in the south of Kruger National Park has a granitic geology and is dissected by a large density of streams and slightly undulating catenas [11]. A catena is a hillslope with different soil types and properties arranged in zones from its crest to its footslope. Particles travel downslope creating an environmental gradient in which different vegetation types are associated with the different soil types and soil properties of the zones [12,13]. There is a clear turnover in nutrients and vegetation structure from the uplands of a catenal sequence (nutrient-poor soils associated with broad-leaved savanna type) to the bottomlands (clay-rich, nutrient rich soils associated with fine-leaved savanna type) [7,14].

It was hypothesised in this study that some mammal species might use certain zones on the catena with higher frequency than others, since the diverse vegetation types across a catena create different habitat patches for mammals (food plants available, vegetation structure, space, cover, etc.) The aims of this study were to (1) provide a basic list of mammal species (>mongoose) that are present in the different zones of one catenal slope and at three waterholes in close vicinity, (2) indicate the feeding guild and body size of mammals present and (3) compare the mammal species richness between three short survey periods during a drought. Factors that influence mammal presence or absence were also included from the literature. This study formed part of a larger multidisciplinary project [15] where certain abiotic and biotic components of this catenal ecosystem were investigated. The study area was deliberately kept small to enable the focus of the larger project to be on providing detail of each of these ecosystem components and to find links between them on a small-scale [16]. This proved to be an important multidisciplinary project that can be expanded to the granite supersite on a landscape scale. This specific study covered here forms the foundation for numerous future research possibilities specifically on mammal diversity and how it might change under different environmental conditions.

2. Methods

2.1. Study Area

The park falls in the Savanna Biome and the study area in the Granite Lowveld vegetation type [17], consisting mainly of mixed woodland and thorn thickets [11,18]. The climate is described as semi-arid subtropical with two distinct seasons: a growing season that is hot and occasionally wet and a dormant season that is warm and dry. The average minimum temperature is 5.7 °C in June, and the average maximum temperature is 32.6 °C in January [2,7]. Topography is an undulating landscape derived from granite that covers the sequence of terrain morphology from the bottomlands to the uplands. Uplands are characterized by sandy, coarse, shallow soil overlying rock, while the bottomlands below the seepline are characterized by deep duplex soil—this is a typical catenal pattern. Sodic areas that are found between the crest and drainage line are composed of shallow sand, with high pH and reduced hydraulic conductivity [13,19].

The study was done on one catena/hillslope in the undulating landscape, its closest outcrops and waterholes in the Southern Granite Supersite [11] of Kruger National Park, South Africa. The three waterholes studied had a permanent supply of water throughout the year. Water is extracted from boreholes using either windmill or solar powered pumps and pumped into 2.5 m tall concrete reservoirs with an open top which feeds into a nearby ground-level water trough/artificial waterhole [20]. The catena was divided into four zones based on differences in vegetation and soil types and its position on the hillslope [16]: crest and midslope, sodic patch with small, wet seep area, footslope shrub veld and a riparian area (around the dry drainage line of the Sabi River near Skukuza). In the study area, the pH of the crest was 5, the sodic patch was 8 and the drainage line 6 [16]. The length of the catena from crest to drainage line is about 500 m (0.3 mile), and the width is about 2 km (1.2 mile) on its broadest part, but this is not a true representation of the surface area of the catena since the zones differ in size along its length. The normal annual rainfall of the area is 560 mm. However, a drought was experienced during the study period and according to Skukuza Weather Data only 194 mm rainfall was measured per year during the study period [15]. It was reported as being one of the most severe droughts, due to an El Niño Southern Oscillation event that reached its peak during 2015–2016 [21].

2.2. Procedure

A total of 30 camera traps were distributed randomly on the catena to give the best cover of each zone. This included the mud wallows on the catena, the nearby granite-boulder outcrops (inselbergs) and the three closest permanent waterholes. Bushnell (23), Cuddeback (4), Scoutguard (2) and Little Acorn (1) models with similar trigger response times and field of view ranges were used [15]. Cameras were operational in the growing season for a period of two weeks each during September 2015, March 2016 and March–April 2017 in order to compile the basic list of mammals present and to compare the data of similar survey periods spanning three years. All cameras were checked after one week of operation, and memory cards were replaced. The same positions were used for the three survey periods. Two photographs were taken when a camera was triggered, with a 5 s rest interval in-between.

Cameras on the catena were positioned in such a way to be able to include small (>mongoose) to mega sized mammals at heights ranging from approximately 0.5 m to 1.7 m (higher cameras pointing slightly downwards) depending on how open the view of the camera was [15]. Cameras were facing in a southerly direction as far as possible. Visual surveys of the area were used to determine the positioning of cameras based on recommendations of a camera trapping specialist. Game trials, open clearings, areas with longer distance view, termite mounds and areas where obvious animal activity was noted were selected. To ensure that the entire study area was represented, some areas with denser vegetation were also included. One camera was placed several meters from each waterhole at an average height of 2 m, facing down to include the entire waterhole in the view. This was done to prevent animal tampering that can cause cameras to malfunction (viz. [20]). The waterhole cameras were set to take photos at 5 min intervals, and this was combined with taking photos when the camera was triggered by animal movement. All cameras used infrared flashes to take images during the night, but the cameras were too far for the flash to capture animals at the waterhole during the dark part of the night. Only larger animals in the vicinity of the camera were captured by the waterhole cameras at night. There were also additional cameras placed in vicinity of the waterholes but not looking directly at the waterhole.

2.3. Data Analyses

Data of all the cameras that were positioned in the same catenal zone were combined to determine animal presence in that zone. The waterholes, mud wallows and granite-boulder outcrops were treated as three additional zones/areas. For the purpose of this study, a trigger event is described as the image/s recorded of an individual or group of a mammal species triggering the motion sensor of the camera at a specific time. If the species could not be identified due to blurred photos, it was indicated as Unknown. The date and time stamps on the photographs were used to determine separate events. A new event was recorded when there was an absence of the group or individual for at least 30 min, approximately.

The type of feeder and body size of each species present were confirmed by Estes [22] and tabulated. The total number of trigger events (in other words the number of observations) of each species was calculated per zone. The data were graphically presented as a colour gradient in different blocks—white blocks indicate no observation of that species, while the darker the colour, the higher the total number of events/observations (range) that were noted for that species. The three survey periods were indicated on this colour figure for each zone (including mud wallows, waterholes and granite outcrops, separately). The number of events was counted for all mammal species observed at each of the three waterholes during a survey period and that was totalled per species. The maximum number of individuals of a species that occurred together in a group at the waterholes during one event was indicated in a table for that survey period. Other smaller groups and solitary individuals were observed for the majority of the species visiting waterholes, but only the maximum group size was tabulated.

The Shapiro–Wilk test was used to test for statistical normality of the data. Since data were not normally distributed, the Kruskal–Wallis test was used to determine significant differences between mammal presence (indicated with a 1 if present and 0 if absent) in each catenal zone and between different survey periods, respectively. A 5% level of significance was used. The species richness was measured by the number of different species observed in each zone during a survey period, while the Shannon–Weiner Index measured the diversity and evenness. The zones were included separately in the calculations and the sum totals of the number of events per species were included for the catena and the waterholes including the surrounding areas. A two-way ANOVA was performed on these values to determine significant differences in number of events between zones and survey periods. The vegan package in R was used for the analyses [23].

3. Results

The species richness was rather high for the nutrient poor granites, with 33 mammal species observed in total. These species were subdivided into the following feeding guilds (Table 1): 18 herbivore species (seven grazers, six browsers, two mixed feeders and three general vegetarians), 10 carnivores, two insectivores, and three omnivore species. Eight species are classified as small mammals (mongoose, squirrel, etc.), two as dwarf antelopes (steenbok, duiker), 11 as medium (impala, leopard, etc.), six as large (zebra, lion, etc.) and six as mega-sized mammals (elephant, rhino, etc.)

Due to the global rhino poaching crisis, all detail of rhinoceros species that can be used to determine their exact location was removed from the figures and text. For the remainder of the species, their presence in each zone on the catena (Figure 1a) (including the additional zones/areas—Figure 1b,c) was indicated for each survey period based on number of events/observations. Species with darker colour blocks on Figure 1 were observed with higher frequency (during different events/observations) on the cameras than species with lighter colour blocks. The common species found in all zones, were buffalo, elephant, greater kudu, grey duiker, impala and lion, while the other common species that were only absent from the granite-boulder outcrop area (Figure 1c) were blue wildebeest, giraffe, plains zebra and spotted hyena. Steenbok (water-independent species, like the grey duiker) was only absent at the mud wallows and waterholes (Figure 1b). Mammal species richness was the highest at waterholes (21 species), followed by the midslope (19) and sodic patch (16) on the catena. Four species were found only in the vicinity of a waterhole and not on the catena, namely, banded mongoose, side-striped jackal, vervet monkey and waterbuck.

Table 1. Total list of mammal species, including their scientific names, observed on the catena, granite outcrops and nearby waterholes. Their feeding guild and body sizes relative to each other are also indicated.

Common Name	Scientific Name	Feeding Guild	Size
Aardvark	*Orycteropus afer*	Insectivore	Medium
African wild dog	*Lycaon pictus*	Carnivore	Medium
Banded mongoose	*Mungos mungo*	Carnivore	Small
Black rhinoceros	*Diceros bicornis*	Browser	Mega
Blue wildebeest	*Connochaetes taurinus*	Grazer	Large
Buffalo (Cape)	*Syncerus caffer*	Grazer	Mega
Bushbuck	*Tragelaphus scriptus*	Browser	Medium
Chacma baboon	*Papio ursinus*	Omnivore	Medium
Civet	*Civettictis civetta*	Omnivore	Medium
Dwarf mongoose	*Helogale parvula*	Carnivore	Small
Elephant (African)	*Loxodonta africana*	Mixed feeder	Mega
Genet species	*Genetta* species	Carnivore	Small
Giraffe (South African)	*Giraffa giraffa* (*G. camelopardalis*—old name)	Browser	Mega
Greater kudu	*Tragelaphus strepsiceros*	Browser	Large
Grey/Common duiker	*Sylvicapra grimmia*	Browser	Dwarf
Hippopotamus	*Hippopotamus amphibius*	Grazer	Mega
Impala	*Aepyceros melampus*	Mixed feeder	Medium
Leopard	*Panthera pardus*	Carnivore	Medium
Lion (African)	*Panthera leo*	Carnivore	Large
Plains zebra	*Equus quagga*	Grazer	Large
Porcupine	*Hystrix africaeaustralis*	Vegetarian	Medium
Scrub hare	*Lepus saxatilis*	Vegetarian	Small
Serval	*Leptailurus serval*	Carnivore	Medium
Side-striped jackal	*Canis adustus*	Carnivore	Medium
Slender mongoose	*Galerella sanguinea*	Carnivore	Small
Spotted hyena	*Crocuta crocuta*	Carnivore	Large
Steenbok	*Raphicerus campestris*	Browser	Dwarf
Tree squirrel	*Paraxerus cepapi*	Vegetarian	Small
Vervet monkey	*Chlorocebus pygerythrus*	Omnivore	Small
Warthog	*Phacochoerus africanus*	Grazer	Medium
Waterbuck	*Kobus ellipsiprymnus*	Grazer	Large
White rhinoceros	*Ceratotherium simum*	Grazer	Mega
White-tailed mongoose	*Ichneumia albicauda*	Insectivore	Small

Mammal species observed at each of the waterholes in closest vicinity to the catena could be distinguished more easily (Table 2). During the 2015 survey period, the De la Porte waterhole was closed for maintenance and no data is available. The herd sizes of elephants visiting waterholes differed, including herds of 6, 9, 12, 18, 21 and 30, while impala herd sizes were 5, 12, 20, 40 and 70 over the different survey periods. Species observed at all three waterholes were baboon, buffalo, elephant, giraffe, impala and warthog. Some species that were also present on the catena were observed at only one of the waterholes, such as blue wildebeest, grey duiker, greater kudu and plains zebra. The larger predators were also only observed at one of the three waterholes, i.e., lion, leopard, wild dog and spotted hyena (latter observed at two waterholes), but these results can be biased since accurate night observations were impossible because of the way the cameras were set-up at waterholes. Vervet monkey, bushbuck, waterbuck and hippopotamus were also only captured at one waterhole, albeit different waterholes (Table 2). The differences that are evident between data presented in Figure 1 and Table 2 (i.e., banded mongoose, civet, dwarf mongoose, side-striped jackal, etc.) are because of the additional cameras that were placed at waterholes to cover the vicinity of the waterhole as well, and these data were included in Figure 1 but not in Table 2 where only data from the waterhole itself are presented.

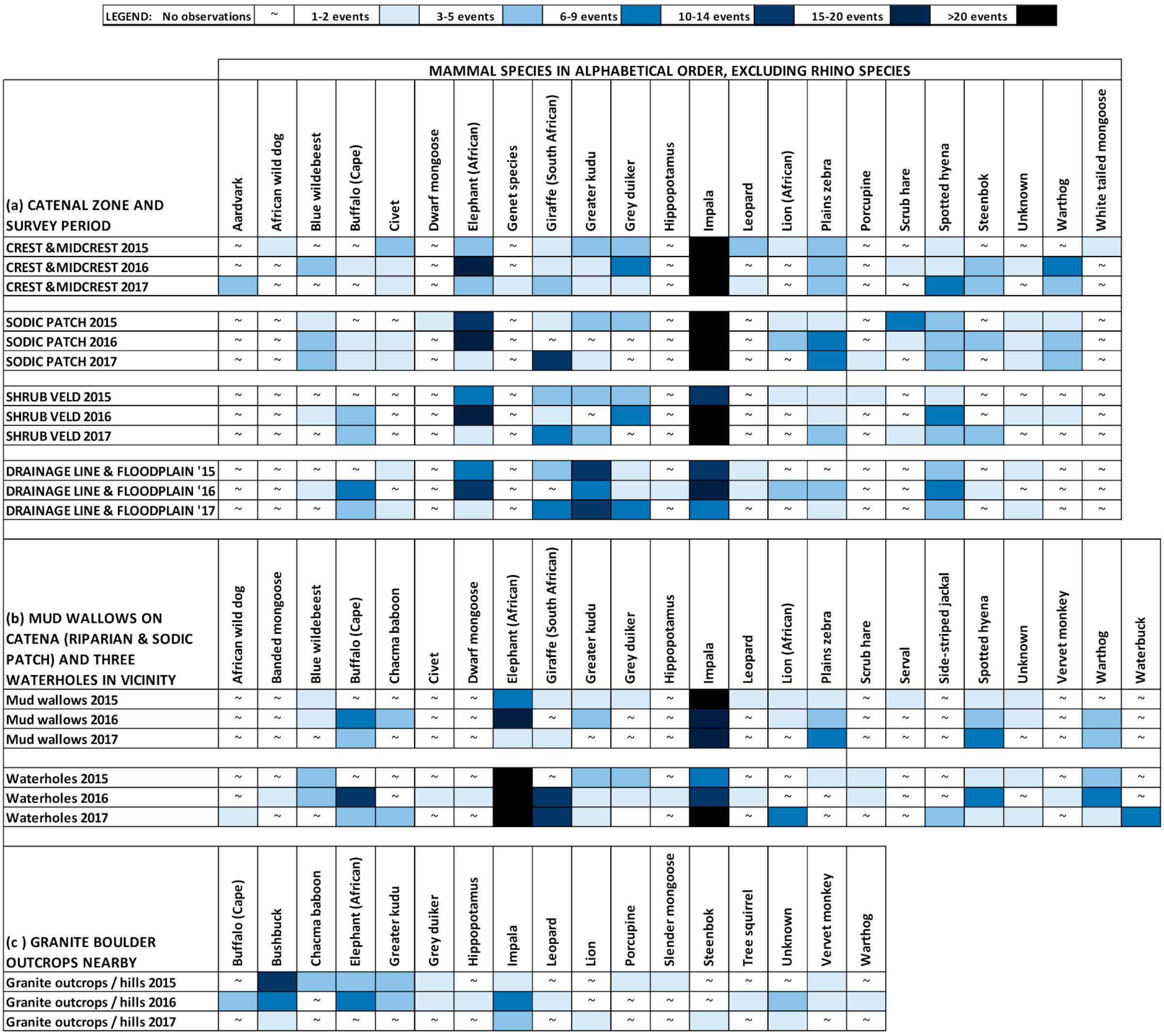

Figure 1. Mammal species (excluding rhino species) present in different zones during three survey periods: (**a**) catenal zones; (**b**) mud wallows, waterholes and (**c**) granite-boulder outcrops. The colour gradient is used to indicate number of events (observations) of each species where increasing numbers were represented by darker colours.

Table 2. Number of events (observations) of the mammal species (excluding rhinos) and the maximum group size observed at each of the three waterholes during that survey period.

Species	Number of Events			Total Events	Max Number of Individuals		
	2015	2016	2017		2015	2016	2017
	De la Porte waterhole						
Baboon	0	1	2	**3**	0	2	2
Buffalo	0	0	1	**1**	0	0	1
Elephant	0	10	25	**35**	0	14	18
Giraffe	0	3	0	**3**	0	11	0
Hippopotamus	0	2	0	**2**	0	5	0
Spotted hyena	0	4	0	**4**	0	1	0
Impala	0	0	4	**4**	0	0	8
Scrub hare	0	1	0	**1**	0	1	0
Warthog	0	1	0	**1**	0	1	0

Table 2. *Cont.*

Species	Number of Events			Total Events	Max Number of Individuals		
	2015	2016	2017		2015	2016	2017
	Kwaggaspan waterhole						
Baboon	0	1	0	**1**	0	2	0
Buffalo	0	4	3	**7**	0	22	30
Bushbuck	0	1	0	**1**	0	1	0
Elephant	14	30	5	**49**	16	21	6
Giraffe	1	1	0	**2**	0	3	1
Grey duiker	4	0	0	**4**	1	0	0
Impala	1	0	2	**3**	1	0	3
Leopard	0	1	0	**1**	0	1	0
Plains zebra	1	0	0	**1**	5	0	0
Scrub hare	1	0	0	**1**	1	0	0
Warthog	4	1	0	**5**	2	1	0
Waterbuck	0	0	9	**9**	0	0	7
	Renosterkoppies waterhole						
Baboon	0	1	1	**2**	0	2	1
Blue wildebeest	1	4	0	**5**	1	3	0
Buffalo	0	5	0	**5**	0	3	0
Elephant	13	16	3	**32**	30	18	1
Giraffe	0	5	10	**15**	0	1	1
Greater kudu	3	1	0	**4**	5	10	0
Impala	3	5	56	**64**	2	70	90
Lion	0	0	7	**7**	0	0	3
Spotted hyena	1	0	0	**1**	1	0	0
Vervet monkey	0	2	0	**2**	0	1	0
Warthog	1	5	1	**7**	0	4	3
Wild dog	0	0	2	**2**	0	0	9

The total number of events and the total number of species per zone were summarised in Table 3. The diversity index values indicating the species richness and evenness in each zone from the number of events were also included, for the sake of completeness. The riparian area (2016 and 2017), granite outcrops (2016) and crest–midslope (2017) had the highest diversity indexes. ANOVA (number of events per species) revealed that all main (Zone and Survey period, respectively: $F(10,10) = 2.077$, $p = 0.132$ and $F(1,10) = 0.287$, $p = 0.604$) and interaction effects ($F(10,10) = 0.324$, $p = 0.955$) were not significant. Small differences were also noted (Figure 1) in presence/absence of some species in the different zones ($H = 2.227$, n = 96, $p = 0.5267$) and between survey periods ($H = 0.180$, n = 99, $p = 0.9139$), but they were not statistically significant. Consequently, there was not enough evidence to test the hypothesis that species may be associated with specific zones. A longer time period is needed for the study and the zones are probably too small, relatively, to limit the mammals to one specific zone.

Table 3. Summary of the sum total of events (observations), species richness (number of species) and the Shannon–Weiner Diversity Index values per survey period for each zone. Total values of the catena and the waterholes (including their surrounding areas) are also indicated.

Zone	Survey Period	Total Events	Species Richness	Shannon Index
Crest and midslope	2015	54	12	1.91
	2016	97	14	1.74
	2017	58	12	2.01
Sodic patch	2015	93	12	1.61
	2016	136	11	1.34
	2017	86	11	1.67
Shrub veld	2015	33	9	1.85
	2016	61	9	1.69
	2017	52	9	1.76
Riparian area	2015	43	8	1.75
	2016	68	13	2.18
	2017	50	9	1.97
Catena total	2015	209	17	1.89
	2016	335	17	1.67
	2017	248	17	2.08
Mud wallows	2015	40	11	1.65
	2016	59	9	1.84
	2017	45	7	1.66
Granite outcrops	2015	28	9	1.83
	2016	36	11	2.03
	2017	9	4	1.15
De la Porte Waterhole	2015	0	0	0.00
	2016	17	7	1.20
	2017	32	4	0.73
Kwaggaspan Waterhole	2015	26	7	1.41
	2016	38	7	0.81
	2017	19	4	1.23
Renosterkoppies Waterhole	2015	22	6	1.28
	2016	44	9	1.89
	2017	80	7	1.05
Waterhole total	2015	73	10	1.38
	2016	150	17	1.98
	2017	191	11	1.36

4. Discussion

4.1. Species Richness and Habitat Description

Mammal species richness on the catena was 23 in total (Table 3) and highest at the crest—midslope (19 species) followed by sodic patch (16), riparian area (15) and shrub veld (14). Similar numbers of species in different zones and between survey periods represent different species that make up the total (Figure 1). In the context of this study, species richness can be defined as the number of different mammal species present in the ecological community [24] associated with the catena and its nearest waterholes. It is merely a count of species and does not take their abundance or distribution in KNP into consideration.

There were little differences (not statistically significant, $p = 0.53$) between species observed across the catenal zones, but a few species could be linked to specific areas outside the catena (Figure 1). The granite-boulder rock outcrops and waterholes delivered some species that were absent in the zones on the catena. A higher-than-expected number of species were noted in vicinity of the outcrops (16 species, Figure 1c), possibly because mammals pass the nearby outcrops en route to one of the waterholes. Rock hyrax and klipspringer (name literary means rock-jumper) are known to be in the area [18] and were expected to be present at these outcrops because they are adapted to such a xeric habitat, but they were not captured on the cameras and thus not included in the results.

Common species found at the catena in this current study were buffalo, elephant, greater kudu, grey duiker, impala, lion, blue wildebeest, giraffe, plains zebra, spotted hyena and steenbok. Siebert and Scogings [7] list similar common species on the catena approximately 40 km away (adjacent to the Sabi River), namely, impala, elephant, hippo, black and white rhino, blue wildebeest, Cape buffalo, plains zebra, greater kudu, steenbok, giraffe and scrub hare. Gertenbach [2] and Sutherland et al. [20] also list the following common species in the larger landscape: impala, greater kudu, steenbok, giraffe, elephant, buffalo, plains zebra, wildebeest, warthog, hippo (at the rivers), lion, leopard, wild dog and spotted hyena.

The zones of the catena, from the crest to the drainage line, consist of different plant communities composed of different densities of trees, shrubs and herbaceous plant species [25] that create different habitat patches for mammals. A large proportion of these plant species are palatable [18] and will most probably be used in different degrees by the herbivore species present, based on their feeding guild. The sodic patch in the study area is reported to be more fertile than the surrounding catenal zones [14], but the grass cover is relatively low, i.e., the sodic patch had a 16% grass cover and the shrub veld zone 32%. The riparian zone at the drainage line had the highest tree canopy cover (33.6% on a 100 m line transect) and the sodic patch the lowest cover (2.7%) [25]. Sodic soils are regarded as a stressful environment for vegetation that is usually sparse but more attractive than the upland vegetation [7]. Sodic areas are attractive to herbivores because of more nutritious vegetation than surrounding areas, predator vigilance, dietary salts or anti-acidosis minerals [13], water in ephemeral depressions and green foliage at wet seep areas. These sodic areas with higher nutrients usually form grazing lawns that are maintained by grazers in a "short-cropped state of high nutritional value", according to Martin et al. [26] (p. 2). However, in comparison to other areas in the KNP, gabbro substrates in the west-central parts of KNP and basalt plains in the eastern parts generate soils of higher fertility leading to more nutritious grazing lawns, while the sandy granitic soils (study area) are less fertile supporting predominantly sourveld [18,26]. The distribution of herbivores in the park is determined by this variation, with higher densities in general in the eastern basaltic soils than on the western granitic soils [19].

It is known that herbivores generally concentrate their foraging in zones that shift through the seasonal cycle up and down with the catenary gradient formed from the crests downward. They move progressively down the slope of the catena in the dry season when availability of nutritious and moist, green food declines upslope, while moving up the profile again during the wet season [8,27]. This catenary movement was not recorded down to the river in this small-scale study—the last part of the catena studied was the third order, dry drainage line. However, the Shannon Diversity Index (H = ~2) was the highest at this drainage line (riparian area) for two survey periods during the drought compared to all the other zones in the study (Table 3). Areas that are closer to rivers have valleys with more drainage lines, and thus, these areas have more moisture than areas on the catenary landscape that are further from rivers, representing the drier crests of the catena [27]. Consequently, the association patterns with rivers suggest that KNP's browsers and mixed feeders prefer these areas closer to the drainage lines in the dry season for the forage it provides [27].

Areas occupied for longer periods contribute to the utilization distribution of the animal and can be connected to activities performed and thus benefits derived, while predator avoidance strategies and accessibility can result in limited use of other areas [28]. A home range is generally defined as a larger general use area traversed by an animal species during routine activities (find food, water, shelter and a mate, avoid predators, etc.) that includes the areas used during different seasons [29,30]. Some areas in the demarcated home range may be occupied simply in transit, i.e., to reach surface water for drinking and seasonal food patches or for escaping predators. Availability of resources and habitat requirements will determine the extent of the area that needs to be traversed in order to fulfil the animal's needs [30]. These among other factors will impact on the species' absence or presence in certain locations and/or zones.

4.2. Waterholes and Ephemeral Mud Wallows

The waterholes had a high mammal species richness in total (21 species), but separately, each waterhole had low species richness and diversity (Table 3). This total number can probably be higher since the smaller and nocturnal mammals might have been missed because of the way the camera traps were set up to cover the entire waterhole and some of the surrounding area. Sutherland et al. [20] reported 26 mammal species at the same three waterholes but also including an additional fourth waterhole during a similar time period. They indicated that carnivores and small herbivores were observed during the night at these four waterholes, while large herbivores and primates visited mostly during the day. Some species, such as elephants and large predators, may monopolise water sources and prevent other species from drinking [5]. This was not observed during the short period of this study, as large numbers and a variety of mammal species were observed at the waterholes, even at the peak of the drought. The three permanent waterholes are located on granitic soils in close vicinity to the study area. They constantly provided drinking water in the drought, since they are filled with underground water by solar pumps and windmills, while ephemeral areas dried up at the beginning of the dry season.

Common species found at the catena were also captured at the waterholes (Figure 1 and Table 2). The black and white rhino were captured at some of the waterholes, but this information is classified. Results from Sutherland et al. [20] correspond roughly to results from this study, i.e., they found an average of 6–7 species at De la Porte for the dry and wet seasons; 3–8 species at Kwaggaspan; and 10–11 species at Renosterkoppies waterholes (compare to Table 2). It is interesting that they reported total numbers of 3 for blue wildebeest, 5 for hippo and 1 warthog that correspond exactly with group sizes observed in this current study. They also listed 3 grey duiker, 2 leopards, 7 scrub hares and 5 side-striped jackals observed in total, but these might be different events and not different individuals. These species were also noted with lower numbers in this study but mostly solitary or in pairs. Species listed by Sutherland et al. [20] that were not captured at the waterholes in this study were cheetah, black-backed jackal, honey badger, southern springhare, steenbok, serval, large spotted genet and white-tailed mongoose that were all captured during the dark part of the night. Some of these species listed were found at the catena or granite outcrops (Figure 1), and only the first four species were completely absent from our results. It is not mentioned at which waterhole these animals were captured, and it may be that these species are present at the N'waswitshaka waterhole included by these authors or that we did not record them during the night.

Based on number of events (Table 2), blue wildebeest, impala and greater kudu seemed to prefer Renosterkoppies waterhole which is the nearest to the catena studied (3.3 km in a straight line), while plains zebra was only captured at the Kwaggaspan waterhole (4.6 km in straight line). Hippopotamuses depend on water-related landscapes but are also known to graze several kilometres from water [18,22,31]. In the study area, hippos were observed quite far from the perennial water sources (i.e., the closest point to the Sabi River is 13.2 km in a straight line) and were found in the drainage line (riparian zone) (Figure 1) and at two of the nearest waterholes only during 2016 at the peak of the drought. Elephant are also known to occur 15–24 km from water in drought conditions [31]. Hippo was captured in 2016 at the De la Porte waterhole, which was the furthest from the catena studied, namely 6.2 km in a straight line, while waterbuck only occurred at the Kwaggaspan waterhole during 2017 at the end of the drought. These latter two species have water-related habitat requirements and are known to stay in close proximity of surface water. The grey duiker is known to be water independent and was not captured while drinking at the Kwaggaspan waterhole, it was just passing by the camera probably en route to reach specific forage patches in its territory.

Water-dependent species require water regularly and can range 5–6 km (non-mobile species: impala, bushbuck, warthog) or up to 10 km distances (mobile species: buffalo, zebra, blue wildebeest) from water [31,32]. Some of the listed species (Table 2) prefer to stay close to surface water, e.g., waterbuck, and they were not expected at the catena which is further away. Buffalo and waterbuck were found farther from surface water where lower forage quantity was available in dry years, while zebra, wildebeest, elephant and impala were found farther with lower forage quality [5,28,33,34]. In the nutrient poor granites (compared to the basalts), the quality and quantity of food are lower, and animals have to travel further from water than in basalt areas where their forage and water needs can be satisfied closer to the waterholes [27].

Irregular availability of water in semi-arid savannas can affect the distribution of mammals, together with the distribution of forage and certain habitat effects. Animals often migrate long distances in response to food and water availability [9,27,35]. In areas where permanent water is provided artificially, the significance of water as a limiting resource or as driver for migration patterns in dry periods is suppressed, as is the case in KNP [5]. If herbivores aggregate near waterholes, predators may also concentrate in the vicinity [26]. Grazers occurred closer to water than expected by Smit et al. [27], while mixed feeders and browsers occurred at high densities close to the rivers but at low densities close to waterholes. Waterbuck and elephant are very water-dependent and tend to be more associated with rivers than with artificial waterholes, while buffalo were found to use both rivers and waterholes. Rivers provide water, habitat and forage to these species [27]. The three waterholes are less than 6 km from the centre of the study area and the closest point to the perennial Sabi River is 13.2 km from the study area, so the area is still within reach of many of the water-dependent species, especially the more mobile species. According to Smit and Grant [5] (p. 69), "An increase in distance to the closest water source implies higher costs in terms of energy spent during travelling, as well as energy "not gained" due to time spent travelling instead of foraging." Additionally, they also state that a larger distance travelled may increase the chances of encountering predators and increase calf mortality due to exhaustion.

The distance to permanent water sources together with many other factors plays a role in the use of ephemeral sources by a mammal species, including the number of animals that can be supported by the ephemeral source, quality and accessibility of the water, other specific conditions that can be limiting and the period of time that the source contains water [31]. Ephemeral water source location depends on the topography and geology of an ecosystem together with rainfall fluctuations in that area. These water sources differ over a range of temporal scales, from small pans or mud wallows formed by rainstorms during the dry season that only contain water for a few days or weeks to pools formed in seasonal rivers that are available throughout the dry season [31,34].

Mud wallows in the study area are located on the sodic patch (with shallow rock beds) and in the riparian area. It contained water during the 2015 and 2016 survey periods but not during 2017. Mud wallows are depressions (small pans) in the ground that temporarily fill with rainwater, hold the water for a certain period thereafter and are maintained by wallowing of animals [15]. These wallows were favoured by species that cover their bodies with mud (i.e., buffalo, elephant, warthog, black and white rhino), while most of the mammals also quenched their thirst at the larger temporary holes on the catena (15 species in total were observed using mud wallows).

Other authors found that herbivores dissipate in KNP and use waterholes less after the first rains when pans and other ephemeral depressions fill with water [20,36]. This enables animals to use areas slightly further away from permanent water. If cover and forage are abundant, animals will probably stay close to the perennial water sources and minimize predation risk by travelling to satisfy water requirements, while the scarcity of food and cover in these areas as result of drought can result in animals dispersing to areas with ephemeral water sources [31]. This will depend on the animal's body size and water dependence. Redfern et al. [31] hypothesized that the distribution of large and mobile water dependent herbivores will be more influenced by ephemeral water sources than perennial sources, while distribution of smaller herbivores that have a fixed territory or specific water related habitat requirements will be limited by perennial water sources.

4.3. Feeding Guild and Body Size

Foraging commonly makes up the largest portion of an animal's mobile activity, especially for large mammals, and basically determines their space occupation [30]. The mammals listed in this study were therefor divided into two main categories, namely, feeding guild and body size. Activity patterns of the mammals observed during the study period were covered in another study [15].

Different feeding guilds were represented in the data, from herbivores to carnivores, scavengers (i.e., jackal, hyena, etc.), insectivores and omnivores (Table 1). These different feeding guilds can indicate a working ecosystem on the catena, especially if it can be linked to different habitats in the zones that include certain biotic and abiotic factors of the catena ecosystem. Herbivores were subdivided into the following dietary classes: grazers that feed mostly on grass and herbaceous material; browsers that feed mostly on leaf material from woody plants, including the concentrate selectors (steenbok and duiker) that select the more nutritious plant parts and fruit; mixed feeders that feed on grass and browse material; and general vegetarians that feed on plant material, such as roots, geophytes, bark, fruits, nuts, etc. Insectivores that feed mostly on insects such as ants, termites and other invertebrates; and omnivores (feed on plant and animal material) [22,37] were also noted.

The order Carnivora contains predators, scavengers and animals that also include large proportions of insects in their diet, such as civet, genet, banded mongoose, dwarf mongoose, slender mongoose and white-tailed mongoose found in this study. Few species are strictly carnivorous; most supplement their diet with fruits, bone, carrion, insects and other invertebrates making it difficult to group them into insectivores, omnivores or carnivores [22]. The majority of predators use the resource 'live prey', but it can be classified into various prey classes with the following characteristics: prey type, size, sex, age, activity periods and habitat needs [38]. Ambush predators (lion and leopard) prefer to hunt in areas with more cover and they are usually more successful during the night [26]. Cursorial predators (wild dog and hyena) need more open areas to run the prey down to exhaustion and then kill it. Some predators (serval, jackal) specialize in rodents and birds and use pouncing and jumping techniques to hunt [22]. All of these carnivores were present in the study area but not limited to specific zones.

Mammalian herbivores that feed on different plant types and parts can optimally utilize the diversity in vegetation resources in the same space [37]. Selective preferences for specific food resource types can generally be expressed by the herbivore either staying in profitable areas for longer times and/or by returning frequently to such areas [26]. Interspecific competition mostly occurs in the dry season when adequate quality forage becomes depleted due to most plants being dormant [28].

Mammal species that are less common generally specialize on a narrow range of resource types, while species that are more abundant usually exploit a wider range of resource types and habitat conditions, according to the niche breadth concepts [3]. Du Toit [8] and Macandza et al. [39] list several authors that describe the various scales at which distinctions in habitat occupation (presence or absence of mammal species) can be recognized, from landscape or biome to vegetation types, habitat to plant species composition of local patches and specific plant parts. Animal factors such as social and behavioural aspects, home range sizes, high- or low-density species, water-dependence, predation, age, sex, among others, also play a role in areas occupied [15]. At landscape scale, some features of resource heterogeneity include vegetation structure of woody plants, soil fertility, distance to water, topography, geomorphology, etc. [39]. Thus, according to Macandza et al. [39] (p. 176), "coexistence among large herbivores may be enabled by distinctions in resource use at one or more of these scales, underlain by differences in body size and morphological adaptations".

A large variety and range in body sizes were indicated in Table 1, from the smallest ruminant antelope, the steenbok (0.5 m shoulder height, 11 kg), to the largest land mammal, the elephant (4 m, 5000 kg), is present in the study area, spanning three orders of magnitude in body mass [8], while carnivores range from dwarf mongoose (0.07 m, 0.27 kg) to lion (1.2 m, 190 kg). There are various mechanisms that regulate food intake that can be connected to body size. Small herbivores usually require less feeding time, and they can spend relatively more time to search for higher quality food items, giving them a patchy distribution. Larger herbivores need to maintain their intake when forage is limited (quantity) and may be forced to consume a lower quality diet resulting in a more even distribution over larger areas in general [10,31,40]. Small mammal distribution may be influenced more by location of cover than distribution of larger species [31], but they may competitively displace the larger guild members away from feeding sites in a horizontal plane for grazers and vertical plane for browsers [8]. However, distribution of large and small species may actually overlap in areas that are resource rich [28,40]. The granite landscape is not nutrient rich compared to other areas in the KNP and only the sodic patch, drainage lines and termite mounds [19] have more nutritious vegetation than the surrounding study area (as explained earlier), but still a variety of mammal species and body sizes were recorded. These species may occupy the same local area because they use different food sources at different heights (based on their body size, morphological and digestive adaptations), and they are not limited to this area only, since they can include other areas in the larger landscape (distribution differences) at different times to meet their nutritional needs and so reduce competition.

4.4. General Discussion

There were small differences between observations in the different survey periods (Figure 1). The Pareto charts for each survey period included in Janecke and Bolton [15] clearly indicate the differences in species presence and frequency of observations. Most of the differences can probably be ascribed to the extreme drought that reached its peak during 2016 and the beginning of 2017 in this area. Some of the smaller mammals were not observed during this period or with low numbers of events (four mongoose species, tree squirrel, scrub hare), while other species might have already been absent at the start of the drought before the study commenced. Vegetation was sparse and the ground bare during the drought. As a result, it could not provide enough cover for mammals, while food resources became limited [15,25,41]. There was variation found in the use of grass communities by the grazers in KNP during this specific drought that was driven by erratic rainfall in different areas of the park, an increase in nutritional stress and in the perceived predation risk and by large-scale variation in the severity of the drought in different areas [21]. Donaldson et al. [21] reported that grazers used the nutritious basalt grazing lawns (Satara area of KNP) much more during the early drought phases in 2014–2015 but that they left in the second drought season (2015–2016) and did not return even after rainfall events.

Food selection, movement rates, dispersion of larger herbivores and other mechanisms that happen at small scales can contribute to explain foraging patterns observed across the landscape at a larger scale. Selection of specific patches and feeding sites (collection of patches in a spatial area that animals forage in during one feeding bout) may play a role in grazing distribution patterns [10]. This may also explain some of the mammal presence or absence in the study area. In heterogeneous habitats, herbivores tend to select nutrient-rich sites more often than sites that are less productive. Large herbivores have spatial memories that are quite accurate, and they will avoid areas with little or no food, as well as patches where food has been depleted based on their memory [10].

Kruger National Park is a large, open park (almost 20,000 km^2—[18]) where the movement of mammals through the park is not limited, except if mammals are bound by their own intraspecies territorial boundaries or by available space [29,42] and food (due to high numbers of animals, geomorphological features or accessibility of food sources) or if they are habitat specific (meaning they can only survive in a specific environment, or vegetation type [8,39]) or influenced by predation risk, to name a few. Thus, a large variety of species that are present in the bigger park can also be present on a small scale at the granite catenas and vice versa. Movement of animals is a key mechanism that allows them to cope with the highly dynamic resource productivity in environments that are spatially heterogeneous [26,35].

5. Conclusions

A total of 33 mammal species were observed in the study area, including the two rhinoceros species. A variety of mammals were present in the study area, but the basic list of mammals provided here can be expanded if a larger area in the same supersite can be included, more camera traps (especially at the waterholes) and longer survey periods (including seasonal and climatic differences) can be used. On the one granitic catena (hillslope) alone, 23 mammal species were found across all four zones, 21 species at the waterholes and their surrounding areas, 16 species at the granite-boulder outcrops and 13 species at the mud wallows, excluding the two rhino species. Some of these species were similar between different zones and areas. A few species only occurred at the outcrops and waterholes but were not observed on the catena. The hypothesis, that specific mammal species might frequent or associate with certain zone/s on the catena, could not be investigated properly in this current study. This could be due to zones being too small to limit mammals to a specific zone in such an open, natural system. Most mammals also need to pass through certain zones to reach waterholes located outside the catena studied. Some species stay close to the waterhole, while others move larger distances away to feed. The two closer waterholes were less than 4.5 km from the centre of the study area and that is close enough for non-mobile water dependent species to reach, while the furthest one was 6 km away and can even be reached by mobile water-dependent species.

If more than one catena can be included in future studies, it could provide a better understanding of how these mammals use similar zones on other hillslopes in the area and how the various feeding guilds interact with the environment on a landscape scale. Small differences were found in mammal species presence between the three survey periods but the extreme drought possibly limited species richness. The presence of a variety of different sized mammals (small to mega-sized) from different feeding guilds (herbivores to carnivores and omnivores) and dietary classes (grazer to browser and mixed feeder) most probably indicate a functioning ecosystem consisting of various interlinked trophic levels.

Some mammal species may not have been recorded because of the extreme drought during the study period (lack of predator cover and food availability forced them to leave the area), normal movement or migration (they are only present during a certain season or opportunistically arrive when conditions are right—which might have been outside the survey periods) or simply because they travelled outside the view of the cameras in the study area. There is thus scope for future studies to add to the basic list of mammals observed during this study to make it more complete, such as to include a longer time period, a wetter period with normal precipitation, seasonal variation, other types of animals (i.e., birds, reptiles, amphibians, small rodents, invertebrates), etc. It is also known that the numbers of certain mammal species (group sizes) can fluctuate seasonally due to availability of food—in summer they aggregate into large groups, while in winter or when conditions become less favourable; they break up into smaller groups and disperse more widely in search of food. All of these factors and more can contribute to the total variety and species richness of catenas inside the Southern Granite Supersite during different climatic, seasonal or environmental conditions. All the knowledge from this study can be beneficial in monitoring and conservation of species in Kruger National Park.

Funding: This research was partially funded by the University of the Free State (UFS) Strategic Research Fund and the NRF Thuthuka Grant (TTK14052267732). The UFS Central Research Fund provided the funds to publish this article.

Institutional Review Board Statement: The study was conducted according to the guidelines of the Declaration of Helsinki and approved by the University of the Free State Interfaculty Animal Ethics Committee (UFS-AED2019/0121 on 22 August 2019).

Informed Consent Statement: Not applicable.

Data Availability Statement: There is no data available from this specific study, but some of the larger multidisciplinary project's data are available at the SANParks Scientific Services repository.

Acknowledgments: Jeremy Bolton, camera trapping specialist from Bushcam Consulting is acknowledged for his part in camera trapping procedures and assistance with data processing of some results. Errol Cason from Department of Animal Science, UFS, is thanked for his assistance with Table 3. The multidisciplinary team of the UFS is acknowledged. Staff at Scientific Services in Skukuza and the game guards from SANParks are also thanked for all their assistance.

Conflicts of Interest: The author declares no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses or interpretation of data; in the writing of the manuscript or in the decision to publish the results.

References

1. Maurer, B.A. The relationship between distribution and abundance in a patchy environment. *Oikos* **1990**, *58*, 181–189. [CrossRef]
2. Gertenbach, W.P.D. Landscapes of the Kruger National Park. *Koedoe* **1983**, *26*, 9–121. [CrossRef]
3. Brown, J.H. On the relationship between abundance and distribution of species. *Am. Nat.* **1984**, *124*, 255–279. [CrossRef]
4. Gaston, K.J. The multiple forms of the interspecific abundance-distribution relationship. *Oikos* **1996**, *76*, 211–220. [CrossRef]
5. Smit, I.P.J.; Grant, C.C. Managing surface-water in a large semi-arid savanna park: Effects on grazer distribution patterns. *J. Nat. Cons.* **2009**, *17*, 61–71. [CrossRef]
6. Tosh, C.A.; Reyers, B.; Van Jaarsveld, A.S. Estimating the abundances of large herbivores in the Kruger National Park using presence-absence data. *Anim. Cons.* **2004**, *7*, 55–61. [CrossRef]
7. Siebert, F.; Scogings, P. Browsing intensity of herbaceous forbs across a semi-arid savanna catenal sequence. *S. Afr. J. Bot.* **2015**, *100*, 69–74. [CrossRef]
8. Du Toit, J.T. Large herbivores and savanna heterogeneity. In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*; Du Toit, J.T., Biggs, H.C., Rogers, K.H., Eds.; Island Press: Washington, DC, USA, 2003; pp. 292–309.
9. Bergstrom, R.; Skarpe, C. The abundance of large wild herbivores in a semi-arid savanna in relation to seasons, pans and livestock. *Afr. J. Ecol.* **1999**, *37*, 12–26. [CrossRef]
10. Bailey, D.W.; Gross, J.E.; Laca, E.A.; Rittenhouse, L.R.; Coughenour, M.B.; Swift, D.M.; Sims, P.I. Mechanisms that result in large herbivore grazing distribution patterns. *J. Range Manag.* **1996**, *49*, 386–400. [CrossRef]
11. Smit, I.P.J.; Riddell, E.S.; Cullum, C.; Petersen, R. Kruger National Park research supersites: Establishing long-term research sites for cross-disciplinary, multiscaled learning. *Koedoe* **2013**, *55*, Art. #1107, 7p. Available online: https://koedoe.co.za/index.php/koedoe/article/view/1107/1489 (accessed on 12 February 2021). [CrossRef]
12. Weil, R.R.; Brady, N.C. *The Nature and Properties of Soils*, 15th ed.; Pearson Education Limited: Harlow, UK, 2016.
13. Khomo, L.M.; Rogers, K.H. Proposed mechanism for the origin of sodic patches in Kruger National Park, South Africa. *Afr. J. Ecol.* **2005**, *43*, 29–34. [CrossRef]
14. Bouwer, D.; Le Roux, P.A.L.; Van Tol, J. Identification of hydropedological flowpaths in Stevenson-Hamilton catena from soil morphological, chemical and hydraulic properties. *Koedoe* **2020**, *62*, a1584. Available online: https://koedoe.co.za/index.php/koedoe/article/view/1584 (accessed on 12 February 2021). [CrossRef]
15. Janecke, B.B.; Bolton, J.G. Variation in mammal diversity and habitat affect heterogeneity and processes of a granite catena. *Koedoe* **2020**, *62*, a1592. Available online: https://koedoe.co.za/index.php/koedoe/article/view/1592 (accessed on 12 February 2021). [CrossRef]
16. Janecke, B.B.; Van Tol, J.; Smit, I.P.J.; Van Aardt, A.C.; Riddell, E.S.; Seaman, M.T.; Swart, W.J.; Du Preez, P.J.; Le Roux, P.A.L. Biotic and abiotic connections on a granitic catena: Framework for multidisciplinary research. *Koedoe* **2020**, *62*, a1600. [CrossRef]
17. Mucina, L.; Rutherford, M.C. (Eds.) *The Vegetation of South. Africa, Lesotho and Swaziland*; Strelizia 19; South African National Biodiversity Institute: Pretoria, South Africa, 2006.
18. Hilton-Barber, B.; Berger, L.R. *Prime Origins Guide to Exploring Kruger. Your Key to Unlocking Kruger's Wildlife Treasure*; Prime Origins: Cape Town, South Africa, 2007.
19. Grant, C.C.; Scholes, M.C. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biol. Conserv.* **2006**, *130*, 426–437. [CrossRef]

20. Sutherland, K.; Ndlovu, M.; Perez-Rodriguez, A. Use of artificial waterholes by animals in the southern region of the Kruger National Park. *Afr. J. Wildl. Res.* **2018**, *48*, 1–14. [CrossRef]
21. Donaldson, J.E.; Parr, C.L.; Mangena, E.H.; Archibald, S. Droughts decouple African savanna grazers from their preferred forage with consequences for grassland productivity. *Ecosystems* **2020**, *23*, 689–701. [CrossRef]
22. Estes, R.D. *The Behavior Guide to African Mammals: Including Hoofed Mammals, Carnivores, Primates*, 20th ed.; University of California Press: Berkeley, South Africa, 2012.
23. Oksanen, J.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.; O'Hara, B.; Simpson, G.; Solymos, P.; Stevens, H.; Wagner, H. Vegan: Community Ecology Package; R Package 2.2-1. 2. 1-2. 2018. Available online: https://www.researchgate.net/publication/313502495_Vegan_Community_Ecology_Package (accessed on 12 February 2021).
24. Colwell, R.K. Biodiversity: Concepts, Patterns and Measurement. In *The Princeton Guide to Ecology*; Simon, A.L., Ed.; Princeton University Press: Princeton, NJ, USA, 2009; pp. 257–263.
25. Janecke, B.B. Vegetation structure and spatial heterogeneity in the Granite Supersite, Kruger National Park. *Koedoe* **2020**, *62*, a1591. Available online: https://koedoe.co.za/index.php/koedoe/article/view/1591 (accessed on 12 February 2021). [CrossRef]
26. Martin, J.; Benhamou, S.; Yoganand, K.; Owen-Smith, N. Coping with Spatial Heterogeneity and Temporal Variability in Resources and Risks: Adaptive Movement Behaviour by a Large Grazing Herbivore. *PLoS ONE* **2015**, *10*, e0118461. [CrossRef]
27. Smit, I.P.J.; Grant, C.C.; Devereux, B.J. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial water sources in a large African savanna park. *Biol. Conserv.* **2007**, *136*, 85–99.
28. Redfern, J.V.; Ryan, S.J.; Getz, W.M. Defining herbivore assemblages in the Kruger National Park: A correlative coherence approach. *Oecologia* **2006**, *146*, 632–640. [CrossRef] [PubMed]
29. Carnaby, T. *Beat About the Bush—Mammals*, 2nd ed.; Jacana Media: Johannesburg, South Africa, 2010.
30. Owen-Smith, N.; Martin, J. Identifying space use at foraging arena scale within the home ranges of large herbivores. *PLoS ONE* **2015**, *10*, e0128821. [CrossRef]
31. Redfern, J.V.; Grant, C.C.; Gaylard, A.; Getz, W.M. Surface water availability in the management of herbivore distributions in an African savanna ecosystem. *J. Arid Environ.* **2005**, *63*, 406–424. [CrossRef]
32. Grossman, D.; Holden, P.L.; Collinson, R.F.H. Veld management on the game ranch. In *Veld management in South Africa*; Tainton, N.M., Ed.; University of Natal Press: Pietermaritzburg, South Africa, 1999; pp. 261–279.
33. Redfern, J.V.; Grant, R.; Biggs, H.; Getz, W.M. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* **2003**, *84*, 2092–2107. [CrossRef]
34. Gaylard, A.; Owen-Smith, N.; Redfern, J. Surface water availability: Implications for heterogeneity and ecosystem processes. In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*; Du Toit, J.T., Biggs, H.C., Rogers, K.H., Eds.; Island Press: Washington, DC, USA, 2003; pp. 171–188.
35. Fryxell, J.M.; Sinclair, A.R.E. Causes and consequences of migration by large herbivores. *Trends Ecol. Evol.* **1988**, *3*, 237–241. [CrossRef]
36. Thrash, I.; Theron, G.; Bothma, J.D.P. Dry season herbivore densities around drinking troughs in the Kruger National Park. *J. Arid. Environ.* **1995**, *29*, 213–219. [CrossRef]
37. Bothma, J.d.P.; Van Rooyen, N.; Van Rooyen, M.W. Using diet and plant resources to set wildlife stocking densities in African savannas. *Wildl. Soc. Bull.* **2004**, *32*, 840–851. [CrossRef]
38. Volmer, R.; Hertler, C. The effect of competition on shared food resources in carnivore guilds. *Q. Int.* **2016**, *413*, 32–43. [CrossRef]
39. Macandza, V.A.; Owen-Smith, N.; Cain, J.W. Habitat and resource partitioning between abundant and relatively rare grazing ungulates. *J. Zool.* **2012**, *287*, 175–185. [CrossRef]
40. Du Toit, J.T.; Owen-Smith, N. Body size, population metabolism, and habitat specialization among large African herbivores. *Am. Nat.* **1989**, *113*, 736–740. [CrossRef]
41. Malherbe, J.; Smit, I.; Wessels, K.; Beukes, P. Recent droughts in the Kruger National Park as reflected in the extreme climate index. *Afr. J. Range For. Sci.* **2020**, *37*, 1–17. [CrossRef]
42. Joubert, S.C.J. Animal behavior. In *Game Ranch Management*, 6th ed.; Bothma, J.d.P., Du Toit, S.G., Eds.; Van Schaik Publishers: Pretoria, South Africa, 2016; pp. 385–391.