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Defining the mechanisms driving grass community (composition and functional trait) shifts in African savannas

Jason Ernest Donaldson

RESPONSE TO REVIEWERS

REVIEWER 1

MAJOR COMMENTS:

COMMENT: My only real criticisms of the thesis were (1) the lack of integration with the broader literature on these subjects, with most of the cited work coming from South Africa,

RESPONSE: Thank you to the reviewer for pointing out the lack of certain east African literature. I apologise for missing certain citations and have added several new citations and text to include the studies that were highlighted. Many of these were directly added to the reviewers' suggestions and I appreciate his advice in relevant literature.

COMMENT: and (2) the strong reliance on a false dichotomy between "fire" versus "herbivore" controlled landscapes.

Regarding point (2): As revealed by most of the work presented. In this thesis, fire and herbivores are complementary and interactive drivers of savanna structure and function. Herbivores can indeed reduce or even eliminate the spread of fire in grassland/savanna landscapes, as has been shown by work on multiple continents. In that sense, one could view heavily grazed semi-arid landscapes as existing in a state where fire has been excluded. This only occurs under a very restricted set of circumstances, as shown by Chapter 2. In the Great Plains of North America, even semi-arid rangelands with precipitation < 400 mm and moderate cattle densities (consuming on average 40% of ANPP) can support fires, provided the dominant grasses have a prostrate structure that allows for fuel contiguity. Only drought and/or extremely high grazing pressure from burrowing rodents can exclude fire from this grassland system. But this does not represent what ecologists define as an alternate stable state — if the herbivores are removed, the system return without outside perturbation back to one that includes fire.

RESPONSE: The first point to be made here is that I do not refer to competition between herbivores and fire but rather between fire and grazers. In contrast to browsers, grazers are reliant on the same grass biomass that supports fire. The reviewer himself has given examples of grazers limiting fire, whether they require high numbers to exclude the fire seems irrelevant to the fact that they are using the same resource. Regarding his last point, my understanding of competition between organisms would lead me to believe that in any competitive relationship when one competitor is removed from a system it would be expected

that another competitor will benefit from their removal and greater access to the relevant resource. This is the exact relationship he describes.

On the other side of this "black/brown world" dichotomy, I am unaware of any case where fire has excluded herbivores from a grassland or savanna system. The 2016 paper by Archibald and Hempson is cited throughout the thesis in support of the idea that fire and herbivores are competitors, but that paper does not present supporting evidence for such competition — it just says "clearly fire and herbivores compete". Here in North America, an extensive, contiguous area of tallgrass prairie (~5000km2) is burnt in its near entirety every year. This black landscape is able to support abundant large herbivores (cattle), and a profitable ranching industry. Without fire, in the short term (several years) the system would support far lower herbivore densities due to bulk limitation of forage quality to ruminants in these types of mesic grasslands/savannas. In the long term, removing fire leads to woody encroachment dramatic decline in the ability of the landscape to support herbivores. Similar patterns have been observed in many African savannas, where fire exclusion has led to woody encroachment and ultimately the decline and/or loss of grazing ruminants. Fire is an essential facilitator of large herbivores, rather than a competitor. This is also true in many East African savannas where I have worked. I don't think it is useful to generalize about fire-grazer interactions without specifying the spatial and temporal patterns of fire in the system and how human inhabitants interact with weather, herbivory, and soil fertility to drive those patterns. In this regard, clear description of the burning regime within the Satara landscape would be useful. This is revealed in part in Chapter 5, but would benefit readers if explained clearly in all papers submitted for publication.

RESPONSE: I appreciate the reviewers' disagreement with the idea that fire can exclude grazers from a system. I also agree that fire facilitates grazing in the short term in the method he describes above. My major point in presenting this dichotomy was to bring the reader's attention to the idea that frequent large fires can lead to changes within the grass community and related grass community traits that have very clear impacts on small-bodied grazers. In doing so I aim to move away from the status quo in current literature which is to ignore fire size when analysing the effects of fire on grazers both in the short and long term. The reviewer has requested that I add a more detailed description of the fire dynamics in the study system and I have added an appendix to aid readers in gaining a clear understanding of the fire within the experimental system. I would like to point out that contrary to the suggestion

that this thesis makes generalisations about fire, this thesis discusses at numerous points the complexities regarding what burn regimes are appropriate where and when.

COMMENT: My only other minor criticism of the thesis is the lack of integration with the broader literature from outside southern Africa. Chapter 4, as well as some element of other chapters, are similar to the work I did for my dissertation in Kenya; hence you can imagine my disappointment that those publications are ignored in the dissertation. Similarly, Chapter 3 makes claims about being novel that only true it the sense that the author is not aware of other studies that have already done this kind of work. This is not a major shortcoming, as I have seen far more egregious omissions of relevant literature by other dissertations, but I still provide some specific instances of omissions below. Overall, this is an excellent thesis and should lead to four high-quality publications that provide important new insights to fire-grazer interactions in savannas.

RESPONSE: Thank you to the reviewer for pointing out the lack of international literature. I apologise for missing certain citations and have added several new citations and text to include the studies that were highlighted. Many of these were directly added to the reviewers' suggestions and I appreciate his advice in relevant literature as I feel these have added to the quality of this work.

MINOR COMMENTS

COMMENT: Page 22: Owen-Smith and Novellie 1982 seems like a strange citation in third to last line —whole books and many more comprehensive papers on this subject have been written since 1982. I suggest starting with Van Soest book from 1994 on ruminant nutrition.

RESPONSE: I have changed this to a more relevant citation – Gordan & Illius 1996 Journal of Animal Ecology

COMMENT: Figure 1.1: "Large fires" needs to be defined.

RESPONSE: I have added text to better describe that I am referring to landscape scale fires in this explanation.

COMMENT: Pg 24, last sentence of the first paragraph does not make logical sense. Fire itself IS the disturbance that promotes grazing.

RESPONSE: Changed to - “In systems managed for wildlife neither management practice is practical, and thus at landscape scales it is unlikely that once a grassland develops into a stable fire driven system that it will switch back to one that promotes grazing without some external effort to change the dominant fire regime.”

COMMENT: Chapter 1 —I would also suspect that the history of human settlements in Kruger has given rise to some of its grazing lawns — humans have been a part of that landscape for thousands of year prior to European settlement, and likely played major role in the fire and the nutrient regime.

RESPONSE: This is certainly the case and is something accepted by most ecologists in Kruger National Park. I do not think that there is anywhere in my thesis where I suggest anything to the contrary.

COMMENT: Page 36 - Specify the scale at which current fire management is focused on increasing heterogeneity.

RESPONSE: I have added the suggested edit. Moreover I have added a more comprehensive description of the current KNP fire management policy to the appendices and separate chapters in line with the second reviewer’s comments.

COMMENT: Page 59 —Re-read the papers at the end of this page carefully. Given the definition of "alternative stable state" in these papers, this dissertation does not provide evidence for two different alternative stable "grazer driven" versus "fire driven" states. Burning a pasture leads to formation of a grazing lawn, but if you remove the grazers, it will go right back to a burnable state —thus the grazing lawn not an alternative stable state.

RESPONSE: I have read these papers carefully and given substantial thought to the comments provided by both reviewers. I have also been through my thesis thoroughly to see where the objections raised here materialize.

At no point in this thesis do I suggest that I am presenting evidence of alternative stable states. I admit that the inclusion of both the terms “alternate” and “alternative” at different points in this thesis have caused unnecessary confusion for which I apologise, but it should be noted that I only use the term “alternative stable states” when presenting arguments made by other authors in my introductory remarks. It was not my intention to suggest that I have shown in this thesis the presence of alternative stable states. Rather, I intended to highlight

the presence of positive consumer-grass feedbacks that maintain alternate states. These alternate states vary in their degree of temporal and spatial stability depending on the extent to which the feedbacks driven by one consumer negatively impact the presence of the other consumers within a given system. I believe that I adequately discussed this topic in the majority of the thesis, but following criticism by both reviewers I have removed mention of Scheffer and Carpernter (2003) which appears to be the main source of confusion.

COMMENT: Page 71. A table listing basic traits of each of these species, such as whether they are rhizomatous, stoloniferous, or bunchgrasses perennial vs. annual, degree of plasticity in leaf angles, etc. would help readers not familiar with the specific study system.

RESPONSE: I have added such a table to appendices.

						Culm orientation (cm)		Internode length (cm)		Leaf length (cm)	
Species	Life history	Stolons	Flowering Height (cm)	Leaf Table Height (cm)	C:N ratio	No grazing	Grazing	No grazing	Grazing	No grazing	Grazing
Aristida congesta congesta (Roem. & Schult)	Perrenial	Absent	79.44	50.88	34.45	80.00	39.17	11.62	3.48	19.44	8.22
Brachiaria eruciformis (Sm.)	Annual	Absent	32.11	25.80	16.93	51.78	1.50	5.39	3.19	11.12	4.06
Bothriochloa radicans (Lehm.)	Perrenial	Present	100.33	80.12	33.23	84.67	73.56	9.73	3.70	19.50	7.84
Cenchrus ciliaris (L.)	Perrenial	Present	77.90	85.02	33.64	77.17	No value	2.94	No value	28.15	No value
Chloris virgata (Sw.)	Perrenial	Present	93.20	68.71	30.68	71.56	26.00	9.49	4.17	14.46	5.76
Digitaria eriantha (Steud.)	Perrenial	Present	98.79	45.77	39.03	83.11	26.11	14.12	8.46	38.22	25.12
Eragrostis cilianensis (All.)	Annual	Absent	53.49	40.90	31.69	78.22	59.11	6.31	5.56	15.09	7.26
Eragrostis superba (Pehr.)	Perrenial	Absent	81.22	63.45	30.65	77.00	4.00	12.63	3.78	28.12	5.81
Heteropogon contortus (L.)	Perrenial	Absent	74.09	49.85	45.34	83.05	54.89	15.42	3.83	14.46	3.42
Panicum coloratum (L.)	Perrenial	Present	106.36	90.85	27.82	79.33	23.28	10.92	4.84	29.46	7.91
Panicum maximum (Jacq.)	Perrenial	Present	103.09	78.30	20.54	85.44	56.89	10.08	7.59	35.91	17.93
Schmidtia pappophoroides (Steud.)	Perrenial	Present	60.03	41.13	32.77	86.78	No value	8.27	No value	17.62	No value
Setaria incrassata (Hochst.)	Perrenial	Absent	106.16	75.29	33.64	81.00	80.00	11.96	7.29	49.03	26.74
Sorghum versicolor (Anderss.)	Annual	Absent	120.81	92.61	25.37	85.00	80.33	12.39	6.01	28.66	14.44
Themeda triandra (Forssk.)	Perrenial	Absent	113.11	88.95	37.36	48.11	14.33	3.50	2.21	3.37	2.43
Tragus berteronianus (Schult)	Annual	Present	23.70	14.79	20.46	79.00	57.50	14.38	6.57	24.29	8.98
Urochloa mosambicensis (Hack.)	Perrenial	Present	96.85	74.53	21.81	80.89	1.75	7.12	4.04	27.70	3.75

COMMENT: Do nutrient inputs from the grazers alter soil nutrient availability on the patch burns as they turn into grazing lawns? See Augustine et al. (2003) for documentation of grazers leading to net nutrient inputs to grazing lawn patches.

RESPONSE: I have read Augustine et al. (2013) and found it an immensely thorough study of the impacts of nutrient additions by herbivores to glades in Kenya. My inclination is that the feeding patterns that we observed during the dry season and the drought by both wildebeest and impala would lead to similar nutrient inputs on burn patches as those observed in Kenya. I believe that both impala and wildebeest are feeding in the broader landscape and using patches as relatively safe resting areas at night. This daily pattern would result in the same process of nutrient input observed by impala in Augustine et al. (2013). Furthermore,

while cattle in the Kenyan system removed nutrient value from these patches this would not occur in the system studied for my thesis where cattle are absent. Unfortunately, we did not have the time or resources to test changes in soil nutrient quantities in detail in the current study.

COMMENT: Page 79: The senescence of the lawn grasses in the absence of post-drought grazing is very interesting. In my study of a Kenyan savanna, I found that after a severe drought, grazers that had emigrated from the study area returned rather quickly after the first rains, and maintained the lawns in a productive state. But where we excluded grazer from lawns, the grasses started to self-shade after approx. 2 month, and declined in productivity (see Augustine and McNaughton 2006). To the extent that a lack of post-drought grazing on lawns is a concern (in terms of those lawns fading out), could another patch burn or bringing cattle in to graze the lawns help solve the problem?

RESPONSE: I appreciate the reviewers' interest in this section of my study. I have added this reference to this chapter to help explain further the patterns I found in this study. I believe that there could certainly be benefits to brining cattle in to not only maintain lawns but also to create lawns in similar ways to those documented by the reviewer and others in east Africa. Unfortunately, I do not believe that the management of KNP is currently in a position to carry such experiments out.

COMMENT: Page 82: You state that "comparative experiments on community-level productivity in African savannas are lacking. See Augustin and McNaughton (2006) and Augustine et al. (2003) for examples from Kenya. I believe the McNaughton (1985) reports on productivity of multiple communities including both bunchgrass and lawn grasses from Serengeti.

RESPONSE: I appreciate the reviewer's distress at my omission of those studies in this statement and I have added text to include these studies.

"Experiments on community level productivity in African savannas have focused on the effects of fire and grazing on tall grass communities (Fay *et al.*, 2003; Knapp *et al.*, 2012) or grazing lawns (Mc Naughton, 1985; Bonnet *et al.*, 2010) separately with comparative experiments in east Africa indicating higher productivity on grazing lawns occurring on abandoned cattle bomas (Augustine et al. 2003; Augustine and Mc Naughton 2006)."

COMMENT: Page 86: Why are the data presented as "relative productivity"? Report the data as actual rather than relative primary productivity. You have used robust methods here (better than what many people use), and can calculate actual primary productivity.

RESPONSE: I have reassessed the values I estimate in the figure and these represent net primary productivity. I have therefore changed the text to indicate this.

COMMENT: Page 90, section on Grass Productivity. This is very similar to the pattern of rain during the drought that I studied in Kenya. See Augustine and McNaughton (2006). The difference in productivity that you report between burned vs. unburned bunchgrass communities in mid-drought rain is very interesting! I suggest you highlight this result in the abstract.

RESPONSE: I appreciate the reviewers' enthusiasm in this regard and will consider adding this to journal submissions.

COMMENT: Page 94, section 5.1. In East Africa, animals do not necessarily move from lawns into tallgrass during drought. You state that "during the late dormant season wildebeest remained on lawns at night and restricted their use of lawn edges where tall bunch grasslands concealed lions, with animals only moving into high risk bunch grasslands in the day time. The patterns of grazer use in this study were largely driven by wildebeest and impala and both these species are likely to be using lawns for predator avoidance even during drought." This is exactly what I document for impala in East Africa — see Augustine (2004).

RESPONSE: Thank you for bringing my attention to this. I have adjusted the text here to include this reference and moved away from the less comprehensive study that I had used to reference the previous statement (Riginos 2015). After looking over the relevant literature again I see that the Augustine (2004) study was far more meticulous in its monitoring of animal use when compared to Riginos (2015) that only utilized two dung counts over the entire year.

"Continued use of lawn systems by grazers during droughts aligns with work done by Augustine (2004) that found similar patterns during a local drought in east Africa where impala in a Kenyan rangeland fed in bunch grasslands during the day but remained on grazing lawns at night to avoid predation. This pattern of use resulted in an overall high utilisation of short grass areas throughout the drought"

COMMENT: Page 95: Same thing in East Africa - in a one-year drought, the few buffalo died, and many cattle died, but most species just showed reduced reproduction (e.g. impala, eland). Zebra migrated out, but later declined due to mortality other locations (Georgiadis et al. 2003; J of Applied Ecology).

RESPONSE: Thank you for the comment. I have added a sentence drawing on this link to work in east Africa.

COMMENT: Last sentence of 5.1: See Boone (2007 in Landscape Ecology) for a nice modelling study demonstrating exactly what you state here. See also Augustine (2010; Aft J of Ecology) for a description of spatial patterns of ungulate responses to a drought.

RESPONSE: Thank you for highlighting this literature.

COMMENT: Section 5.2 — define an "agricultural grazing system". I know many grazing ecosystem that have livestock that I would consider "non-agronomic', and of course many small-scale livestock production systems that are highly "agronomic".

RESPONSE: Changed to “fenced commercial grazing systems”

COMMENT: Note that your system is not "free roaming" — the herbivores are.

RESPONSE: Corrected

COMMENT: Last sentence of section 5.2: what does "if burnt" refer to here - burning the entire landscape, or just burning smaller patches? Why not just apply patch burns on the lawns that are experiencing self-shading, to reinitiate grazer attraction?

RESPONSE: Corrected to “if burnt in large landscape scale fires”

It should be possible to generate the same patches using small burns after the drought on self-shading lawns. However, the point of this particular chapter was to look at the resilience of grazer-grazing lawn feedbacks through a drought event and not suggest management protocols to maintain lawns.

COMMENT: Last paragraph of Chapter 4: Be explicit about the size of fires you are referring to here. I like the concluding sentence, which emphasize; the non-independence of fire and grazing. See also Fuhlendorf et al. 2012 for an entire paper about this conclusion.

RESPONSE: I understand why the reviewer has requested that size of fire be included in the concluding remarks due to the nature of the entire thesis. However, I disagree that is necessary to include in this section of my thesis as here I am referring to any fire event prior to, or during a drought. The size of fires becomes less important during droughts (I show this in Chapter 5) as grazers can maintain substantially larger fires in a short cropped state when productivity is low during drought events. I have therefore not changed the words here.

COMMENT: Chapter 5 — to what extent might the persistence of lawns after drought be related to soil nutrients?

RESPONSE: The persistence of lawns on the Basalts of KNP is almost certainly strongly linked to the underlying soil properties of those areas. Although the underlying soil properties within the study region is fairly ubiquitous (Gertenbach 1983) there is evidence that nutrient concentrations related to extinct and active termite mounds can cause a threefold increase in grazer densities around mounds during the growing season (Grant and Scholes 2006). Moreover, areas with high sodic levels can attract fourfold the grazing densities of the surrounding landscape with the majority of these short-grass grazers. There is therefore a definite impact of the underlying soils but I was unable to disentangle this at the coarse scale I worked at and with the coarse soils data utilized.

REVIEWER 2

MANDATORY CORRECTIONS AND ADDITIONS:

COMMENT: Definition of grazing lawn. This study is centred on grazing lawns; comment about them made repeatedly throughout the introduction. However, the reader encounters no clear definition of a grazing lawn by the end of the introduction. I therefore request a brief, robust definition applicable to all chapters to be presented in the introduction. Refer to comment about grazing lawns in the section "PhD theses should contain a comprehensive literature review" at the end of this report.

RESPONSE: I have added a definition and description of grazing lawns to the introduction.

“African grazing lawns have been defined as grassland areas where grazing by large mammalian herbivores has driven a large depletion in the grass sward height to the extent that grass tillers have been activated resulting in the growth of a prostrate, dense canopy (Mc Naughton, 1984). These short stature, dense canopies are seldom associated with fire as they do not maintain sufficient biomass to burn except under extreme conditions. Rather, the high density fresh regrowth provides nutritious forage for mammalian grazers resulting in active selection for grazing lawns by numerous grazing species (Mc Naughton, 1984; Waldram, Bond and Stock, 2008; Anderson *et al.*, 2010; Kleynhans *et al.*, 2010). Moreover, stimulated grazing lawn growth as a result of defoliation has been shown under controlled experimental conditions (Anderson, Dong and Mc Naughton, 2006; Anderson *et al.*, 2013) and repeated grazing by mammalian herbivores seems to be a requirement for the continued existence of grazing in numerous African systems (see Hempson *et al.*, 2015 for review), leading to suggestions of a co-evolutionary history (Mc Naughton, 1984). Thus, grazing lawns represent grassland systems dominated by grazer dynamics with very little direct influence on their functioning by fire. Despite the definition provided by Mc Naughton (1984) there is still scope for interpretation of what exactly constitutes a grazing lawn in African savannas and defining them in the field can require more detailed definitions. Thus, within each chapter of this thesis I will further define grazing lawns in terms relevant to the work presented.”

COMMENT: Study area appendix. Experimentally created small burns were the foundation for this study (chapters 2, 3, 4); their attraction for grazers the key focus. Use of these experimental burns was monitored using dung counts, a sound technique. In reading through the results of each chapter, lack of knowledge about two factors preclude strong conclusions

being reached. How much other recently burnt area was available to grazers in each year of study, and how many grazers were present in the defined study area that might use the experimental or other burns? That is, if there are large expanses of alternative recently burnt areas in close proximity, the experimental burns might not be well utilised, and vice versa (recognised in Figure 1.1). If herbivore numbers are low, owing for example to mortality or long-distance movement, then attractive experimental habitats might be poorly utilised. I therefore deem it necessary that information is provided on these two aspects. This information will in any event fortify the candidate's position in publications. I suggest it is best included as an appendix so as to minimise disruption to the layout of the thesis. Please note that the required information on fire is already presented in chapter 5 (Figure 5.3, page 113) but not at a resolution by which the reader can judge effects on the experimental burns. For example, from figure 5.3 I speculate that, relative to where I think the experimental plots are positioned in the figure, a very large area to the south burnt in both 2012 and 2014, plus a conspicuous patch in the northeast and the northwest corner burnt in 2014, may have been of sufficient scale to have attracted the more mobile herbivores, specifically wildebeest, zebra and buffalo, away from the experimental site. Figure 5.3 also seems to suggest that other quite large patches were burnt quite close to the experiment in 2015 that would have been attractive during the 2017 season, possibly close enough to have influenced the movement of impala. There is sufficient evidence shown in these maps to expect that fire distribution in the broader landscape would have affected the temporal pattern of herbivore use, but comment about the differences in habitat use seen across herbivore species during a specific period would be sound (equal bias). I read no mention of ungulate density in the study area other than a general reference to Du Toit about large abundances (page 38, line 1). Literature is cited indicating variation in ungulate numbers over the park, so were numbers of relevant species high, average or low over the period of study? This appendix should therefore present data on mammal numbers in the study area for the years of interest, or as best as can be achieved in this regard. The candidate appears to have recognised this shortcoming in his comment about the limitations of experimental work during drought (page 126, lines 4 to 2 from bottom). However, this limitation also applies to field experimental study during non-drought periods. In fact, any field experiment is subject to prevailing influences — they are not truly deserving of the term 'experiment' because all other factors are not held constant. Owing to the importance attributed to predation in his discussion on the use of grazing lawns, it would be useful if this appendix also included information about the densities of lion, spotted hyena, leopard, cheetah, and wild dog in the study area.

RESPONSE: I have added a detailed description of the fires that may have impacted our experiment to the Appendices as requested by the reviewer. This description includes a high resolution figure depicting fires in the landscape during the course of the experiment. I feel that this sufficiently prepares the reader to interoperate the results in the context of interference by external fires.

The reviewer requests on several occasions a detailed outline of the herbivore numbers within the Kruger National Park and specifically the Satara land system. Considering that KNP land managers and scientific services with considerably more resources at their disposal do not have reliable estimates in this regard I feel it is unrealistic to expect a PhD candidate to produce such information. In my opinion, providing the reader with the estimates that do exist for grazer and predator numbers in this region of the park would only prove to give the reader a false impression that accurate species densities and changes in densities are known, which is incorrect.

COMMENT: Description of study area in each chapter. A main purpose for describing a study area in any publication is to enable a reader to make comparison with another site based on the extent of similarity. The candidate has written for a reader already familiar with African savannas and to some extent the Kruger National Park. The amount included about the study area has varied chapter to chapter based on the content of the chapter in question, but I request that all chapters contain a brief statement of the following: mean annual rainfall, coefficient of variation of rainfall, seasonality of rainfall, rainfall for the study years, some statement about summer and winter temperatures, geological substrate, topography, and soil type (SA or USA classification).

RESPONSE: I appreciate the reviewers' concern in this regard and I have thus added substantially more detail to the site descriptions within each chapter. This now includes rainfall, temperature, soil, geological substrate and topography information.

COMMENT: Throughout the thesis I saw no source for authorities of species cited. Include one. It should probably be stated for each chapter considering they have been prepared as individual papers.

RESPONSE: I have corrected this and included binomial authorities in each chapter.

COMMENT: Note that a few Latin binomials are incorrectly spelt on occasion.

Urochloa mosambicensis has only one 's' in 'mos'. berteronianus Page 74, line 2. Both Latin binomials contain incorrect spelling. Page 84, Paragraph second last line. `mosambicensis'. Page 87, section 3.4. Line 8. `mosambicensis' and line 9 `berteronianus'. Page 104. Study area, line 12. `mosambicensis'. Page 107, line 2. `mosambicensis'; space after period for 7.1; plus others.

Setaria incrassata not Setaria incrassate.

RESPONSE: Corrected

COMMENT: Circa should be used only in the context of time, it is not a synonym for approximately. Even days' (page 37) is not an appropriate use. Change to an acceptable term.

RESPONSE: I have corrected this to “approximately”.

COMMENT: The accepted symbol for a statistical mean is X with a bar above, not M. Change throughout.

RESPONSE: Corrected

COMMENT: 'Owen-Smith' and Owen-smith' text and references. Acceptable if the mistake of 'Owen-smith' is as the name appears on the paper.

RESPONSE: Corrected

COMMENT: 'Alternate stable state' and 'alternative stable state'. Choose one version and stick with it. See comment below in "Alternate (alternative) stable states" about the concept. 'Alternate' and 'alternative' are not synonyms.

RESPONSE: I have changed all text to alternate state.

COMMENT: Inappropriate use of an em-dash. An em-dash if skilfully employed can add emphasis to the noun being elaborated (it should only be used following a noun) which renders it a useful punctuation mark in fiction writing. It is, however, not well suited to formal writing such as a thesis and should be used sparingly. In the majority of cases in this thesis em-dashes should be replaced by commas. In many cases in this thesis a hyphen has mistakenly been used in place of an em-dash. Some examples: Abstract: both uses on page 3. Page 26. Replace em-dash either side of 'the white rhino' with commas. Page 103, Line 15,

use em-dashes not hyphens, or preferably use commas. Page 117, Line 20, mixture of em-dash and hyphen, commas recommended.

RESPONSE: I appreciate the reviewers' advice and have corrected all errors in the thesis.

COMMENT: Study area of empirical chapters. Are the very exact co-ordinates (two decimal places) for the study area or for the Kruger National Park (which would be incorrect)?

RESPONSE: These coordinates were for the study area and have been moved in the text accordingly to make this less ambiguous.

COMMENT: Page 21. 1' sentence of first true paragraph. Change to 'availability of forage over time'.

RESPONSE: Corrected

COMMENT: Page 21, last line. This is a first reference to 'tall bunch grasslands' that is subsequently used throughout the thesis for Themeda-dominated grassland in the study area. These are not tall grasslands, neither in a South African nor in a global context, but would usually be referred to as medium-height grassland. Hyparrhenia grassland in West Africa or Konza prairie grassland is tall. There are two options for correction. Qualify use of the term at first mention in the thesis and leave the other statements as they stand, or in anticipation for publication that many reviewers' would not accept the term used change all mention of tall grassland to an international norm of 'medium-height grassland'. Note that this nomenclature is also well established for North American prairies.

RESPONSE: Thank you for pointing this out. I will edit accordingly for publication but in this thesis I have added a definition after the first mention that holds for this thesis.

COMMENT: Page 22, line 7. Remove hyphen after 'from'.

RESPONSE: Corrected

COMMENT: Page 23, 1St sentence below Fig 1.1. Change 'tillers' to 'meristems' — existing tillers are destroyed by fire other than the basal portion within the protected crown, each of which carries a meristem for regrowth.

RESPONSE: Corrected

COMMENT: Page 24, line 9. Change 'practical' (an adjective) to 'practicable' (an adverb).

RESPONSE: Corrected.

COMMENT: Page 28, line 10. Change 'responses' to 'response'

RESPONSE: Corrected.

COMMENT: Page 32. Point 5 mentions impala but there is no mention of impala in any of the preceding points.

RESPONSE: Corrected. I have added a sentence explaining the response of impala.

COMMENT: Page 36. Study site. There is no statement about the general climate of the study area, the rainfall of the study period, any detail about the soils other than that they were clayey, or woody cover (make reference to Table 2.1 or at least give summary value), making it very difficult to compare these results with other study areas. This detail must be included.

RESPONSE: As mentioned in the response above I have added substantially to the site description.

COMMENT: Page 37 line 1. Does Van Oudtshoorn (1999) makes any mention about the dominant grasses of the Satara Land System? A citation should offer direct support for the statement in question.

RESPONSE: I have removed Van Oudtshoorn (1999).

COMMENT: Page 38 line 8, and elsewhere - 'found in grass heights' should be rephrased.

RESPONSE: Corrected

COMMENT: Page 38 lines 3-5. Authorities or source (e.g., Skinner and Chimamba 2005) for mammal binomials should have been given.

RESPONSE: Corrected

COMMENT: Page 39 line 1. "Similar amounts of woody cover and similar abiotic conditions." State the average percent woody cover and state which abiotic variables are similar, preferably using an abbreviated quantitative statement.

RESPONSE: Corrected

COMMENT: Page 39 Table 2.1. Amend the caption to explain the meaning of values placed parentheses. According to mean grass height before the burn, that early season burn had a significantly taller sward than either of the other two treatments. Was this tested? How might it influence interpretation of results?

RESPONSE: Corrected

COMMENT: Page 40 lines 11-14. Describe how grass height was measured. Was it the highest standing piece of grass, with heights therefore distorted by isolated tall culms? Was it average leaf table height? Was it measured or visually estimated?

RESPONSE: I have better described this method as measuring grass leaf table height.

COMMENT: Pages 40/41. What constituted a dung count needs to be described. Line 1 of section 3.4 refers to 'dung events' implying discrete groups of excretory products could be discerned. For buffalo, was it individual pats assuming incorrectly that only one pat is voided during a single excretory event? For impala, was it the number of pellet groups or individual pellets (the latter would possible have given a better indication of total biomass assuming number of pellets scales with body size)? What about summer when an aggregate of impala pellets might be replaced by a soft, semi-fluid pat. For zebra, could individual events be discerned or were the balls of an individual event too scattered?

RESPONSE: I have slightly altered the text in this description to explain that a dung event refers to a single cluster of unique dung. The request seems an over reach of what is realistically possible. To count individual pellets would require over a month to do on most plots alone, and to exactly tell which droppings are from separate individuals would require watching every animal and defeat the purpose of an indirect method. There are obvious and well discussed difficulties with using dung counts as indirect proxy estimates of animal densities. I have addressed these throughout the thesis and our methods follow best practice to reduce error wherever possible.

COMMENT: Figure 2.2 caption. Change 'for each month of 2013' to an accurate description of what is actually shown (figure does not show all months, figure extends into 2014).

RESPONSE: Corrected

COMMENT: Page 46, last true sentence of text. It states "...failed in half the early burn...." but table 2.3 lists failure for two of eight plots which is a quarter. There seems to be an error.

RESPONSE: Corrected to “…failed in a quarter of the early-burn…”

COMMENT: Page 48, line 5 from bottom. Do you mean 'wildlife breeding' — why would national parks support breeders?

RESPONSE: Removed

COMMENT: Page 50, line 6. "and highlights issues with using agricultural-style burning in natural ecosystems" This statement appears to me to unequivocally imply that the manner of burning is a primary reason for decline of the wildebeest population in the KNP. If so, this is not a properly supported conclusion appropriate for a PhD thesis. While this work offers useful evidence for such an influence, a long history of research on the subject has also identified an influence of disruption of migration routes by fencing with escalated adult mortality as an observed consequence, culling, and possible roles of predator pits. Tweak the statement.

RESPONSE: Changed to

“…suggests that wildebeest populations already impacted by the loss of natural migratory routes, heavy predation and culling may be further impacted by loss of habitat resulting from large scale fires in KNP.”

COMMENT: Page 59, line 2 from bottom, page 60, line 2. Upper case 'M' in `Nloy-Meir unless the paper was published with this mistake.

RESPONSE: Corrected

COMMENT: Page 60, line 2. 'successful shift' — value judgement implied, rephrase.

RESPONSE: Corrected to “shift”

COMMENT: Figure 3.1. caption, and on page 62. "Fires occurred once in 2015 on the no-burn plots labelled 2 and 3 due to a runaway lightning ignition." Surely the lightning fires influenced what was presented in figure S2.3 and S2.4 but there is no mention that sample size was adjusted in these figures in order to accommodate this influence. State in the caption as well that the lightning fires occurred during October.

RESPONSE: I have added text to explain this.

COMMENT: Page 62 describes that KNP managers extinguished other fires in the area of the experiment but there is no insight as to the area concerned and how many unplanned fires burnt a portion anyway. This information is central for the reader to understand the availability of other burn patches that might have influenced the attractiveness of the experimental burns. See section "Study area appendix".

RESPONSE: I have added a detailed description of fires to Appendix A.

COMMENT: Page 63, section 3.2, first sentence. Choice of percentage sand should be justified. If a soil sample was obtained, then why was a full textural analysis not done? Percent clay is the most important characteristic of soil texture for both soil fertility and soil water availability.

RESPONSE: A full texture analysis was performed and as stated percent clay could have been used but auto correlated with percentage sand (as would be expected) – I therefore used percent sand to prevent autocorrelation issues within the RDA and related analyses.

COMMENT: Line 5, and throughout. Change 'meters' to 'metres' as a measure of distance because American English has for the most not been used. (But note it remains a disc pasture meter in English.)

RSPONSE: Corrected

COMMENT: Line 6. Change to 'and sand percentage'.

RESPONSE: Corrected

COMMENT: Line 7. Change 'had shown' to 'shows'.

RESPONSE: Corrected

The description about use of a disc to determine the proportion of the plot that had been bitten is ambiguous and needs to be clarified. Was the procedure in fact "we placed a 30 cm diameter disc every 2 m along a transect line and determined for each placement whether there was any bitten grass under the disc". It appears it matters not if it was one or every blade of grass that was eaten. This is fine although it is a low resolution approach, but if correct then it does not give an estimate of "the proportion of the plot that had been bitten". Instead, it gives the frequency with which at least one bite occurs in a 30 cm diameter area. The approach appears to have delivered worthwhile results but the approach would have been

stronger had the proportion of leaves bitten or biomass taken by herbivory been estimated. I suggest that the crudeness of the measure used has obfuscated differences over years and across treatments that are shown in figure 3.2.

RESPONSE: I appreciate the reviewers' specific requests in this regard and I have corrected the wording to better represent these issues both in text and figure captions.

COMMENT: Page 63, second last sentence. If dung was sampled for one month prior and two months following a burn, and each plot was burnt only once a year, then surely it is a total of three and not six months of data collection per plot per year?

RESPONSE: Corrected to three months.

COMMENT: Page 64, Section 3.3. Species composition data.

Use of radius implies tussocks were circular— can this be assumed?

RESPONSE: Yes

COMMENT: Page 64, Section 3.4. Species trait data.

Delete 'Finally'

RESPONSE: Corrected

COMMENT: Line 2. I suggest mention of 'climax' is deleted brings into consideration the nature of successional dynamics of this vegetation, which would be problematic for many reasons. Simply say "we designated an unburned grass patch".

RESPONSE: I agree with the reviewers' comment although climax fire grass is a term well used in the literature. I have deleted it throughout.

COMMENT: Page 65, Section 3.5. Statistical analysis. The method of Hill and Smith (1976) needs a brief descriptive clause to be inserted in order for the reader to gain some insight about this technique—the reader cannot be expected to consult Legendre and Legendre in order to comprehend what is going on.

RESPONSE

COMMENT: Section 4.3. Title — Hypothesis in full.

RESPONSE: Corrected

COMMENT: Figure 3.4 caption. Italicise species names; Ivirgatai; 'incrassata' Page 70, lines 5-7. 'recently ungrazed or unburned' — grazing history of sampled plants before the current growth pattern is not known.

RESPONSE: Corrected

COMMENT: Page 73, section 5.1 'Grass community response to pyric herbivory'. The observation of a negative relationship between cover of Bothriochloa radicans and grazing pressure is not easily reconciled with earlier claims in the thesis that this is a particularly unpalatable species. Is the statement correct?

RESPONSE: I do not agree. Grazing was intense across the plots after fire and resulted in grazing on even low quality grasses. I describe this numerous times within the text and it clearly aligns with this statement.

COMMENT: Page 75, Figure 3.5 caption, and Figure S3.3 caption. Both captions state 2015 whereas the text implies but does not state Figure S3.3 should be 2017.

RESPONSE: Corrected

COMMENT: Page 73, lines 6-7. Change "management of landscapes for commercial pasture" to "use of savannas for livestock grazing" because 'pasture' planting of suitable species for livestock grazing.

RESPONSE: Corrected

COMMENT: Line 8. Delete 'climax'.

RESPONSE: Corrected

COMMENT: Page 73, line 6 from bottom. Lower case `triandra'.

RESPONSE: Corrected

COMMENT: Page 74, Line 11. Change to "a result of our trait selection", i.e., 'of' missing, not 'the'.

RESPONSE: Corrected

COMMENT: Page 74/75. The sentence based on a personal communication with Caroline Lehmann needs to be deleted as no proper evidence has been put forward. Citation of this example awaits its publication.

RESPONSE: Deleted

COMMENT: Page 75, section 5.2. Line 12 of section. Delete 'Once again,' as it is too colloquial.

RESPONSE: Corrected

COMMENT: Page 75, section 5.2. Line 5 of 2nd paragraph. The hyphens should be em-dashes but in any case I would suggest commas are used.

RESPONSE: Corrected

COMMENT: Line 13. Change “palatable" species' to 'species palatable to livestock' or 'species palatable to cattle' so that the reader does not have to second-guess your misgivings about previous use of the term.

RESPONSE: Corrected

COMMENT: Page 75, section 5.2, 2nd paragraph, first sentence. Insert a comma following 'congesta'. This species is not an annual but potentially a short-lived perennial (both congesta congesta and congesta barbicollis) although it may flower and seed in its first season. If it was a true annual Aristida species, then I suggest it was misidentified. In any event, Aristida species in general are recognised as relatively drought-adapted species.

RESPONSE: Species were taken to the SANBI herbarium for confirmation. Aristida congesta is explained in Van Oudsthoorn as an annual or short-lived perennial. In this system during the drought individual plants were seldom present longer than a single season.

COMMENT: Page 76, section 5.3, line 3. 'function' and 'functioning are not the same meaning — a repeated action should take the present participle.

RESPONSE: Corrected

COMMENT: Point 1, line 1. "Droughts are stochastic events" is not a supportable statement; all the work of Tyson and colleagues dating back to the 1970s has been ignored. Inter-annual rainfall variability has been strongly patterned throughout the summer rainfall region of

South Africa. There is evidence emerging that these patterns are and will be affected by global change, but not to my knowledge that it has become a stochastic event. Use another term; this applies throughout the thesis.

RESPONSE: I have removed the term stochastic from in all text.

COMMENT: Point 1, question 1. "When do grazers use lawn grass, bunch grass and burnt bunch-grass communities as their main resource". The question can only be properly addressed if the foraging patterns of grazers are followed in order to determine the proportion of intake contributed by each and every community. Examination of use of plots in only three communities can only reveal the relative use of those three communities. By contrast, questions 2 and 3 are well defined for the study method used. Please alter the phrasing.

RESPONSE: I appreciate the reviewers' criticism here. I have altered the question to indicate that my methods had no clear way of identifying the periods animals spent in all available habitats but rather the time spent within those focused on.

"(1) when do grazers use lawn grass, bunch grass and burnt-bunch grass communities during and after drought events?"

COMMENT: Point 2, line 2. I suggest change to "looking at dung deposition" meaning of 'events' not clear.

RESPONSE: Corrected

COMMENT: Point 3, line 1. Change to "during drought events", i.e., not 'droughts'. Also, 'events' implies more than one drought but the drought is described above as a single drought lasting from 2014 to 2016.

RESPONSE: Corrected

COMMENT: Point 3, lines 3 and 4. Presenting means of this nature to two decimal places is false accuracy. The SE should be reported to one decimal place greater than a mean. Reporting an SE without sample size is pretty meaningless as the reader cannot compute a confidence interval in order to make a comparison with published values. My opinion is that there is no need for statistics of this nature in an abstract. The reader would be better informed if the results were reported something along the lines of "….there was a nine- and

two-fold greater rate of dung deposition on x than on y or z, respectively". The results section can present the hard statistics.

RESPONSE: Corrected. I appreciate the reviewers' personal views on this matter and will consider this when preparing papers for publication.

COMMENT: Point 3, last sentence. Write in past tense. Change "loss" to "reduction". The sentence needs to rewritten because its meaning is not clear. It is a long sentence with a conditional clause whose meaning is not clear plus a second main clause after 'and' that is not a logical sequitur of the preceding main clause.

RESPONSE: Corrected to "However, the most severe impact on lawn productivity was the reduction of grazing pressure after droughts when grazers did not return to feed on the same lawn patches they had frequented pre-drought resulting in grasses self-shading and senescing."

COMMENT: Point 4, line 3. "that (iii) this"

RESPONSE: Corrected

COMMENT: Page 80, line 2. "is the result" — function (functioning) is either singular or an uncountable noun which also takes the singular.

RESPONSE: Corrected

COMMENT: Page 82, line 5. A bunchgrass is also a clonal pattern of growth (see Briske's work). Is it meant to be "capture space through stoloniferous or rhizomatous growth"? Rephrase.

RESPONSE: Corrected

COMMENT: Page 82, line 10. Rephrase "productivity stops" because a rate cannot 'stop' although can decline to zero. Growth can stop.

RESPONSE: Corrected

COMMENT: Page 82, line 4 from bottom. "structurally different" incorrect use of 'divergent'.

RESPONSE: Corrected

COMMENT: Page 83, first paragraph. Rapid recolonization of ground exposed by drought dieback is achieved part by species capable of stoloniferous (and rhizomatous) growth (e.g., Digitaria species) from surviving tufts as compared with a slow, usually less successful process of seedling regeneration bunchgrass. Two relevant references are: (1) Von Maltitz G P (1990) The effect of spatial scale of disturbance on patch dynamics. MSc thesis, University of the Witwatersrand, Johannesburg. (2) O'Connor TG (1991) Patch colonisation in a savanna grassland. Journal of Vegetation Science 2, 254. I would have expected these sorts of relations and attributes to have been revealed by a literature review.

RESPONSE: I have added these references to this section of text and explained in more clear terms that there was evidence of these trends beforehand.

"…with O'Connor (1991) showing that species can rapidly recolonise bare ground after drought dieback if they are capable of rhizomatous or stoloniferous growth compared with those that need to reseed."

COMMENT: Page 83, line 5 from bottom. Question 1 is not addressed by this study because the sources of intake by different herbivore species has not been determined. Instead, the candidate as studied the differences in herbivore use among three vegetation communities. Tweak the statement so that is correct.

RESPONSE: Addressed above

COMMENT: Page 85, Figure 4.1 caption. No need for acronyms in a caption if the full name has been given.

RESPONSE: Corrected

COMMENT: Page 86. Nice study approach but please double check you mean 50 cm^2 for ME and PP plots. This is approximately 7 by 7 cm in size which seems too small for reliable measures of productivity. If a 5 by 5 cm quadrat (i.e., 25 cm' quadrat) was harvested, this means allowing a 1 cm edge effect. Such a fine-scaled approach needs justification. It may be good enough for a true lawn but 1 am not aware of anyone ever having successfully worked at such a fine scale in semi-arid bunchgrass grassland unless the references stated (e.g., Knapp et al 2012) used this scale.

RESPONSE: I thank the reviewer for noting this error. This has been changed to indicate that cages were 25 cm by 25 cm (625 cm^2).

COMMENT: Page 86, line 12 from bottom. Change to "grass growth has stopped" — reason given above. Page 86, final paragraph. I suggest delete the opening clause because it is redundant. What is the motivation for looking at tussock death — is it tied into opening up of space by drought and hence loss of surface area supporting production? The statement implies tussocks entirely comprised the lawn community, with no stoloniferous or rhizomatous species present.

RESPONSE: Corrected

COMMENT: Page 87, section 3.4. Grazer utilisation. Last sentence of first paragraph. Information content of sentence is poor. State the approximate woody cover and approximate values of the abiotic variables considered.

RESPONSE: Corrected to include these details.

COMMENT: Page 90, Table 4.2. The caption states standard deviation but the same values are presented as standard error in the preceding text. Which is it? Reporting of SD or SE is meaningless unless sample size is given.

RESPONSE: Corrected

COMMENT: Page 90, section 4.2, second true sentence. Productivity is a rate, defined in this thesis as gm'month-1. 'Production' is the amount over a defined time period (e.g., monthly production). So the second sentence should commence 'Primary production' not 'Primary productivity'.

RESPONSE: Corrected

COMMENT: Page 90, line 3 from bottom. No evidence presented that self-shading was the cause of senescence.

RESPONSE: Removed

COMMENT: Page 91. Figure 4.2. Either (a) and (b) have been switched the caption or the respective axes were incorrectly labelled.

RESPONSE: Corrected

COMMENT: Last line of caption. "grass growth has stopped" – reason given above.

RESPONSE: Corrected

COMMENT: Page 92, lines 1-2. Reference to carbon stores etc should be deleted from a results section because no evidence is offered. Mechanisms should be discussed in the discussion section following presentation of evidence of grazing pressure in section 4.3.

RESPONSE: Corrected

COMMENT: Page 93, section 5, line 1 of discussion. I suggest change 'Popular theory' to 'Current understanding' doubt this is a formal theory; if it is then 'popular' would not be an acceptable adjective.

RESPONSE: Corrected

COMMENT: Page 93, section 5 'Discussion'. Statements in the opening paragraph are not properly supported the results on account of study design. The study has provided good evidence on differences in herbivore use across three habitats but has not defined the full set of feeding habitats which support each of these species. The findings may well be consistent with the pattern they describe, and this pattern may be in accord with what was shown by Yoganand and Owen-Smith, but it does not constitute evidence that "goes against this for all our study species". Conclusion about the importance of different habitats for each herbivore species would require quantification of the amount of forage harvested from each habitat type. First, even if a unit area of bunch grasslands is not used much, there is a large area of bunch grassland that may result in an overall substantial contribution to intake. (He shows lawns do not cover a large surface area.) Second, only three grass communities have been examined in this study. There are other communities which may prove important, for example, sub-canopy habitat, sodic patches, riparian habitats. Third, especially in the case of impala but also for buffalo, an increasing amount of browse is taken when grass availability declines. However, the main issue is that the design of the study does not allow for comment on the overall importance of these habitats to each herbivore species. This might be poorly received by reviewers so I suggest it is rephrased.

RESPONSE: I thank the reviewer for highlighting these issues. In response I have changed the text in this paragraph to focus more on the higher than expected use of lawns by grazers during the drought. This aligns with the reviewer’s comments that I cannot draw conclusions

of the value of all habitats to grazing species and instead focuses on the unique finding of the intensive use of lawns even during drought.

“Current understanding dictates that having large areas of bunch grasslands in rangeland savannas provides reserve forage for local grazers during the dormant season (Owen-Smith and Novellie, 1982). Our work does not dispute that bunch grasslands provide resources to grazers during droughts but highlights the importance of short grass patches to all study species. Wildebeest in particular were found in high densities on lawn systems when compared with bunch grasslands in the 2015 dormant season and continued to frequent lawns during the 2015/2016 growing season even when rainfall and productivity was severely limited. This is not a unique finding within this system, Yoganand and Owen-Smith (2014) found that wildebeest in the western Kruger National Park rarely use bunch grasslands in average rainfall years with both high predation risk and low forage quality making bunch grasslands an unattractive resource even when alternative food resources are limited. But what is novel for the Kruger National Park that we have shown, is that this trend extends even one season into a severe drought when available graze on lawns is almost completely depleted and the perceived benefits of remaining on lawns by grazers is unlikely to be a nutritional decision.”

COMMENT: Page 94, section 5.1. Second sentence needs to be rewritten. The main problem seems to be that "Owen-Smith" following the closing em-dash (mistakenly a hyphen was used) should probably mark the beginning of a new sentence. Also, this study is compared with one by Riginos but with no information provided about her study other than that it was of a rangeland in East Africa. How different are lion densities? Also change "by Riginos (2015)"; line 5 change "looked at" to "studied".

RESPONSE: I have substantially altered the text in this section due to comments made by other reviewers. This comment is thus no longer relevant.

COMMENT: Page 95. Section 5.2. Line 1. Change 'drop-off' to 'decline'.

RESPONSE: Corrected

COMMENT: The opening sentence is clumsy. I suggest split it into two and start with the statement contained the second main clause

RESPONSE: Corrected

COMMENT: Page 96, line 7, and line 2 from bottom. Change to "grazing pressure"

RESPONSE: Corrected

COMMENT: Last line. Change 'dropping-off to 'declining'. Page 97, line 7 from bottom. Change to 'devoid'.

RESPONSE: Corrected

COMMENT: Lines 4 to 3 from bottom. It can be 'one of the few' or 'the only' but I do not see how it can be ‘on of the only'.

RESPONSE: Corrected

COMMENT: Page 99, line 1. Is it meant to be "Each of fire and grazers"?

RESPONSE: Corrected

COMMENT: Line 3. Delete 'purely'. Should `to establish' not be `to maintain'? This distinction goes to the core of this thesis.

RESPONSE: Corrected

COMMENT: Line 5. Change to 'may become' because climate change is 'expected' not an already demonstrated fact in the area of interest.

RESPONSE: Corrected

COMMENT: Page 99. Somewhere in the study area state the total area mapped in order that the areas stated toward the bottom of page 99 can be better comprehended.

RESPONSE: Added

COMMENT: Page 99, last line. Delete 'stochastic' unless its use can be justified.

RESPONSE: Corrected

COMMENT: Page 101. Line 6 from bottom. What is 'domesticated wildlife system'?

RESPONSE: Corrected

COMMENT: Page 102, second true paragraph, line 3. 'competitive' and 'fast growing' are not generally considered to be complementary traits (e.g., Tilman, Grime). Please tweak so that the implied meaning becomes clearer.

RESPONSE: Corrected

COMMENT: Page 102, second true paragraph, Line Replace 'pasture' for the reason stated earlier.

RESPONSE: Corrected

COMMENT: Page 102, final paragraph, line 2. The statement that these grasses are 'non-grazing adapted' would not receive support. The issue with grazing impacts is the sustained severity of grazing and its timing in relation to phenology. Grasses can also become adapted to grazing in different ways, which Briske in particular has explored well. Rephrase.

RESPONSE: I agree with this voew and have altered the statement to refer to their adaptation as fire-adapted species.

COMMENT: Page 104. Study area, Lines 12 and 13. If Cromsigt and to Beest are the source, that is a study undertaken at a point in time, I question whether it can be stated 'in order of abundance' for a list that contains a number of annual species because their abundance fluctuates markedly over time in an individual manner. Rephrase.

RESPONSE: I have removed the statement in order of abundance.

COMMENT: Lines 6 to 4 from bottom. Is it meant that the original Kruger fence limited the historical migration of wildebeest but that they now have this potential migration route available, or is it meant that the current western boundary limits the potential migration route of wildebeest? Rephrase.

RESPONSE: Corrected to emphasise that the fence has continued to limit any migration.

COMMENT: Figure 5.1 caption. Change to "by Gertenbach (1983)."

RESPONSE: Corrected

COMMENT: Section 3.2, line 1. 'the majority' Line 'becoming dormant' Line Instead of 'well below' give a percentage.

RESPONSE: Corrected

COMMENT: Figure 5.2. In the other chapters the rainfall stations from which data were sourced are named. This graph is probably based on a different source because it covers a different geographical area. Please indicate which stations were used.

RESPONSE: I have added this information to the figure caption.

COMMENT: The figure appears to give total annual rainfall for calendar years, which is inappropriate for this region. Rather, a rainfall year of July to June inclusive should be plotted.

RESPONSE: Ignored as this seems completely irrelevant given the study is described in years.

COMMENT: Page 106, section 3.3, last line. "products developed by Buccini and Hannan (2007)."

RESPONSE: Corrected

COMMENT: Section 3.4, line 6. The sentence commencing 'We followed' needs revision. It is too long and has too many clauses. Issues: 'and measured standing'; 'and recorded the presence of lawn or not'.

RESPONSE: Corrected

“We followed the methods of Cromsigt and te Beest (2014) and walked 750 m transects. Along each transect we measured standing grass height every 2 m using a disc pasture meter (DPM) calibrated for KNP (Zambatis *et al.*, 2006).”

COMMENT: Page 109. Was there any means of assessing the accuracy of a global soil map?

RESPONSE: We have tried this with very little success for a number of other products.

COMMENT: Page 110. Table 5.1 caption, first sentence. The caption appears to be incorrect because it refers to herbivore utilisation of grass communities whereas the text and entries in the first column refer only to change in vegetation state.

RESPONSE: Corrected

COMMENT: Page 111, section 4.2, 1st true paragraph. Concerning statistical statement, reference table rather than repeating statement in the text.

RESPONSE: Corrected

COMMENT: Page 113, Figure 5.3. The figure should have a distance scale and should show north.

RESPONSE: Corrected

COMMENT: Page 114, line 8. Change "for the duration of" to "during the course of"; the former implies this low level was maintained throughout the study.

RESPONSE: Corrected

COMMENT: Page 120, sentence 1. "The interaction between fire and herbivory as shapers of vegetation has received remarkably little attention" is simply incorrect for African savanna woody vegetation. The combined influence of fire and elephants on both savanna and forest vegetation in East Africa had been clearly established by the 1960s and a wealth of quantitative empirical effort concert with modelling was in place by the 1980s.

COMMENT: Page 121, 2nd (1" true) paragraph, line 3. Change to "why do grazer not limit".

RESPONSE: Corrected

COMMENT: Page 121, 2nd (1" true) paragraph, Line 9. 'underutilised' is a value judgement. Rephrase. Figure 6.1, point 4. Change to 'drought results' as only one drought was studied.

RESPONSE: Corrected

COMMENT: Page 125, line 16. 'Ben-Shahar', i.e., an upper case '5' unless printed with a lower case in the paper.

RESPONSE: Corrected

COMMENT: P130. 'Bibliography' should be changed to 'Literature cited'. A bibliography on a subject would be an attempt to list all relevant work on the subject of interest, which is a far cry from the action of the candidate. Instead, he has in keeping with the demand of many journals listed mainly references post 2000. The thesis reads as though almost no

understanding of African savannas existed prior to 2000. I do not think his pattern of citation will be challenged during the publication process and also accept that the format adopted by the candidate is a by-product of university rules which encourage submission of a PhD as a collection of papers. I am, however, disappointed that the university's approach has denied the candidate an opportunity to show his depth of philosophical insight about his subject of study by not requiring a true literature review including pre-2000 material.

RESPONSE: Ignored

COMMENT: Table S2.1. It is not clear whether all species have been reviewed for the column headed 'Evidence of active short grass selection', that is, does `No' mean the species in question does not actively select short grass or that the review based on apparently only four references did not consider these species. 'Short grass' needs to be defined in the table as well.

RESPONSE: I have added an explanation of short grass.

POINTS FOR CONSIDERATION

COMMENT: I thought it may be useful for the candidate to receive comment on a number of points for which I believe there is a different interpretation, or methods which I think could have been done differently. The candidate and supervisors can sift through these when preparing publications or when conceiving future studies that rely on the foundation set in this effort. Alternate (alternative) stable states. Two issues require deeper consideration. The first is the choice between 'alternate' and 'alternative', unless it is argued they are synonyms, with which many workers would not agree. Debate took place about the choice of term when the concept was developed in the 1970s (e.g., May 1975), which concluded that 'alternate' was the correct term. 'Alternate' conveys the notion that one state will come after the other state, that is, an entity can only exist as one or the other at a point in time. 'Alternative' may also be applied to two mutually exclusive states, but practise of choice by the entity is commonly implied in its meaning which is inappropriate for the dynamic under consideration. This distinction has broken down in contemporary literature, with 'alternative' now being commonly employed especially by American workers. Although I prefer 'alternate', I suggest the candidate should choose one and consistently.

RESPONSE: I appreciate the comment and description of the issue. I have changed my writing to refer to alternate state and reframed from referring to stable states throughout my work.

The second issue is the claim of a 'stable' state, based on definition offered by Scheffer and Carpenter (2003) (page 59). The criteria which should be met in order to conclude one is dealing with an 'alternate stable state' are rigorous — Petraitis (2013; Multiple stable states in natural ecosystems. Oxford University Press, New York) offers one statement of such conditions that is too lengthy to recount here (based on Peterson CH 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? The American Naturalist 124, 127-133). He is also critical of some of the Dublin et al example of an alternate stable state resulting from elephants and fire. I am not advocating that the candidate need accept the position of this or other writers, but simply that he become aware that the term 'alternative stable state' could come under critical scrutiny in the rather loose manner in which it is used and confusion in the literature surrounding the concept. Furthermore, the Scheffer and Carpenter (2003) definition presented "alternate states can exist in the same abiotic space if attractors or feedbacks maintain them within a relatively stable average" has implications for this study. First, it may well be the change in abiotic space resulting from nutrient concentration by grazers that emerges as possibly the single most critical process of maintaining grazing lawns, which would arguably be in contradiction of this definition. Requirement for the 'same abiotic space' is listed in most contemporary definitions of alternate stable states, a point which I believe requires more rigorous theoretical examination. Another point is how to measure that your new system is stable, or at least to identify the relevant variables. Is it stability of composition, structure, foliage nutrient content, productivity, or some combination? Certainly for compositional stability, average longevity of constituent species is critical. A number of the species listed as characteristic of grazing lawns initiated through small burns are annuals or short-lived perennials (Chapter 3); highly variable composition can therefore be expected from year to year.

RESPONSE: I appreciate both of the reviewers' critique on these points. I have removed the citation of Scheffer and Carpenter (2003) as I feel it complicated the message I was trying to present.

COMMENT: I found the thesis a little ambivalent in assessing its contribution to theory. (Although clarification of the difference among hypothesis, concept, and theory is first

required.) Although use of insights gained for application in management are clearly and compellingly articulated, state shifts are accorded rather cursory comment. Indeed, despite having introduced alternate stable states as a key lynchpin of theoretical advancement in preceding chapters, I noted that neither state shifts nor any theory about alternate stable states were addressed in the final chapter. From my reading the candidate will not be in a position to make strong comment about state shifts, but he should rather emphasise insight gained about positive feedback processes. They are under-ignored and he has original insight to offer. To this end, please find some relevant comments below in "What is a grazing lawn?", especially regarding fire as a potential agent for initiating a positive feedback process.

RESPONSE: Thank you for the comments in this regard. I have done what I can to reduce the comment on state shifts and tried to focus more on feedbacks and the processes involved in their creation and maintenance. I have not added substantial text in this regard, but rather tweaked numerous small sections of the thesis. I will also be taking these comments into account when preparing work for publication.

COMMENT: Management and conservation issues regarding lawns. At various points throughout the thesis (e.g., pages 121, 124) the candidate argues for increasing the proportion of lawns in KNP at the expense of tall grassland; he accordingly expresses criticism of current fire management policy in KNP. However, as he notes (page 128, section 1.4), fire is used for a number of reasons including controlling bush encroachment, controlling tick loads, improving visibility for tourists, managing grazing resources, and manipulating herbivore movement. I suggest greater caution should be evident in his call for grazing lawns to become the priority, they need to be evaluated within the context of multiple objectives. This task is well beyond the scope of this thesis, but he would face a strong challenge convincing most that grazing lawns are more important than containing bush encroachment. In order to create more lawns using small fires the total area burnt would decrease, a recipe for rapid bush encroachment that would transform substantial area of open grassland. One cannot convincingly argue for a single management objective in the face of competing management challenges. Note also that this is environmental engineering order to attain a pre-determined ideal, and for me was of very similar flavour to logic previously expounded in favour of culling first predators then some prey species in KNP. History has not reflected well on those decisions. As an aside, does the candidate posit that burning policy for KNP on its own explains the amount of lawn grassland currently supported in this system, and why the area of lawn grass has not expanded over time?

RESPONSE: Thank you for the comment. I have repeatedly stated in this thesis that much of the queries the reviewer raises above are personal and subjective, I therefore do not feel that they require incorporation into the thesis. I have also been clear throughout the thesis that fire is not the only driver of lawn loss – low rhino densities and the collapse of the wildebeest migration are repeatedly cited as major drivers of the low lawn cover.

COMMENT: Dung counts. Dung counts were used in this study as an index of herbivore use, a good choice in opinion. The technique is well developed and well researched, such that the methodology used in this study could have been improved. A count of dung of all species lumped together does not recognise that species produce dung at different rates and that different kinds of dung decompose at different rates. An ideal variable would therefore have been to derive the number of individuals of each species. This can be derived from dung counts if the rate of production and the rate of disappearance of dung are known. Rate of dung deposition for each of these species is available in the literature. Rates of disappearance need to be estimated in the field, but this is not an onerous task. The candidate has recognised that dung beetles can cause rapid disappearance of dung in the wet season. Termites can also cause relatively rapid disappearance of dung during the dry season (e.g., Ferrar). The area sampled for dung also needs some consideration. A larger area is needed for a large-bodied mammal that defecates infrequently. I would recommend to the candidate that he employ these elaborations in any future work.

RESPONSE: I appreciate this comment and will take it into account during future work.

COMMENT: Drought as a stochastic event. Drought is repeatedly referred to a stochastic event throughout the thesis. 'Stochastic' is commonly defined as 'governed by the laws of probability' but I understand him to mean that drought might occur in an unpredictable manner (e.g., page 59, 15t true paragraph, line 8; use of 'erratic'). This is not generally accepted. Inter-annual rainfall variability including drought has shown a strong temporal pattern in the summer rainfall region of southern Africa at least up until the 1990s (see Tyson, P.D. & Preston-Whyte, R.A. (2000). The Weather and Climate of Southern Africa. Oxford University Press). The candidate also predicates discussion about the drought he studied on an anticipated increased frequency of drought resulting from global change (pages 59, 75). This is important, but relevant discussion can also be legitimately predicated on the simple fact that drought is a natural component of savanna climate, one whose effect is not well studied.

RESPONSE: I accept that I was incorrect in using the term stochastic and value the reviewers' criticism of this. Furthermore, I appreciate the final comment that climate change is not a necessity for developing the story and will take this into account in future writings.

COMMENT: Multivariate statistics. The candidate has used Redundancy Analysis (RDA) for examining botanical composition. A strong, interpretable pattern was revealed contributing to the success of the study. For purposes of publication, please be aware of the following. RDA is a constrained form of Principal Components Analysis (PCA). It is therefore a linear technique, that is, an assumption for the technique to be valid is that individual species will show a linear response along a latent variable. This is usually judged by the number of zero values in the species-by-sites matrix — there should be very few, ideally none for RDA and PCA. Figure 3.4 suggests that this may not have been the case. (Also note that patterns can be checked a posteriori). It is further noted that three environmental variables, namely distance from water, percentage bitten, and dung, all represent herbivory. Two of these may be redundant, which can affect the pattern extracted in a constrained ordination. I therefore suggest that consideration be given to identifying and removing redundant environmental variables, and to using an alternative ordination technique if there are too many zero values.

RESPONSE: I worked closely with Alan Gardener who wrote the Vegan package in R and works intensively with ordination techniques. I therefore feel confident that this work was carried out correctly. Further, redundant environmental variables were removed as explained in the methods.

COMMENT: Fire as a cognisant entity. The candidate has followed precedent set by others in using terminology which comes close to conferring organismal qualities to fire, not dissimilar to the supra-organism qualities ascribed to vegetation successional states by Clements which eventually were universally rejected. It is obviously part of writing for effect, but an alternative argument is that if ecology is to develop into a respected, mature science, then it needs to employ an accurate, unambiguous lexicon. You may pass this off as unadulterated ravings of incipient senility, but fire does not 'prefer' grasses (what about the vast expanses of conifer forest in the northern hemisphere which regularly burn), it is not a 'consumer because a fire cannot make active choices in the same manner that herbivores make decisions. There is no design to fire unless imposed by human management — its ability to 'consume' is a completely fortuitous outcome of whether there is sufficient fuel of appropriate dryness and contiguity across the landscape experiencing climatic conditions

conducive to the spread of fire fortuitously at the time ignition takes place. Herbivores may reduce fuel load through consumption or increase it through transforming biomass into litter or necromass. An individual fire is an entirely probabilistic outcome with no design. Fire does not therefore 'compete'. The candidate has been successful in drawing contrast between fire and grazing as agents affecting savanna dynamics, but phrasing such as "Fire — inferior competitor but dominant consumer" appears to me to be misplaced. There are limits to what can be achieved through employing simile for grazing and fire but is also obvious that comparison for some aspects is trivial because herbivores take one bite at a time and have to continue taking bites throughout the year if they are to survive. The spatial and temporal patterning of the bites is important, decision by decision, with more opportunity for choice in a relatively open-ended system such as the KNP compared with closed livestock systems. Impact of grazers is by intention, they know their world and decide what to do accordingly. Fires do not —they are not organisms. The candidate has made valuable progress in redefining the relation between fire and grazing for savanna dynamics, but I am not convinced by the terminology employed.

RESPONSE: I accept this criticism from the reviewer. However, I feel he has misinterpreted his own philosophical beliefs as fact. Similar arguments about fires design and decision making could be transferred onto grazing species. I appreciate that understanding the readers comfort in the use of certain terms is not unimportant when looking to publish papers but I would argue that there should be room to engage different audiences and display one’s own interpretation of systems functioning.

COMMENT: Grass swards as forage. Chapter 2 has been accepted publication but for future efforts I suggest better measures can be obtained than simply using sward height. Grazing herbivores select a sward structure in order to maximise intake rate, which is determined by biomass density within a height above ground appropriate for the size and shape of their mouthparts. Non-destructive measures such as the comparative yield method in conjunction with structural measurements offer an alternative for time-efficient measurement of available forage. If the dry-weight rank method is used in conjunction, available forage on a species basis is easily calculated. An alternative of using a disc pasture meter for estimating biomass (chapter 4) raises some problems if the meter has not been calibrated for a target vegetation type. Has it been calibrated for lawns in KNP? Using a DPM for gaining an index of height can also prove problematical because the disc invariably flattens the sward, unless a very light disc is used (which should then be stated).

RESPONSE: I will consider this in future work.

COMMENT: What is a grazing lawn? The subject of study was the initiation and maintenance of grazing lawns. I would therefore have expected the candidate, in a literature review, to present a clear, robust definition of a grazing lawn, describe associated characteristics including expected functional traits of constituent species, identify the circumstances under which lawns may or may not develop, and to catalogue known or likely agents responsible for their initiation. The candidate can rightly counter that all these have been presented but snippets of insight appear throughout the thesis, although the candidate acknowledges that establishment of a grazing lawn is not yet defined (page 126, last sentence of section 1.2). It may be argued that references cited cover all this but the strength of philosophy of a thesis — grazing lawns are, after all, the whole point of this exercise — need to be judged on what is presented not on what can be read elsewhere. For example, a first definition of a grazing lawn appears on page 35. "We defined grazing lawns as areas where high grazing pressure limits grass height below levels required to carry fire, that is, grazing lawns are formed when positive feedbacks promote their maintenance and restrict fire." This perhaps serves as an adequate functional definition for the purpose of the chapter in question, but the definition approaches a tautology in that the central study question of the effect of excluding fire is also the foundation of the definition. It pays no attention to the types of species comprising a lawn. First mention of using composition as a characteristic appears in section 3.4 "Grazer utilisation" (page 87). "We defined lawns as areas where >80% grass and dominated by *Urochloa mossambicensis* (sic) and *Tragus berteroneanus* (sic)". This expansion of definition is logically placed when considering the subject matter of the chapter but it would have been useful for a reader to know what they were dealing with from the outset. This is also a utilitarian definition developed for the study area in question rather than one based on first principles — it would not apply in East African savannas where these species do not occur. Similar statements can be made about inclusion of traits.

The definition should also have been properly motivated. By most standards use of the term 'lawn' implies a near complete dominance of short-statured species growing mainly by means of stoloniferous or rhizomatous growth. The two defining species named above do neither. One is a loosely tufted perennial while the second is an annual. I should like to have read a justification of this state being classed a grazing lawn rather than simply a closely grazed grassland. It is further stated in the opening paragraph of results (page 90) that bunchgrasses were absent from lawns, implying that only species like *Themeda triandra* and *Bothriochloa*

radicans were considered bunchgrasses, not species like *U. mosambicensis*. I am not confident this distinction would be universally accepted; at the least it begs clear definition of the growth form of the last mentioned. My confidence decreased further when reading that bunchgrasses are not clonal — quite the opposite, they are an extremely successful clonal strategy.

RESPONSE: A review including a definition of African grazing lawns has already been published and includes the reviewers' name (see Hempson et al. 2015), re-hashing this work would have done little to improve the work presented in my thesis. I have added a definition to the introduction to improve the readers understanding of a grazing lawn in the initial stages of the thesis. However, as the reviewer points out a number of times above, grazing lawn systems are complex and vary by region and circumstance making "utilitarian definitions" the most readily interpretable to readers in different systems. I have added a table to better indicate the life-history traits of the grass species discussed in the study. I have also ensured that the term "clonal" has been removed.

COMMENT: Agents responsible for initiation of grazing lawns are listed in order to justify the design of the experiment. The list is short: termite mounds, mud wallows, dung middens, sodic sites, and white rhino, all under a general umbrella of disturbances. Hippopotamus are briefly mentioned elsewhere in the thesis although they were arguably the vanguard for work on grazing lawns in African savannas. White rhinos are accorded special recognition, underscoring the need for recognition of the influence of relations among body size, digestive pattern, mouthparts on feeding ecology commented on below. Is this a complete range of agents? What is the relative contribution of each agent, does this contribution change in character in relation to environment (climate, soils) or to the spatial scale of the system it relates to herbivore movement? Are the same agents responsible for the maintenance of a lawn? Does development of a lawn mean a degree of abiotic change has occurred, especially in regard of soil fertility? The above empirical list has not identified a unifying causal agent (nutrient enrichment appears to be a common denominator). An alternative approach is to attempt to identify why a small patch might be formed which becomes attractive to, and subsequently positively reinforced by, grazers. It is unlikely there is a complete answer yet available, and this thesis makes a useful contribution, but the value of its contribution would have been more clearly evident if the context had been comprehensively presented in a literature review. A review could also have explored questions surrounding the role of small fires, the focus of the study, serving as a natural agent of lawn formation. Although chapters

two, three and four provide compelling evidence that small fires can be used by management to redress any perceived imbalance in lawn cover, would small fires have served in a natural system as a causal agent of grazing lawns? (This is related to comment elsewhere about the ambivalence of the main intent of this thesis — is it intended to resolve key theoretical issues or develop management approaches, or both?) If positive feedback of grazing on patch development is most likely when there are a few small burns in an otherwise large unburnt area during a period when there is a relatively high density of wildebeest, impala and zebra, among others, resident in the same landscape, then a number of questions could have been reviewed. What is the distribution of fire size in relation to both temporally varying and spatially varying factors? Under what circumstances might small fires occur? What is the probability of the same small patch being burnt more than one year in a row in an otherwise lightly burnt landscape? Interesting observation was made on lightning-induced fires, might these not be pivotal for this dynamic? If definition of a grazing lawn is critically dependent on height (see especially chapter 2) then influences which maintain short grass should be reviewed. The candidate alludes to one important influence of mean annual rainfall on lawns becoming tall or not (page line 4 from bottom; page 127, opening sentences of 1st true paragraph) but this statement, in fact, reflects a general influence of plant water availability. In a semi-arid climate prone to drought with heavy clay soils (his study environment), plant available water is dependent not only on rainfall but also on factors influencing water retention and water loss. I make a few comments because I gained the impression that the importance of water loss was not recognised for his study conditions. Water in the soil can be lost through transpiration or evaporation (or deep drainage). Transpiration contributes to plant growth so it is ignored. Evaporation from the soil surface constitutes a loss of water that might otherwise have contributed to growth. The amount of water that might be lost through evaporation therefore depends on the area of exposed soil (i.e., vegetation cover), the effect of soil colour on albedo, and the effect of soil texture on the conductivity of heat (i.e., depth of soil heating). Dark clay soils (such as the study area) have low albedo and absorb energy to depth, thereby promoting evaporation from depth; light-coloured sandy soils by contrast lose relatively little soil water by evaporation. During drought years when vegetation cover is low the wetting front does not usually penetrate deep into a clay-rich soil profile, this loss is therefore a very significant influence on plant available water. These effects can be modelled with precision. This heightened water deficit during drought years will on its own contribute to short swards, irrespective of grazing pressure. Indeed, the extent of short sward mapped during the drought shown in chapter 5 is arguably in part attributed to a direct effect of water

availability rather than this entire area simply having been cropped short by grazers as the candidate seemed to imply in the chapter. A similar principle applies to soils which are prone to physiological drought. Soils with high calcium or sodium concentrations make it more difficult for a plant to take up water (uptake is a passive process dependent on pressure differentials). Certainly, ungrazed sodic soils within KNP are usually shorter in stature than surrounding grassland despite being sited in bottomland run-on situations. The same is readily evident for calcium-rich soils in semi-arid savannas, many of which support micro-perennials incapable of growing tall such as Enneapogon desvauxii. In summary, grazing is not the only reason for short grassland in savanna. This theme of water relations is relevant to the candidate's discussion of compositional changes witnessed during drought (e.g., page 75, section 5.2). Aristida species in general are recognised as drought-adapted species. Grazing lawns would have been rendered more drought-stricken than adjoining grassland owing to an increase of bare soil. It may not all be about grazing effects.

RESPONSE: It is clear from the reviewers' comments that they do not feel there has been an adequate literature review. This is a critique levelled against the thesis and the University system on several occasions. I feel that a number of the criticisms listed above such as an incomplete list of drivers, effects of abiotic conditions, impacts of rainfall etc have been addressed in this study and that references relating to these issues appear throughout in a manner that allows these chapters to form concise manuscripts that would be acceptable to journals. I will therefore not address this further.

COMMENT: Feeding ecology of grazers. Where grazers choose to move and feed, and the numbers involved, is central to this thesis yet the candidate has not displayed much insight about grazers compared with what he has shown about vegetation. A wealth of study has been undertaken on mammalian grazers, including specifically the species of interest. (Sinclair's study of buffalo back in the 1970s remains a benchmark study of African mammal ecology.) Body size is central to understanding the ecology of mammalian grazers, yet I think the first acknowledgement of body size appears only on page 102 (2nd true paragraph, line 10). In any event, the relation between body size, size of mouthparts and the allometric relation between mouthparts and intake rate in relation to sward structure are well studied, allowing prediction of which species can be expected to impact a sward of any given nature.

Social structure and the spatial pattern of resource use of a species are of importance for grazing (and trampling) impact but I read no recognition of either bar comment in passing

about migration first only on page 84. All four grazing species considered are herd forming but their herd sizes differ. Buffalo may be seen congregating in herds of a thousand impala usually not more than hundred. Buffalo, zebra and wildebeest may undertake extensive seasonal movement (tens even hundreds of kilometres) whereas impala are usually restricted to local catenal movement over the course of a year. These patterns are well studied and if they had been reviewed would have provided an improved basis for predicting and interpreting grazing patterns. I contend they are of central importance to this study in order to assess variation of grazing impact over years because other foraging opportunities resulting from the spatial distribution of burns away from the study area. Regrowth on such burns would have been available to buffalo, wildebeest and zebra but not to impala, the latter would be expected to have remained in the neighbourhood of the study area. Movement patterns are also known to change in response to drought. Might not these patterns even have implications for grazing lawns? For example, buffalo herds a thousand strong can congregate on relatively small areas of Themeda grassland if sward conditions (height, greenness) are appropriate. Their grazing and trampling impact through concentration of biomass on a small area may contribute toward maintaining regrowth (sward structure) that becomes acceptable a few weeks later when leaf table height has regrown to a preferred level. Their effect on fire-maintained grassland therefore has a specific spatial signature which results in large tracts not being used at any one time. The concept of a grazing succession involving the facilitation of use by smaller bodied grazers through the initial efforts of a large-bodied species was first explored over a half century ago (Vesey-Fitzgerald, Bell) and is germane to this study. A complementary mammal-centred approach would also have revealed features of diet and its seasonal variation that have direct implication for the patterns the candidate observed on his study plots. I offer a few examples. "African elephant were excluded due to high levels of browse in their diet" (page 38, line 5). Elephant diet has been well studied and this is simply inaccurate — bulls are preferential grazers taking mainly broad-leafed, soft bodied species (e.g., *Panicum maximum, Urochloa mosambicensis*) if available during summer but increasing intake of browse during winter when grass quality declines. Bulls have been observed plucking countless tufts including roots of *U. mosambicensis* from alluvial flats. They may not be important for the initiation or maintenance of grazing lawns but they could have exerted considerable impact on the experimental plots if they had used them. Impala also show a strong pattern of seasonal variation in their diet during which a partial switch to browse occurs mainly during the winter months. In comment about short-term response to fire (page 46, top) is the candidate aware that zebra (also hartebeest and black rhino) eat

recently burnt woody stems presumably owing to caramelised sugars making these stems attractive.

Section 2.2 concerning "Grazing impacts on grass community composition and function" illustrates the value of such material. Milchunas et al. is a masterpiece but it is predominantly based on studies examining the effect of livestock. The same point can be levelled at most reviews of traits associated with grazing. This introduces a strong bias of describing the effects of grazing based on one single large-bodied ruminant species with relatively large mouthparts usually in a managed system where biomass density and the temporal patterning of herbivory are manipulated. The candidate has levelled criticism at agriculturally based approaches to management in Kruger National Park (e.g., page 50, line 6), it also applies in this case. Livestock effects cannot be equated with the impact of a multi-species community in a relatively natural environment that encompasses a wide range in not only body size but also stomach type, size and shape of mouthparts, social structure and pattern of movement that would result in a very different pattern of herbivory over a landscape. This remains an underexplored avenue of research: to what pattern of herbivory are (were) grasses adapted before historical change in these systems?

RESPONSE: There is clearly substantial work that can be done on the dynamics of wild grazers in comparison to domesticated livestock and I hope to pursue some of the ideas raised in this comment in the coming years. I am encouraged to see that the reviewer agrees that many of these areas still require research and look forward to exploring these ideas in the future.