The effect of seasonality and post-fire on habitat preferences of the endangered Swayne’s hartebeest (Alcelaphus buselaphus swaynei) in Maze National Park, Ethiopia

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Abstract

Introduction The availability of preferred habitats determine the spatial and temporal distribution of herbivores in savanna ecosystems and is crucial for developing conservation strategies of targeted wildlife species. Habitat preference of large grazers in connection to grass height and post-fire effect has been debated for the last century. Here, we examined Swayne's hartebeest's (Alcelaphus buselaphus swaynei) seasonal habitat selection, grass height preferences and post-fire effect on their habitat preferences in Maze National Park. Data for seasonal habitat selection were collected using both visual observation along established transect routes and pellet counting using permanently established plots. Every month, we measured fresh bite grass height that was grazed by Swayne's hartebeest in grassland habitat. Starting from the first week of burning, we recorded the abundance of Swayne's hartebeest in both burned and unburned grassland areas. Results From detected pellets, 94.3% were recorded in the grassland habitat indicating that other habitat types are less used despite their extensive cover > 50% of the Park. During wet and early dry seasons, Swayne's hartebeest exclusively preferred grassland habitat. We found that 85.2% (n=1079) and 85.3% (n=593) of individuals observed in areas with a grass height below 30 cm during wet and early dry seasons, respectively; while 70.9% (n=2,288) preferred grass height below 30 cm during the dry season. The density of Swayne's hartebeest in burned grassland area was higher than unburned grassland areas upto 150 days since burning. However, in unburned grassland areas, the density was initially low but showed increasing trend for consecutive days, reaching similar abundance with burned areas after 150 days since burning. Conclusion Swayne's hartebeests exclusively preferred grassland habitat, particularly during wet and early dry seasons, shortest available grass height in all seasons and were attracted to burned grassland areas. Our results suggested that fire played an important role in maintaining habitat quality in grassland, and that management should continue using controlled burning as a tool for the conservation of Swayne's hartebeest. However, we remain cautious of our findings given the paucity of information regarding other confounding factors and the absence of long-term data on fire disturbance.

Introduction

Identifying the most preferred and quality of different habitat types are crucial for developing conservation strategies of targeted wildlife species [1-5]. Herbivores prefer suitable habitat to maximize their forage intake [6, 7] and reduce predation risk [5, 8]. There are several factors that determine the spatial and temporal distribution of herbivores in savannas ecosystems. Availability of resources [3, 9-12], predation risk [5, 8], fire [13-15], grass height [16-18], human settlement and livestock density [19-23] determine the spatial distribution of wild herbivores, but there is also variation among species.

During the past, several papers were published to develop a general trend of large grazers’ habitat preference on grass height and how they respond to post fire effect. The outcomes are however controversial suggesting species specific study in particular for endangered species which needs a careful conservation management plan is needed. There is a general consensus that grass height has a major influence of the spatial and temporal distribution of herbivores [16, 24, 25]. Larger body sized
herbivores (above 100 kg body weight; [24, 26] are expected to graze tall grass to meet their quantitative food requirements [18, 27], while smaller body-sized herbivores can achieve an adequate amount of food intake from short grass swards [28-30]. In theory, shorter grasses are generally leafy with higher proportion of nutrients and preferred by many small body-sized herbivores [24, 31], while larger body-sized herbivores can tolerate poorer quality food provided by the taller grasses [18, 26]. However, field based studies for different large mammals revealed contrasting results. For instance, large sized herbivores such as white rhino (*Ceratotherium simum*), wildebeest (*Connochaetes gnou*) and gravy's zebra (*Equus grevyi*) were found to be more attracted to shorter grass heights [24]. In contrast, the small-bodied impala (*Aepyceros melampus*) preferred the grass heights intermediate between those grazed by zebra and wildebeests [24]. Other smaller herbivores like mountain reedbuck (*Redunca fulvorufa*) and oribi (*Oreobia orebi*) feed mainly on fairly tall grass tufts [28, 30].

Fire is an important factor in the ecology and evolution of grassland ecosystems [13, 32, 33]. In African savannas, frequent burning of grass influences the habitat selection of herbivores due to impacting forage quality and reducing predation risk [15, 18]. Fire has historically, and still today, been used as a tool for the management of grassland vegetation [34]. Understanding how fire affects the movement of large herbivores and habitat selection in grasslands remains an important question for wildlife managers.

Post-fire regrowth of grass determines the dry season habitat use of many herbivore species [35, 36]. Small body-sized herbivores (below 100 kg), such as Thomson’s gazelle (*Gazella thomsoni*), Grant’s gazelle (*Gazella granti*) and impala (*Aepyceros melampus*), were significantly attracted to burned areas, while large body-sized herbivores (above 100 kg) such as topi (*Damaliscus korrigum*) and zebra (*Equus burchelli*) were not [37]. However, other studies have found contrasting results on the association between burned area selections and herbivores body size [15, 17, 24, 25]. Negative relationship between body mass and burned area preference were also documented [16, 29]. Large body-sized herbivores such as tsessebe (*Damaliscus lunatus*) and roan antelope (*Hippotragus equinus*) were frequently attracted to burned areas [31].

Swayne’s hartebeest (*Alcelaphus buselaphus swaynei*) is one of the large body-sized herbivores in Maze National Park, Ethiopia, weighing between 100 to 200 kg [38]. Swayne’s hartebeest was once widely distributed in Ethiopia, Somalia and Djibouti [39], but currently its range is confined to Ethiopia [40-42] and listed as endangered sub-species by IUCN Red list [43]. In our recent study, we documented the largest population size of Swayne’s hartebeest in Maze National Park which remains unstudied and gets little attention from the scientific community (Misganaw et al. unpublished). Ecological studies in particular on habitat preference, foraging scale in connection with grass height in different seasons and effects of use of fire as a management tool is crucial to develop a proper conservation management plan. In this study, we aimed to examine: (1) general habitat selection of Swayne’s hartebeest among the available habitat types in Maze National Park such are (grassland, riverine forest, three bushland habitat types), (2) grass height preference of Swayne’s hartebeest from four categories (below 30, 31 – 50, 51 – 100 and above 100 cm), and (3) how the they responded to post fire effect from density of Swayne’s hartebeest in burned grassland areas in consecutive days since burning.
Materials And Methods

Study area

Maze National Park is located at (6°25′N, 37°14′E) in southern Ethiopia (see Fig. 1). The Park covers an area of 175 km$^2$ and was established in 2005 to conserve the rare and endangered Swayne's hartebeest, which is considered the flagship species for the Park. The elevation of the study area ranges between 900 – 1,300 m asl. It is semi-arid and drought prone area with low and erratic rainfall (mean annual rainfall is below 800 mm) with high mean monthly temperature not less than 30°C. The Park has sufficient water sources for wildlife. The Maze River and several small tributaries, such as Daho, Lemasea and Domba flow throughout the year in the Park.

Maze National Park has a variety of habitat types, including riverine forests, plain grassland habitats with scattered trees (hereafter called grassland), sloppy bushland habitat, plain bushland habitat, rugged bushland habitat with small valleys and neighborhood agricultural land (Fig. 1). At the beginning of the wet season, the grass was growing fast and Swayne's hartebeests congregated in specific sites in the Park where the grass heights were shortest. Starting from September up to the next burning date, the grass height in most parts of the Park reached above a meter. The Park is surrounded by mountains, farmland and communal grazing lands. The grasslands are primarily dominated by annual grass species, such as Exotheca abyssinca, Heteropogon contortus, Loudentia spp., Setaria incrassate, and Hyparrhenia filipendula with scattered woody plants such as Combretum terminalia. Burning of the grasslands has occurred by the wildlife managers since the Park was established.

Swayne's hartebeest sampling design

The Park was initially divided into 10 blocks using features such as roads, rivers, vegetation cover and valleys for a total count of hartebeest to each of habitat types and burned/unburned grassland for a given block. In each block, the habitat types and burned/unburned grassland areas were demarcated by using GPS with in approximately 30m differences depending up on the nature of the habitat types and the size of each habitat types and blocks were estimated using ArcGIS 10.3. In each block, we established permanent parallel transect routes spaced approximately 150 – 200 m apart. In the plains areas (i.e. open grassland and plain bushland areas), 37 transect routes were spaced in 200 m gap, whereas in the forest and rugged bushland areas where observation from distance was impossible, 15 transect routes were spaced 150 m apart. The number and length of transects varied among blocks depending on the size of the blocks. In each transect, we randomly established 4 m × 5 m plots for Swayne's hartebeest pellet presence/absence detection. The plots were established based on an average calculation of 10 plots for one km transect route. A total of 400 plots in the grassland, 100 plots in the plain bushland, 119 plots in the sloppy bushland, 191 plots in the rugged bushland, 148 plots in the riverine forest habitat and 44 plots in the agricultural land adjacent to the Park boundary were permanently established. The GPS coordinates and habitat types were recorded at each plot.

Swayne's hartebeest habitat selection
The general habitat use of Swayne's hartebeest from the available five habitat types (grassland, riverine forest, three bushland habitat types) were conducted for one year (i.e. from December 2016 – November 2017). Since the grass height varied before and after burning the grassland habitat, we divided the dry season into early dry season (before burning) and dry season (after burning). During the dry season (i.e. from December – May), we counted the pellet samples across the 1,002 plots established in the whole Park. Pellet-groups that were more than 50 cm apart in a plot were recorded as pellet from different individuals. Freshness of pellet samples also gave clues for being defected from different individuals. We visited each plot for an average of 36 times during the dry season. After a pellet-group was detected, it was removed from each plot to avoid redetecting during the subsequent surveys.

In the wet seasons (i.e. from June – August) and early dry (i.e. from September – November), we used visual observation of Swayne's hartebeest along transect routes as pellet sampling was difficult due to dense habitat cover. During both seasons, habitat use of the Swayne's hartebeest was estimated through transect counting aided with 10x42 binoculars. Whenever the Swayne's hartebeests were observed, habitat types and abundance of the Swayne's hartebeests were recorded for the center of the group [44]. We surveyed each transect 12 times during each season, and to avoid double detections of individuals, all transect routes of a block were surveyed at the same time. The timing of survey was carried out at early morning from 6:00 – 10:00 a.m. and late evening from 3:00 – 6:00 p.m. when Swayne's hartebeests were active [45].

**Swayne's hartebeest grass height preferences**

In Maze National Park, grass height varied over seasons. Grass heights were measured on 464, 193 and 133 central point of random plots of 1 m$^2$ area to estimate average grass height during the dry, wet and early dry seasons within the grassland habitat, respectively. During the three seasons, the feeding sites of Swayne's hartebeests were studied to determine the grass height preferred by Swayne's hartebeest by walking on the 37 transects designed in the grassland areas. The surveys were carried out for 5 – 8 days in every month for one year (i.e., from December 2016 – November 2017). Whenever an individual or a herd of Swayne's hartebeest was observed on the transect walk in both sides of a transect route, the total number of Swayne's hartebeests was recorded. The first grazing Swayne's hartebeest seen was chosen as a focal animal and its feeding location was identified using the nearby landmarks like trees or bushes. It was then displaced and fresh bites were identified at the site. Fresh bites were identified by the white coloration at the bite, whereas old bites turn brown [44]. Once the bites were identified, a 1 m$^2$ quadrat was placed over the grass patch. Within each quadrat, the height of the grass of same grass species to the immediate grass grazed by Swayne's hartebeest was measured using a ruler or a meter tape with the assumption that grass of same species in close proximity will have same grass height.

**Effect of fire on hartebeest grazing**

The Maze National Park management conducted controlled burning on some parts of the grassland at the end of the wet season every year (mostly from October – November, depending on when the rain
ends). During this study period, the burning time was end of November. Only part of the grassland is burned in every year. During the survey year, 21.4 km$^2$ of the grassland area was burned while 30.2 km$^2$ remained unburned. In both habitat types, we carried out 36 times transect count (a transect might cross both grassland types) from the first date of the burning (i.e. from the beginning of December – to mid-May and count the number of Swayne’s hartebeest individuals. In both grassland areas, we counted the grazing hartebeests twice every week to record how long Swayne’s hartebeests grazed in those areas. We summed the number of observed individuals for each surveying days in the burned and unburned grassland areas, separately. Counting was conducted in the morning 6:00 – 10:00 a.m. and late evening from 3:00 – 6:00 p.m. to correspond with peak Swayne’s hartebeest grazing time [45].

Data analysis

General habitat use

We used Ivlev’s selectivity calculations as a measure of relative habitat selection of Swayne’s hartebeest among the different habitat types using pellet presence data. Following [44], we used the equation $E_i = (r_i - n_i) / (r_i+n_i)$ where $r_i$ is the proportion pellet detected in each habitat types within the survey period and $n_i$ is the proportion of plots in each habitat types during the surveying period available from the total area represented by the survey period.

We used linear mixed effect model [46] to evaluate the relationship between density of Swayne’s hartebeest pellet (response variable) and habitat types during the dry season. We also used linear mixed effect model to evaluate the relationship between density of Swayne's hartebeest (response variable) and time (i.e. Julian date as explanatory variable) during early dry and wet seasons, separately. Block and transects were used as random factors to account for variations among areas and transects. We used generalized linear model to estimate the relationship between grass height (response variable) and Julian date (explanatory variable) for one year. We used generalized linear mixed model [47] for Swayne’s hartebeest seasonal grass height preference using density of Swayne’s hartebeest as a response variable with season (at three levels: wet, early dry and dry) and grass height as predictor variables. Block and transects were used as random factors to account for variations among areas and transects. We also used generalized linear mixed model to estimate Swayne's hartebeest abundance (response variable) in relation to burning (categorical variable at two levels: burned and unburned), and days since burning as predictor variables. Block was used as random factor to account for variations among areas. All analyses were done in R version 3.5.1[48].

Results

Habitat selection

During the dry season, we detected 6,288 Swayne’s hartebeest pellets. Of these, 5931 (94.3%) were in the grassland habitat, 131 (2%) in the riverine forest, 119 (1.9%) in the plain bushland habitat. The rest 107 (1.7 %) pellets were found in sloppy bushland, rugged bushland and neighboring agricultural areas.
Swayne's hartebeests select grassland habitat, while avoiding the rest five habitats (Table 1). Additionally, the grassland habitat had a significantly higher pellet density than the other habitat types (Fig. 2).

We recorded a total of 154 and 93 of either an individual or herds of Swayne's hartebeest observation points during wet and early dry seasons, respectively. All observations were exclusively recorded in grassland habitats. We could not observe Swayne's hartebeests in other habitat types in both seasons. Of those observation points, we recorded 1,269 and 723 Swayne's hartebeests during wet and early dry seasons, respectively.

The densities of the Swayne's hartebeests were aggregated in small range and the density did not vary across the three months of wet season. However, during the early dry season, the Swayne's hartebeests were more dispersed to the periphery and the density varied across months. The density (km$^{-2}$) of Swayne's hartebeest did not vary during the wet season; but showed significant decrease with increasing time during the early dry season (Table 2).

**Grass height preferences**

The random grass height measurements in Maze National Park showed a significant increase of grass height with increasing time (Fig. 3)

During the dry season, we recorded a total of 3,225 grazing Swayne's hartebeests in different grass heights. Of these, 2288 (70.9%) individuals were recorded below 30 cm grass heights. The rest 540 (16.7%), 258 (8%) and 139 (4.3%) of Swayne's hartebeests were recorded between 31 – 50 cm, 51 – 100 cm and above 100 cm grass heights, respectively. In all months of the dry season, we recorded the highest number of Swayne's hartebeests grazing below 30 cm grass heights. During the wet season, we recorded a total of 1,266 grazing Swayne's hartebeests. Of which, 1079 (85.2%) individuals were recorded below 30 cm grass heights. The rest 156 (12.3%), 29 (2.3%) and 2 (0.2%) hartebeests were recorded between 31 – 50 cm, 51 – 100 cm and above 100 cm grass heights, respectively. During the early dry season, we recorded a total of 695 Swayne's hartebeests. Of these, 593 (85.3%) hartebeests were recorded below 30 cm grass height. The rest 78 (11.2%) and 24 (3.5%) individuals were recorded between 31 – 50 cm and above 50 cm grass heights, respectively.

Our study showed that Swayne's hartebeests strongly preferred shortest available grass height in all seasons, with a decrease in the density of animals (km$^{-2}$) with increasing grass height (Fig. 4; Table 3). The decrease was stronger during wet and early dry seasons compared to dry season. Areas with taller grasses are more used during the dry season than other seasons (Fig. 4).

**Impact of fire on Swayne's hartebeest habitat use**

Swayne's hartebeest was attracted by burned grassland areas since the day of burning. In the first 30 days since burning, 54.5% of the observed Swayne's hartebeests were found in burned grassland areas. From 31 – 60, 61 – 90, 91 – 120 and >121 days since burning, we found 90.8%, 89.1%, 66% and 47.5% of
individuals in burned grassland areas from the total observed Swayne's hartebeests, respectively. The density of Swayne's hartebeest in burned grassland area was significantly higher than unburned grassland areas (Table 4). The burned grassland area has attracted Swayne's hartebeests up to 150 days after the initial burning (Fig. 5).

**Discussion**

Swayne's hartebeests strongly preferred open grassland habitat and short grasses throughout the year similar to some other large body-sized wild herbivores, such as wildebeest (*Connochaetes gnou*), gravy's zebra (*Equus grevyi*) and white rhino (*Ceratotherium simum*) [24], confirming that they are exclusively grazers and use high percentage of grass in their diet [49]. However, few number of Swayne's hartebeest pellets were detected in bushland habitats and riverine forests during the dry season walking to a water source. We did not find Swayne's hartebeest in agricultural land and rugged habitats except in a rare occurrence mostly when they were chased by predators (i.e. lion, their main predator).

The study revealed that the Swayne's hartebeest grass height preference did not follow the hypothesis that large body-sized herbivores prefer taller grass height. Maze National Park is a lowland area, and the grass grows fast and reaches above a meter when wet season begins (Fig. 4). However, Swayne's hartebeests almost abandoned the taller grass height every month, and consistently preferred the smallest available grass height areas in the Park. Throughout the year, large numbers of Swayne's hartebeests were grazing in grass stands below 30 cm tall.

Grass height preferences of Swayne's hartebeest determine their distribution in Maze National Park at different seasons. Previous studies also revealed that forage influences the distribution of herbivores [25, 37, 50]. The influence is demonstrated on the distribution of herbivore on its bite size [50]. During wet season, Swayne's hartebeest populations were concentrated in small patches over three months where the grass heights were shortest. These areas are rocky and the grass was growing slowly unlike other grassland areas. The density of Swayne's hartebeest was not significantly different in months of the wet season. It was due to their congregation at shortest grassland sites for three months (i.e., from June – August) of the wet season. Starting from September up to the next burning date (i.e. early dry season), the grass height in most parts of the Park became above a meter and the Swayne's hartebeests dispersed toward the periphery of the Park to find short grass sward that showed significant difference of Swayne's hartebeest density in relation to the Julian dates of the season.

The result from this study revealed that Swayne's hartebeests are highly attracted to burned grassland areas. This supports the hypothesis that herbivores are more attracted to burned grassland areas, since this has been found in several previous studies [2, 31, 34-36, 51-53]. Swayne's hartebeests also exist in unburned grassland areas, although the burned area attracted more than the unburned grassland areas. Herbivores foraging in savanna ecosystems within burned areas may demonstrate a trade-off between acquiring quality forage and avoiding risky of predation [44]. The two hypotheses why burned areas attract herbivores can be ascertained because most burned areas quickly flush new grass shoots that
attract herbivores due to easily digestible forage [34, 44] and herbivores are attracted to the burned areas due to increased safety from predators [44]. This is because decreasing fire frequency helps to increase vegetation cover and tree density and provide more cover for predators. It decreases the detection and visibility of predators and the subsequent ability of herbivores to escape from predators. As a result, herbivores mostly avoid areas with relatively taller vegetation or denser woody cover and spend more time in relatively open areas.

However, Swayne's hartebeests’ attraction to burned areas might be due to obtaining quickly flushing new grass shoots for their forage. This is because the predator (lion) killing areas of the Swayne's hartebeest during the survey period were not limited only in denser vegetation habitats. Out of the 13 carcasses (by visual observation during the field work) of Swayne's hartebeests, six were predated in the burned grassland habitats. Swayne's hartebeest also have been observed close to the forest areas more frequently once the grass is burned. Another reason for the preference of burned grassland area might be due to the biomass ratio. Previous studies indicated that burning directly decreases the live: dead biomass ration and increases herbivores attraction [10, 15, 53]. During the survey years, burning time in Maze National Park was in November when the green grass was prevalent at unburned areas and the burned areas contain clumps of dead biomass that was not burned and short new grass shoots. That might attract Swayne's hartebeests to burned areas. The short newly growing grass shoots in burned areas are younger and have higher nutrient content than green grass of the unburned areas [15].

The other possible reasons that Swayne's hartebeests preferred burned areas might be to avoid parasites, specifically ticks and flies [10, 54] or to acquire minerals from ash that are not obtained from available forage [55]. Ecto-parasites like ticks and flies can negatively affect the health of herbivores [56]. During the field survey period, Swayne's hartebeests were observed in the burned grassland area immediately during second day of burning. This supports the hypothesis that herbivores can ingest ash from burned areas by licking the burned soil [55]. This is because ash is high in Ca, potassium carbonate (K₂CO₃), phosphate (PO₄) and trace minerals [55], and so Swayne's hartebeest might use ash as a nutrient supplement from the burned grassland areas.

The study revealed that the burned areas significantly attract Swayne's hartebeests for 150 days since burning. This might be the preference of fresh grass in burned areas when the grass height and nutrient contents are not significantly different between burned and unburned areas [14, 15]. Similar results were obtained on Thomson's gazelles and Impala [15]. Many herbivores studies report similar trends that preferred fresh grass in burned area over unburned green grass in the first months of post-fire in equatorial grassland ecosystem [14, 34, 36]. This may help to predict when the attraction will end up, and up to when the nutrient and grass height have no longer differences between burned and unburned areas. Additional post-fire studies and vegetation monitoring may help substantiate our results.

**Conclusions**
Swayne's hartebeests in Maze National Park preferred grassland habitats, indicating that they are purely grazers. The Swayne's hartebeests highly preferred available shortest grass heights throughout the year, and similarly their preference of burned grassland areas was higher. Hence, since the Swayne's hartebeest is an endemic herbivore residing only in two prime habitats (Maze National Park and Senkele Swayne's Hartebeest Sanctuary); and controlled burning of the grassland areas should be taken as conservation action to ensure their persistence in Maze National Park.

Abbreviations

CEES: Centre for Ecological and Evolutionary Synthesis; IUCN: International Union for Conservation of Nature; MNP: Maze National Park; EWCA: Ethiopian Wildlife Conservation Authority; GPS: Global Positioning System

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors’ contribution

Misganaw Tamrat designed the study with close follow up from Anagaw Atickem, Afework Bekele and Nils Chr Stenseth. Misganaw Tamrat collected the data; Misganaw Tamrat, Diress Tsegaye and Anagaw Atickem analyzed the data; Misganaw Tamrat wrote the first draft. Afework Bekele, Anagaw Atickem, Paul Evangelista and NilsChrStenseth revised the manuscript extensively and then all authors and coauthors revised subsequent versions of the manuscript. All authors read and approved the final manuscript.
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References

1. Illius A, Gordon I. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia. 1992; 89: 428-434.

2. Klop E, van Goethem J. Savanna fires govern community structure of ungulates in Bénoué National Park, Cameroon. Journal of Tropical Ecology. 2008; 24: 39-47.

3. Ogutu JO, et al. Herbivore dynamics and range contraction in Kajiado County Kenya: climate and land use changes, population pressures, governance, policy and human-wildlife conflicts. The Open Ecology Journal. 2014; 7.

4. Paudel PK, Hais M, Kindlmann P. Habitat suitability models of mountain ungulates: identifying potential areas for conservation. Zoological Studies. 2015; 54:37.

5. Rapp E. Micro habitat selection of herbivores in response to perceived predation risk and forage quality in Hluhluwe-iMfolozi game reserve. 2017.

6. Martínez-Freiría F, et al. Contemporary niche contraction affects climate change predictions for elephants and giraffes. Diversity and Distributions. 2016; 22:432-444.

7. Schuette P, Creel S, Christianson D. Ungulate distributions in a rangeland with competitors, predators and pastoralists. Journal of applied ecology. 2016; 53:1066-1077.
8. Guo K, et al. Habitat selection and their interspecific interactions for mammal assemblage in the Greater Khingan Mountains, northeastern China. Wildlife Biology. 2017.
9. Bell RH. A grazing ecosystem in the Serengeti. Scientific American. 1971; 225:86-93.
10. Olubayo R, et al. Comparative differences in densities of adult ticks as a function of body size on some East African antelopes. African Journal of Ecology. 1993; 31:26-34.
11. Voeten MM, Prins HH. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia. 1999; 120:287-294.
12. Mobæk R, et al. Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. Oikos. 2009; 118:209-218.
13. Sankaran M, Ratnam J, Hanan N. Woody cover in African savannas: the role of resources, fire and herbivory. Global Ecology and Biogeography. 2008;17:236-245.
14. Hassan SN, Rija AA. Fire history and management as determinant of patch selection by foraging herbivores in western Serengeti, Tanzania. International Journal of Biodiversity Science, Ecosystem Services & Management. 2011; 7:122-133.
15. Eby SL, et al. The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. J Anim Ecol. 2014; 83:1196-205.
16. Laca E, et al. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and forage science. 1992; 47:91-102.
17. Massé A, Côté SD. Habitat selection of a large herbivore at high density and without predation: trade-off between forage and cover? Journal of Mammalogy. 2009; 90:961-970.
18. Bjørneraas K, et al. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oecologia. 2012; 168:231-243.
19. Fritz H, De Garine-Wichatitsky M, Letessier G. Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour. Journal of Applied Ecology. 1996;589-598.
20. Lamprey RH, Reid RS. Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? Journal of Biogeography. 2004; 31:997-1032.
21. Vavra M. Livestock grazing and wildlife: developing compatibilities. Rangeland Ecology & Management. 2005; 58:128-134.
22. Sitters J, et al. Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. Biological Conservation. 2009; 142:738-750.
23. Atickem A, Loe LE. Livestock-wildlife conflicts in the Ethiopian highlands: assessing the dietary and spatial overlap between mountain nyala and cattle. African journal of ecology. 2014; 52:343-351.
24. Arsenault R, Owen-Smith N. Resource partitioning by grass height among grazing ungulates does not follow body size relation. Oikos. 2008; 117:1711-1717.
25. Treydte AC, et al. Grazing ungulates select for grasses growing beneath trees in African savannas. Mammalian Biology-Zeitschrift für Säugetierkunde. 2011;76:345-350.
26. Bhola N, et al. Comparative changes in density and demography of large herbivores in the Masai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya. Biodiversity and Conservation. 2012; 21:1509-1530.

27. Hopcraft JGC, et al. Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. Journal of Animal Ecology. 2012; 81:201-213.

28. Oliver J. Population ecology of oribi, grey rhebuck and mountain reedbuck in Highmoor State Forest Land. South African Journal of Wildlife Research-24-month delayed open access. 1978; 8:95-105.

29. Demment MW, Van Soest PJ. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. The American Naturalist. 1985;125:641-672.

30. Reilly B, Theron G, Bothma JDP. Food preferences of oribi Ourebia ourebi in the Golden Gate Highlands National Park. Koedoe. 1990; 33:55-61.

31. Gureja N, Owen-Smith N. Comparative use of burnt grassland by rare antelope species in a lowveld game ranch, South Africa. South African Journal of Wildlife Research-24-month delayed open access. 2002;32:31-38.

32. Van Langevelde F, et al. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology. 2003;84:337-350.

33. Bond WJ, Keeley JE. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in ecology & evolution. 2005;20:387-394.

34. Pacifici M, et al. Fire policy optimization to maximize suitable habitat for locally rare species under different climatic conditions: A case study of antelopes in the Kruger National Park. Biological conservation. 2015;191:313-321.

35. Moe SR, Wegge P, Kapela EB. The influence of man-made fires on large wild herbivores in Lake Burungi area in northern Tanzania. African journal of Ecology. 1990; 28:35-43.

36. Parrini F, Owen-Smith N. The importance of post-fire regrowth for sable antelope in a southern African savanna. African Journal of Ecology. 2010;48:526-534.

37. Bailey DW, et al. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management. 1996;49:386-400.

38. Yalden D, Largen M, Kock D. Catalogue of the Mammals of Ethiopia: 5. Artiodactyla. Monitore Zoologico Italiano. Supplemento. 1984;19:67-221.

39. Datiko D, Bekele A. Population status and human impact on the endangered Swayne's hartebeest (Alcelaphus buselaphus swaynei) in Nechisar Plains, Nechisar National Park, Ethiopia. African Journal of Ecology. 2011;49:311-319.

40. Lewis J, Wilson R. The ecology of Swayne's hartebeest. Biological Conservation. 1979;15:1-12.

41. Vié J. The IUCN Red list: a key conservation tool. W: J.-C. Vié, C. Hilton-Taylor and SN Stuart (eds). The 2008 Review of The IUCN Red list of Threatened Species. IUCN Gland, Switzerland, ss. 16. 2008.

42. Mamo Y, et al. Status of the Swaynes Hartebeest (Alcelaphus buselaphus swaynei) meta-population under land cover changes in Ethiopian Protected Areas. International Journal of Biodiversity and
Table 1 Number of permanent plots established along the transect routes and the number of pellets detected during the dry season (one plot is 4 x 5 m = 20 m$^2$; $ri$ = is the proportion of all Swayne’s hartebeest pellet detected; $ni$ = is the proportion of plots representing a habitat type; $Ei$ = Ivlev’s selectivity index)
| Habitat type     | Number of plots | Number of pellets detected | $r_i$ | $n_i$ | $E_i = (r_i - n_i) / (r_i + n_i)$ |
|-----------------|-----------------|----------------------------|-------|-------|----------------------------------|
| Grassland       | 400             | 5,931                      | 0.90  | 0.40  |                                  |
| Plain bushland  | 100             | 119                        | 0.02  | 0.10  | -0.67                            |
| Sloppy bushland | 119             | 76                         | 0.01  | 0.12  | -0.83                            |
| Rugged bushland | 191             | 16                         | 0.00  | 0.19  | -1.00                            |
| Riverine forest | 148             | 131                        | 0.02  | 0.15  | -0.76                            |
| Agricultural land | 44              | 15                         | 0.00  | 0.13  | -1.00                            |
| **Total**       | **1,002**       | **6,288**                  |       |       |                                  |

Table 2 Swayne’s hartebeest density (km$^{-2}$) during the wet and early dry seasons in Maze National Park analysed using linear mixed effect model

| Season    | Effects     | Estimate | SE    | t-value | P-value |
|-----------|-------------|----------|-------|---------|---------|
| Wet       | Intercept   | 48.277   | 26.183| 1.844   | 0.070   |
|           | Julian date | -0.169   | 0.132 | -1.287  | 0.209   |
| Early dry | Intercept   | 27.624   | 8.788 | 3.143   | 0.003   |
|           | Julian date | -0.065   | 0.027 | -2.412  | 0.012   |

Table 3 Estimates of Swayne’s hartebeest density in grassland habitat in relation to season and grass height in Maze National Park analyzed using general linear mixed-effects model. Early dry season was used a reference level for season categorical variable

|                      | Estimate | SE    | t-value | P-value |
|----------------------|----------|-------|---------|---------|
| Intercept            | 12.428   | 1.286 | 9.666   | < 0.001 |
| Dry season           | -2.174   | 1.107 | -1.963  | 0.050   |
| Wet Season           | 2.394    | 1.423 | 1.682   | 0.093   |
| Grass height         | -0.102   | 0.018 | -5.556  | < 0.001 |
| Dry season × Grass height | -0.064 | 0.025 | -2.556  | 0.012   |
| Wet season × Grass height | -0.100 | 0.034 | -2.906  | 0.004   |
Table 4 Swayne’s hartebeest abundance in grassland habitat in relation to fire disturbance (burned vs unburned) in Maze National Park analyzed using generalized linear mixed effect model

|                          | Estimate | SE   | z-value | P-value |
|--------------------------|----------|------|---------|---------|
| Intercept                | 3.451    | 0.080| 43.14   | <0.001  |
| Un-burned vs. burned     | -1.754   | 0.058| -30.41  | <0.001  |
| Days vs. burned          | -0.002   | 0.000| -6.07   | <0.001  |
| Un-burned × Days         | 0.009    | 0.001| 16.97   | <0.001  |

Figures

Figure 1
Map showing the study area and habitat types in Maze National Park, Ethiopia

Figure 2

Swayne’s hartebeest pellet density per square meter area in different habitat types during the dry season in Maze National Park

Figure 3

Grass height across Julian date in Maze National Park analyzed using a fixed effect model with 95% confidence interval in Maze National Park. The grass heights were randomly measured from random
plots in each month for a year

Figure 4

Predicting the density of Swayne’s hartebeest in relation to grass height preference in three seasons in Maze National Park
Figure 5

Predicted Swayne’s hartebeest abundance both burned and unburned grassland areas in Maze National Park in relation to days since burning