The effect of season 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

Background: The availability of preferred habitats determines the spatial and temporal distribution of herbivores in savanna ecosystems. Understanding habitat preference of a targeted wildlife species is crucial for developing effective conservation strategies. Habitat preference of large grazers in connection to grass height and post-fire effect has been debated for the last century. Here, we examined the effects of season, grass height and burning on the habitat preference on Swayne's hartebeest (Alcelaphus buselaphus swaynei) in Maze National Park. Data for seasonal habitat selection were collected using both direct observation along established transect lines and pellet counting using permanently established plots. Every month, we measured grass height commonly preferred 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 patches. 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=1,079) 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 up to 150 days since burning. However, in unburned grassland areas, the density was initially low but showed increasing trend for consecutive days, reaching similar density with burned areas after 150 days since burning. Conclusion: Swayne's hartebeest 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.

Background

Identifying the most preferred and quality of different habitat types are crucial for developing conservation strategies of a targeted wildlife species [1-5]. Herbivores prefer suitable habitats 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 though these factors have variation in effect among species. Since a habitat does not always contain adequate resources, the trade-offs between costs and benefits associated with searching, visiting and utilizing limit its selection by herbivores [24]. Moreover, spatial variation in relative availability of different habitat types may result in dissimilar habitat selection among individuals of the same species [25, 26].

During the past, several papers [17, 24, 25] were published to develop a general trend of large grazers' habitat preference in response to grass height and post-fire effect on vegetation. There is a general consensus that grass height has a major influence on the spatial and temporal distribution of herbivores. Herbivores could optimize their daily forage need where they are able to access sufficient quality forage, effectively, and resource partitioning among species occurs through differential selection of grass height [27, 28]. It has been demonstrated to exert a major influence on bite size that in turn impacts on food intake rate achieved by grazing herbivores [26, 29, 30].

Larger body sized herbivores (above 100 kg body weight) [24, 31] are expected to graze tall grass to meet their quantitative food requirements [18, 32], while smaller body-sized herbivores can achieve an adequate amount of food intake from short grass swards [33-35]. In theory, shorter grasses are generally leafy with higher proportion of nutrients and preferred by many small body-sized herbivores [24, 36], while larger body-sized herbivores can tolerate poorer quality food provided by the taller grasses [18, 31]. When grass grows and matures, commonly its quality decreases for grazers [9, 18, 29, 37], which is mainly due to changes in proportions on various parts of the grass and their nutrient contents. This can be demonstrated by the decrease proportion of leaves and the nitrogen content (both indicating high grass quality) in the grass with increasing grass mass in savanna ecosystem [38].

In African savannas, frequent burning of grass influences the habitat selection of herbivores due to impacting forage quality and reducing predation risk [15, 39], and it is a key element in predicting habitat selection by specific species [26]. Fire plays a determinant role in the ecology and evolution of grassland ecosystems [13, 40, 41], and it has historically, and still today, been used as a tool for the management of grassland vegetation [42, 43]. Post-fire regrowth of grass determines the dry season habitat use of many herbivore species [42, 44]. However, there have been arguments among ecologists how burning affects habitat selection of large body-sized herbivores.

Small body-sized herbivores might prefer burned areas more than large body-sized herbivores due to differential preferences in relation to forage quality [45]. However, another study [25] revealed that fire does not have relationship between body size and use of burned areas. Several studies [14, 25, 46] evidenced that decreasing fire frequency increases vegetation cover and tree densities, which in turn decreases visibility and the subsequent ability of herbivores to detect and escape from predators. As a result, herbivores may avoid areas with relatively denser vegetation cover or spent more time in those areas for vigilance rather than foraging [14]. Hence, herbivores foraging in burned areas may represent either acquiring quality forage or avoiding predators.

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 [47]. It was once widely distributed in Ethiopia, Somalia and Djibouti [48], but currently its range is confined to Ethiopia [49-51] and listed as endangered sub-species by IUCN Red list [52]. In our recent study, we documented the largest population size of Swayne's hartebeests in Maze National Park (Misganaw et al. unpublished) which remains unstudied and gets little attention from the scientific community. Therefore, the aim of this study was to examine: (1) the

general habitat selection of Swayne's hartebeest among the main habitat types in Maze National Park, (2) the grass height preference of Swayne's hartebeest, (3) the density of Swayne's hartebeest in different seasons, and (4) how Swayne's hartebeest respond to post-fire effect in consecutive days since burning in grassland areas.

Results

Habitat selection

During the dry season, we detected 6,288 Swayne's hartebeest pellets. Of this, 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 selected 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 did not observe Swayne's hartebeests in other habitat types, because they did not use other habitat types except grassland in both seasons. Of those observation points, we recorded 1,269 and 723 Swayne's hartebeests during wet and early dry seasons, respectively. During the wet season, no monthly variation on density (individuals/km^2) of Swayne's hartebeest was found. However, during the early dry season the Swayne's hartebeests were more dispersed to the periphery and the density showed significant decrease with increasing time across months (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 events while studying their grass height preference. Of this, 2288 (70.9%) individuals were recorded below 30 cm grass heights. The rest 540 (16.7%), 258 (8%) and 139 (4.3%) of grazing events were recorded between 31–50 cm, 51–100 cm and above 100 cm grass heights, respectively. During the wet season, we recorded a total of 1,266 grazing events. Of this, 1079 (85.2%) were recorded below 30 cm grass heights. The rest 156 (12.3%), 29 (2.3%) and 2 (0.2%) grazing events 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 grazing events. Of this, 593 (85.3%) were recorded below 30 cm grass height. The rest 78 (11.2%) and 24 (3.5%) grazing events were recorded between 31–50 cm and above 50 cm grass heights, respectively. Swayne's hartebeests strongly preferred shortest available grass height in all seasons, with a decrease in the density of animals with increasing grass height (Table 3, Fig. 4). 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 up to 150 days after the initial burning (Table 4, 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 [53]. However, few number of Swayne's hartebeest pellets were detected in bushland habitats and riverine forests during the dry season, this occurred probably when they were walking to a water source. Swayne's hartebeests were not encountered in agricultural land and rugged habitats except in a rare occurrence; this might be 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 one meter within a month after the wet season begins (Fig. 3). However, Swayne's hartebeests almost abandoned the taller grass height, and consistently preferred the shorter (below 30 cm) available grass height areas in the Park. Previous studies [24, 39, 53] also confirmed that large body-sized herbivores, such as hartebeests and roan antelope in Nazinga Game Ranch, Burkina Faso, preferred short grass height. Other herbivore species, such as wildebeest and zebra, generally preferred grass height below 25 cm during the wet season in Serengeti Park, Tanzania [15]. White rhino preferred short grass height (below 24 cm) during the dry season in Hluhluwe-iMfolozi Park, South Africa [24]. However, Swayne's hartebeests utilized taller grass height during the dry season rather than the rest two seasons in Maze National Park (Fig. 4). This is also in agreement with a study in Burkina Faso, where hartebeests during the hot dry season utilized tall grass height when availability of fresh and shorter grasses become scarce, and they are attesting to their apparent ability to acquire scarce regrowth from taller grass height [53].

Throughout the year, large numbers of Swayne's hartebeests were grazing in shorter grass heights. This might be due to higher digestibility and nutritional quality and bite rates of shorter grasses, or it could be due to predation risk despite low density of carnivores (mainly lions) in the Park (Misganaw et al., unpublished data). Shorter grasses have less lignin with lower carbon to nitrogen ratios which are more

palatable and digestible for grazers [38]. Shorter grasses also have higher nutritional quality [28, 54], and percentage of green leaves that allow higher bite rates for herbivores foraging [30], while predation by carnivores might also have effect on habitat preference of herbivores [55-57].

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 [58-60]. The influence is demonstrated on the distribution of herbivore on its bite size [29]. During wet season, Swayne's hartebeest populations were concentrated in three small grassland patches over three months where the grass heights were shortest. The patches have shorter grass heights unlike the surrounding area covered by much taller grasses of the same species possibly as a result of soil types. The density of Swayne's hartebeest was not significantly different in months of the wet season as the rest of the grassland covered by tall grass height. 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 [43, 46, 61]. For instance, quality of forage in burned patches of grassland habitat highly attracted hartebeests in Burkina Faso [53]. Other herbivores such as wildebeest and zebra also preferred annually burned grassland patches [39]. Herbivores foraging in savanna ecosystems within burned areas may demonstrate a trade-off between acquiring quality forage and avoiding risky of predation [39]. The two hypotheses on why burned areas attract herbivores are because most burned areas quickly flush new grass shoots that are highly nutritious and easily digestible [39, 61] and because the absence of taller vegetation allows herbivores to see predators from greater distances [39]. As a result, some herbivores may avoid areas with relatively taller vegetation or denser woody cover preferring open areas for safety. The Swayne's hartebeest are still vulnerable to predation by lions in the open burned areas. During our surveys, we encountered 13 carcasses of Swayne's hartebeests; of these six were predated in the burned grassland habitats (Misganaw et al, unpublished data).

Swayne's hartebeest have also 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 of the grass. Previous studies indicated that burning directly decreases the live: dead biomass ration and increases herbivores attraction [10, 15, 62]. During the survey year, 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, 63] or to acquire minerals from ash that are not obtained from available forage [64]. Studies have shown that burning grassland in Ngorongoro Crater, Tanzania during the dry season virtually eliminated tick populations [65]. Ecto-parasites, such as ticks and flies, can negatively affect the health of herbivores [65]. 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 [64]. This is because ash is high in Ca, potassium carbonate (K_2CO3), phosphate (PO4) and trace minerals [64], 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. After 150 days however, there was little in utilizing the burned or unburned areas, possibly because both areas had the same nutrition content [14, 15]. Similar results were observed 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, 42, 61]. 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.

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 a 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), steep bushland habitat above 15° slope (hereafter sloppy bushland habitat, see Additional file 1), plain bushland habitat, riverine forest, rugged bushland habitat with small valleys and neighborhood agricultural land (Fig. 1). The Park is surrounded by mountains, agricultural land 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 Swayne's hartebeest in each of habitat types and burned/unburned grassland patches. In each block, the habitat types and burned/unburned grassland patches were demarcated by using GPS within approximately 30 m accuracy and the extent was estimated using ArcGIS 10.3. In each block, we established permanent parallel transect lines spaced approximately 150–200 m apart. In the plains areas (i.e. open grassland and plain bushland areas), 37 transect lines were spaced at 200 m gap, whereas in the forest and rugged bushland areas where observation from distance was impossible, 15 transect lines were spaced 150 m apart. The length of transects varied due to the difference in size of each habitat types with average length of 5.9 km (±1.5 SD). In each transect, we randomly established 4 m × 5 m plots for Swayne's hartebeest pellet presence/absence detection. We established plots systematically along transect lines at every 100 m regular intervals (thus, the total is 10 plots per 1 km). 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 six 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 direct observation of Swayne's hartebeest along transect lines 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 [39]. We surveyed each transect 12 times during each season, and to avoid double detections of individuals, all transect lines of a block were surveyed at the same time. The surveys were 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 [66].

Because Swayne's hartebeests were found in concentrated in three patches in grassland habitat during the wet season, we delineated the area by using GPS coordinates with 30 m intervals resulting 0.7 km^2, 2.3 km^2, and 2.5 km^2 (see Additional file 2). During the early dry season, we also found the Swayne's hartebeests in the peripheral part of the park leaving the three patches used during the wet season and covering 3.4 km^2, 4.7 km^2 and 5.3 km^2 areas (see Additional file 2). The density was then derived by dividing the population estimate of the Swayne's hartebeest during the transect count to the area where they found in the wet and early dry season.

Swayne's hartebeest grass height preferences

To estimate average grass height in the grassland habitat during each season, grass heights were measured for 464, 193 and 133 central points of random plots of 1 m^2 area during the dry, wet and early dry seasons, respectively. The average grass height was varied across seasons in the Park. From the randomly measured grass heights, overall grass height for the survey year was 56.8±60.4 cm (mean ± SD); while for dry, wet and early dry season was 32±39.9 cm, 70.2±51 and 121.7±76 cm, respectively. Based on this estimate, we subjectively categorized the grass heights as below 30 cm, 31-50 cm, 51-100 cm, and above 100 cm.

During the three seasons, the grazing events of Swayne's hartebeests were recorded to determine the grass height preferred by Swayne's hartebeest by walking on the transect lines established 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 was observed on the transect walk within 150 m of either side of a transect line (i.e., 300 m width) for open habitats (i.e., grassland, plain bushland, sloppy bushland and agricultural land), while within 100 m (i.e., 200 m width) for riverine forest and rugged bushland habitats, 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 [39]. Once the bites were identified, a 1 m^2 quadrat was placed over the grass patch. Within each quadrat, heights of the preferred grasses by Swayne's hartebeest were measured, but only those escaped from fresh grazing during the observation time.

Effect of fire on Swayne's hartebeest habitat use

The Maze National Park management conducted controlled burning on some parts of the grassland habitat at the end of the wet season every year (mostly from October – November, depending on when the rain ends). Only some portion of the grassland habitat is burned in every year. Burning practice in the Park is mainly maintained by the Park managers with scheduled time in a year for herbivores use. However, in some places mostly at the periphery the local farmers also conduct burning. During this study period, the burning time was end of November. 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 Swayne's hartebeests twice (two days) every week to record how long Swayne's hartebeests were attracted 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. [66].

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 [39], we used the equation $Ei = (ri - ni) / (ri+ni)$ where ri is the proportion pellet detected in each habitat types within the survey period and ni 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 from the package lme4 [67] 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. We used generalized a 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 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 for the above models [68]. 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 [68]. We checked residuals and all the models met the assumption of normality. All analyses were done in R version 3.5.1 [69].

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, Diress Tsegaye, Paul Evangelista and Nils Chr Stenseth 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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Tables

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	0.4	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	0.020

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

Effects	Estimmate	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

Effects	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

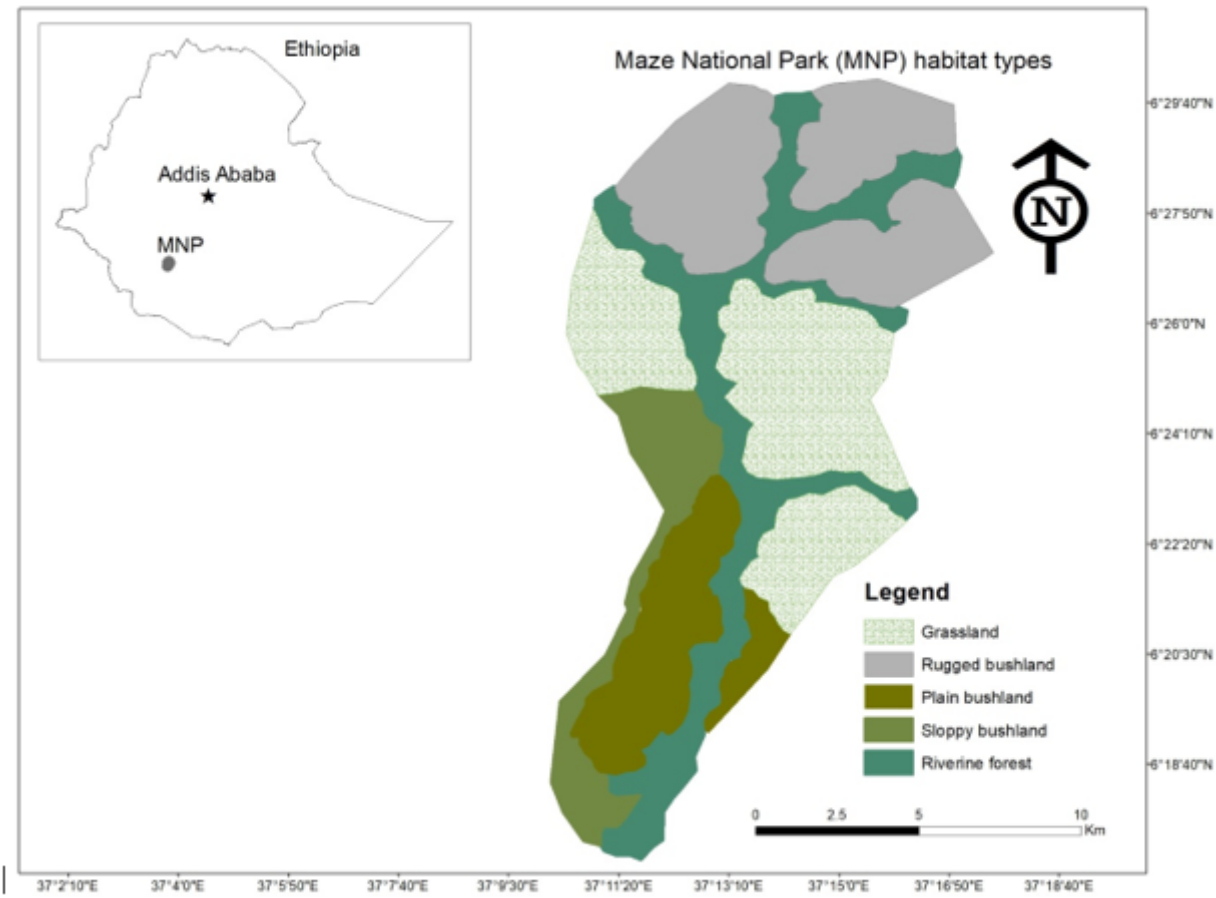

Figure 1

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

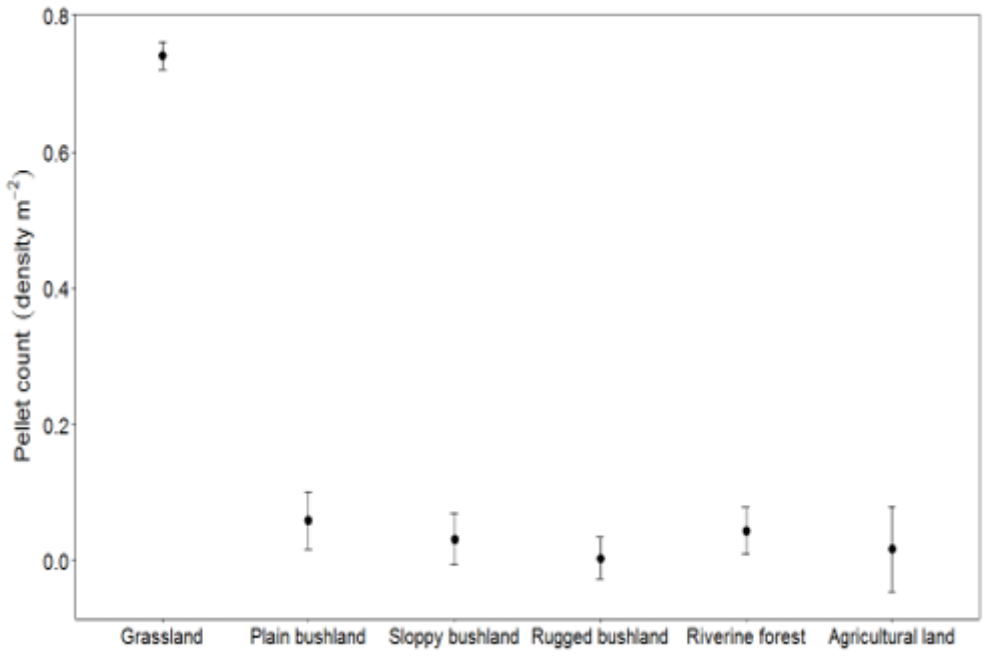

Figure 2

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

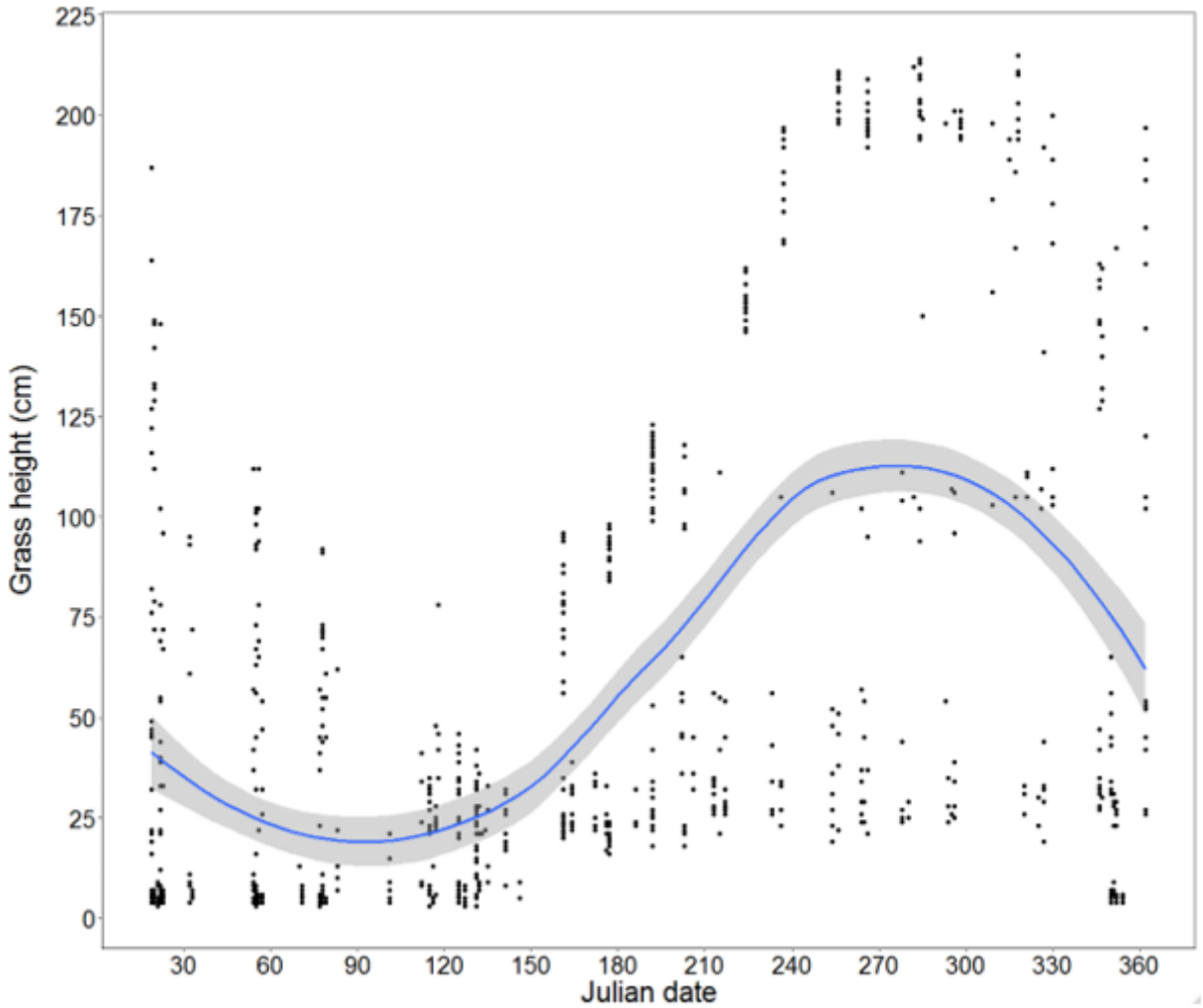

Figure 3

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

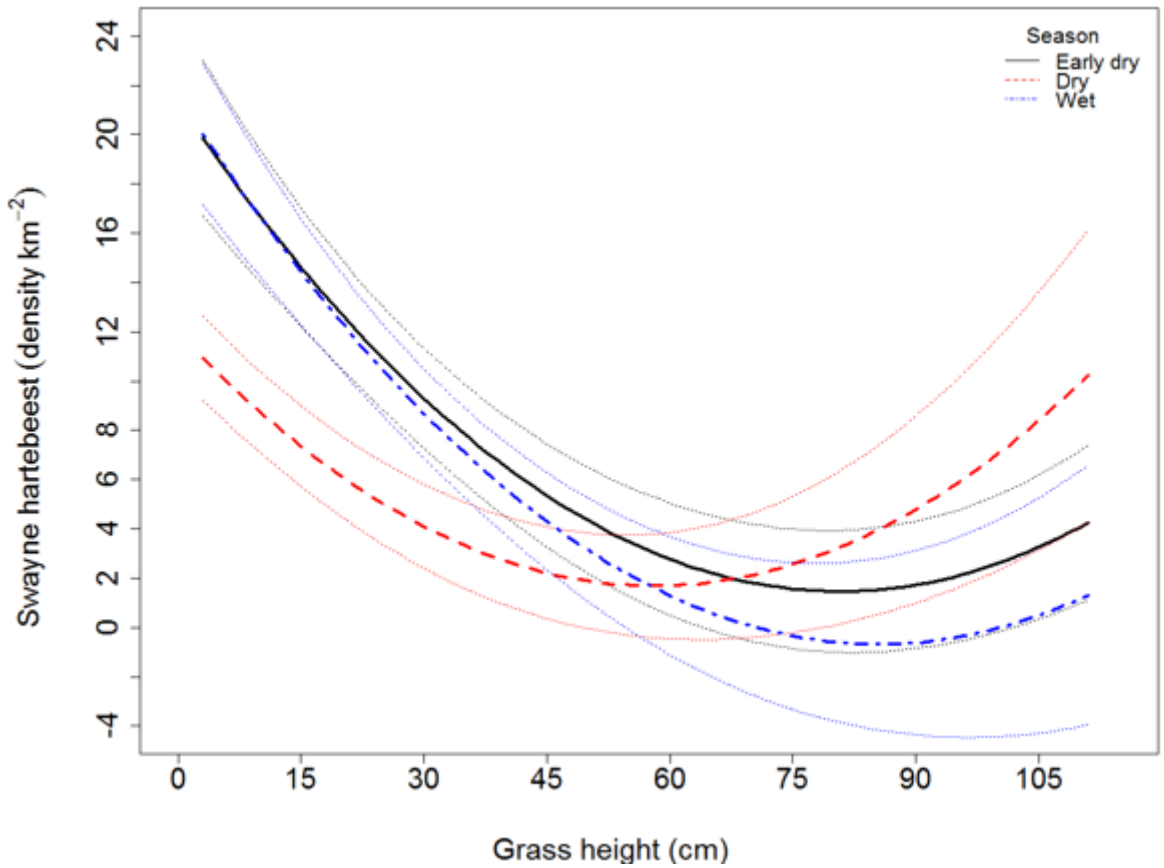

Figure 4

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

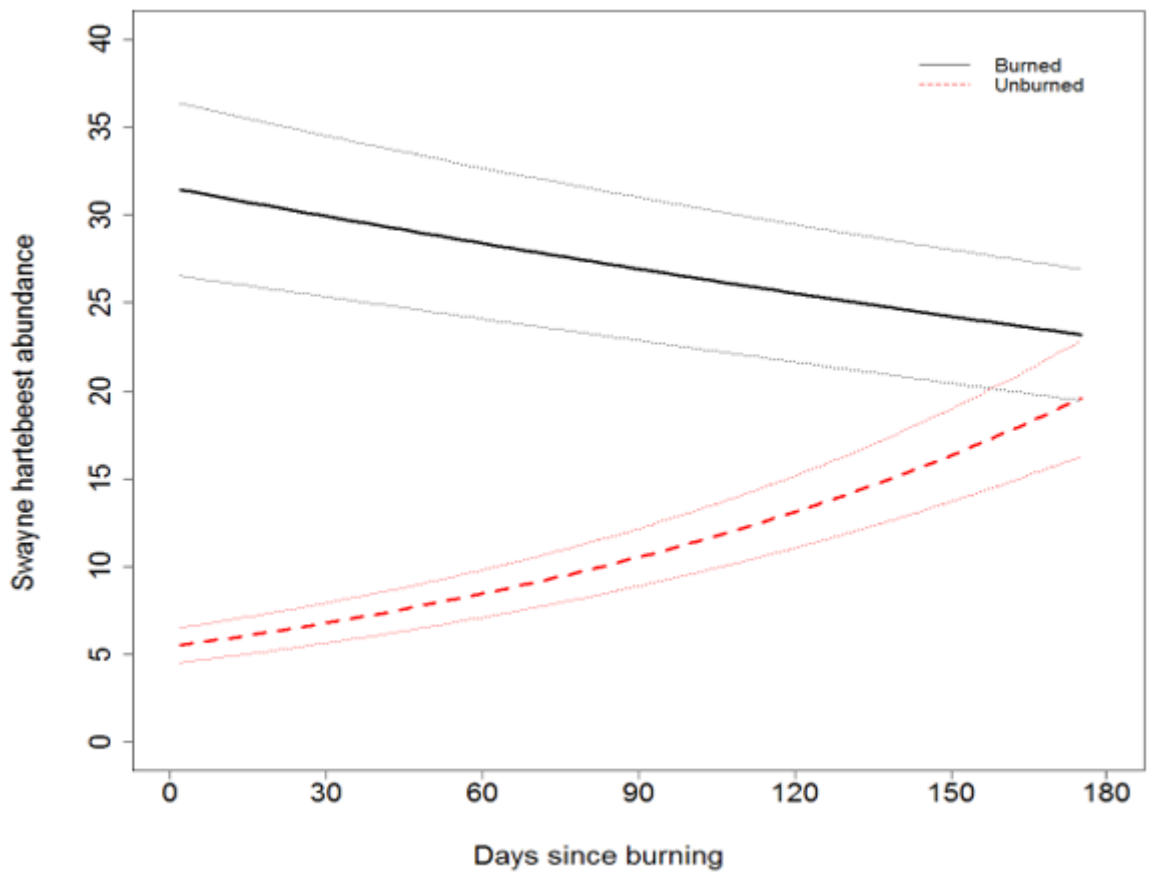

Figure 5

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

Supplementary Files

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