Running head: Swayne's hartebeest time and space use

Swayne's hartebeest (*Alcelaphus buselaphus swaynei*): home range and activity patterns in Maze National Park, Ethiopia

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Home range and activity patterns of animals are important elements for wildlife management and conservation practices. We examined seasonal home range and daily activity patterns of the endangered Swayne's hartebeest (*Alcelaphus buselaphus swaynei*) in Maze National Park, Ethiopia. We tracked two groups of Swayne's hartebeests in open grassland for 1 year. Each group's daily activities (0700-1900 hours) and GPS locations were recorded at 15-minute intervals on 5 days every month. Activities were grouped into five behavioral categories:

feeding, resting, travelling, vigilance, and other. In addition, we carried out nocturnal monitoring during full moon periods to further document movements patterns. We produced 95% and 50% kernel density estimates (KDE) of home range sizes for each group. Home range estimates did not vary across seasons. Feeding and travelling peaked during the early morning and late afternoon, whereas resting occurred most frequently during the mid-day hours in both seasons. The proportion of time spent feeding was higher during the dry season, whereas a greater proportion of time was spent resting during the wet season. Vigilance behavior occurred consistently throughout the day during both seasons. Time spent feeding and travelling did not vary significantly between seasons. Activity patterns of Swayne's hartebeest's are strongly influenced by both time of day and season, while home range size is less influenced by seasonality and may instead reflect temporal variation in food availability. Our findings will help to inform management strategies and conserve one of the last two extant populations of Swayne's hartebeests.

Key words: activity budgets, behavior, open grassland, seasonal variation, space use

The home range concept describes how animals use space, and is defined as an area of limited spatial extent over which an animal repeatedly travels to meet its basic needs (Burt 1943; Powell and Mitchell 2012) . The extent and patterns of animal space use may be directly linked to numerous factors, including variation in the availability of resources for survival and reproduction (Corriale et al. 2013; Tucker et al. 2014). Ecological factors, such as habitat type and quality, disturbance, and changes in population and predator density influence home range size and shape (Nilsen et al. 2008; Kie et al. 2010; van Beest et al. 2011; Powell and Mitchell 2012). The size of an animal's home-range can also vary seasonally (Quirici et al.

2010) or irregularly, in response to its metabolic requirements, reproductive behavior, or diet (Ofstad et al. 2016).

Habitat types explain important characteristics in terms of the quantity and quality of an individual's diet (Naidoo et al. 2012; Ofstad et al. 2016). Further, the distribution and characteristics of habitat features—for instance, plant biomass—determine the quality of forage and generates variation in space use among herbivores (Ford 1983; Hopcraft et al. 2012). Seasonality affects phenology, duration of vegetative growth, and the spatial distribution of plants, which in turn, affect seasonal space use by herbivores (Lindstedt et al. 1986; McLoughlin and Ferguson 2000). Herbivores therefore should adjust their space use in response to these seasonal changes, to minimize any negative consequences on fitness (Relyea et al. 2000; Kelt and Van Vuren 2001). Seasonal changes in home range size also provide insight into how herbivores are able to cope with such seasonal variability (Worton 1987; Börger et al. 2006).

In addition to having access to sufficient resources in their home range, herbivores also need to adjust their activity patterns in relation to seasonal changes (Tobler et al. 2009; Valeix et al. 2009; Blake et al. 2012). Daily activity patterns of herbivores may be driven by a variety of external factors, including availability of forage (Tobler et al. 2009; Valeix et al. 2009; Sanusi et al. 2013), sex, age, and body mass (Lizcano and Cavelier 2000; Ofstad et al. 2016). African herbivores forage mainly during daylight hours (Sanusi et al. 2013; Kasiringua et al. 2017). For instance, a study of the activity patterns of red hartebeest (*Alcelaphus buselaphus caama*), eland (*Taurotragus oryx*) and buffalo (*Syncerus caffer*) at Waterberg National Park (Namibia) found that they rested most in the middle of the day and fed most in the early morning and late afternoon (Kasiringua et al. 2017). Larger-bodied herbivores exhibit lower relative adjustments to their diurnal activity patterns in response to hourly variations of ambient temperature than smaller-bodied herbivores (Taylor et al. 2006; Smith and Cain III 2009; Valeix et al. 2009). This probably plays an important part in the animals' energy relations, particularly for feeding, resting, thermoregulation, antipredator strategies, and various forms of social interactions (Valeix et al. 2009; Blake et al. 2012; Sanusi et al. 2013).

We examined the diurnal activity patterns and seasonal home range sizes of Swayne's hartebeest (*Alcelaphus buselaphus swaynei*) at Maze National Park, Ethiopia. The Swayne's hartebeest weighs between 100 and 200 kg and is endemic to Ethiopia (Lewis and Wilson 1979), with a geographic range that has contracted due to habitat loss and displacement by livestock since the 1950's (Mamo et al. 2012; Kumssa and Bekele 2013). Further, population sizes declined following a rinderpest outbreak transmitted from introduced cattle (*Bos taurus*) at the end of 19th century; extensive hunting also is implicated in its decline (Hunt 1951; Lewis and Wilson 1977). The IUCN Red List of Threatened Species listed Swayne's hartebeest as Endangered in 1986, and it has remained at this status since (IUCN 2019). Currently, it only is found in Maze National Park and Senkele Swayne's Hartebeest Sanctuary, Ethiopia. Over a one-year period of direct observation we aimed to investigate Swayne's hartebeest (1) seasonal home range sizes, (2) hourly variation in activity patterns, and (3) seasonal variation in activity patterns.

MATERIALS AND METHODS

Study area.—Maze National Park is located between 6°30′40"N - 6°16′40"N and 37°9′30"E - 37°16′30"E in southern Ethiopia. The park covers an area of 175 km^2 at elevations between 900 – 1300 m asl and was established in 2005 to conserve Swayne's hartebeest. Maze National Park experiences a short rainy season from March to April, a longer rainy season from June to August, and a dry season from November to February (Refera 2005; Mamo et al. 2012). The mean monthly minimum temperature is 15.3°C and the mean monthly maximum is 35.5°C (Mamo et al. 2012). The Daho, Lemasea, and Domba Rivers flow through the park, providing water throughout the year. The major habitat types of the park include grasslands with scattered trees, sloped bushland (i.e., slopes of > 15°), flat bushland, riverine forest, and rugged bushland (Tamrat et al. 2020). Grasslands are dominated by annuals of the family Poaceae, such as: *Exotheca abyssinca*, *Heteropogon contortus*, *Loudentia* spp., *Setaria incrassate*, and *Hyparrhenia filipendula*, interspersed with scattered woody plants, mainly *Combretum* spp. (Myrtales: Combretaceae). Grass growing during the wet season (June to August), becomes taller in the early-dry season (September to November), then senesces in the first few months of the dry season (December to May) (Tamrat et al. 2020).

In addition to Swayne's hartebeest, other large (>10 kg) mammals present in Maze National Park include waterbuck (*Kobus ellipsiprymnus*), greater kudu *(Tragelaphus strepsiceros)*, oribi (*Ourebia ourebi*), and lions (*Panthera leo*). Swayne's hartebeest is designated as a flagship species of the park. Despite its Endangered status, the population size in Maze National Park has been increasing for the last decade (Tamrat et al. 2020). In the park, Swayne's hartebeest prefer open grasslands during the dry season, and use grasslands exclusively both during the early-dry and wet seasons (Tamrat et al. 2020). Since the park was established, controlled burning of grassland has been carried out to remove litter and senescent biomass from previous years. Following burning, grasses and forbs are scarce and scattered until the rain returns, promoting new growth of high quality (Burkepile et al. 2013; Eby et al. 2014). During our study, 21.4 km^2 of grassland were burned at the end of November while 30.2 km^2 remained unburned.

Home range and activity patterns.—We collected data on diurnal activity patterns for two study groups of Swayne's hartebeests. The two groups were separated by 6 km of riverine forest. We tracked both groups in relatively open grassland areas containing scattered trees. To estimate mean grass height in each group's home range, we measured grass heights of 73, 33, and 30, central points of random plots of 1 m^2 area in Group 1's range and 74, 44, and 34, in Group 2's range during the dry, wet, and early-dry seasons, respectively.

We observed study groups predominantly on foot from early morning (0700 hours) to late afternoon (1900 hours). Five days of observation were undertaken each month in three different seasons: early-dry season (September to November), dry season (December to May), and wet season (June to August), over a one-year period (October 2018 to September 2019). Early-dry season refers to months of the dry season before burning of some grassland patches. Number of individuals in Group 1 ranged from 31 – 34 while Group 2's size ranged from 22 – 27 individuals.

Hartebeest follows were facilitated by an established network of routes used by wildlife managers and occasional photo safaris. Observations of activities and GPS locations of each group were recorded every 15 minutes by scan sampling (Shannon et al. 2008; Vymyslická et al. 2011). The same observers were assigned to each group throughout the study period to maintain consistency and habituate animals. To supplement our diurnal observations, we conducted night monitoring during the full moon to document nocturnal space use and provide a 24-hour profile. Full moon nights offered good visibility conditions to carry out observations, particularly in areas such as open grassland that lacked dense vegetation (Crosmary et al. 2012). We carried out a total of 35 night surveys: 18 for Group 1, and 17 for Group 2. Observations were made with the help of spotting lights suspended from platforms, tree hides, or a car parked 40 – 50 m away, to avoid disturbing the study animals (Crosmary et al. 2012).

With the aid of binoculars, we noted the activities and age and ex classes (i.e., adult female, adult male, sub-adult female, sub-adult male, and juvenile) of every recorded animal. We identified the age-classes and sex using the animals' reproductive organs and horn morphology (Mamo et al. 2012). We divided individual activities (hereafter 'activity type') into five categories: feeding, travelling, resting, vigilance, and other (i.e., drinking, fighting, reproduction, excretion, and grooming; Table 1). We recorded activities of the first five individuals (from left to right and from right to left, alternately, during consecutive scans) during each scan. Then, to characterize diurnal activity patterns, we calculated the proportion of time spent on each activity type. The activity patterns were collected for the wet, early-dry and dry seasons separately.

Data analyses.—We estimated home range sizes during each of the three seasons by each of the two groups of Swayne's hartebeests employing 95% and 50% Kernel Density Estimation (KDE) using the R package "adehabitat HR". We used linear models to compare changes in 50% and 95% KDE home range size for each group, separately. We used linear models to evaluate the relationship between grass height and Julian date for each group of Swayne's hartebeest, separately. We also added a squared term for Julian date to capture the curvilinear trend (i.e. non-linear).

Because we did not find variation in the activity patterns of Swayne's hartebeests between the dry and early-dry seasons during a preliminary analysis, we merged these seasons into a single 'dry season' in subsequent analyses. We used a general linear mixed effects model from the package lme4 to evaluate time spent per hour (response variable) in relation to activity types and time of day for each season (i.e., wet and dry seasons), separately. We performed log transformation of the response variable (i.e., percent of time spent) to avoid lack of fit of the model. We also added a squared term to capture the curvilinear trend. Sites for the two selected groups were used as random factors to account for variation between groups. All analyses were carried out in R version 3.5.1 (R Core Team 2018).

RESULTS

During the one-year study period, we recorded 5,585 GPS locations for the two study groups (Group 1: n = 2,638 day, 155 night; Group 2: n = 2,635 day, 157 night). During the dry season, GPS points were scattered and spread over wide areas in both groups, whereas during the wet season, points were more condensed and distributed across much smaller areas in Group 1 (Fig. 1). The means ± SD of the 95% and 50% KDE home range sizes across the three seasons were 4.81 km^2 ± 2.74 and 1.19 km^2 ± 0.80 for Group 1, and 6.46 km^2 ± 3.54 and 1.18 km^2 ± 0.58 for Group 2, respectively (Fig. 2; Table 2). However, the home range sizes did not vary significantly among seasons except for the early-dry season range of Group 1 (Supplementary Data SD1).

The random grass height measurements in both groups' ranges showed increasing of grass height with time except during the wet season in Group 2's range (Fig. 3). The means ± SD of dry, wet, and early-dry, seasons' grass heights for Group 1's range were: 21.0 cm ± 16.0, 37.2 cm ± 18.6 and 47.4 cm ± 31.4. The corresponding data for Group 2 were: 15.0 cm ± 11.8, 11.3 cm ± 4.3 and 41.7 cm ± 26.4.

A total of 26,382 activity observations (Group 1: *n* = 10,160 dry season, *n* = 3,030 wet season; Group 2: *n* = 9,982 dry season, *n* = 3,210 wet season) were recorded during the one-year study period. For Group 1 during the dry season, resting was the most observed activity (33.1%) followed by feeding (28.7%). During the wet season, time spent resting (46.8%) increased while feeding (25.3%) decreased slightly. Similarly, during the dry season, Group 2 was observed resting (32.0%) most, followed by feeding (30.4%). During the wet season, time spent resting (54.1%) by Group 2 increased substantially while feeding (24.4%) decreased (Supplementary Data SD2). Feeding varied significantly with the other activity types and their interaction with time except travelling during both the wet and dry seasons (Supplementary Data SD3).

During both seasons, time spent feeding peaked in the early morning (0700 – 1000 hours) and late afternoon (1500 – 1800 hours; Fig. 4). Time devoted to travelling also peaked in the early morning and late afternoon during the dry season, but temporal variation in travelling time was negligible during the wet season. Conversely, time spent resting peaked during the middle of the day (1000 – 1500 hours) during both seasons. Time spent on vigilance and other activities exhibited limited temporal variation in both seasons, though vigilance declined late in the day (1600 – 1800 hours) during the wet season.

DISCUSSION

Although the home ranges of Swayne's hartebeest did not vary at different seasons in Maze National Park, there are distinct seasonal space use variations between the two study groups. We also noted the proportion of home range variations between the two study groups based on the home range size models. This might be explained by seasonal grass height variation between sites and grass height preferences in different seasons (Tamrat et al. 2020). In much of the park, the grass starts to grow during the wet season and reaches above one m during the early-dry season until some grassland patches are burnt.

The park management carried out controlled burning every year on some parts of the grassland habitat, mostly from October to November, depending on when the rain ends. During the survey year, several areas of grassland were burned, totaling 21.4 km^2. While fire reduces much of the forage at the time of burning, it also results in new shoots once the rains return (Eby et al. 2014; Pacifici et al. 2015). Although this study does not specifically examine the relationship between daily or seasonal activities and controlled burning, Tamrat et al. (2020) found that Swayne's hartebeest were attracted to post-fire regrowth and short grass height, ranging over larger areas during the dry season.

Increased dietary resource selection by hartebeests, particularly when the resources are less available, possibly resulted in larger home range size during the dry season (Casebeer and Koss 1970; Schuette et al. 1998). The increased space use of Swayne's hartebeest during the dry season might represent a response to seasonal senescence of taller grasses (Tamrat et al. 2020) and fire (Burkepile et al. 2013; Eby et al. 2014). During the wet season, however, the space use of the two groups was highly variable, which could be due to the availability of shorter grasses on specific patches in Group 1's range where Swayne's hartebeests congregate (Tamrat et al. 2020).

Although we cannot evaluate the potential role of all other confounding factors that impact the home range size and usage patterns of Swayne's hartebeest in Maze National Park, there are few potential predators (i.e., lion population estimated to be seven individuals, (Tamrat et al. 2020) in the park). We also only witnessed two lion attacks on Swayne's hartebeest over our one-year study period. Thus, predation may be a less important factor influencing their seasonal home range patterns than spatiotemporal variation in resource availability. Here, we highlighted the importance of understanding the space use of two sub-populations at different seasons. Such knowledge could provide an impartial tool to make comparisons across species and ecosystems that would contribute to delineating general mechanisms of home range behavior (Powell and Mitchell 2012; Fauvelle et al. 2017).

Activity patterns of herbivores are considered an adaptation to seasonal and diurnal variation in environmental factors (Lizcano and Cavelier 2000; Taylor et al. 2006; Sanusi et al. 2013), and represent a complex compromise between optimal foraging time, resting and environmental factors (Sanusi et al. 2013; Kasiringua et al. 2017). Feeding by Swayne's hartebeest in Maze National Park peaked during the early morning and late afternoon in both the wet and dry seasons, consistent with observations in Nechisar National Park (Vymyslická et al. 2011). Although Swayne's hartebeests were recently extirpated from Nechisar National Park, previous studies reported that they had spent more time foraging and walking during the early morning and late afternoon, and more time standing and resting during the middle of the day (Vymyslická et al. 2011). Time spent feeding during the dry season was greater than during the wet season, likely because of the lower availability of shorter and more nutritious grasses during the drier months (Vymyslická et al. 2011).

Travelling and feeding appeared to be associated in Swayne's hartebeest at Maze National Park. Specifically, Swayne's hartebeest both fed more and travelled more during the early morning and late afternoon hours. Conversely, they spent more time resting between 1000 and 1500 hours, probably because of the need to minimize thermal stress during the hottest part of the day during both seasons (Kasiringua et al. 2017; Tan et al. 2018). The diurnal activity patterns of Swayne's hartebeest followed diurnal variation in ambient temperature similar to wildebeest (*Connochaetes taurinus*) at Kruger National Park, South Africa (Treydte et al. 2011). However, during the wet season, the peak in time spent resting was extended from 0900 to 1600 hours, likely facilitated by the greater abundance of forage during the wet season (Hopcraft et al. 2012; Tamrat et al. 2020). Hartebeest previously have been reported to cope with periods of restricted resources by searching more widely for food and increasing time spent on feeding (Schuette et al. 1998). Our results suggest that the general activity patterns of Swayne's hartebeest were similar to those of other large herbivore species including red hartebeest and wildebeest (Taylor et al. 2006; Valeix et al. 2009).

Our data improve our understanding of seasonal variability in the home range and diurnal activity dynamics of Swayne's hartebeest. We found that Swayne's hartebeest is a sedentary herbivore that tends to have fairly stable ranges. Our study also revealed that the abundance of food resources is a major limiting factor in determining the home ranges of the Swayne's hartebeest. The dynamic nature of resource availability in Maze National Park in different seasons explains the variation in activity patterns of the Swayne's hartebeest over time. The IUCN Red List of Threatened Species lists the Swayne's hartebeest as Endangered, and several subpopulations have been extirpated within their historical range (Vymyslická et al. 2011; Tamrat et al. 2020). The only site aside from Maze National Park where Swayne's hartebeest still occurs is Senkele Swayne's Hartebeest Sanctuary, where the population is under pressure from overgrazing, lack of water, and human settlement, and may need translocations of animals into it to maintain a sustainable population (Tamrat et al. 2020). Knowledge of the space use of Swayne's hartebeest may be used as a complement to management and conservation strategies including conservation planning, habitat management, and reintroduction efforts, to conserve this taxon. We hope this study will help to inform management strategies in Maze National Park and conserve one of the last two extant populations of Swayne's hartebeests.

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Supplementary Data

Supplementary Data SD1.—Kernel density home range estimates (KDE) for two groups of Swayne's hartebeest in relation to season (early-dry, dry and wet) in Maze National Park, Ethiopia.

Supplementary Data SD2.— The total number of recorded activities and their proportions for two selected groups of Swayne's hartebeest during the wet and dry seasons over a one-year period (October 2018 to September 2019).

Supplementary Data SD3.— Estimates of Swayne's hartebeest diurnal activity patterns during the wet and dry seasons in Maze National Park, analyzed using a general linear mixed effects model. Feeding was used as the reference level for categorical activity variables.

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Figure legends

Fig 1.—Map showing the home range estimates for the two study groups of Swayne's hartebeests in Maze National Park, Ethiopia. The blue refers to the 50% and the purple to the 95% kernel density estimate (KDE) for the early-dry, dry, and wet seasons. The points represent the GPS locations of each ranging point collected during this study.

Fig 2.—Home range estimates for two study groups of Swayne's hartebeest during the early-dry, dry and wet seasons based on kernel density estimates (KDE) in Maze National Park, Ethiopia

Fig 3.—Mean grass height across the different Julian dates of a one-year cycle at the grassland sites occupied by our study groups of Swayne's hartebeest in Maze National Park, Ethiopia analyzed using a linear model.

Fig 4.—Trends of the daily activity patterns of Swayne's hartebeest during the wet and dry seasons in Maze National Park, Ethiopia.

Table 1.- Description of different activity patterns of Swayne's hartebeest in Maze National Park, Ethiopia

Activity	Description
Feeding	Grazing (biting and swallowing) or searching food over short distance with the head bent down
Travelling	Locomoting with head held upright, including walking and running often between sources of forage
Resting	Standing (quadrupedal posture with head held upright) OR lying down, without showing vigilance in open space or in the shade
Vigilance	Looking towards external stimuli such as predators, domestic livestock, human or other wildlife.
Others	Other behavior, including drinking, fighting, sexual behavior, excretion, and grooming.

Table 2. Home range sizes for two groups of Swayne's hartebeests in Maze National Park, Ethiopia based on 95% and 50% kernel density estimates.

Groups	Season	95% KDE (km^2 ± SD)	50% KDE (km^2 ± SD)
Group 1	Early-dry	5.60±4.01	1.41±1.09
	Dry	5.92±1.65	1.52±0.54
	Wet	1.79±0.32	0.28±0.04
	Mean	*4.81±2.74*	*1.19±0.80*
Group 2	Early-dry	4.09±2.81	0.72±0.44
	Dry	7.72±3.76	1.33±0.47
	Wet	7.02±3.48	1.34±0.82
	Mean	*6.46 ±3.54*	*1.18 ±0.58*

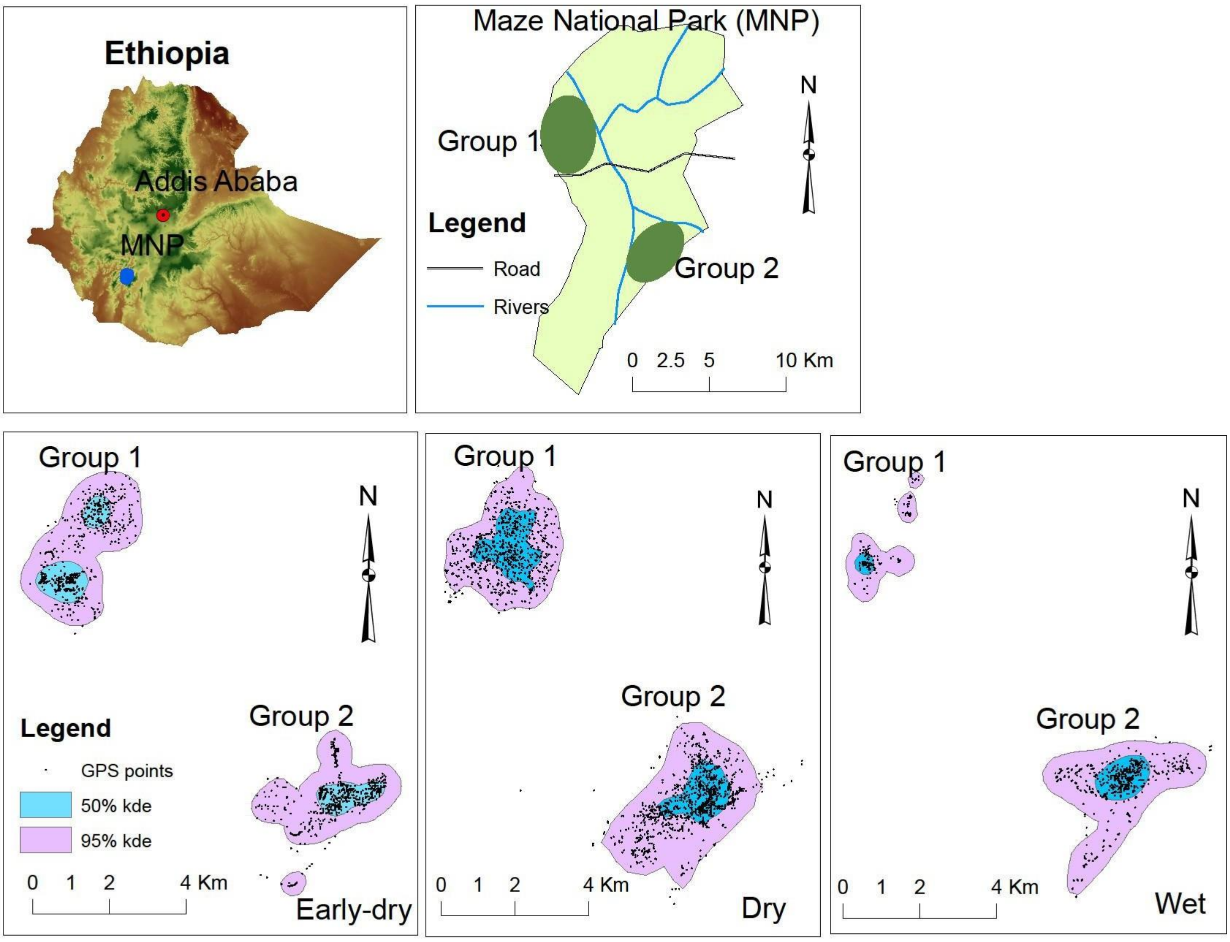

Fig 1.-Map showing the home range estimates for the two study groups of Swayne's hartebeests in Maze National Park, Ethiopia. The blue refers to the 50% and the purple refers the 95% kernel density estimate (KDE) for the early-dry, dry, and wet seasons. The points represent the GPS locations of each ranging point collected during this study.

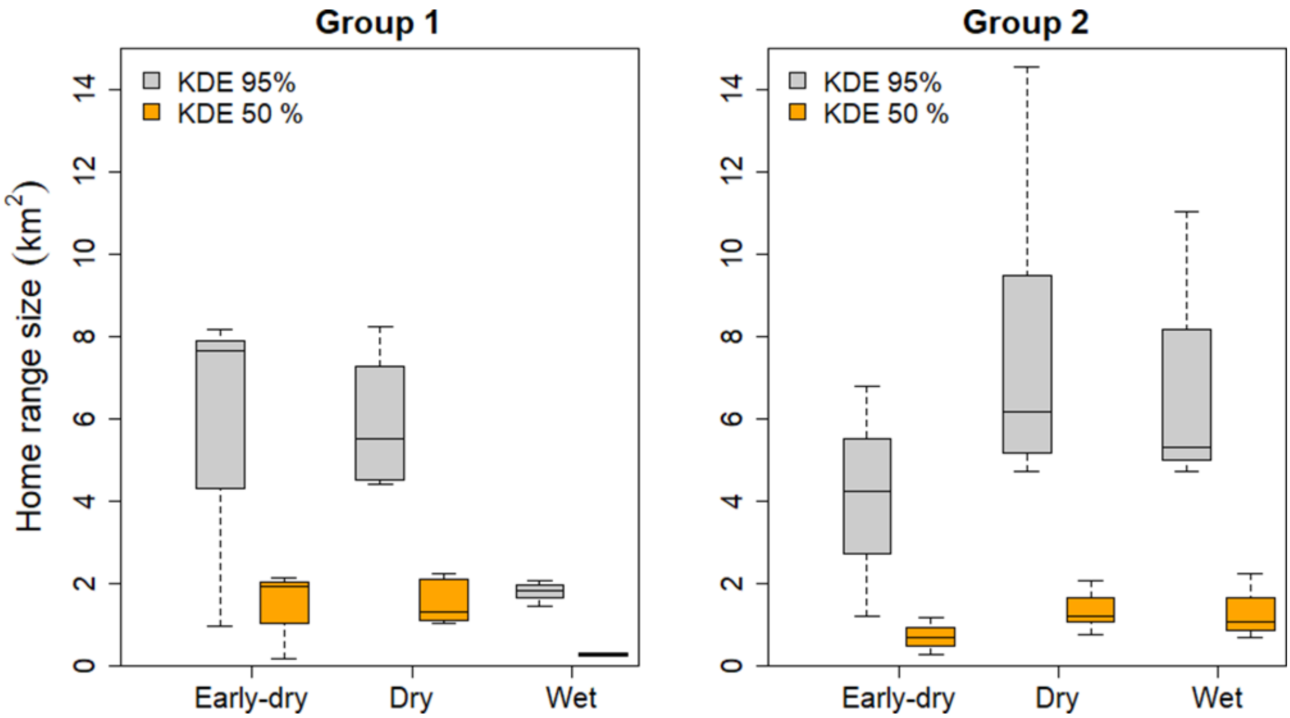

Fig 2.-Home range estimates for two study groups of Swayne's hartebeest during the early-dry, dry and wet seasons based on kernel density estimates (KDE) in Maze National Park, Ethiopia.

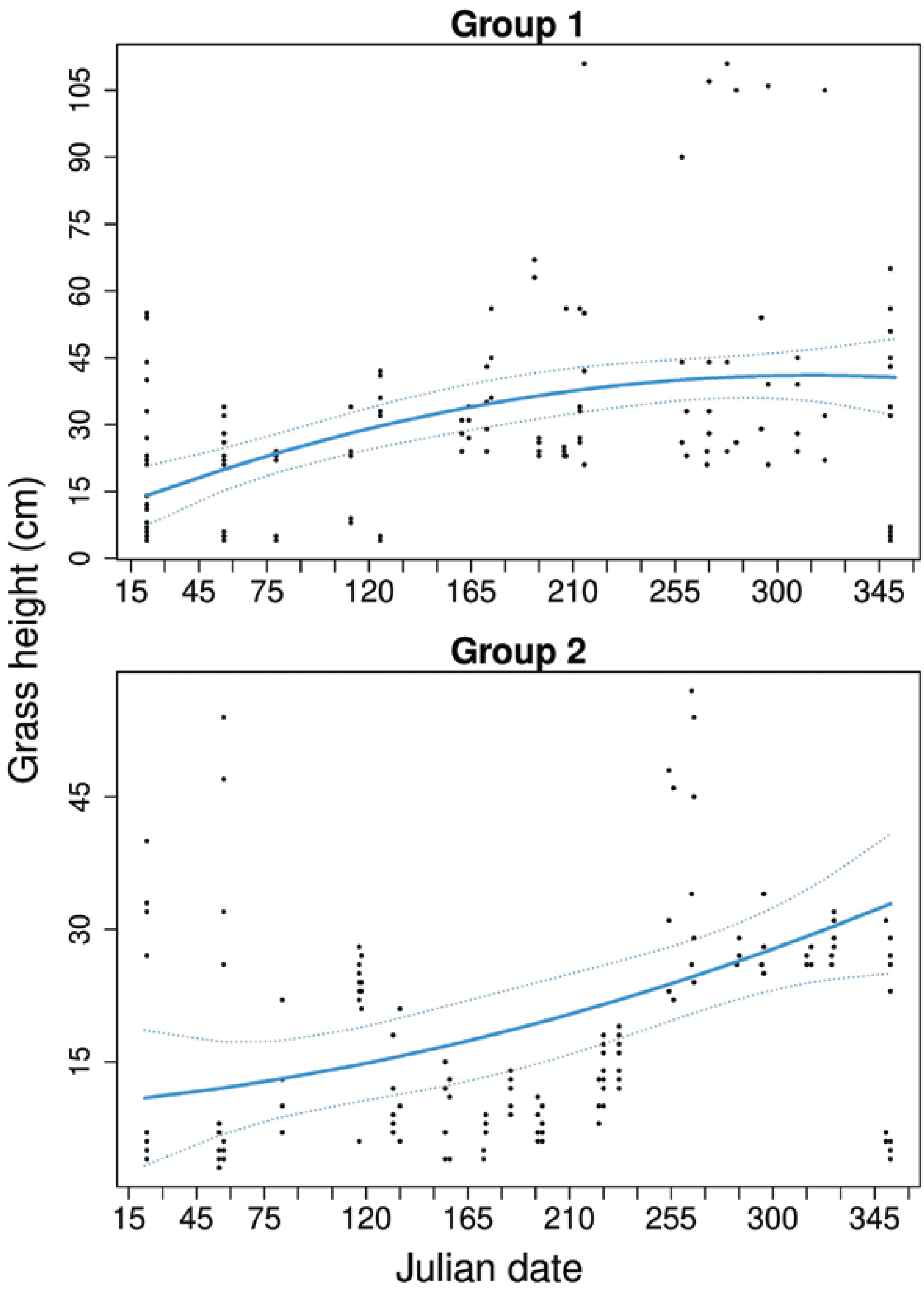

Fig. 3.—Mean grass height across the different Julian dates of a 1-year cycle at the grassland sites occupied by our study groups of Swayne’s hartebeest in Maze National Park, Ethiopia analyzed using a linear model.

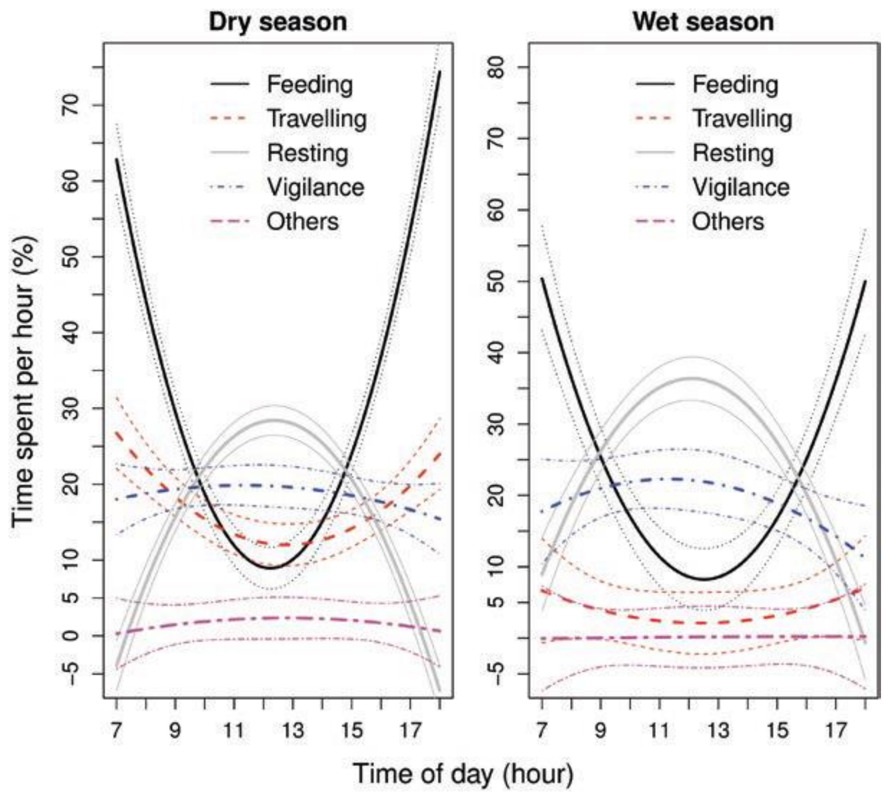

Fig. 4.—Trends in the daily activity patterns of Swayne’s hartebeest during the wet and dry seasons in Maze National Park, Ethiopia.