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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 h) and GPS locations were recorded at 15-min intervals on 5 days every month. Activities were grouped into five behavioral categories: feeding, resting, traveling, 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 traveling peaked during the early morning and late afternoon, whereas resting occurred most frequently during the midday 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 traveling did not vary significantly between seasons. Activity patterns of Swayne's hartebeests are strongly influenced both by 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 also can 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 these species 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 in ambient temperature than smaller-bodied herbivores (Taylor et al. 2006; Smith and Cain 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 1950s (Mamo et al. 2012; Kumssa and Bekele 2013). Further, population size of Swayne's hartebeest 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 SSC Antelope Specialist Group 2019). Currently, it is found only in Maze National Park and Senkele Swayne's Hartebeest Sanctuary, Ethiopia. Over a 1-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 km² at elevations between 900 and 1,300 m a.s.l. 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 (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 hartebeest 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 km² of grassland were burned at the end of November while 30.2 km² 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 m² 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 h) to late afternoon (1900 h). 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 1-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 to 34 while Group 2's size ranged from 22 to 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 min 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 undertook night monitoring during the full moon to document nocturnal space use and provide a 24-h 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 sex classes (i.e., adult female, adult male, subadult female, subadult 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, traveling, 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., nonlinear).

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 for food over short distances with the head bent down
Traveling	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 behavior
Vigilance	Looking towards external stimuli such as predators, domestic livestock, humans, or other wildlife.
Others	Other behavior, including drinking, fighting, sexual behavior, excretion, and grooming.

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 1-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 1-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 traveling during both the wet and dry seasons (Supplementary Data SD3).

During both seasons, time spent feeding peaked in the early morning (0700–1000 h) and late afternoon (1500–1800 h; Fig. 4). Time devoted to traveling also peaked in the early morning and late afternoon during the dry season, but temporal

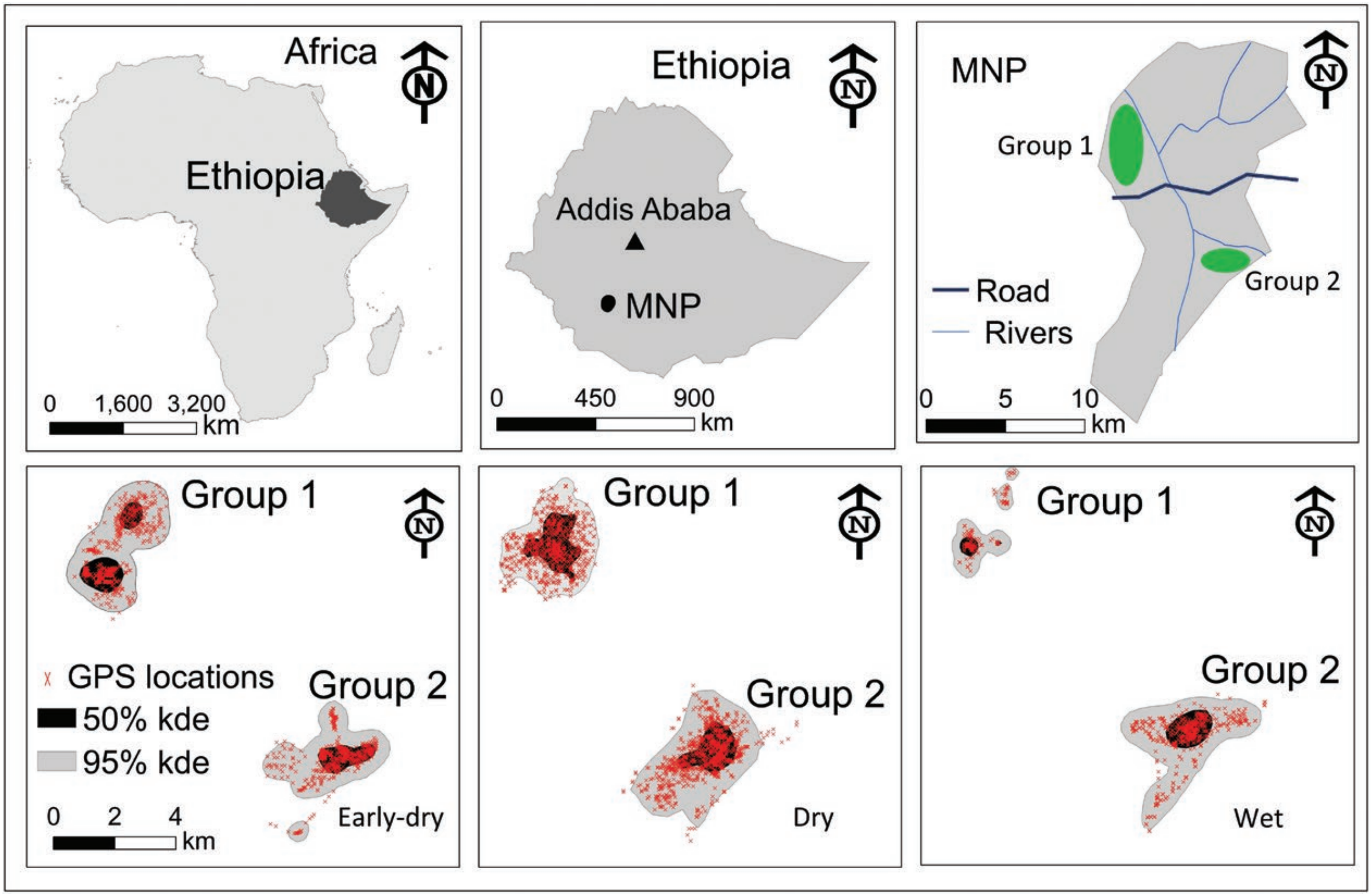

Fig. 1.—Map showing the home range estimates for the two study groups of Swayne's hartebeests in Maze National Park, Ethiopia. The black refers to the 50% and the gray to the 95% kernel density estimate (KDE) for the early-dry, dry, and wet seasons. The red marks represent the GPS locations of all ranging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

variation in traveling time was negligible during the wet season. Conversely, time spent resting peaked during the middle of the day (1000–1500 h) 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 h) 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 1 m during the early-dry season until some grassland patches are burnt.

The park management carries 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 postfire 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., the lion population in the park is estimated to be just seven individuals—Tamrat et al. 2020). We also only witnessed two lion attacks on Swayne's

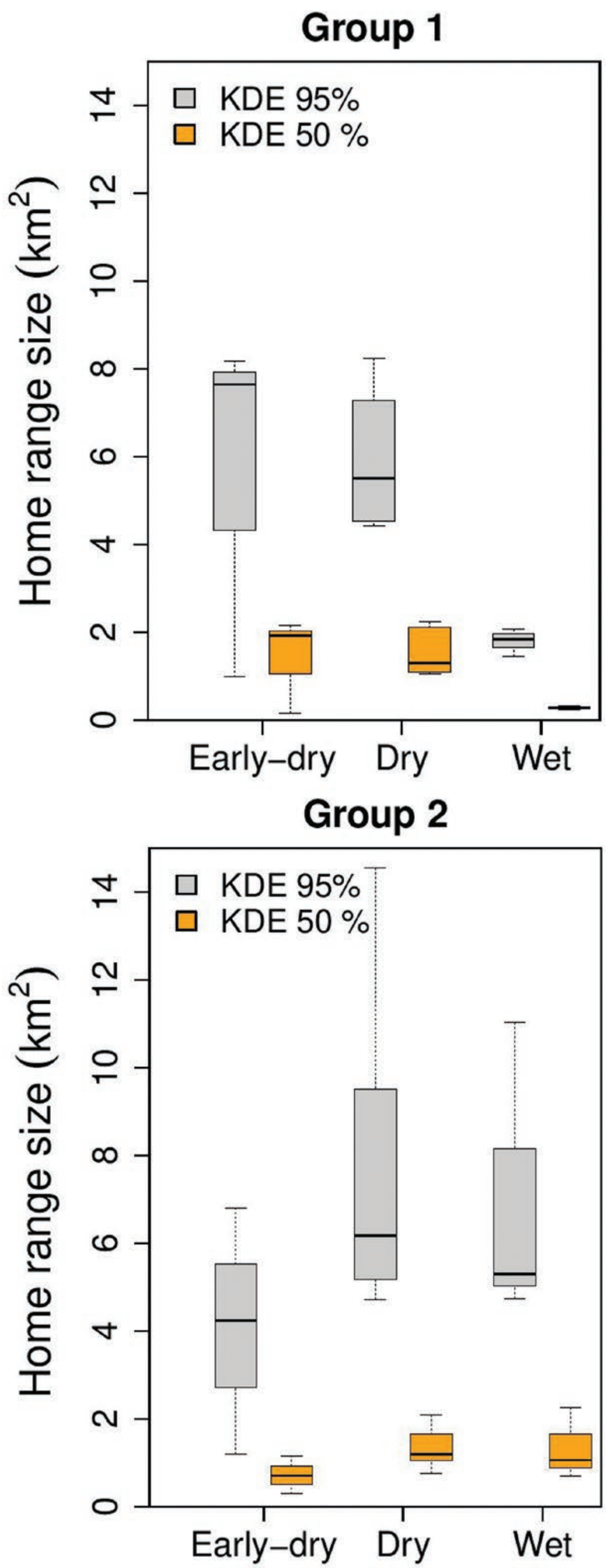

Fig. 2.—Home range estimates for two study groups of Swayne's hartebeest during the early-dry, dry, and wet seasons based on kernel density estimates (KDE) in Maze National Park, Ethiopia.

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 (KDE).

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

hartebeest over our 1-year study period. Thus, predation may be a less important factor influencing Swayne's hartebeest seasonal home range patterns than spatiotemporal variation in resource availability. Here, we highlighted the importance of understanding the space use of two subpopulations in 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).

Traveling and feeding appeared to be associated in Swayne's hartebeest at Maze National Park. Specifically, Swayne's hartebeest both fed more and traveled more during the early morning and late afternoon hours. Conversely, they spent more time resting between 1000 and 1500 h, 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 h, 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.

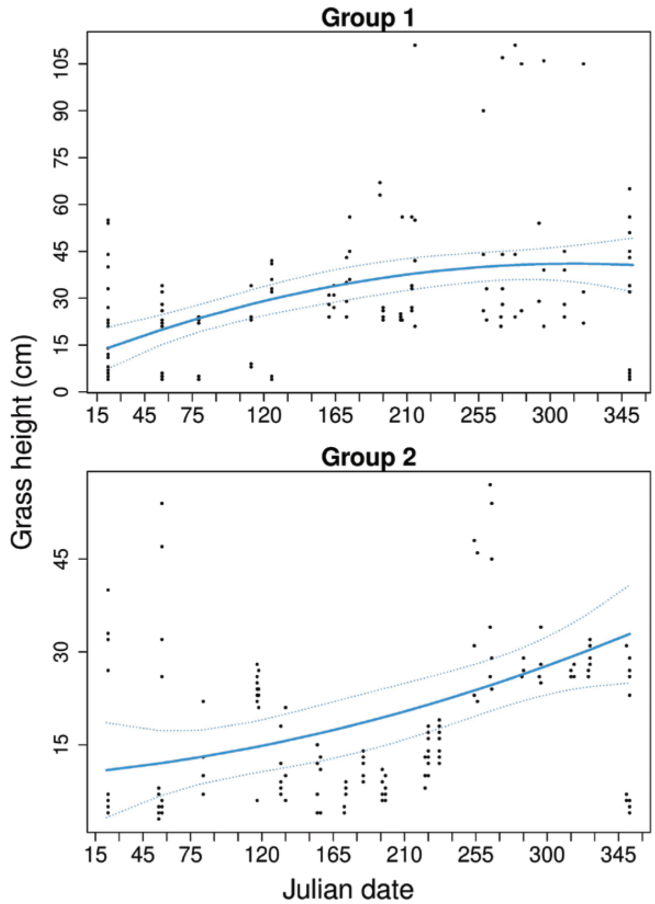

Fig. 3.—Mean grass height across the different Julian dates of a 1-year cycle at the grassland sites occupied by our study groups of Swayne's hartebeest in Maze National Park, Ethiopia analyzed using a linear model.

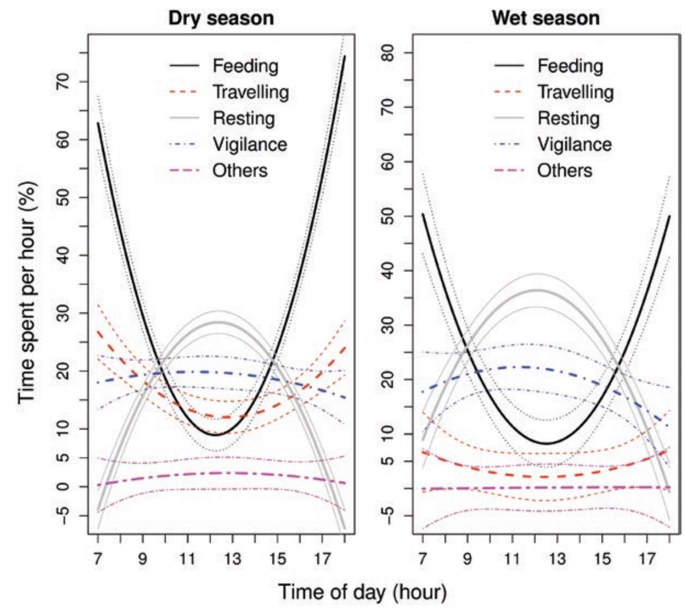

Fig. 4.—Trends in the daily activity patterns of Swayne's hartebeest during the wet and dry seasons in Maze National Park, Ethiopia.

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 are available at *Journal of Mammalogy* online.

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 1-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.

Literature Cited

Blake, J. G., D. Mosquera, B. A. Loiselle, K. Swing, J. Guerra, and D. Romo. 2012. Temporal activity patterns of terrestrial mammals in lowland rainforest of eastern Ecuador. Ecotropica 18:137–146.

Börger, L., et al. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. The American Naturalist 168:471–485.

Burkepile, D. E., et al. 2013. Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces. Ecosphere 4:139.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Casebeer, R., and G. Koss. 1970. Food habits of wildebeest, zebra, hartebeest and cattle in Kenya Masailand. African Journal of Ecology 8:25–36.

Corriale, M. J., E. Muschetto, and E. A. Herrera. 2013. Influence of group sizes and food resources in home-range sizes of capybaras from Argentina. Journal of Mammalogy 94:19–28.

Crosmary, W.-G., M. Valeix, H. Fritz, H. Madzikanda, and S. D. Côté. 2012. African ungulates and their drinking problems: hunting and predation risks constrain access to water. Animal Behaviour 83:145–153.

Eby, S. L., T. M. Anderson, E. P. Mayemba, and M. E. Ritchie. 2014. The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. The Journal of Animal Ecology 83:1196–1205.

Fauvelle, C., R. Diepstraten, and T. Jessen. 2017. A meta-analysis of home range studies in the context of trophic levels: implications for policy-based conservation. PLoS ONE 12:e0173361.

Ford, R. G. 1983. Home range in a patchy environment: optimal foraging predictions. American Zoologist 23:315–326.

Hopcraft, J. G., T. M. Anderson, S. Pérez-Vila, E. Mayemba, and H. Olff. 2012. Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. The Journal of Animal Ecology 81:201–213.

Hunt, J. A. 1951. A general survey of the Somaliland Protectorate 1944–1950; final report on "An economic survey and reconnaissance of the British Somaliland Protectorate 1944–1950," Colonial Development and Welfare Scheme D. 484. The Chief Secretary. Hargeisa, Somaliland Protectorate.

IUCN SSC Antelope Speclialist Group. 2019. *Alcelaphus buselaphus* (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2019: e.T811A143160967. https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T811A143160967.en. Accessed 3 July 2019.

Kasiringua, E., G. Kopij, and Ș. Procheș. 2017. Daily activity patterns of ungulates at water holes during the dry season in the Waterberg National Park, Namibia. Russian Journal of Theriology 16:129–138.

Kelt, D. A., and D. H. Van Vuren. 2001. The ecology and macroecology of mammalian home range area. The American Naturalist 157:637–645.

Kie, J. G., et al. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of the Royal Society of London, B: Biological Sciences 365:2221–2231.

Kumssa, T., and A. Bekele. 2013. Human-wildlife conflict in Senkele Swayne's hartebeest sanctuary, Ethiopia. Journal of Experimental Biology and Agricultural Sciences 1:32–38.

Lewis, J., and R. Wilson. 1977. The plight of Swayne's hartebeest. Oryx 13:491–494.

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

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology 67:413–418.

Lizcano, D. J., and J. Cavelier. 2000. Daily and seasonal activity of the mountain tapir (*Tapirus pinchaque*) in the Central Andes of Colombia. Journal of Zoology 252:429–435.

Mamo, Y., G. Mengesha, A. Fetene, K. Shale, and M. Girma. 2012. Status of the Swayne's hartebeest (*Alcelaphus buselaphus swaynei*) meta-population under land cover changes in Ethiopian Protected Areas. International Journal of Biodiversity and Conservation 4:416–426.

McLoughlin, P. D., and S. H. Ferguson. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience 7:123–130.

Naidoo, R., P. Du Preez, G. Stuart-Hill, L. C. Weaver, M. Jago, and M. Wegmann. 2012. Factors affecting intraspecific variation in home range size of a large African herbivore. Landscape Ecology 27:1523–1534.

Nilsen, E. B., S. Pedersen, and J. D. Linnell. 2008. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecological Research 23:635–639.

Ofstad, E. G., I. Herfindal, E. J. Solberg, and B.-E. Sæther. 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. Proceedings of the Royal Society of London, B: Biological Sciences 283:20161234.

Pacifici, M., et al. 2015. 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 191:313–321.

Powell, R. A., and M. S. Mitchell. 2012. What is a home range? Journal of Mammalogy 93:948–958.

Quirici, V., et al. 2010. Seasonal variation in the range areas of the diurnal rodent *Octodon degus*. Journal of Mammalogy 91:458–466.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Relyea, R. A., R. K. Lawrence, and S. Demarais. 2000. Home range of desert mule deer: testing the body-size and habitat-productivity hypotheses. The Journal of Wildlife Management 64:146–153.

Sanusi, M. M. A., M. Shukor, W. W. Juliana, and C. Traeholt. 2013. Activity pattern of selected ungulates at Krau Wildlife

Reserve. Pp. 325–330 in The 2013 UKM FST Postgraduate Colloquium: Proceedings of the Universiti Kebangsaan Malaysia, Faculty of Science and Technology 2013 Postgraduate Colloquium (A. M. H. Murad et al., eds.). AIP Conference Proceedings no. 1571. AIP Publishing, American Institute of Physics. Melville, New York.

Schuette, J. R., D. M. Leslie, Jr., R. L. Lochmiller, and J. A. Jenks. 1998. Diets of hartebeest and roan antelope in Burkina Faso: support of the long-faced hypothesis. Journal of Mammalogy 79:426–436.

Shannon, G., B. R. Page, R. L. Mackey, K. J. Duffy, and R. Slotow. 2008. Activity budgets and sexual segregation in African elephants (*Loxodonta africana*). Journal of Mammalogy 89:467–476.

Smith, S. M., and J. W. CainIII. 2009. Foraging efficiency and vigilance behaviour of impala: the influence of herd size and neighbour density. African Journal of Ecology 47:109–118.

Tamrat, M., A. Atickem, D. Tsegaye, P. Evangelista, A. Bekele, and N. C. Stenseth. 2020. The effect of season and post-fire on habitat preferences of the endangered Swayne's hartebeest (*Alcelaphus buselaphus swaynei*) in Maze National Park, Ethiopia. BMC Ecology 20:5.

Tamrat, M., et al. 2020. Human–wildlife conflict and coexistence: a case study from Senkele Swayne's Hartebeest Sanctuary in Ethiopia. Wildlife Biology 2020:wlb.00712.

Tan, W. S., et al. 2018. Observations of occurrence and daily activity patterns of ungulates in the Endau Rompin Landscape, peninsular Malaysia. Journal of Threatened Taxa 10:11245–11253.

Taylor, W. A., J. D. Skinner, and R. Krecek. 2006. The activity budgets and activity patterns of sympatric grey rhebok and mountain reedbuck in a highveld grassland area of South Africa. African Journal of Ecology 44:431–437.

Tobler, M. W., S. E. Carrillo-Percastegui, and G. Powell. 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. Journal of Tropical Ecology 25:261–270.

Treydte, A. C., J. G. van der Beek, A. A. Perdok, and S. E. van Wieren. 2011. Grazing ungulates select for grasses growing beneath trees in African savannas. Mammalian Biology-Zeitschrift für Säugetierkunde 76:345–350.

Tucker, M. A., T. J. Ord, and T. L. Rogers. 2014. Evolutionary predictors of mammalian home range size: body mass, diet and the environment. Global Ecology and Biogeography 23:1105–1114.

Valeix, M., et al. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90:23–30.

van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? The Journal of Animal Ecology 80:771–785.

Vymyslická, P., P. Hejcmanová, M. Antonínová, M. Stejskalová, and J. Svitálek. 2011. Daily activity pattern of the endangered Swayne's hartebeest (*Alcelaphus buselaphus swaynei* Sclater, 1892) in the Nechisar National Park, Ethiopia. African Journal of Ecology 49:246–249.

Worton, B. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277–298.

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