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Decorum in nature: impala *(Aepyceros melampus melampus)* dung middens follow spatial point patterns in Mukuvisi Woodland, Zimbabwe

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ABSTRACT

Guided by the Optimum Foraging Theory,the Avoidance Concept, and assuming that the impala *Aepyceros melampus melampus* defecate purposevely at dung middens, we hypothesized that the impala's dung midden locations do not: (1) follow complete spatial randomness; (2) cluster along park tracks; and (3) cluster along the waterways. Using geolocation data for all *impala* dung middens in the Mukuvisi Woodland, Zmbabwe, the *G(r)* function revealed a clustered pattern at 0–100 m. Additionally, the 2nd Order *Gcross* function showed evidence of spatial aggregation of dung middens to within 25 m of park tracks, but no evidence of spatial aggregation between impala dung middens and waterways. Our findings give insight into possible evolutionary decorum for optimum olfaction, energy-saving, disease,pest avoidance, and contamination avoidance.

Introduction

Communal defecation sites (henceforth referred to as "dung middens") are common to genera, including the antelope e.g., *Alcelaphinae, Antilopinae, Hippotraginae, Reduncinae,* and *Cephalophinae* that are native to Africa and Eurasia (Mungall, 2007). African savannas, which cover approximately 65% of the continent (Augustine & Mcnaughton, 2004) include our study area and support a range of antelope species, especially in the southern region, including Zimbabwe. These species include the Thomson's gazelle, *(Gazella thomsonii);* greater kudu, *(Tragelaphus strepsiceros);* eland *(Tragelaphus Oryx);* roan antelope, *(Hippotragus equinus),* as well as impala, *Aepyceros melampus melampus* (Ezenwa, 2004; Mooring et al., 1996). Some antelope species, e.g., the impala have evolved conspicuous behavior whereby members of a group defecate at several common latrines/dung middens) located within or at the periphery of territories or habitats (Estes 1991) following Optimum Foraging Theory.

The impala has a complex life history, including synchronized birthing at the beginning of the rain season (Nersting & Arctander, 2001; Sinclair et al., 2000) to offspring whose longevity spans 0–12 years (Spinage, 1972). Predation by canids, felids, and snakes (e.g., lion *(Panthera Leo),* cheetah *(Acinonyx jubatus),* wild dog *(Lycaon pictus),* black-backed jackal *(Canis mesomelas)* as well as the African rock python *(Python sebae)* and other predators, after man is a significant cause of mortality to impala (Thaker

et al., 2011; Valeix et al., 2009). Parasites and diseases also exert extensive costs on impala, including reductions in growth, fertility, and death (Ezenwa, 2004). In Zimbabwe, for example, impala are vulnerable to tick attacks (Mooring et al., 1996), especially the brown ear-tick *(Rhipicephalus appendiculatus)* (Minshull & Jacqueline, 1982). Gastric nematodes (e.g., *Longistrongylus spp)* also affect impala, e.g.,, in the Kruger National Park (Pletcher et al., 1984).

For many antelopes and impala, evolutionary traits for predator-encounter avoidance are not limited to group living, temporal, and spatial changes in movement patterns, rearrangements in group size, and synchronized birthing (Valeix et al., 2009). Group living fosters anti-predator tactics (Fritz & De Garine-Wichatitsky, 1996). For example, impala have been observed in multispecies assemblages including, with warthog, wildebeest, and zebra to obtain predator-avoidance benefits through the increased total alertness associated with bigger groups (Hunter & Skinner, 1998). The impala's behavioral responses against parasites include scratch grooming against tick attacks (Mooring et al., 1996). Dung middens are also thought to have evolved as a behavioral response to diseases, and parasites, avoiding food contamination, marking territory as well as sharing mating statuses (Attum et al., 2006; Curtis, 2014; Miller, 1996). However, some studies, e.g., Apio et al. (2006), suggest that dung middens may not be a significant response to parasites, while Ezenwa (2004) suggested that dung

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midden-use may increase the risk of parasitic infections. Additionally, many animals use olfactory based on scent marks, which may be deposited at dung middens to communicate with one another for reproduction, dominance, and territory defence, as well as to discriminate conspecifics from heterospecifics (Kollikowski et al., 2019). Dung middens may also be used as a strategy for predator encounter avoidance but the notion is not supported in the literature.

Dung middens (the equivalence of communal latrines) are defecation points, which stand out as scattered mounts of excreta for the respective species (Shillito et al., 2008). For impalas, dung middens are used consistently by all members of the herd and defecating on non-dung midden location is minimized (Ezenwa, 2004); thus, members of the herd spend energy walking to the common latrine for defecation or for olfactory reasons. As such, the spatial distribution of dung middens in the habitat/territory of a species is expected to enable members to use minimum energy to access the middens.

Following the Optimum Foraging Theory, dung middens must be located strategically in the entire habitat for the impala to obtain the afore-mentioned benefits (Charnov, 1976). The Optimum Foraging Theory states that animals in pursuit of food and other resources tend to keep the searching distance short from their main area of operating. Thus, animals strive to save energy in getting to their critical functional activity locationsin this case, for impalas and other antelopes; dung middens, in their foraging activities. For example, if the dung middens are difficult to access or very far from regularly used resource sites (e.g., water), the impala would spend a lot of energy traveling to the nearest dung midden to defecate at any given time.

As such, dung midden points should form some patterns within the habitat of the herd. However, there is a dearth in the literature that formally investigates the spatial point pattern of dung middens. Our study formally investigated the spatial point pattern of impala dung middens. Following the Optimum Foraging Theory concept (Klein and Fairall 1986), we hypothesize that (1) the impala dung middens' locations do not follow complete spatial randomness in space; (2) they cluster along park tracks to minimise energy in locomotion to defecate at middens; and (3) they cluster along the waterways where the impala spends time drinking water. We tested these hypotheses using geolocation data for impala dung middens collected from Mukuvisi Woodland, Harare (Zimbabwe).

Methods and materials

Study area

Mukuvisi Woodland (latitude 17° 50 "S-17° 51' S and longitudes 31° 04' E-31° 06" E) is a fenced nature reserve covering nearly 275 hectares, which are surrounded by residential area ~7 km south-east of the central business district of Harare, Zimbabwe (Mareya et al., 2018) (Figure 1). The nature reserve was designated as a wildlife protected area in 1910 to serve as a recreational facility for urban wildlife enthusiasts (http://www.mukuvisiwoodland.co.zw/). Visitors mainly school classes use the entire park for activities including treasure hunts. Other people also use the park for hiking, jogging, biking, and horse riding which is confined the man-made tracks (Figure 1). Motorized automobiles are not allowed in the park. Field observation suggests that both man and wildlife including the impalas use the tracks. Camping is also
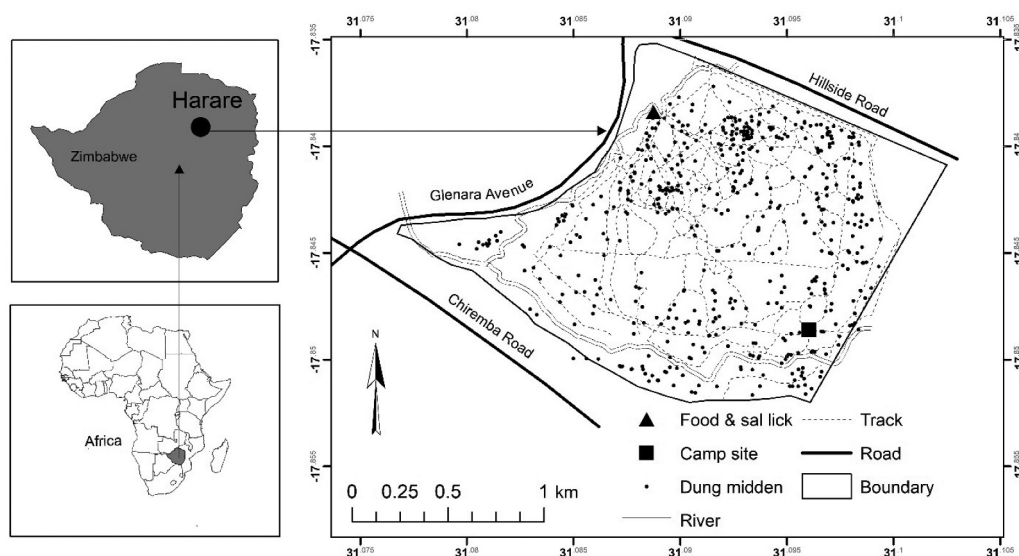
Figure 1. Location of Mukuvisi Woodland, dung midden points, rivers, camping site, animal feeding, and salt lick point and tracks, Harare, Zimbabwe.

allowed in the nature reserve but is confined to the camping site as indicated in Figure 1.

Mukuvisi Woodland experiences a tropical savanna climate, with a mean annual temperature of 18°C and 800–1,000 mm of rainfall (Bulton, 1995). The precipitation occurs between November and March with peaks in January and February (Bulton, 1995). The woodland lies at a mean altitude of 1,440 m above sea level and is underlain by coarse-textured sandy soils (Bulton, 1995). Two perennial streams flow through the woodland as well as an extensive network of animal trails (Figure 1). The park has three distinct land cover types. Grassland covers the approximately 9% of the nature reserve to the north. The dominant grass species include *Sporobolus pyramidalis*, *Hyparrhenia filipendula*, *Heteropogon contortus* and *Hyparrhenia dissoluta* (http://www.mukuvisi woodland.co.zw/). Forest, described as dry miombo woodland dominated by *Burkea africana*, *Parinari curatellifolia,* and *Brachystegia spiciformis* occupy approximately the entire 90% of the nature reserve (Mareya et al., 2018). A very small area comprised the riparian area of the perennial Mukuvisi River and its nameless tributary.

The woodland is habitat to diverse fauna species including animals, birds, reptiles, and fish (http://www.mukuvisiwoodland.co.zw/). Impala population book-keeping records by the time of our study revealed that 56 mature impalas were present in the entire nature reserve. These animals use tracks to get to and from the animal feeding and salt lick point (Figure 1). The animals (particularly the impalas and zebras) appeared to be habituated to the presence of human because they did not seem to be bothered by the presence of the fieldwork team. As such, the presence of human activity in the park was not expected to influence the spatial distribution of impala dung middens. Our own fieldwork showed that impalas utilize the entire park. We also observed the African rock python and black-backed jackals, which are potential predators of the impala in the study area. While no formal investigation of the real potential predation threat of the pythons and the jackals on the impalas, it is plausible to assume that the presence of those predators modifies the behavior of the impala. This is so because while foraging, the impala may avoid dense vegetation minimize encounter with predators, which may ambush from the thick vegetation cover (Hunter & Skinner, 1998).

Data acquisition

This study used impala dung midden location data; park tracks as well as park streams collected in October 2015. The geolocation of impala dung middens data was collected using the sweeping technique (Whitesides et al. 1988). The sweeping field survey technique is an extension of belt transect means of field survey. The sweeping method considers accounting for almost every accessible area in an almost ~50 cm overlaps of one belt to other. This technique enabled us to survey all impala dung middens in the study area. To achieve this, we used hand-held Global Positioning System (GPS) devices to record location coordinates of every impala dung midden in the Mukuvisi Woodland. We swept 10 m-apart swaths along north-south oriented straight lines for the entire study area. To avoid swath overlaps and dung midden omissions, we used the GPS devices to navigate in straight lines connecting predetermined 10-m-apart start and end points (Figure 2).

Each fieldworker identified and recorded impala dung middens within 5 m on either side of the straight-line swath at walking pace (~4 km/hr) to avoid misses. Using this method, we collected 540 geolocations of impala dung middens in the entire study area (Figure 1). Middens which occurred within 5 m of each other were recorded as one. Their boundaries were clearly defined by virtue of them being heaps of dung. This study did not classify the middens as active or not active because we wanted to understand the spatial location patterns of middens in the entire nature reserve.

The tracks and rivers were digitized from Geo Eye 1 images using the Open Layers capability in QGIS 2.18 following Mareya et al. (2018). All visible tracks including the hiking, horseback, and bike trails were digitized for the entire park.

Data analysis

First, we interrogated the dung midden point data for clustering against the hypothesis of complete spatial randomness using the Diggle's *G(r)* function for two-dimensional spatial point data following Dixon (2002). The G*(r)* function considers point interaction based on the complete incident distribution of points from neighboring points (Dale et al., 2002) in determining cluster pattern process within a bounding box. To minimize errors associated with too large bounding boxes, we transformed our study area into a minimum convex hull polygon so that our subsequent point pattern analysis computation used a bounding box resembling the distribution shape of our point data. We considered clustering to be present when the observed *G*(*r*) curve was above the theoretical curve and dispersion when below the theoretical *G*(*r*) curve (Diggle, et al., 1976; Gatrell et al., 1996; Rowlingson & Diggle, 1993).
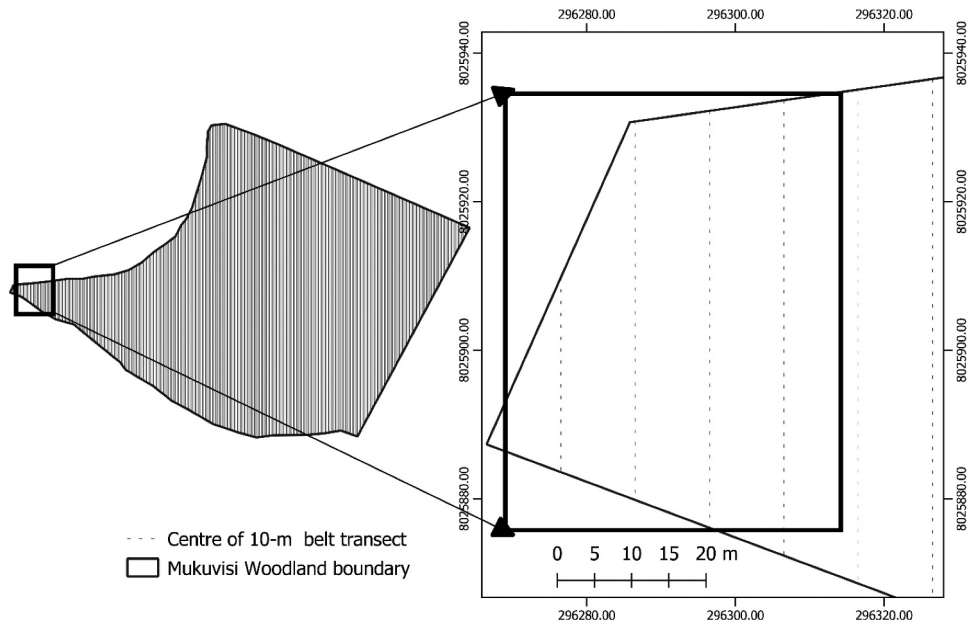
Figure 2. Outline of the 10-m apart transect used during fieldwork.

Because we hypothesized that there is a spatial attraction between the dung middens to water and tracks, we then used the 2nd Order *Gcross* function to test for spatial aggregation between impala dung middens to both rivers/streams and tracks in R software following Ndaimani et al. (2016). The *Gcross* spatial analytical method is premised on considering distance-based aggregation of points, a variable (dung middens) to a parameter (tracks and rivers). This helps in figuring out the density of dung middens in relation to distance from tracks or rivers. Just like the G(r)-function, which considers successive incremental distances (r) to decide a spatial point pattern of interest; *Gcross* takes into account incremental distances of the spatial distribution of dung middens in relationship to tracks or rivers to test for spatial aggregation/attraction. The *Gcross*-function was chosen because we assumed that impala dung midden location behavior is landscape selective so a distance separation-based analysis was deemed appropriate. Because *Gcross* is a spatial point pattern analysis technique, we first used the maptools (sp and spatstat) packages in R software to convert our tracks and rivers line data into points (Oksanen, 2010; Perry, 1995). We then ran the 2nd Order *Gcross* function using the resulting points, which represented the rivers and the tracks and the impala dung midden data. We ran the *Gcross* with 499 replications and made 95% confidence interval simulation boundaries around the theoretical (CSR) function following Ndaimani et al. (2016). We inferred spatial aggregation when the observed *Gcross* function was above the theoretical function and its 95% envelopes, and segregation when the observed Gcross was below the upper 95% confidence envelopes following Ndaimani et al. (2016).

Results

Our test for point clustering with the *G(r)* function revealed that the impala dung middens point pattern did not follow complete spatial randomness but a clustered pattern between 0 and 100 m (Figure 3). This observation generated a question, i.e., what do the dung middens cluster on? The next two results provide answers to that question.

Our test for spatial aggregation using the 2nd Order *Gcross* function showed evidence of spatial aggregation of impala dung midden locations to tracks within 25 m from tracks, no attraction between 25 and 40 m, and segregation at all distances >40 m (Figure 4).

The 2nd order *Gcross* test for spatial attraction showed significant spatial segregation between impala dung middens and rivers at all distances (Figure 5).

Discussions

Our work is among the first attempts to explain the spatial distribution of impala dung middens as well as report attraction of impala dung middens to tracks. In support of our first hypothesis, we observed that impala dung middens cluster in space, i.e., they do not follow complete spatial randomness. In support of our second hypothesis, we also observed that impala dung middens are aggregated along the park tracks. However, our third hypothesis did not get support because we observed segregation between the dung middens and waterways.

The mechanisms explaining the clustering of the dung midden in space are many. In agreement with the Optimum Foraging Hypothesis (Charnov, 1976), we speculate that the impala may be clustering their
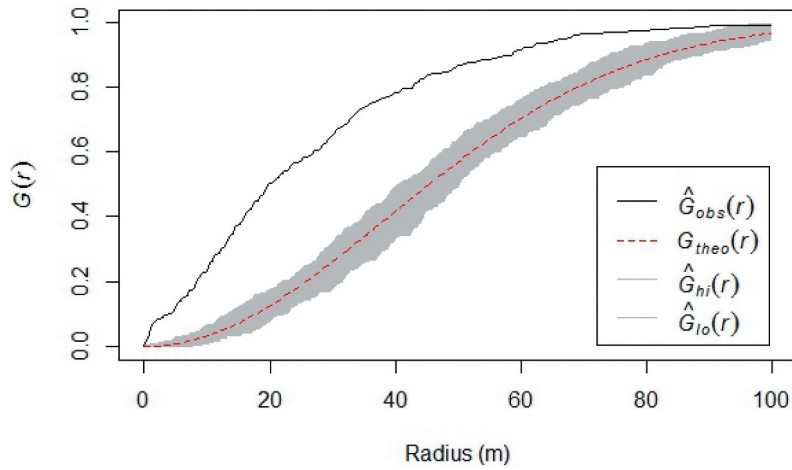
Figure 3. $G(r)$ plot showing significant spatial point pattern clustering of impala dung middens within approximately 0 - 100m $[\bar{G}_{obs}(r) > \bar{G}_{theo}(r)]$ and no clustering at distances >100m $[\bar{G}_{obs}(r) = \bar{G}_{theo}(r)]$. The shaded region represents the 95% confidence interval around the theoretical complete spatial randomness function.
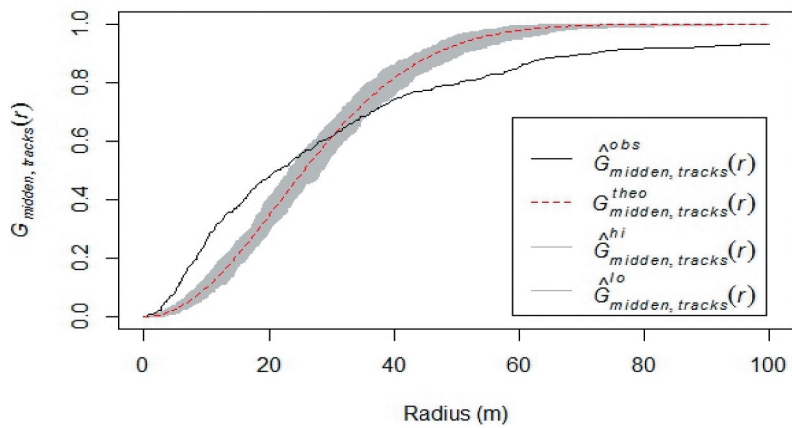
Figure 4. 2nd Order G*cross* plot showing significant spatial aggregation of impala dung middens to tracks within

~25m $[\widehat{G}_{midden.\,tracks}^{obs}(r) > \widehat{G}_{midden.\,tracks}^{theo}(r)]$, a random association within ~25 – 40m $[\widehat{G}_{midden.\,tracks}^{obs}(r) = \widehat{G}_{midden.\,tracks}^{theo}(r)]$ as well as

segregation at distance >40m distance $[\widehat{G}_{midden.\,tracks}^{obs}(r) < \widehat{G}_{midden.\,tracks}^{theo}(r)]$. The shaded region represents the 95% confidence interval around the theoretical complete spatial randomness function.
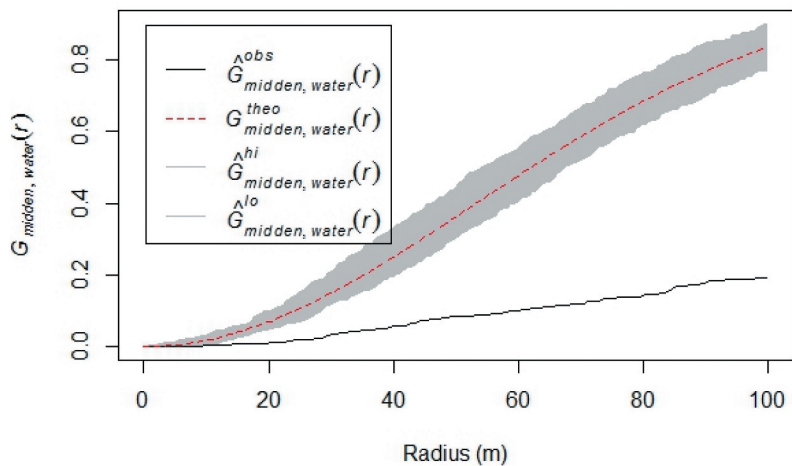
Figure 5. 2nd Order G*cross* plot showing significant spatial segregation of impala dung middens from rivers at all distance $[\widehat{G}_{midden.\,tracks}^{obs}(r) < \widehat{G}_{midden.\,tracks}^{theo}(r)]$. The shaded region represents the 95% confidence interval around the theoretical complete spatial randomness function.

dung middens along the tracks in order to minimize the energy required in regularly navigating to a dung midden for defecation or olfactory reasons. Thus, in our study, the observed aggregation of impala dung middens with park tracks suggests that the impala has evolved mechanisms to optimally locate their defecating points in their habitat to conserve energy because tracks do not have barriers (e.g., vegetation and difficult terrain) that hamper locomotion.

Our other observation of spatial segregation between the dung middens and waterways was in contradiction to our hypothesis that was based on the Optimum Foraging Theory. With this theory, we expected the dung middens to cluster along the waterways (drinking water sources for impala) because impala intensively uses water resources (Gaidet and Lecomte 2013). In line with the Optimum Foraging Theory, clustering of dung middens to waterways is expected for the reasons of conserving energy when regularly walking to dung middens for various reasons. However, our observation that impalas site dung middens away from water sources could be an evolved strategy to minimize contamination of water sources with parasites including gastric nematodes following the avoidance mechanisms (Nersting & Arctander, 2001; Titcomb et al., 2021)

Dung middens are also used by breeding males to mark territories (Brashares & Arcese, 1999; Roberts & Lowen, 1997) and by breeding females to communicate readiness for mating (Black Decima & Santana, 2011; Tribe & Burger, 2011). In addition, the middens are also an activity hotspot for dung beetles as well as other beetles that access the middens for food and mates (Ocampo & Philips, 2005). Some insectivore birds are reported to utilize dung middens for foraging purposes (Kemp & Kemp, 1975). Thus, an enhanced understanding of the spatial pattern of dung middens in the landscape could, therefore, heighten understanding of these and other complex processes and patterns in the landscape.

The major strength of our study is that our analyses were based on a complete count of dung middens in the study area. Our sampling design allowed us to sweep the entire study area to map all dung middens during fieldwork. In addition, we digitized all the tracks and streams that were later used in point pattern analyses. We, therefore, advance that our results from spatial analyses represent a comprehensive picture of dung midden pattern in the study area. Based on our thorough mapping of dung middens, tracks, and streams, we emphasize that our findings are reliable and can, therefore, be used with confidence.

Recognising that ecosystems are complex with no one theory to explain everything, we note a number of weaknesses inherent in our study. First is that our findings were made in a relatively small, fenced study area where impala choices could be limited by the restricted space. The pattern of impala dung middens in a larger study site might yield to different observations. Second, we drew conclusions based on observations made in one protected site with potentially limited threats to the impala. For example, potential impala predator species in our study are few, thus the effect of predation on the dung midden behavior could be anecdotal. The pattern of impala dung middens in a study area with significant predators could be different from our observations.

Future work could include replicating the study in a larger study area, which is not fenced. Other work could involve replication of the study in landscapes with different environmental variables to establish whether findings are consistent. Such studies could also investigate the influence of patch quality, temporal dynamics, and seasonality on the spatial distribution of impala dung middens. Our study also ushers inroads into multiple investigations including the influence of dung middens on olfactory, soil nutrient dynamics, disease transmission, parasite spread, and predator avoidance.

Conclusion

In this study, we observed that impala dung middens show attraction to tracks but show segregation from water points. Clustering along tracks could be an energy saving strategy, while segregation from water sources could be a strategy to minimize contamination of water sources. Our findings give insight into possible mechanisms for energy saving in antelopes as well as contamination avoidance dynamics regarding predators, diseases, parasites in ecosystems.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Designed the experiment: Paradzayi Tagwireyi, Hardlife Muhoyi, Henry Ndaimani, Kudzai Shaun Mpakairi
Collected data: Hardlife Muhoyi, Paradzayi Tagwireyi, Henry Ndaimani,
Analyzed data: Paradzayi Tagwireyi, Hardlife Muhoyi
Wrote the manuscript: Paradzayi Tagwireyi, Hardlife Muhoyi

Data accessibility statement

The primary data used in developing this scientific report is available here: https://figshare.com/articles/dataset/impala_dung_middens_geolocation/21916143

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