Title: Spatial mapping shows that some African Elephants use cognitive maps to navigate the core but not the periphery of their home ranges

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Abstract

Strategies of navigation have been shown to play a critical role when animals revisit resource sites across large home ranges. The habitual route system appears to be a sufficient strategy for animals to navigate while avoiding the cognitive cost of traveling using the Euclidean map. We hypothesize that wild elephants travel more frequently using habitual routes to revisit resource sites as opposed to using the Euclidean map. To identify the elephants' habitual routes, we created a python script, which accounted for frequently used route segments that constituted the habitual routes. Results showed elephant navigation flexibility traveling at Kruger National Park landscape. Elephants shift strategies of navigation depending on the familiarity of their surroundings. In the core area of their home range, elephants traveled using the Euclidean map, but intraindividual differences showed that elephants then converted to habitual routes when navigating within the less familiar periphery of their home range. These findings are analogous to recent experimental results found in smaller mammals that showed that rats encode locations according to their familiarity with their surroundings. Additionally, as recently observed in monkeys, intersections of habitual routes are important locations used by elephants when making navigation decisions. We found a strong association between intersections and new segment usage by elephants when they revisit resource sites, suggesting that intersection choice may contribute to the spatial representations elephants use when repeatedly revisiting resource sites.

Keywords: navigation flexibility, animal navigation, spatial cognition, African elephants, habitual routes, Geographic Information System.

Introduction

In the wild, species regularly navigate away from, and then return to, specific locations within their home range. In doing so, they rely on strategies of navigation that vary according to their cognitive ability and the constraints of their environment. Currently, a significant amount of evidence indicates that animals' navigational skills rely on acquiring particular spatial information, memorizing this information, and then getting familiar within their environment (Wehner et al. 1996; Graham et al. 2003; Wehner et al. 2006; Dolins 2009; Wystrach & Graham 2012). Such findings demonstrate the different mechanisms many animals use to efficiently navigate in various contexts (Wehner et al. 2004; Sommer et al. 2008). Experimental studies on small mammals show that pyramidal cells in the hippocampus remap (remap in this context refers to the brain cells reassembling their fields in "an entirely new representation") themselves according to the location the animal experiences (Sommer et al. 2008).

Social insects are known to be skilled navigators, and it is hypothesized that they store spatial and visual information by familiarizing themselves with their environment (Menzel et al. 2005). For example, ants (*Melophorusbagoti*) use landmarks as guides to select the travel routes associated with frequently visited food sources (Graham & Cheng 2009; Collett 2010; Wystrach & Graham 2012) and familiarize themselves with the routes they travel, repeating and maintaining proximity to their habitual routes (Wehner et al. 2006).

In general, it is expected that wild animals use an efficient and reliable navigation system to return to resources and that many animals likely combine more than one strategy of navigation. Repeating routes seems to be the default navigation system among the majority of studied species in contrast to the more cognitively demanding Euclidean map (McNamara & Shelton 2003; Haun et al. 2006; Di Fiore & Suarez 2007; Noser & Byrne 2007; Sommer et al. 2008). In a route based

map, animals would maintain an internal representation of a sequence of landmarks and create intersections of routes to detect their goal while constantly repeating routes and route segments (Sigg & Stolba 1981; Poucet 1993; Byrne 2000; Sommer et al. 2008). When animals travel using the Euclidean map the location and orientation of the species is centered on features in their surrounding environment that they can use to get distance and direction knowledge (Poucet 1993; Byrne 2000). If the Euclidean map is the dominant approach, wild animals will be able to travel by creating new segments of routes and departing from different locations (Menzel et al. 2005; Presotto & Izar 2010; Suarez 2014) to reach already visited resources. Animals may also show flexibility in combining both strategies depending on the environmental context, just as humans do (Burgess 2006; Presotto & Izar 2010). The Euclidean map approach may be more utilized in areas where food resources are unpredictable and subject to change. On the other hand, in landscapes where food sources, like fruits, experience a smaller interval of fructification and plant species are predictable year-round, creating new routes or route segments might be unnecessary energy spent since resource locations do not change (Izar et al. 2012). Additionally, it is possible that in the wild animals need to switch between navigation strategies based on seasonal changes in food availability (Presotto & Izar 2010).

Small mammals in experimental settings demonstrate flexibility in navigational strategies. In manipulated environments, rats switched strategies to navigate according to their familiarity with the location (Hayman et al. 2003; Alme et al. 2014). The intraindividual variation found in rats occurred when the same individual changed from one strategy to another depending on how they internally represent their environment (Cheng 1986; Shettleworth 1998; Jeffery et al. 2004).

In the wild, it is challenging to compare animal behavioral responses to findings in experimental settings. Yet, vector data produced by the animal movement can elucidate the different context

animals use to navigate their home range within their core and peripheral areas. Wild primates

offer important insights into strategies of navigation regarding various systems based on resource

distribution (Presotto & Izar 2010; Presotto et al. 2018). The majority of primate species are

reported to travel over habitual routes (Milton 2000; Byrne 2000; Di Fiore & Suarez 2007; Noser

& Byrne 2007; Suarez 2014), whereas a select few create new segments when they revisit food

sources (Haun et al. 2006; Normand et al. 2009; Presotto & Izar 2010). As for other taxa, primates

may rely on familiarizing themselves with locations they are likely to return to while searching

for food. As for primates, if food availability is a constant variable, an animal would be able to

memorize its environment through the consistent repetition of routes. When the availability of

food is not a constant, an animal could encode specific locations and create new segments by

using these locations as a reference, thus increasing the chance of finding resources.

In this paper, we investigated wild African elephants' strategy of navigation traveling within their

core and peripheral areas. We classified the routes and route segments that four female African

elephants (*Loxodonta africana)* used to revisit resource sites. We also evaluated the spatial role of

intersections along the elephants' habitual routes. Elephants are strong candidates to study

strategies of navigation since they travel long distances (Viljoen 1989; Douglas-Hamilton 1998;

Blake et al. 2001; Leggett 2006), visit a variety of resources daily (Chamaill-Jammes et al. 2013),

and exhibit effective spatial memory (Polansky et al. 2015). A well-developed hippocampal

structure likely provides elephants with the potential for high learning capacity similar to humans

and other primates (Nissani 2004).

For this study, a *route* is a collection of GPS points within one given day comprised of many

segments. *Route segments* are the distance between two GPS points at one-hour intervals and an

intersection is defined as a fixed point along the routes where the elephant intersected a

previously used travel route. Locations where two routes merged, traveled in parallel but did not

transect each other were not considered intersections. To investigate if elephants frequently repeat

route segments when revisiting resources, we applied the habitual route analysis method

(HRAM), which identifies route segments that are used repeatedly. This study attempts to expand

on three ideas. First, we compared elephants' patterns of navigation to investigate interindividual

and intraindividual navigational differences within their home range in the savannah of KNP.

Second, we tested if elephants primarily travel over habitual routes. Finally, we examined the role

of intersections of routes within the route network system and modeled the probability of

intersections occurring as a function of landscape covariates, including distance of human

influences.

Methods

The data collected represent the daily movements of four female elephants (3A, 4A, 43, and 45)

of reproductive age that lived and overlapped each other within the southern portion of Skukuza,

Kruger National Park (KNP), South Africa (Fig. 1). Each of the four elephants was fitted with a

GPS collar as part of a separate study concerned with the effects of immunocontraception on

female elephants (Fayrer-Hosken et al. 1997). The data obtained via the collars were a record of

all geographic locations visited by all subjects between October 1998 and February 1999. The

data collection period corresponds to the regional transition from the dry season to the wet season.

Elephant visited locations were collected by GPS collars with each coordinate pair recorded

hourly (supplementary material, Fig. 1). All first visited resource sites in this study were coded as

"first-time visit" in our data model, but these first-time visit locations may have been visited

before our study commenced.

FIGURE 1 AROUND HERE

To investigate intraindividual differences, elephant 4A's travel routes were classified as 4A-South

(core area) and 4A-North (periphery) to distinguish between the travel routes 4A used in its core

area at Skukuza in the southern portion of 4A's home range and the peripheral area further north

at Satara in the northern portion of 4A's home range. Two months after the data collection started,

4A traveled 36 km to the north of Skukuza to Satara. Individual home ranges were defined by the

Minimum Convex Polygons (MCPs), or the smallest polygon that no internal angle exceeds 180

degrees and contains all sites recorded with the presence of each elephant position (Aebischer et

al. 1993).

Repeated versus new segments

To define potential food and water resources elephants visited throughout their home range,

woodland and water locations were extracted using remote sensing techniques (see method

below). We then identified and manually classified *new* and *repeated* route segments each

elephant used to repeatedly reach these locations. A route segment is considered *new* if a) it was

further than 300 m from an existing route segment to a resource location or b) the elephants

changed the cardinal direction of travel from all previously used segments and did not return to

the cardinal direction in which they came from using 45° as minimum angulation (supplementary

material, Fig. 2a). A route segment is considered a *repeated* route segment if it is less than 300 m

and/or less than 45° of an existing route segment to a resource location (supplementary material,

Fig. 2b). 300 m was a conservative estimate of the distance an elephant may see in this

environment based on specialist observations (Frayer-Hosken; personal communications; see

Data and Procedures section below for further details). Initially, the first route segment used to

reach a resource site was identified and the direction where the animal came from identified as North, South, East, or West. Next, we identified the second route segment traveled when the individual returned to that location, classifying the segment as *new* or *repeated* accordingly. This procedure was repeated as many times as the elephant revisited a resource site for all route segments across all elephants.

We also expected the elephants to repeat route segments more often than create new segments, especially over short time intervals. Short intervals between revisits may lead animals to repeat route segments because resources may occur for a period in the same location (Normand et al. 2009). To control for short interval revisit bias that may be introduced by the analysis we conducted a descriptive and mean analysis of the distribution of intervals in days that the elephants used to revisit resources sites.

Intersections

All intersections elephants traversed before revisiting woodland and water locations were visually identified and counted. Intersections were separated by the ones detected by the HRAM (see method below) or clustered intersections occurring along habitual routes and the intersections occurring outside the habitual routes that occurred once. Intersections occurring outside of the habitual routes were detected visually by overlaying all, non-repeated routes across all elephants. If intersections were not important locations to link route segments that compose the habitual routes, both types of intersections should play a similar role in elephants' choice to use repeated or create new route segments to reach repeated locations. We expected no significant differences between these two types of intersection.

In an attempt to replicate what was recently found for monkeys (Presotto et al. 2018), using binary logistic regression, the probability of elephants using intersections outside their habitual

routes/intersections along habitual routes as a function of intersection locations was modeled. To fit the logistic regression assumption, we excluded all repeated measurements. To eliminate repeated measurements, intersections clustered at 50 m from each other were grouped. For each one of the 44 groups of reused intersections only one intersection was randomly assigned to each group. Therefore, we assumed independency of the observed intersections. To test intersection locations, the environmental covariates located within the elephants' home range were used as predictors:

a) *the distance to tourism facilities*, which are locations created by KNP for animals sighting. Elephants may not frequently travel in closer proximity to these locations to avoid human presence (Blake et al. 2008);

b) *the distance to main rivers* because rivers/water are considered the main drivers for elephants and can be spatial references in the topography (Bohrer et al. 2014);

c) *the distance to water bodies*. Water bodies in KNP are man-made locations to provision water to animals during the dry season. These are human influenced locations but that provide water resources to elephants;

d) *the terrain steepness (slope/topography)*, which gives animals better visibility to the horizon, which in turn could allow them to make decision based on visibility (Presotto et al. 2018);

e) *the orientation of the terrain steepness (aspect)* plays a role on vegetation predominance, which could influence the location of the intersections;

f) *the presence of woodland/water in the land cover (1), and any other type of land cover (0)* was used to observe if woodland/water influenced on intersection location (see land cover method below) and finally;

g) *the intensity of space usage* since within their home range animals may use more or less intensively determined areas (Willems & Hill 2009) (supplementary material, Fig. 3). Intersections outside the habitual routes were classified as non-success (0) and intersections along habitual routes were classified as success (1) (p) being between 0 and 1. We tested intersection locations for spatial autocorrelation using Morans' I = 0.22 (z score = 4.28, p = 0.000) followed by a binary logistic regression controlled for spatial autocorrelation (Rangel et al. 2010; Seltman 2012). Following (Presotto et al. 2018) we ranked the individual covariates, employing the Akaike Information Criterion (AICc) and used only the statistically significant exploratory variables in the final logistic regression model as follow:

$$p = \frac{exp^{(a+b1x1+b2x2+b3x3...)}}{1 + exp^{(a+b1x1+b2x2+b3x3...)}}$$

where *p* is the probability of using intersections outside of habitual routes (0) or probability of using intersections along habitual routes (1); exp = 2.72; *a* the constant of the equation, and *b* the coefficient of the predictor variables.

If intersections were key locations used by elephants as a spatial reference to revisit resource sites, we expected elephants to use intersections in association to *new* route segments. Every intersection of a route segment used immediately before the elephants reached every repeated resource site were detected for each time they revisited that site. We applied a chi-square to test the null hypothesis, which assumed no association between using an intersection when departing from a *new* route segment of using a *repeated* segment to revisit resource sites. Thus, four categories were tested: a) travel over a *new* route segment with intersection usage; b) travel over a *new* route segment without intersection usage; c) travel over a *repeated* route segment with intersection usage; and d) travel over a *repeated* route segment without intersection usage. A post

hoc analysis of the chi-square results based on z values was conducted. This test was a

comparison of the result of the p-value with the Bonferroni p-value (p=0.05/4, or the number of

the cross categories), assuming that if the calculated p-value based on the adjusted residuals was

larger than the Bonferroni value the distribution was not significant.

The z-value and the p-values represented the statistical significance of the index values at 95%

confidence level.

Data and Procedure

We classified woodland and water using Landsat 5 imagery at approximately 30 m resolution

(supplementary material, Fig. 4). Our study area falls within the Landsat path 168 and row 77.

The scene utilized was scene ID LT51680771998278JSA00, and it was acquired on 10th of

October 1998. For elevation creation, we used ASTER DEM again at approximately 30 m

horizontal resolution. We generated five land cover classes that consisted of grassland, mixed

vegetation, woodland, bare soil, and water by conducting a pixel-based supervised classification a

maximum likelihood algorithm. The classification was validated using the confusion matrix,

which compares the category-by-category basis between the core classification and higher

resolution imagery classification. The classification accuracy was 82% for water and 75% for

woodland. Resource sites were only revisited sites located on woodland and water. Therefore, to

avoid accounting for repeated locations that did not represent potential resources all other land

cover classes were eliminated from the analysis. This approach was used to be conservative

detecting locations of patchily distributed resources. We assumed that the mixed vegetation areas

in savannas would show dispersed resource locations where elephants would feed on-the-go and

not necessary returning to areas where resources were previously encountered (Hills 2006).

The GPS-enabled tracking collars were produced by Lotek Fish and Wildlife monitoring systems. A detailed analysis of the GPS collars specifications, accuracy, and reliability was performed by (Douglas-Hamilton 1998). The location data from the collars were stored in a dedicated bank of non-volatile RAM within the collar's GPS unit and retrieved at the end of the study. During the study, the data set consisted of approximately 600 total daily routes constructed by connecting individual daily sequential geographic coordinate pair for each elephant. From the total dataset, across all elephants, 116 days were excluded due GPS collars loss of connection with satellite for more than six hours. Thus, the total days used in this study were 484.

To investigate the existence of a route-network system used by elephants we applied the *Habitual Route Analysis Method (HRAM)* (supplemental material, Readme). The habitual route infers that: (a) repeated routes and route segments occur more often than newly created segments when revisiting resource sites and the usage of (b) well-defined intersections along the routes. HRAM isolates a daily route and delineates a buffer around the route, which should have as an input the specie-specific visual site range. The buffer distance applied in this study is based on the sight range derived from the species ability to see in their given habitat. Unfortunately, visual acuity studies in African elephants lack conclusive findings. Male elephants' visual acuity is estimated to be four to five time less than a normally sighted human; apparently elephants can see nearby objects to differentiate between food sources, but there is limited evidence of how far they can see towards the horizon (Shyan-Norwalt et al. 2010). For elephants in savannas, we assumed an arbitrary extended sight range of 300 m. The 300 m applied is most likely an overestimated distance for an elephant's visual range in our study area. Yet, the site range can be affected by the terrain topography, which may play a role in the capability the elephants have to navigate as they do for some taxa (Benhamou and Poucet 1998; Menzel et al. 2005; Wystrach et al. 2011). The

300 m distance was used to eliminate the potential effect of visual reach on the memorization of locations. Thus, all daily route buffers assume 300 m distance. HRAM requires an input value for the buffer distance based on the data projection's unit of measurement. For example, the data in this study use WGS_1984_UTM_Zone_36S projection, which uses meters as its unit of measurement. The buffer distance in this study is adjusted according to the species-specific visual range. Once the daily route buffer of 300 m is created, other daily routes generated from the same elephant overlay onto the buffer for the entire study period, excluding the month, which the daily route's buffer fell within. For example, in this study, if elephants repeated a specific location October 1st and then repeated the route segment on October 15th, then this segment was excluded to eliminate the possibility that elephants traveled using habitual routes and revisited the same resource site because it happened within the same month (Presotto & Izar 2010). All segments within the 300 m buffer of all daily routes composed the habitual routes used by each elephant (Fig. 2).

FIGURE 2 AROUND HERE

The resulting habitual routes were then used to investigate how far the elephants traveled from these segments. We tested the distance the elephants deviated from the habitual routes by creating zones of a predetermined distance around the habitual route. We calculated the percentages of all geographical coordinates that fell within 500 m, 1000 m, 1500 m, 2000 m, 2500 m, 3000 m, 4000 m, 5000 m, and greater than 5000 m from the habitual routes for each elephant.

The land cover classification was conducted using ESRI ArcGIS 10. Geospatial Modelling Environment (GME) was used to created routes from the sequence of geographic coordinates by

day, Spatial Analysis for Macroecology (SAM) was used to conduct the spatial logistic regression model, and SPSS 23 to conduct descriptive statistics, Mann-Whitney and Kruskal-Wallis statistical tests. To create the HRAM, which identifies route and route segment repetition, we used a combination of python and structured query language (SQL) within Pgadmin by PostGres. Pgadmin is an open source object-relational database management system, which utilizes a spatial extension called PostGIS. HRAM is freely available on Github and on our data repository.

Results

The Kruskal-Wallis test (H = 4, p = 0.406) showed elephants did not differ in the size of area they explored during the studied period, but they differ in the mean daily travel distance (H = 34.8, p = 0.000) they navigated. The Mann-Whitney two-tailed test (U = 2, p = 0.879) showed no intraindividual difference for 4A when it traveled the North and South of its range for the same variable (supplementary material, Table 1).

Route segments and repeated segments distance

For 484 days elephants navigated over 7,766 route segments, repeating 25% of the total (N=1,977). The distance of the repeated route segments used by elephants significantly varied among themselves (Kruskal-Wallis test H = 68, p = 0.000), with no intraindividual significant difference (Mann-Whitney two-tailed test U = 63, P = 0.144) (supplementary material, Table 2). We expected elephants finding resources in close proximity to the habitual routes. The total number of locations elephants used did not fall equally within predetermined distance bands around their habitual routes (Fig. 3). In the north, 4A showed the largest percent of locations used in close proximity to its habitual route.

FIGURE 3 AROUND HERE

New versus repeated route segments

From the 1,977 repeated route segments, only route segments that ended on repeated woodland and water (*N*=774) were classified as *new* or *repeated*. Except for 4A traveling in the South, elephants repeated route segments significantly below than expected by chance when revisiting resource sites in their core area, whereas 4A traveling in the North repeated route segments above than expected by chance when revisiting resource sites in the periphery (Table 1), with no inter (Kruskal-Wallis test H = 1.94, *p* = 0.745) nor intraindividual (Mann-Whitney two-tailed test U = 9, *p* =0.867) statistically significant difference in the usage of *repeated* and *new* route segments to revisit resource sites.

TABLE 1 AROUND HERE

Elephants revisit resource sites the most during the first five days after their first visit. They all decrease repetition of the site after the first five days and continued decreasing within the same month (supplementary material, Fig. 5). Yet, the elephants were most often using *new* than *repeated* route segments to revisit resource sites. There was an interindividual significant statistic difference in the interval elephants waited to revisit resource sites (Kruskal-Wallis test H = 20.6, *p* = 0.000) and also an intraindividual significant difference (Mann-Whitney two-tailed test U = 7, *p* = 0.006). 4A in the North showed shorter intervals to repeat resource sites than when traveling in the South.

Intersections of route segments

From the total 8,750 fixes, about 10% (*N*=867) were intersections elephants used to revisit resource sites (3A *N*=184; 43 *N*=207; 45 *N*=170; 4A in the South *N*=104; 4A in the North *N*=202). From the total number of used intersections, 51% occurred along habitual routes selected by the HRAM.

There were no statistically significant differences between intersections outside the habitual routes/intersections along habitual routes for terrain steepness (Mann-Whitney two-tailed test U = 98, *p* = 0.295). Both, intersections outside the habitual routes and intersection along habitual routes faced the south of the elephants' home range. Intersections along habitual routes showed higher usage than intersections outside the habitual routes (Mann-Whitney two-tailed test U = 103 *p* = 0.007), intersections along habitual routes were significantly closer to water bodies than intersections outside the habitual routes (Mann-Whitney two-tailed test U = 60,1, *p* = 0.000), intersections along habitual routes were significantly farther from the main rivers than intersections outside the habitual routes (Mann-Whitney two-tailed test U = 116,4, *p*= 0.000), and finally intersections along habitual routes were significantly closer to tourism facilities than intersections outside the habitual routes (Mann-Whitney two-tailed test U = 36,9, *p* = 0.000 (Table 2). Table 3 in the supplementary material shows descriptive landscape differences between intersections outside the habitual routes and intersections along habitual routes.

TABLE 2 AROUND HERE

The comparison between the dichotomous intersections outside the habitual routes (0)/intersections along habitual routes (1) showed negative relationship with (a) distance of tourism facilities (r_s = -0.525, *p* = 0.000), (b) distance to water bodies (r_s = -0.311, *p* = 0.000), and

positive relationship with (d) distance to main rivers ($r_s = 0.208$, $p = 0.000$), and (e) intensity of space usage ($r_s = 0.092$, $p = 0.007$) $N= 867$. All relationships were significant at the 0.01 level. Intersections outside the habitual routes/intersections along habitual routes did not show any relationship in regards to terrain steepness ($r_s = 0.036$, $p = 0.295$), and direction of terrain steepness ($r_s = 0.058$, $p = 0.088$) $N=867$.

The logistic regression model showed that distances from main rivers, water bodies, tourism facilities and the intensity of space usage were the best predictors for intersections occurring along habitual routes (Table 3). The total area under the curve was set as 1 for a perfect prediction accuracy (Fig. 4). The probability of that an intersection along habitual routes was used appeared to be related to how far intersections were from tourism facilities and water bodies, how close they were to main rivers, and the proportion of route segments used.

TABLE 3 AROUND HERE

FIGURE 4 AROUND HERE

Intersection usage with new route segments vs. intersection usage with repeated route segments

Results showed a clear association between the uses of intersections associated with the uses of *new* route segments. We found that elephants were more likely to use intersections when traveling over *new* segments than when traveling over *repeated* segments (Chi-square test $\chi^2(1, N= 774) = 16.63$, $p < 0.000$, supplementary material, Table 4a). Although all elephants were more likely to

use *new* route segments in association with the intersections, intraindividual statistical significant

differences showed the most robust association between the uses of intersection with *new* route

segments when 4A was in the peripherical-North of its home range. In 52% of the observations,

4A traveled over *new* route segments when route segments were associated with the use of

intersections in the North, against 21.9% of intersections associated with *repeated* route segments

(Chi-square test χ^2(1, *N*=310) = 27, *p* = 0.000). When 4A traveled by *repeated* route segments in

the North, intersections were not used in 78% of the observations. In the South we did not find a

significant difference when 4A traveled over *new* nor *repeated* route segments associated with

intersections.

Discussion

African elephants in the savannah of KNP exhibited flexibility in navigation and mostly did not

rely on habitual routes to travel in their home range. The elephants explored different area sizes

and traveled significantly different daily distances. Though elephants showed significant

differences in distance and explored area size, they did use the same strategies of navigation

within their core area.

At least in the core area, the data did not show heavy usage of the habitual routes and in the

periphery, we found strong evidence of switching strategies in a similar manner to primates

(Normand & Boesch 2009; Presotto & Izar 2010). These results did not support the hypothesis

that African elephants in KNP travel most of the time over habitual routes. From the total route

segments used, only 25% were reused continuously, while 75% of the route segments elephants

used to revisit resource sites were new. Elephants in the core area created multiple new route

segments and departed from any point of their home range to revisit resource sites. This finding

was similar to what was found for chimpanzees in the Tai forest, where chimpanzees were able to

find the resources departing from different points of their home range without the use of habitual routes (Normand et al. 2009). The navigation strategies of both chimpanzees and elephants appear similar.

Although similar to chimpanzees, elephant strategies of navigation differed from other primates such as capuchins in the rainforest of Brazil that traveled most of the time by creating new route segments to revisit resource sites when outside of their core area (Presotto & Izar 2010). While chimpanzees and elephants used a high proportion of new route segments in their core area, supporting that familiarity may play a role in memory of locations (Mangan & Webb 2009), in the rainforest capuchins used a higher proportion of habitual routes within their core area and used new route segments most frequently while traveling in the periphery (Presotto & Izar 2010).

For elephants, it appears that familiarity with locations may play a role in their navigation at least within their core area. In the savanna of KNP elephants may familiarized themselves with their core area and revisited resources departing from any point to reach well-known locations like other elephants living in different areas do when visiting waterholes (De Beer et al. 2006). At Etosha National Park (ENP), Namibia elephants can reach waterholes departing from different directions suggesting that familiarity with waterholes allowed the animals to understand the distance they needed to travel when shifted from one waterhole to a different one (De Beer et al. 2006).

With no formal studies showing how far elephants can see towards the horizon of savannas, it is possible that our estimation of 300 m may not be accurate for elephants' capacity of visual-reach. However, if habitual routes were visible elephants could easily repeat them without the cognitive cost of triangulating information to reach resource sites. By eliminating route visibility, the use of new route segments to revisit locations showed that elephants have spatial knowledge about

resource sites (Polansky et al. 2015). We eliminated the possibility that short intervals between

revisits to resource sites could allow elephants to remember the routes and easily repeat them by

removing from the analysis resources occurring in the same month. Resource sites repetition

occurred the most in the first five days after the first visit and decreased after the first month.

Therefore, we showed that elephants potentially remembered resource sites even when they do

not regularly revisit them. Elephants may use other senses (e.g., the scent of water) to locate

resources but these effects were not considered in this study. These results shed light on recent

suggestions that elephants were likely traveling using the Euclidean-cognitive map (Polansky et

al. 2015).

We also tested the hypothesis of no association between the uses of an intersection of routes in

association with a higher proportion of new route segments. We did not confirm this hypothesis

because we found that elephants were more likely to use intersections while traveling over new

route segments than when traveling over repeated route segments. The strongest association,

however, occurred when an elephant switched its navigation strategy. Intraindividual differences

showed that an elephant used habitual routes when it traveled the peripheral area of its home

range. While in the core area elephants showed a high proportion of new route segment usage. 4A

in the North shifted its strategy from creating new segments to repeating them. The strategy used

by 4A in the North opposed the strategy used by 4A in the South. Though the South-core area, 4A

used the same strategies that the other elephants did. Once it arrived at the North-peripheral area,

4A increased the number of repeated route segments, increased the number of used intersections,

and visited resource sites closer to the habitual routes. This intraindividual difference suggested

that using habitual routes when the location is not well-known might be a way to learn the route

segments until they become familiar. Once the habitual routes become familiar elephants may

starting to create new route segments to revisit resource sites, which potentially can shorten the distances between two resources (De Beer et al. 2006). 4A in the North increased the use of repeated route segments approximately to 75%. While 4A in the South explored 66% of the resource sites at 500 m from the habitual route, in the North it explored around 80% of the resource sites at 500 m from the habitual routes. The habitual route 4A used in the South was composed of 233 repeated route segments, whereas in the North its habitual route was composed of 634 repeated route segments. Eighty-five percent of all resource sites 4A visited in the North were repeated, while in the South 4A only revisited 15% of all resource sites (Fig. 5a, 5b, and 5c).

FIGURE 5 AROUND HERE

Finally, the hypothesis that intersections were used more often when elephants traveled over new route segments with the strongest association found for 4A in the North was accepted. In 52% of the times, 4A in the North traveled over new route segments these segments were associated with the use of intersections, while the use of intersections associated with repeated route segments dropped to 22%. It is valuable to mention that while traveling over repeated segments in the North 4A did not use intersections in 78% of the observations. If intersections of routes were a key location to making a navigation decision, it is possible that 4A in the North needed time to create a spatial representation of these locations and therefore traveling over habitual routes likely minimizes the need of having key locations when in the peripheral areas. As suggested by (Polansky et al. 2015), when the landscape varies in time and space, elephants seem to adapt their navigation strategy. As with primates, elephants may adjust their strategy of navigation according to resource distribution (Presotto & Izar 2010). Also, creating new route segments may allow

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elephants to first learn the routes to have fast access to resources and then improve the strategies similarly to humans (Zhang et al. 2014). As for other taxa, the use of intersection as locations to make decisions appears to play a role in elephant navigation too (Presotto et al. 2018). We suggest that the intraindividual difference found in this study may be time-dependent. If animals travel most of the time over their core area, they may need certain period to internally represent the periphery of the home range to acquire similar spatial knowledge that they have within their core area. The observation required to answer this question could not be obtained, but it is known that strategies of navigation may change based on memory degradation (Chen et al. 2011).

The role of intersections in an animals' home range needs further analysis to understand if intersections are used as decision-making locations. In the savanna of KNP, distinct woodland and water distribution along the landscape may work as very distinct features to memorize the location of place. When intersections were located along the habitual routes, they occurred close to the main rivers. This is likely due fact that water is considered a critical resource that helps shape elephant navigation (Polansky et al. 2015). The intersections also occurred in the most intensively used areas within the elephants' home range, which suggest that these intersections were not randomly chosen by the elephants. These intersections may represent places with landscape similarities as for other taxa (Cartwright & Collett 1987).

The data appears to show that wild elephants convert from Euclidean map to habitual routes just as capuchins have demonstrated (Presotto & Izar 2010). Over time, we would expect the elephants become familiar with the locations and convert back to the strategy of Euclidean map (Zhang et al. 2014).

Our results open a new avenue to further understanding navigation strategies used by elephants within their core and peripheral areas. These findings contribute to highlight that the distribution

of features in a divergent landscape may play a greater influence in the animals' internal representation of space than the attribution these features were given in the past. The ability to acquire and maintain spatial information may be related to phylogenetically proximity, yet, it seems that the way each animal deals with their natural landscape may also determine convergence in navigation among them.

Compliance with ethical standards

Conflict of interest: The authors declare no conflict of interests.

Author contributions Presotto analyzed data and wrote the paper. Fayrer-Hosken collected data. Curry developed the python script and contributed to language improvement. Madden contributed to data analysis. All authors contributed to comments and improving the manuscript.

Data availability: The datasets analyzed during the currently study are available on Salisbury University repository.

Ethical approval: Data collection used in this research complied with protocols approved by the Animal Behavior Society and the Animal Research Ethics Committee of the School of Veterinary of the University of Georgia, Athens, GA, USA and SANParks legal requirements under the permit BERHJ9.

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Figure captions

Fig. 1. Study site location.

Fig. 2. a) All January 1998 routes and November 11th, 1997; b) all January 1998 days and segments that repeated the location used November 11th, 1997; c) Route segments repeated and intersected in January previously used November 11th, 1997.

Fig. 3. Zones of the predetermined distance around the habitual routes show all geographical coordinates that fell within the distance bands (500 m, 1,000 m, 1,500 m, 2,000 m, 2,500 m, 3,000 m, 4000 m, 5,000 m, >5,000 m).

Fig. 4. Results for binary logistic regression model using four explanatory variables: distance of tourism location, distance from water bodies, distance from the main rivers, and intensity of space usage. The area for the logistic regression model was 77% prediction accuracy for intersections outside of the habitual routes=0/intersections along the habitual routes=1: McFadden's Rho-Squared: 0.3847, χ^2= 43971, $P = 0.000$, AIC = 712.

Fig. 5. a) The habitual route from 4A's b) 4A-North's repeated segments, and c) 4A-South's repeated segments.