Spatial behaviour of translocated African elephants (*Loxodonta africana*) in a novel environment: using behaviour to inform conservation actions

Noa Pinter-Wollman[1)]

(Animal Behaviour Graduate Group, University of California, One Shields Avenue, Davis, CA 95616, USA)

(Accepted: 15 January 2009)

Summary

When animals encounter a novel environment they can either reject it and leave or accept it and explore their new home. It is important to understand what governs animals' response to a novel place because of the fitness consequences and wildlife management implications entailed. Here I examine the spatial behaviour of translocated African elephants (*Loxodonta africana*) upon arrival at a novel environment. I monitored the movement patterns of 12 radio-collared elephants for a year post-translocation. I documented the first account of both female and male African elephants homing back to their natal habitat. More males than expected left the release site, but female–calf units also homed to their natal habitat, demonstrating that homing is not confined to one sex or age. When examining the spatial behaviour of elephants that remained near the release site I did not find a relationship between habitat exploration and last distance from release site, elephant age, or social association. However, I did find a negative correlation between habitat exploration and distance from human activities. This work provides biological insights regarding individual variation in spatial activity of animals in a novel environment and offers recommendations for future management actions.

Keywords: African elephant, exploration, individual variation, novel environment, translocation, wildlife management.

[1)] Author's current address: Department of Biology, Stanford University, USA, e-mail: nmpinter@stanford.edu

DOI:10.1163/156853909X413105

Behaviour 146, 1171-1192
Also available online - www.brill.nl/beh

Introduction

Many species encounter novel environments both naturally, e.g., during dispersal (Stenseth & Lidicker, 1992), and due to human activities, e.g., animal relocations (Stamps & Swaisgood, 2007). Upon arrival at a novel environment animals can either remain and assess their new home or reject it and leave.

Rejecting a release site and returning to the source site i.e., homing, is often observed in translocations. Most translocations aim to establish viable populations at the release site (Fischer & Lindenmayer, 2000) or permanently remove animals from the source site (Richard-Hansen et al., 2000). Therefore, it is important to understand the factors underlying homing e.g., life history traits (Tuberville et al., 2005), translocation timing (Belisle et al., 2001), and release procedure (Bangs & Fritts, 1996).

Remaining in a novel environment requires assessing it through habitat exploration (Stamps, 2001). Exploration can provide important information (Clark & Mangel, 1984; Eliassen et al., 2007) but can also entail costs due to predation (Larsen & Boutin, 1994; Yoder et al., 2004), or exhaustion (Baker & Rao, 2004). Despite the potential fitness consequences of exploration, studies of translocated animals often overlook the exploration process and report only the last distance from release site (Musil et al., 1993; Clarke & Schedvin, 1997; van Vuren et al., 1997; Armstrong et al., 1999; Cowan, 2001). Distance from natal nest or release site can affect survival and fitness (Byrom & Krebs, 1999; Hansson et al., 2004) but does not always correspond to the exploration exhibited (Moehrenschlager & Macdonald, 2003; Tweed et al., 2003, Selonen & Hanski, 2006). Thus, both distance and exploration should be addressed when studying spatial behaviour in a new environment.

Linking exploration with other biological variables can provide useful proxies for predicting individual variation in exploration and, thus, in fitness (Dingemanse et al., 2004). Such variables could be age (Mikheev & Andreev, 1993), social behaviour (Sunnucks, 1998; Stoewe et al., 2006) and other behavioural traits (Fraser et al., 2001; Watters & Meehan, 2007). Animals translocated for solving human-wildlife conflict can be easily assigned behavioural measures relating to their fear from humans such as, latency to approach a stationary observer i.e., the ‘human approach test’ (Hemsworth et al., 1989, 1996), and distance from roads (Theuerkauf et al., 2003; Whittington et al., 2005).

African elephants (*Loxodonta africana*) are a vulnerable species that is often translocated in wildlife management actions to reduce human-elephant conflict (Muir, 2000; Wambwa et al., 2001, Dublin & Niskanen, 2003). However, only little information has been thus far provided on the spatial behaviour of translocated male African elephants (Muir, 2000; Garai & Carr, 2001; Slotow & van Dyk, 2004) and none on females. Here I examine the spatial behaviour of both male and female translocated African elephants upon release to a novel environment.

Some life history aspects of African elephants may influence their spatial behaviour in a novel place. Males are the dispersing sex and travel long distances in search for mates; females and their offspring live in matriarchal groups (Moss & Poole, 1983). Therefore, males would be more likely to leave the release site, or explore it more extensively if they remain, than females whose movements may be confined by the physical abilities of young calves. Furthermore, matriarch's age governs both social (McComb et al., 2001) and spatial (Foley, 2002; Foley et al., 2008) knowledge and it has been suggested that old males are information repositories (Evans & Harris, 2008). Thus, older individuals may have prior knowledge about the new habitat, and may explore it less extensively than younger individuals. Finally, elephant social aggregations are hypothesized to serve as a platform for ecological information exchange (Foley, 2002). Therefore, I expect association with conspecifics to reduce self-exploration of the new environment.

In addition to the above life history aspects, I also examine the relationship between exploration and approach distance to human activities to provide an accessible proxy of exploration for future management actions. Previous research has shown a negative correlation between habitat exploration and latency to approach unfamiliar objects in birds (Verbeek et al., 1994). Therefore, I anticipate finding a negative correlation between exploration and approach to human activities.

Material and methods

Translocation and study site

During September 2005, 150 African elephants were translocated from Shimba Hills National Reserve and Mwaluganje Elephant Sanctuary on the coast of Kenya (4–4.3°S and 39.5–39.3°E) to Tsavo East National Park

(2.00–3.70°S and 38.13–39.30°E), a distance of 160 km (Figure 1) as part of Kenya's Wildlife Service (KWS) effort to decrease human-elephant conflict around Shimba Hills. The translocation was conducted by the KWS according to the IUCN elephant translocation guidelines (Dublin & Niskanen, 2003) and funded by the Kenya Government. Elephant groups of fewer than 12 individuals were targeted and transported as intact units. Adult males were targeted based on their location and accessibility by road during the translocation and were moved in pairs. The elephants were released in a 'hard release' method i.e., were allowed to walk directly into the park from the transportation trucks and not kept in an enclosure. Translocating the 150 elephants took 32 days during which 20 groups (average $\pm$ SD group size 6.8 ± 2.5) and 20 adult males were moved.

The release site, Tsavo East, differs greatly from the source site, Shimba Hills, in its climate, vegetation, size, and elephant density. Tsavo East is semi arid with an average annual rainfall ranging from 300 to 700 mm, while Shimba Hills is part of the coastal plateau with an average annual rainfall of 1500 mm and a humid equatorial climate. During the rains, vegetation growth in Tsavo East is spatially heterogeneous and unpredictable, in contrast to the spatially homogeneous and reliable vegetation growth in Shimba Hills (van Wijngaarden, 1985). Tsavo East is the largest national park in Kenya (13 950 km^2) and along with the adjacent Tsavo West National Park forms the largest protected area in the country (20 812 km^2), which is home to approx. 9000 elephants (Blanc et al., 2007); density $=$ 0.43 elephants/km^2. The source site, Shimba Hills is a small (250 km^2) reserve surrounded by human settlements containing approx. 600 elephants (Blanc et al., 2007); density $=$ 2.4 elephants/km^2. These ecological differences between the release site and source site provide a unique opportunity to study the behaviour of elephants in a novel environment, the release site.

Data collection

During the translocation all elephants were individually marked for post-translocation monitoring. All 150 elephants were tagged with yellow zip ties on their tails and painted with a unique white number on their backs for individual identification. Natural ear marks and tusk shapes were also used for individual identification (Moss 1996). The age of each translocated elephant was estimated, based on Moss (1996), according to body measurements (back length and shoulder height) taken during the translocation and observations later in the field. Of the translocated elephants, 12 adults moved on different days (3 independent males chosen haphazardly, and 9 females — the matriarchs of the first 9 groups moved) were fitted with GPS/VHF elephant collars (Sirtrack, New Zealand) to enable detailed post-release tracking of movement patterns. Due to a malfunction in the collars' drop-off mechanism, only one collar was recovered and the GPS data from it retrieved and presented here (the collar of individual No. 89). Spatial data for all other collared individuals are based on radio-telemetry using the VHF signal only.

Post-translocation monitoring was conducted for 380 days after the release of the first group, providing at least a year of data for all translocated elephants. Collared elephants were tracked from the air and ground by locating the VHF signal of their radio collar using a TR-4 Tracking receiver (Telonics, USA). During ground surveys, a three element hand-held folding Yagi antenna (Sirtrack) was used to detect the collar signals. A compass was used to determine the bearing towards the signal and the location from which the bearing was taken recorded using a Geko 201 GPS unit (Garmin, USA). The computer program Locate II (Nams, 2000) was later used to triangulate the elephants' location. Aerial tracking was conducted with a light Super Cub aircraft fitted with wing-mounted antennae. Signal directionality was determined using a TAC-2-RLB Antenna Control Unit (Telonics). Elephants' locations from air were recorded using a Geko 201 GPS unit (Garmin). Each collared elephant was sought at least 2–3 times a week, from air and ground, and located at least once a month. For additional information on the resolution of the spatial data, see Appendix A, Table A-1.

The location and identity of every translocated elephant spotted were recorded providing data on the status of all translocated elephants, and not only collared individuals. Analysis of exploration patterns, however, was based only on data from collared individuals, due to the higher temporal resolution of collared individuals' sightings.

Despite elephants living in matriarchal groups (Moss & Poole, 1983), the number of individuals associating with the collared elephants varied throughout the study due to their dynamic fission-fusion social behaviour (Moss & Poole, 1983; Wittemyer et al., 2005; Pinter-Wollman et al., 2009). Therefore, to examine the correlation between spatial and social behaviour post-translocation, I used the average number of elephants associating with each collared elephant as a measure of sociality. Associating individuals were defined as elephants within 500 m of one another during a time window of 2 h, based on previous work on African elephants' social behaviour (McComb et al., 2000, 2001, 2003; Wittemyer et al., 2005). Additional information about the social behaviour of the translocated elephants can be found in Pinter-Wollman et al. (2009).

Minimal distance between the collared elephants and a stationary observer was estimated for each ground observation, similarly to obtaining minimal distance to observer in a 'human approach test' conducted in farm animals (Hemsworth et al., 1996): When collared elephants were seen during ground surveys I immediately stopped the vehicle and remained stationary. The minimal distance to which the collared elephant approached the stationary observer was estimated based on known distances to prominent topographical features in proximity to the elephants. Observations were carried out until the elephants could no longer be seen, allowing them enough time to sense the observer's presence. Minimal distance to observer was averaged across all sightings for each collared elephant. Statistical analysis was then conducted on the log of this average for normalization purposes.

Data analysis

Last distance from the release site and minimal distance from roads were calculated based on the collared individuals' locations. Last distance from release site was calculated as the straight Euclidian distance between the release site and the location of the collared elephant at the end of the study, approximately a year after release. Distance from roads was calculated as the minimal distance between each collared elephant sighting and the nearest road, using GIS data from the Tsavo East research station. Average distance from roads was computed for each elephant for further statistical analysis. Distance calculations were implemented in ArcView 3.2 (ESRI, USA). Other spatial measures can be found in Appendix A, Table A-2.

A Moving Weighted Centroid (MWC) analysis was developed to accurately describe exploration patterns, taking into account the patchy manner in which elephants use their habitat. Elephants exhibit a heterogeneous usage of their habitat by moving great distances rapidly between areas of high use (Cushman et al., 2005), referred to as streaking (Douglas-Hamilton et al., 2005), also seen in other mammals (Sinclair, 1984; Sheppard et al., 2006). In the MWC analysis I calculated the distance of each collared elephant location (focal location) to the centroid of its locations from the previous 30 days.

The centroid was calculated as a spatio-temporal weighted average:

$$X = \frac{\sum_{i,t_i \leqslant 30} x_i \times \frac{1}{t_i}}{\sum_{i,t_i \leq 30} \frac{1}{t_i}},$$

$$Y = \frac{\sum_{i,t_i \leqslant 30} y_i \times \frac{1}{t_i}}{\sum_{i,t_i \leq 30} \frac{1}{t_i}}.$$

Where X and Y are the x, y coordinates of the centroid; x_i and y_i are the x, y coordinates of a sighting (i) within the 30 days preceding the focal location; and t_i is the number of days separating a sighting (i) from the focal location.

Weighing each location inversely proportional to the number of days separating it from the focal location assigned earlier locations a lower impact on the location of the centroid. Because the centroid for each new location was based on data from the 30 days preceding the focal location (average $\pm$ SD number of sightings available for each point was 7.4 $\pm$ 5.9), the centroid moved over time, and overall effectively created a moving average of the general movement patterns for each elephant.

The MWC is an extension of using a fixed time window, which creates discrete activity centers, as described in Waterman (1986). In expansion of the discrete activity centers, the MWC analysis creates a continuous activity center by employing principles from smoothing techniques, often used to analyze animal movements, such as moving windows (Pace, 2001), moving average (MA), and moving weighted average (MWA) (for a review of smoothing techniques see Hen et al. (2004)). However, in contrast to such smoothing techniques, whose goal is to average the movement pattern, in this study the deviation from the average smoothed movement was of interest here as an exploration measure. A similar approach was previously applied to describe elephants' heterogeneous movement patterns by Cushman et al. (2005).

Calculating the distance (d) of each observation from the MWC provided information regarding the amount of localized movements each elephant exhibited during its exploration of the novel environment. The statistic used to describe the exploration value for each elephant was the median of d for all observations over a course of a year. The median of d and not its mean was used due to the skewed distribution (positive skew) of d. To test the robustness of d values median to sampling effort, I performed a 1000 run 95% cross-validation procedure (Efron & Tibshirani, 1993). The median of d showed small variation (SD = 0.52 km), indicating that d is robust to outliers and uneven sampling. For a comparison of d's median to other spatial measures, see Appendix A, Table A-2. All calculations were conducted in Matlab (MathWorks, USA).

Statistical analysis

To determine whether the probability of translocated independent males (older than 15 years: Poole, 1996) to leave the release site, Tsavo (East and West) National Parks, differed from that of female–calf social units, I used a two tailed Fisher's exact test. Female–calf units were used and not larger social units because some social groups that were captured together broke up (Pinter-Wollman et al., 2009). Variability among elephants in last distance from release site and in exploration was expressed using a normalized measure of variability: coefficient of variation (C_v).

To study the relationship between exploration and other biological variables, linear regression was used when a dependent variable (exploration) and an independent variable (age) could be defined. Because I could not naturally define a dependent and an independent variable for all other cases, Pearson's correlation coefficient was used when comparing exploration with social association, minimal distance to observer, and average distance to roads. Correction for multiple testing was conducted using the False Discovery Rate (FDR) method (Benjamini & Hochberg, 1995). Consequently, statistical significance was set at p-values less than 0.025 for testing the relationship between exploration and other biological variables. Statistical analyses were implemented in Matlab using its statistical toolbox (MathWorks) and in JMP (SAS Institute, USA).

Results

Leaving Tsavo East and West National Parks

Eight of the 109 translocated elephants whose fate is known left the release site, Tsavo (East and West) National Parks, and either returned to Shimba Hills ($N = 6$) or ended up elsewhere on the coast, near Malindi ($N = 2$)

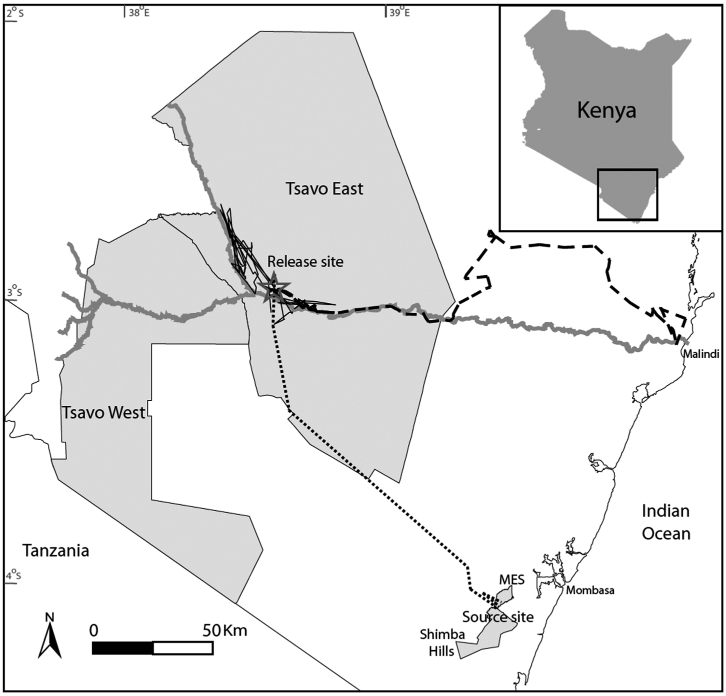

Figure 1. Map of field site and movement paths of three collared elephants. Inset indicates location of field site within Kenya and town names (Malindi and Mombasa) are noted for orientation; light gray polygons represent the protected areas Tsavo East National Park, Tsavo West National Park, Shimba Hills National Reserve and Mwaluganji Elephant Sanctuary (MES); dark gray lines denote permanent rivers; release site is marked with a star; the travel rout of a collared male who reached the coast within 13 days of release is indicated by a dashed black line; the travel rout of a collared female and her calf who reached Shimba Hills within 12 days of release is indicated by a dotted black line; and the travel path of a collared female who remained in Tsavo East, based on locations obtained throughout the year of the study, is presented for comparison by a thin solid black line.

(Figure 1, Table 1). A larger proportion of males left the release site than females with calves. Four of the 15 adult males whose fate is known (26%) left the release site, and two of the 39 translocated female–calf units whose fate is known (5%) left the release site (Fisher's exact test, $p = 0.04$). This finding supports my prediction that males would be more likely than females to leave the release site.

Of the eight elephants that left the release site, two males, one collared and one uncollared, were found on the coast, 170 km east of the release site, 13 and 31 days after release. Both these males were shot by the Problem

Table 1. Details of translocated elephants that left the release site (Tsavo).

ID	Release date	Sex	Age	Collared	Date last seen in Tsavo	Date first found out of Tsavo	End location out of Tsavo	Max number of days before leaving Tsavo*	Comments
15	29-Aug-05	♂	20-25	No	29-Aug-05	20-Feb-06	Shimba Hills	171	
41	3-Sep-05	♀	35-40	Yes	30-Dec-05	18-Feb-06	Shimba Hills	165	
42	3-Sep-05	♀	2-3	No	30-Dec-05	18-Feb-06	Shimba Hills	165	41's calf
50	4-Sep-05	♂	30-35	Yes	14-Sep-05	28-Oct-05	Shimba Hills	54	returned to the southern part of Tsavo East on 20-Aug-06
51	4-Sep-05	♂	40-45	No	4-Sep-05	5-Oct-05	Malindi	31	Shot by PAC in Malindi, 5-Oct-05
89	14-Sep-05	♂	40-45	Yes	22-Sep-05	23-Sep-05	Malindi	9	Shot by PAC in Malindi, 27-Sep-05
96	20-Sep-05	♂	1-2	No	24-Sep-05	2-Oct-05	Shimba Hills	12	98's calf
98	20-Sep-05	♀	20-25	Yes	24-Sep-05	2-Oct-05	Shimba Hills	12	part of group seen in Tsavo east on 2-Jan-06

PAC, Problem Animal Control.

* Number of days between the release date and the date first found out of Tsavo.

Animal Control (PAC) unit of the KWS. A collared female and her calf were found in Shimba Hills 12 days after release. Two other males, one collared and one uncollared, were sighted in Shimba Hills 54 and 171 days after release. The collared male (No. 50) was seen back in Tsavo East almost a year after his original release date. Another collared female and her calf were found in Shimba Hills 165 days after release (see Table 1 for details on all these elephants). This last female and her calf were seen in Tsavo East six weeks earlier, when the rains began, indicating that their homing occurred at least 123 days after release, and not immediately upon release. This last observation implies that ecological factors, such as rain, might play a role in the timing of homing. Both females that homed left their social group behind. Some of the remaining group members were seen in Tsavo East more than half a year after the homing females left.

Two travel paths of elephants that left the release site were closely monitored: the path of male No. 89 that took 13 days to reach the coast (obtained from the GPS component of the collar, providing a location every 4 h) and the path of female No. 98 and her calf No. 96 that took 12 days to reach Shimba Hills (obtained from tracking the VHF signal 3 times a week) (Figure 1). Monitoring these paths revealed direct movements with little exploration around the chosen path. Exploration, as calculated for the collared individuals that remained at the release site, could not be obtained for these individuals due to their short travel duration. Still, a qualitative difference between their movement patterns and those of elephants that remained in Tsavo East can be seen in Figure 1.

Individual variation in spatial use of elephants that remained near the release site

Of the 12 collared elephants, only seven remained in the Tsavo (East and West) National Parks (four collared individuals rejected the release site and were discussed above, and one died four days after release). An average of approximately 80 locations (range: 19–125) were obtained using the collars' VHF signal through triangulation and sightings from ground and air for each of the seven remaining collared elephants (for details, see Appendix A, Table A-1). Last distance from release site varied extensively among the remaining seven collared elephants ($C_v = 77\%$, range $= 9.3$–102.5 km). Furthermore, exploration values, as estimated by the median distance from

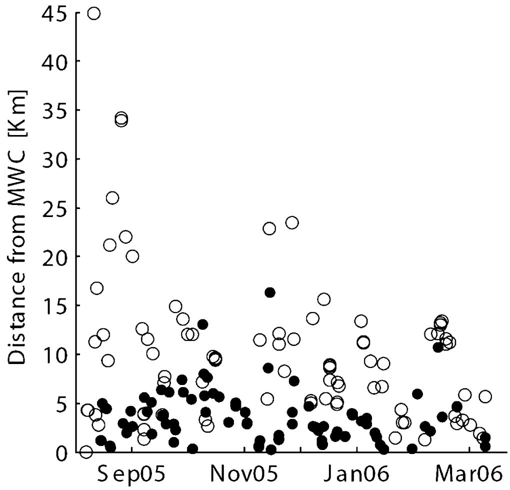

Figure 2. Distance from MWC (d) over time for two translocated elephants. For each sighting, its distance (d) from the spatial centroid of the preceding 30 days is indicated in km on the y axis. Sightings from 6 months post-translocation are shown (time indicated on the x-axis). Open circles are sightings of a collared female with high exploration values. Closed circles are sightings of a different collared female with low exploration values.

the MWC, also varied greatly among these elephants ($C_v = 62\%$, range = 2.2–11.6 km). Each elephant had a different exploration pattern in regard to its MWC: some elephants ranged far from their MWC whereas others remained close (Figure 2).

Interestingly, no relationship was found between exploration and last distance from release site (Pearson correlation, $r = 0.02$, $p = 0.97$, $N = 7$) (Figure 3), indicating that elephants with high exploration values did not necessarily settle far from the release site, and vice versa. This finding supports the notion that exploration behaviour is not necessarily related to an animals' settlement distance from release site, or natal nest and, therefore, should not be ignored when examining the spatial behaviour of animals in a novel environment.

Relationship between exploration and other variables

Minimal distance to observer and distance to roads correlated strongly with exploration but other variables did not. The effect of gender on exploration could not be examined due to insufficient data regarding independent males' exploration (only one of three collared males remained near the release site).

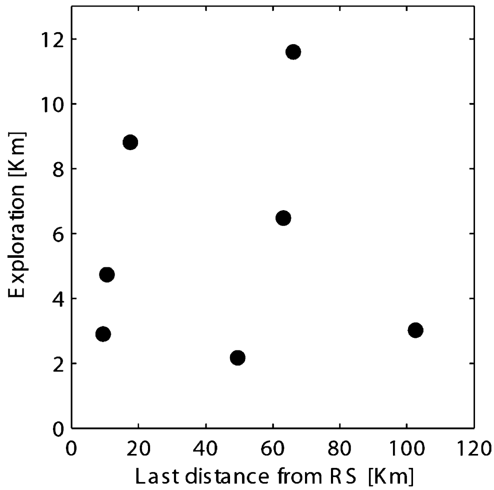

Figure 3. Exploration vs. last distance from release site. Exploration is the median distance from the MWC for each elephant (km). Last distance from release site (RS) is the Euclidian distance between the release site and the location where the elephant was last seen, approx. 1 year after release (km). No correlation was found between these two variables (Pearson correlation, $r = 0.02$, $p = 0.97$).

Exploration patterns did not significantly correlate with age ($r = 0.02$, $p = 0.96$, $N = 7$) or with the average number of conspecifics in association with the collared individuals (Pearson correlation, $r = -0.61$; $p = 0.19$, $N = 6$). Thus, the data did not support or refute my predictions regarding the effects of age and social association on exploration. However, the log of the average minimal distance to observer negatively correlated with exploration (Pearson correlation, $r = -0.89$; $p = 0.02$, $N = 6$) (Figure 4). Average distance to roads also negatively correlated with the exploration patterns observed (Pearson correlation, $r = -0.86$, $p = 0.01$, $N = 7$). Correlations of exploration with distance to observer and with distance to roads achieved statistical significance after correcting for multiple testing ($m = 4$ tests). Thus, as predicted, I found a significant negative relationship between exploration of a novel environment and distance from human activities.

Discussion

When examining the spatial behaviour of African elephants in a novel environment I uncovered three important findings: (1) males were more likely to reject the release site than female–calf units; (2) the exploration of elephants

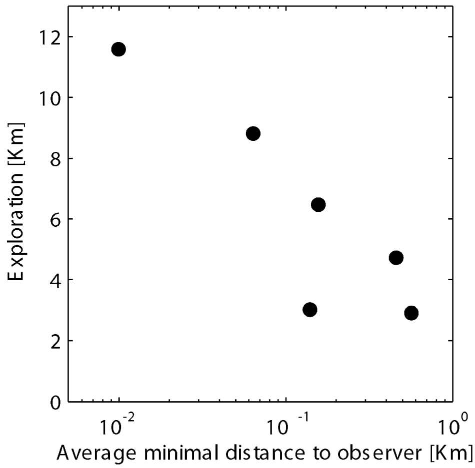

Figure 4. Exploration vs. minimal distance from observer. Exploration is the median distance from the MWC for each elephant (km). Distance from observer is the average minimal distance from observer for all actual sightings from the ground of each elephant (km) and is plotted on a log scale. A strong negative correlation was found between minimal distance to observer and exploration (Pearson correlation, $r = -0.89$; $p = 0.02$).

that remained at the release did not correlate with their final distance from the release site; (3) exploration negatively correlated with distance from human activities.

Leaving the release site and homing

Never before has homing been documented in African elephants on a large scale as the one presented here. Garai & Carr (2001) reported that two translocated African elephant males homed 8 km and Lahiri-Choudhury (1993) reported that a translocated Asian male elephant homed 180 km within three weeks of release. Here I document, for the first time, homing of females and calves in addition to adult male elephants.

Understanding the underlying factors leading elephants to reject the release site is important for reducing homing events in future translations and because excursions from the release site into human settlements may lead to fatal results (e.g., males No. 51, No. 89). Homing was not confined to one sex or age. A greater proportion of translocated males than female–calf units left the release site, supporting the hypothesis that due to males being the dispersing sex (Moss & Poole, 1983) they will be more likely to leave the release site than females. Still, the fact that females and calves also homed to the source site suggests that all elephants, including young calves, are capable of traversing substantial distances over a short time period.

Elephant homing events were not limited to a certain time after release. Some elephants homed back immediately after release, while others waited until the rains before homing. Seasonal variation in movement patterns was previously observed in undisturbed elephant populations (Cushman et al., 2005) and in translocated fox squirrels (Bendel & Terres, 1994). Homing in other species is usually reported only immediately after release (Belisle et al., 2001; Sullivan et al., 2004). Post-translocation monitoring should span all seasons to allow detection of unexpected movement patterns resulting from seasonal change.

It cannot be determined whether the type of release, 'soft' or 'hard' (Hardman & Moro, 2006), affected the translocated elephants' propensity to leave the release site, despite evidence of release method influencing spatial activities in other translocated mammals (Bright & Morris, 1994; Bangs & Fritts, 1996). The elephants in this study were hard released; however, translocated African elephants released in a 'soft release' left their release site as well (Garai & Carr, 2001).

Finally, homing females left their social groups behind, taking with them only their youngest calf. Homing events of entire social groups were not documented here. A possible explanation may be unintentional fracturing of family groups during the translocation and leaving group members behind (Dublin & Niskanen, 2003). Close genetic relatedness was found among elephants captured together as social groups in this translocation (Pinter-Wollman et al., 2009) (genetic data are not available for females No. 41, No. 98, and their groups). Still, the females that homed might have been more closely related to or had stronger social bonds with group members possibly left behind at the source site.

How did the elephants find their way back home? Elephants are capable of traveling great distances (Viljoen, 1989; Thouless, 1995). However, the elephants were translocated in conditions not allowing visual, olfactory, and acoustic cues during transport, and yet they accurately returned to their source site. Two males (No. 51, No. 89) reached the coast, suggesting the use of olfactory cues, brought by coastal winds, or use of river directionality. In addition, one homing male (No. 50) was found in Tsavo East a year after his initial release suggesting that some elephants move between the two sites naturally. This last finding raises the question whether a corridor connecting the two sites may be a more efficient solution for human–elephant conflict in this area than translocation.

Exploration of the novel environment

Individuals that remained in proximity to the release site, varied greatly in their exploration of the new environment, as found in other translocated animals (Moehrenschlager & Macdonald, 2003; Crook, 2004). Explaining such individual variation can provide interesting biological insights and have conservation and wildlife management implications for future translocations and reintroductions (e.g., Moehrenschlager & Macdonald, 2003).

To examine the translocated elephants' exploration I developed the Moving Weighted Centroid analysis. MWC adds a measure of exploration to existing, techniques used for studying spatial behaviour in animals that exhibit heterogeneous movement patterns (Doerr & Doerr, 2004; Cushman et al., 2005). The MWC analysis encompassed a nested model of spatial movement separating small-scale local movements from the general overall movement patterns of the animal. While the overall large-scale movements dictated the end location of the animal, the small scale movements around the centroid described the exploration characteristic of the animal.

In this study, no relationship was found between exploration and last distance from release site, supporting my claim that examining only last distance from release site, or from natal nest, is not sufficient despite its wide use. Settlement distance as an indicator for translocation success (Armstrong et al., 1999; Cowan, 2001) might overlook fitness consequences originating from exploration of an unfamiliar environment. Selonen & Hanski (2006) found variation in pre-dispersal exploration exhibited by juvenile flying squirrels. Some flying squirrels explore the environment before dispersal and settle in a familiar location, whereas others end up in a similar distance from their natal nest but do not explore before dispersal, thus settling in an unfamiliar location. Furthermore, long-distance dispersers often exhibit low levels of exploration (Byrom & Krebs, 1999; Selonen & Hanski, 2006), similar to the direct movements, seen in the homing elephants or those that reached the coast (Figure 1). Thus, both settlement distance and exploration behaviour must be examined to fully understand the settlement process of animals in a novel environment.

No relationship was detected between exploration and the elephants' age or social behaviour possibly due to the small sample size of this study. The non-significant negative trend of exploration and social association suggests that sociality may provide social information about the novel environment, reducing the need for self-exploring it. More data are needed to further examine this point.

Finally, as predicted, a negative significant relationship was found between exploration and the elephants' reaction to human activities: minimal distance to observer and distance from roads. These two variables can be easily measured and assessed in the field both pre- and post-translocation. Uncovering indicators for exploration that can be easily evaluated pre-translocation (e.g., age (Mikheev & Andreev, 1993), social setting (Stoewe et al., 2006), social dominance (Sunnucks, 1998), life experience (Harris & Knowlton, 2001) and boldness (Fraser et al., 2001)) can prove useful for predicting post-translocation behaviour and even survival (Frair et al., 2007; Watters & Meehan, 2007). For example, reaction to novel objects prior to release was found to negatively correlate with survival and positively correlate with movement distance from release site in swift foxes (Bremner-Harrison et al., 2004). Thus, the elephants' response to human activities found here may provide a surrogate for estimating exploration of uncollared elephants and can be an indicator for post-release exploration when targeting individuals for translocation. For example, if the release site is large and the resources in it are widely distributed, individuals that are likely to explore extensively should be targeted for translocation, whereas a small release site with dense resources might call for translocating individuals with limited exploration.

Overall, the results presented here provide an understanding of the factors governing individual variation in animals' spatial activity when faced with a novel environment. The ability to explain such variation by linking it with other biological traits, that can be easily evaluated, can both augment wildlife management actions and provide interesting insights about the spatial behaviour of animals in general.

Acknowledgements

I would like to thank the Kenyan Office of the President for permission to conduct this research and the Kenya Wildlife Service (KWS) for conducting the translocation, and for allowing me to study it. KWS also funded radio collars, tracking equipment, and aerial surveys. Felix Mdamu and the pilots of Tsavo East KWS headquarters assisted in data collection. I am grateful to Judy Stamps for valuable discussion during the preparation of this manuscript;

and to Maxine Zylberberg, Megan Wyman, Lynne Isbell, Lynette Hart, Judy Stamps and several anonymous reviewers for comments on earlier drafts of this manuscript. Funding for this work was provided by the Lincoln Park Zoo, International Elephant Foundation, and UC Davis Animal Behaviour Graduate Group.

References

Armstrong, D.P., Castro, I., Alley, J.C., Feenstra, B. & Perrott, J.K. (1999). Mortality and behaviour of Hihi, an endangered New Zealand honeyeater, in the establishment phase following translocation. — Biol. Conserv. 89: 329-339.

Baker, M.B. & Rao, S. (2004). Incremental costs and benefits shape natal dispersal: theory and example with *Hemilepistus reaumuri*. — Ecology 85: 1039-1051.

Bangs, E.E. & Fritts, S.H. (1996). Reintroducing the gray wolf to central Idaho and Yellowstone national park. — Wild. Soc. Bull. 24: 402-413.

Belisle, M., Desrochers, A. & Fortin, M. (2001). Influence of forest cover on the movements of forest birds: a homing experiment. — Ecology 82: 1893-1904.

Bendel, P.R. & Therres, G.D. (1994). Movements, site fidelity and survival of Delmarva fox squirrels following translocation. — Am. Midl. Nat. 132: 227-233.

Benjamini, Y. & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. — J. Roy. Stat. Soc. B. 57: 289-300.

Blanc, J.J., Barnes, R.F.W., Craig, G.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I. & Hart, J.A. (2007). African elephant status report 2007: an update from the African elephant database. — IUCN/SSC/AfESG occasional paper of the IUCN Species Survival Commission, Gland.

Bremner-Harrison, S., Prodohl, P.A. & Elwood, R.W. (2004). Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). — Anim. Conserv. 7: 313-320.

Bright, P.W. & Morris, P.A. (1994). Animal translocation for conservation: performance of dormice in relation to release methods, origin and season. — J. Appl. Ecol. 31: 699-708.

Byrom, A.E. & Krebs, C.J. (1999). Natal dispersal of juvenile arctic ground squirrels in the boreal forest. — Can. J. Zool. 77: 1048-1059.

Clark, C.W. & Mangel, M. (1984). Foraging and flocking strategies information in an uncertain environment. — Am. Nat. 123: 626-641.

Clarke, M.F. & Schedvin, N. (1997). An experimental study of the translocation of noisy miners *Manorina melanocephala* and difficulties associated with dispersal. — Biol. Conserv. 80: 161-167.

Cowan, P.E. (2001). Responses of common brushtail possums (*Trichosurus vulpecula*) to translocation on farmland, southern North Island, New Zealand. — Wild. Res. 28: 277-282.

Crook, D.A. (2004). Movements associated with home-range establishment by two species of lowland river fish. — Can. J. Fish. Aquat. Sci. 61: 2183-2193.

Cushman, S.A., Chase, M. & Griffin, C. (2005). Elephants in space and time. — Oikos 109: 331-341.

Dingemanse, N.J., Both, C., Drent, P.J. & Tinbergen, J.M. (2004). Fitness consequences of avian personalities in a fluctuating environment. — Proc. Roy. Soc. B Biol. 271: 847-852.

Doerr, V.A.J. & Doerr, E.D. (2004). Fractal analysis can explain individual variation in dispersal search paths. — Ecology 85: 1428-1438.

Douglas-Hamilton, I., Krink, T. & Vollrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. — Naturwissenschaften 92: 158-163.

Dublin, H.T. & Niskanen, L.S. (2003). IUCN/SSC AfESG Guidelines for the *in situ* translocation of the African elephant for conservation purposes. — IUCN, Gland and Cambridge.

Efron, B. & Tibshirani, R.J. (1993). An introduction to the bootstrap. — Chapman & Hall/CRC, Boca Raton, FL.

Eliassen, S., Jorgensen, C., Mangel, M. & Giske, J. (2007). Exploration or exploitation: life expectancy changes the value of learning in foraging strategies. — Oikos 116: 513-523.

Evans, K. & Harris, S. (2008). Adolescence in male Africa elephants (*Loxodonta africana*) and the importance of sociality. — Anim. Behav. 76: 779-787.

Fischer, J. & Lindenmayer, D.B. (2000). An assessment of the published results of animal relocations. — Biol. Conserv. 96: 1-11.

Frair, J.L., Merrill, E.H., Allen, J.R. & Boyce, M.S. (2007). Know thy enemy: experience affects elk translocation success in risky landscapes. J. Wildl. Manage. — 71: 541-554.

Foley, C.A.H. (2002). The effects of poaching on elephant social systems. — Ph.D. dissertation, University of Princeton, Princeton, NJ.

Foley, C., Pettorelli, N. & Foley, L. (2008). Severe drought and calf survival in elephants. — Biol. Lett. 4: 541-544.

Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N. & Skalski, G.T. (2001). Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. — Am. Nat. 158: 124-135.

Garai, M.E. & Carr, R.D. (2001). Unsuccessful introductions of adult elephant bulls to confined areas in South Africa. — Pachyderm 31: 52-57.

Hansson, B., Bensch, S. & Hasselquist, D. (2004). Lifetime fitness of short- and long-distance dispersing great reed warblers. — Evolution 58: 2546-2557.

Hardman, D. & Moro, B. (2006). Optimizing reintroduction success by delayed dispersal: is the release protocol important for hare-wallabies? — Biol. Conserv. 128: 403-411.

Harris, C.E. & Knowlton, F.F. (2001). Differential responses of coyotes to novel stimuli in familiar and unfamiliar settings. — Can. J. Zool. 79: 2005-2013.

Hemsworth, P.H., Barnett, J.L., Coleman, G.J. & Hansen, C. (1989). A study of the relationships between the attitudinal and behavioural profiles of stockpersons and the level of fear of humans and reproductive performance of commercial pigs. — Appl. Anim. Behav. Sci. 23: 301-314.

Hemsworth, P.H., Price, E.O. & Borgwardt, R. (1996). Behavioural responses of domestic pigs and cattle to humans and novel stimuli. — Appl. Anim. Behav. Sci. 50: 43-56.

Hen, I., Sakov, A., Kafkafi, N., Golani, I. & Benjamini, Y. (2004). The dynamics of spatial behaviour: how can robust smoothing techniques help? — J. Neurosci. Methods. 133: 161-172.

Lahiri-Choudhury, D.K. (1993). Problems of wild elephant translocation. — Oryx 27: 53-55.

Larsen, K.W. & Boutin, S. (1994). Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. — Ecology 75: 214-223.

McComb, K., Moss, C., Sayialel, S. & Baker, L. (2000). Unusually extensive networks of vocal recognition in African elephants. — Anim. Behav. 59: 1103-1109.

McComb, K., Moss, C., Durant, S.M., Baker, L. & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. — Science 292: 491-494.

McComb, K., Reby, D., Baker, L., Moss, C. & Sayialel, S. (2003). Long-distance communication of acoustic cues to social identity in African elephants. — Anim. Behav. 65: 317-329.

Mikheev, V.N. & Andreev, O.A. (1993). Two-phase exploration of a novel environment in the guppy, *Poecilia reticulata*. — J. Fish. Biol. 42: 375-383.

Moehrenschlager, A. & Macdonald, D.W. (2003). Movement and survival parameters of translocated and resident swift foxes *Vulpes velox*. — Anim. Conserv. 6: 199-206.

Moss, C. (1996). Getting to know a population. — In: Studying elephants (Kanwanga, K., ed.). African Wildlife Foundation, Nairobi, p. 58-74.

Moss, C.J. & Poole, J.H. (1983). Relationships and social structure of African elephants. — In: Primate social relations: an integrated approach (Hinde, R.A., ed.). Blackwell Scientific Publications, Oxford, p. 315-325.

Muir, C. (2000). Monitoring the impact of the Mwaluganje elephant translocation, Kenya. — Unpublished report to KWS, Nairobi.

Musil, D.D., Connelly, J.W. & Reese, K.P. (1993). Movements, survival, and reproduction of sage grouse translocated into central Idaho. — J. Wildl. Manage. 57: 85-91.

Nams, V.O. (2000). Locate II User's Guide. A program to triangulate radiotelemetry bearings and calculate error ellipses. — Pacer Computer Software, Tatamagouche, NS.

Pace, B.M. (2001). Estimating and visualizing movement paths from radio-tracking data. — In: Radio tracking and animal populations (Millspaugh, J.J. & Marzluff, J.M., eds). Academic Press, New York, NY, p. 189-206.

Pinter-Wollman, N., Isbell, L.A. & Hart, L.A. (2009). The relationship between social behaviour and habitat familiarity in African elephants (*Loxodonta africana*). — Proc. Roy. Soc. B: Biol. 276: 1009-1014.

Poole, J. (1996). The African elephant. — In: Studying elephants (Kanwanga, K., ed.). African Wildlife Foundation, Nairobi, p. 1-8.

Richard-Hansen, C., Vie, J.C. & De Thoisy, B. (2000). Translocation of red howler monkeys (*Alouatta seniculus*) in French Guiana. — Biol. Conserv. 93: 247-253.

Selonen, V. & Hanski, I.K. (2006). Habitat exploration and use in dispersing juvenile flying squirrels. — J. Anim. Ecol. 75: 1440-1449.

Sheppard, J.K., Preen, A.R., Marsh, H., Lawler, I.R., Whiting, S.D. & Jones, R.E. (2006). Movement heterogeneity of Dugongs, *Dugong dugon (muller)*, over large spatial scales. — J. Exp. Mar. Biol. Ecol. 334: 64-83.

Sinclair, A.R.E. (1984). The function of distance movements in vertebrates. — In: The ecology of animal movement (Swingland, I.R. & Greenwood, P.J., eds). Clarendon Press, Oxford, p. 240-258.

Slotow, R. & van Dyk, G. (2004). Ranging of older male elephants introduced to an existing small population without older males: Pilanesberg National Park. — Koedoe 47: 91-104.

Stamps, J. (2001). Habitat selection by dispersers: integrating proximate and ultimate approaches. — In: Dispersal (Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D., eds). Oxford University Press, New York, NY, p. 230-242.

Stamps, J.A. & Swaisgood, R.R. (2007). Someplace like home: experience, habitat selection and conservation biology. — Appl. Anim. Behav. Sci. 102: 392-409.

Stenseth, N.C. & Lidicker, W.Z. (1992). The study of dispersal: a conceptual guide. — In: Animal dispersal (Stenseth, N.C. & Lidicker, W.Z., eds). Chapman and Hall, London, p. 5-20.

Stoewe, M., Bugnyar, T., Heinrich, B. & Kotrschal, K. (2006). Effects of group size on approach to novel objects in ravens (*Corvus corax*). — Ethology 112: 1079-1088.

Sullivan, B.K., Kwiatkowski, M.A. & Schuett, G.W. (2004). Translocation of urban gila monsters: a problematic conservation tool. — Biol. Conserv. 117: 235-242.

Sunnucks, P. (1998). Avoidance of novel objects by rabbits (*Oryctolagus cuniculus l.*). — Wildl. Res. 25: 273-283.

Theuerkauf, J., Jedrzejewski, W., Schmidt, K. & Gula, R. (2003). Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). — J. Wildl. Manage. 67: 706-716.

Thouless, C.R. (1995). Long distance movements of elephants in northern Kenya. — Afr. J. Ecol. 33: 321-334.

Tuberville, T.D., Clark, E.E., Buhlmann, K.A. & Whitfield, G.J. (2005). Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). — Anim. Conserv. 8: 349-358.

Tweed, E.J., Foster, J.T., Woodworth, B.L., Oesterle, P., Kuehler, C., Lieberman, A.A., Powers, A.T., Whitaker, K., Monahan, W.B., Kellerman, J. & Telfer, T. (2003). Survival, dispersal, and home-range establishment of reintroduced captive-bred puaiohi, *Myadestes palmeri*. — Biol. Conserv. 111: 1-9.

van Vuren, D., Loredo, A.J., Kuenziette, V., Leider, A.L. & Morrison, M.L. (1997). Translocation as a nonlethal alternative for managing California ground squirrels. — J. Wildl. Manage. 61: 351-359.

van Wijngaarden, W. (1985). Elephants-trees-grass-grazers: relationships between climate, soils, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya). — ITC, Enschede.

Verbeek, M.E.M., Drent, P.J. & Wiepkema, P.R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. — Anim. Behav. 48: 1113-1121.

Viljoen, P.J. (1989). Spatial distribution and movements of elephants (*Loxodonta africana*) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. — J. Zool. Lond. 219: 1-19.

Wambwa, E., Manyibe, T., Litoroh, M., Gakuya, F. & Kanyingi, J. (2001). Resolving human-elephant conflict in Luwero District, Uganda, through elephant translocation. — Pachyderm 31: 58-62.

Waterman, J.M. (1986). Behaviour and use of space by juvenile Columbian ground squirrels *Spermophilus columbianus*. — Can. J. Zool. 64: 1121-1127.

Watters, J.V. & Meehan, C.L. (2007). Different strokes: can managing behavioural types increase post-release success? — Appl. Anim. Behav. Sci. 102: 364-379.

Whittington, J., St. Clair, C.C. & Mercer, G. (2005). Spatial responses of wolves to roads and trails in mountain valleys. — Ecol. Appl. 15: 543-553.

Wittemyer, G., Douglas-Hamilton, I. & Getz, W.M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. — Anim. Behav. 69: 1357-1371.

Yoder, J.M., Marschall, E.A. & Swanson, D.A. (2004). The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. — Behav. Ecol. 15: 469–476.

Appendix A

Table A-1. Additional information for evaluating the spatial data resolution.

Elephant ID	Sex	Age	*N*	Average time between locations ± SD (days)
2	♀	25–30	112	3.34 ± 6.78
9	♀	30–35	89	4.30 ± 5.99
52	♀	30–35	125	2.96 ± 4.68
61	♀	35–40	27	5.33 ± 8.85
80	♀	30–35	103	3.15 ± 8.77
93	♂	40–45	19	17.98 ± 17.67*
141	♀	20–25	101	3.26 ± 5.93

Information is provided for the collared elephants whose exploration value was presented in this study. *N* is the number of data points obtained (from triangulation, aerial surveys and direct sightings on the ground).

* Despite the long duration between No. 93's locations, its signal was heard several times during air surveys within its home range ('area' below) but the exact coordinates could not always be obtained due to the harsh wind conditions in that region (Tsavo West hills). Signals without exact coordinates were not used for the spatial analysis but affirmed that this individual did not make abrupt movements between days during which accurate coordinates were obtained.

Table A-2. Commonly used spatial measures and the exploration measure used in this study.

Elephant ID	Cumulative distance traveled (km)	Average distance from release site ± SD (km)	Area (km^2)	Exploration (km)
2	973.36	17.03 ± 10.42	2007.4	8.81
9	590.51	17.36 ± 9.73	1083.7	4.74
52	468.8	7.11 ± 3.84	322.9	2.91
61	336	26.61 ± 23.83	2492.1	11.59
80	649.85	11.57 ± 9.57	2088.3	5.77
93	195.72	51.10 ± 14.59	623.3	2.17
141	485.67	12.73 ± 14.01	1309.0	3.01

Area is the total area (MCP, minimum convex polygon) of all locations obtained for each elephant. The exploration values used and described in this paper are median of *d* (km) (see detailed explanation in text). Note that none of the spatial measures aside for exploration takes into account the heterogeneous spatial use exhibited by elephants and explained in the text. Information is provided for the collared elephants whose exploration value was presented in this study.