

The role of elephant *Loxodonta africana* pathways as a spatial variable in crop-raiding location

K. VON GERHARDT, A. VAN NIEKERK, M. KIDD, M. SAMWAYS and J. HANKS

Abstract Short-range elephant *Loxodonta africana* movements were examined in a heterogeneous landscape mosaic of settlements, crop fields and remnant forest in the Caprivi Strip, Namibia. We explored the penetration of the landscape through the use of permanent pathways and determined the impact of pathway use on crop-raiding location. Pathways were linear, devoid of vegetation and maintained by repeated movement. Functional connectivity of pathways was not species-specific, and pathways were used by various species. Elephants travelled in single file at night and we recorded selective pathway use: females selected pathways away from settlements to access water, whereas males used pathways among settlements to launch crop raids. Proximity of raided fields to the nearest pathway was the only significant spatial variable explaining crop-raiding location. Bulls were responsible for all crop-raiding incidents. We conclude that (1) pathways were the most significant spatial variable influencing which fields were raided, (2) crop-raiding from pathways may maximize foraging efficiency by reducing time spent and distance travelled while foraging, (3) pathways may facilitate penetration of the matrix by connecting predictable resources (crops) with preferred shelter areas, crossing points at roads and preferred drinking spots, and (4) access to the Kwandu River is restricted by settlements, predictably resulting in human–elephant conflict. By highlighting the relevance of pathways for movement of elephants we show that an understanding of the use of pathways is important for land-use planning in conservation landscapes, specifically with regard to human–elephant conflict. We also argue for the need to more fully explore pathway occurrence and use at larger spatial scales.

Keywords African elephant, Caprivi Strip, connectivity, human–elephant conflict, land-use mosaic, pathways, transfrontier conservation area

Introduction

Conservation authorities have had a difficult time suppressing conflict between humans and elephants *Loxodonta africana*, a challenge that is widespread and problematic in both Africa and Asia. In Africa, in particular, the resolution of conflict has become a political challenge, as rural chiefdoms may resist mitigation efforts (Osborn & Parker, 2003), which could threaten conservation programmes (Hoare, 1999; Sitati & Walpole, 2006). In the last 2 decades research has increasingly turned to investigating the causes of human–elephant conflict (Naughton-Treves, 1997; Hoare, 1999; Smith & Kasiki, 2000; Parker & Osborn, 2001; Mosojane, 2004; Sitati et al., 2003, 2005; Harris et al., 2008; Jackson et al., 2008; Graham et al., 2009). Although some studies make reference to the possible role of elephant pathways as spatial variables in human–elephant conflict (Smith & Kasiki, 2000; Mosojane, 2004; Chiyo et al., 2005; Sitati & Walpole, 2006), no research to date has investigated the spatial relationship between crop-raiding location and pathways.

Some pathways have been used for 50 years (Haynes, 2006), with their position representative of long-term movements and feeding patterns of elephant populations (Agnew, 1966). Williamson (1975) recorded elephant trails following the troughs of Pleistocene dunes in Zimbabwe. In Botswana, Child (1968) observed that seasonal movement by elephants was reflected by well-defined pathways, especially those leading to pans. Pathways or trails have been mentioned anecdotally in connection with watering holes or drinking areas (Moss, 1988; Payne 1998). Shannon et al. (2009) found that the most heavily used elephant pathways were close to water. Crop damage caused by elephants in the Okavango Delta can be along established elephant pathways (NRP, 2006). K. Leggett (pers. comm.) confirms that desert elephants use pathways seasonally between feeding areas, as well as daily to access preferred drinking spots along the Hoanib and Hoarusib Rivers in Namibia.

In the equatorial forests of central Africa, forest elephants *L. africana cyclotis* play an important role in ecosystem dynamics by opening up clearings, structuring tree-species composition through seed deposition and by creating forest pathways that are subsequently used by other species (Weinbaum et al., 2007). Forest elephant trails can be tens of km long and several m wide (Blake & Inkamba-Nkulu, 2004). It has been suggested that migrations of forest elephants may follow regular pathways rather than being random movements (Turkalo & Fay, 1995). Elephant trails

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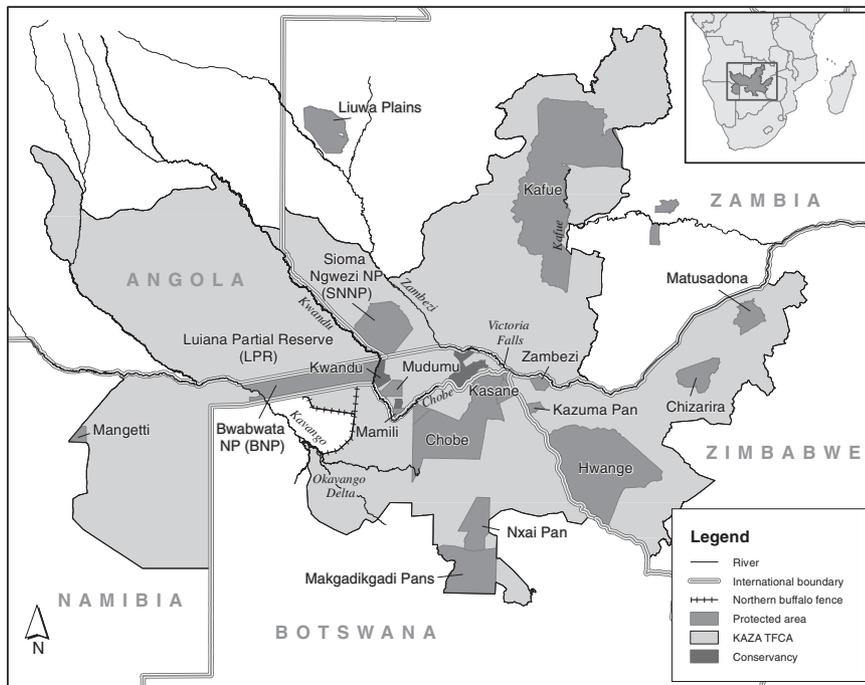


FIG. 1 The study area within southern Africa's Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA). The rectangle on the inset indicates the location of the main map in north-east Namibia.

in the Congo connect forest clearings, which are important social gathering sites, and different sized pathways have different functions, with larger trails used for long-distance faster travel and smaller, more sinuous, pathways used for foraging and accessing resources (Van Leeuwe & Gautier-Hion, 1998).

The identification of elephant pathways, and the landscape elements they connect, may offer insights into habitat requirements in a fragmented landscape. Much like seasonal corridors, pathways could facilitate daily movement, increase feeding efficiency by reducing travelling times to high-nutrient, clustered and stable food sources. Here we report on African savannah elephant *L. africana* movement along pathways, the landscape features (water, forage, refuges) connected by pathways, and the spatial correlates (distance to nearest settlement, refuge, road, protected area, river and elephant pathways) of raided field locations. Our study offers new insights into the spatial variables of human–elephant conflict and provides guidance for land-use planning initiatives and conservation managers.

Study area

The c. 190 km² Kwandu Conservancy occupies the centre of the Caprivi Strip (Fig. 1) in north-east Namibia. Lying central to the Kavango-Zambezi Transfrontier Conservation Area, the Kwandu Conservancy and its southern conservancy neighbours comprise a priority corridor for elephant movement from Botswana's Chobe National Park into Zambia's Sioma Ngwezi National Park

and Angola's Luiana Partial Reserve. The Kwandu Conservancy is situated between two protected areas: Bwabwata National Park in the west, and Caprivi State Forest in the east. The international boundary of Zambia's Sioma Ngwezi National Park and Angola's Luiana Partial Reserve forms the northern boundary. The Kwandu Conservancy is considered a human–elephant conflict hotspot (Hanks, 2006).

The most densely populated conservancy in Namibia, the Kwandu Conservancy is inhabited by 4,300 people. Community-based natural resource management is practised, and elephants are protected by law. Kongola is the largest village. Villages, crop fields, schools and clinics are mostly sited adjacent to the main north–south gravel road. Cultivation is practised in the wet season (November–April), when farmers plant maize, millet and sorghum, which are harvested in April and May. The greater Kwandu Basin is marked by the presence of fossil dunes where shallow, seasonally flooded areas form in the dune troughs and ancient river valleys. The Kwandu River is the western boundary of the Kwandu Conservancy, and both people and elephants rely on the river for water in the dry season (May–October). During the wet season surface water is widely available in numerous waterholes, pans and *omuramba* (ancient river valleys) but by May most of the waterholes have dried up. Rainfall is variable, occurring mainly in summer months between November and April. Mean annual rainfall is 600 mm. Soils are predominantly Kalahari sands and nutrient-poor (Robertson, 2005). The landscape is flat, at altitudes of 930–1,100 m (Mendelsohn & Roberts, 1997). Broad-leafed savannah characterizes the Caprivi Strip. Mopane-*Burkea* and teak woodland, mixed

shrubland and *omuramba* grassland dominate the area, with mature woodlands (*Acacia* spp.) occurring in the region (Mendelsohn & Roberts, 1997).

Methods

Fieldwork to locate and explore elephant pathways was initiated from the Caprivi State Forest border, with the assistance of local game guards. Only permanent pathways, with floors devoid of vegetation and regularly used by elephants, were selected (Blake & Inkamba-Nkulu, 2004). Regular use of pathways by elephants was confirmed through visual observation of dung, feeding damage and elephant footprints. Pathways that did not show any of these signs were excluded from the analyses. Pathways were followed from the border to the Kwandu River in the west. To record pathway length for spatial analyses in *ArcGIS* v. 9.3 (ESRI, Redlands, USA), coordinates (with a global positioning system, GPS), elevation, and pathway width were logged at 100-m intervals. Land use and presence of water pans, fields, roads, crossing points and prints of other species were also noted. Elephant activity along pathways and crossing points was documented over 120 observation days during the peaks of the wet and dry seasons of 2008. Fresh spoor was recorded daily between 06.00 and 07.00. To avoid recounting old spoor, footprints were eradicated after each count, and bull and breeding-herd spoor (including that of offspring) were noted. Male and female elephant groups were distinguished by the presence or absence of footprints of elephants < 6 years old (Balasubramanian et al., 1995; Chiyo & Cochrane, 2005).

Ground surveys were used to register all reported crop-raiding incidents in the peak wet season months (March–April) of 2008, when crops mature. Two hundred and fifty crop fields were georeferenced. Each field was assigned a random number drawn from a uniform distribution. Fields were sorted according to random numbers and the first 100 fields were selected as a random sample. We divided fields into three categories reflecting the protocol of Integrated Rural Development and Nature Conservation, Namibia: if elephants had been present in the field, the incident was recorded as either ‘raided’ (> 25% of field damaged) or ‘non-raided, elephant presence’ (< 25% of field damaged). If no elephants had been to the field, it was categorized ‘non-raided, elephant absence’. Corner points of the fields recorded with a GPS were used to create polygons in *ArcGIS* and the centre of each field was determined using the centroid tool. The 100 fields were mapped and distance measures from each field centre to the nearest pathway, settlement, tar and gravel road, river, forest refuge and protected area (spatial correlates tested in previous human–elephant conflict research; e.g. Naughton-Treves, 1997; Hoare, 1999; Smith & Kasiki, 2000; Sitati et al., 2003,

2005) were determined using *ArcGIS*. One-way ANOVA was used to test for association between whether crop fields were raided by elephants or not, and distance to the nearest settlement, protected area, forest refuge, tarmac road, gravel road, river and pathway, and field elevation.

Results

The 12 elephant pathways connected the Kwandu River with the Caprivi State Forest and the Bwabwata National Park, crossing three land-use types: forest, agricultural land and floodplain. Pathways were used at night, allowing elephants to traverse the anthropogenic landscape in relative safety. Pathways tended to follow an east–west orientation and had low curvilinearity. They connected resource patches such as preferred drinking or crossing points on the Kwandu River (Plate 1), with waterholes, maize fields and crossing points on the main north–south road. Waterholes were found along 50% of the pathways (Table 1). However, 83% of these waterholes were dry by May (the end of the wet season). Female elephants avoided pathways in areas of medium and high settlement density (< 100 people km⁻²) in the south, Mendelsohn & Roberts, 1997), preferring the northern pathways further away from settlements (areas with < 10 people km⁻²). Teak woodland and shrubland constitute the major vegetation type in the forest and includes tree species important for elephant diet in the wet and dry seasons. Crop fields are a mixture of fallow and planted fields, with maize the dominant crop type. Pathways become less defined (i.e. non-linear) after entering crop fields but increasingly linear when approaching road-crossing points and when leading to a river. Crossing points at roads remained 100% consistent, with elephants always crossing at the same locations for all observations. Pathways were used by other species, including the hyaena *Crocuta crocuta*, hippopotamus *Hippopotamus amphibius*, leopard *Panthera pardus*, jackal *Canis mesomelas*, wild cat *Felis libyca*, duiker *Sylvicapra grimmia*, kudu *Tragelaphus strepsiceros* and bushpig *Potamochoerus larvatus*, especially in the north, in areas of decreased human disturbance.

Pathway activity was significantly higher in the peak wet season months (March–April; 60 records) than in the second dry season months (September–October; eight records), with peak activity in April (Fig. 2). Data records of elephant footprints showed that pathway use was highest in the southern, high-density settlement areas and in the extreme northern low-density settlement area. Monthly rainfall and elephant incident data for 2006–2008 showed a clear correlation between timing of rainfall and elephant raids, with raids occurring after above-average rainfall events (Spearman Rank correlation = 0.685). Crop raiding occurred as crops ripened towards the end of the rainy season, with a peak of incidents in April. Of the 168 recorded



PLATE 1 Elephant *Loxodonta africana* pathways within the Kwandu Conservancy were linear, with floors devoid of vegetation (a, b, e). Pathways connected habitat and resource patches such as waterholes (c) and preferred drinking spots on the river (f) with crossing points on the Kwandu Conservancy road (d).

incidents, only 24% comprised actual raids (> 25% of field destroyed). Maize was the most frequently planted crop ($n = 100$), and the most affected by elephant incidents. Mature crops were raided more frequently than interim or immature crops ($\chi^2 = 8.32$, $P = 0.00392$). Bulls were responsible for 100% of reported incidents, and all incidents occurred at night. Bull group size increased with incident type, with larger groups responsible for raids ($z = 2.91$, $P < 0.01$). Seventy-five percent of fields raided in 2007 were

targeted again in 2008 ($\chi^2 = 11.95$, $P = 0.02$). Distance to protected area, forest refuge, tar and gravel roads, river and elevation were insignificant as spatial variables in explaining field-raiding position. Although statistically not significant, fields lying close to settlements tended to be raided less frequently than fields at a distance from settlements. Fields close to pathways were visited by elephants more frequently and raided significantly more often than fields that lay further away (Fig. 3).

TABLE 1 Characteristics of the 12 recorded elephant *Loxodonta africana* pathways, with density of adjacent human settlements, pathway length, width and elevation, number of branches off a pathway, number of adjacent waterholes, whether males or both males and females used the pathway, and season in which the pathway was used.

| Pathway | Settlement density along pathway | Length (km) | Width (m) | Elevation (m) | No. of branches | No. of waterholes | Elephant sex | Seasonal use of pathways |
|---------|----------------------------------|-------------|-----------|---------------|-----------------|-------------------|--------------|--------------------------|
| 1 | High | 5.7 | 0.6 | 973 | 6 | 0 | Male | Wet, dry |
| 2 | High | 4.7 | 0.5 | 978 | 2 | 0 | Male | Wet, dry |
| 3 | High | 3.6 | 0.7 | 980 | 6 | 0 | Male | Wet |
| 4 | Medium | 2.5 | 0.5 | 988 | 6 | 1 | Male | Wet |
| 5 | Medium | 6.8 | 1.1 | 993 | 8 | 3 | Male | Wet |
| 6 | Medium | 3.4 | 1.3 | 993 | 2 | 4 | Male | Wet |
| 7 | Medium | 3.3 | 0.5 | 990 | 4 | 0 | Male | Wet |
| 8 | Low | 3.3 | 0.7 | 972 | 2 | 1 | Both | Wet, dry |
| 9 | Low | 4.6 | 0.5 | 985 | 0 | 0 | Male | Wet, dry |
| 10 | Low | 4.4 | 0.5 | 986 | 0 | 0 | Both | Wet, dry |
| 11 | Low | 2.3 | 0.5 | 989 | 2 | 1 | Male | Wet, dry |
| 12 | Low | 4.3 | 1 | 988 | 0 | 8 | Male | Wet, dry |

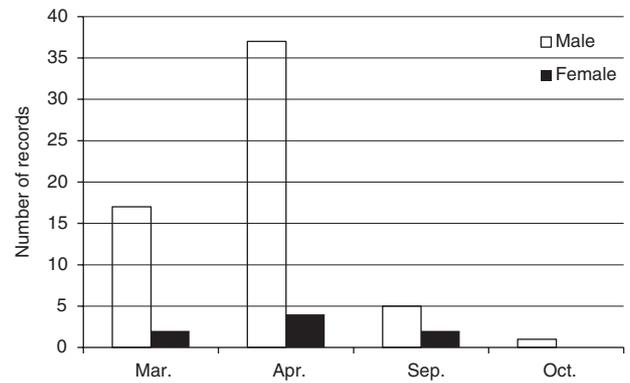


FIG. 2 Number of records of use of pathways in the wettest (March and April) and driest (September and October) months by male and female elephants.

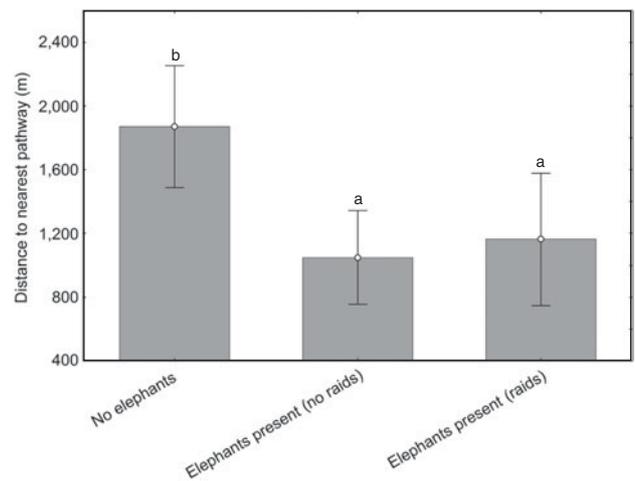


FIG. 3 Fields close to pathways were visited by elephants more frequently and raided significantly ($P < 0.01$) more often than fields that lay further away. Bars with different letters above are significantly different.

Discussion

Many species use pathways, for a host of reasons. The rock hyrax *Procapra capensis* uses foraging trails within its home range (Estes, 1992). The black rhinoceros *Diceros bicornis* in East Africa move along the 'same well worn paths' when moving to and from drinking areas (Ritchie, 1963). Harvester ant *Pogonomyrmex* spp. foragers use a trunk-route system to facilitate exploitation of patchily distributed yet stable food resources (Holldöbler & Lumsden, 1980); trunk trails are consistent over time, with chemical and visual cues along trails contributing to trail persistence.

Hippopotamus pathways in swamp areas are aligned with the prevailing slope and develop into channel systems that keep river channels open. Main trails are connected to lateral trails that lead to grazing areas. Pathway use has been recorded in the forest elephant (Van Leeuwe & Gautier-Hion, 1998), and Shannon et al. (2009) mapped an entire savannah elephant pathway network in South Africa,

TABLE 2 One-way ANOVA testing for association between whether crop fields ($n = 100$) were raided by elephants or not and distance to the nearest settlement, protected area, forest refuge, tar or gravel road, river and pathway, and field elevation.

| Distance to | <i>F</i> | <i>p</i> |
|----------------|----------|----------|
| Settlement | 2.55 | 0.08 |
| Protected area | 1.09 | 0.34 |
| Forest refuge | 1.10 | 0.34 |
| Tar road | 1.45 | 0.24 |
| Gravel road | 0.10 | 0.90 |
| River | 1.33 | 0.33 |
| Pathway | 6.01 | 0.01 |
| Elevation | 0.77 | 0.47 |

recording an increased density of pathways in closed woodland close to water.

Our study is the first to demonstrate the spatial significance of pathways for elephant movements and crop-raiding location. We observed that females use pathways far from settlements to access water, whereas males use pathways throughout the year and irrespective of density of human settlements. Bulls used the pathways not only in the harvesting (wet) season when crops ripen but also at the peak of the dry season, and this suggests that elephants use pathways for reasons other than crop-raiding. Pathways for savannah elephants may be least-effort routes between daily and seasonal resources such as preferred drinking and resting areas, crossing points on roads, and foraging sites. Pathway use in Kwandu Conservancy therefore appears to maximize optimal foraging by facilitating movement in a disturbed matrix and linking predictable resources.

Maximizing optimal foraging

Area-concentrated search is considered vital in patchy environments (Fortin, 2003), where search mode is adapted to habitat structure. Search modes can either be intensive (with low travel speeds and high path sinuosity) or extensive (with high travel speeds along linear paths). Minimizing travel distance between resources is an obvious strategy to maximize the cost-benefit balance (Noser & Byrne, 2007). The procurement of food at the lowest energetic cost forms the basis of optimal foraging theory. The use of least-effort routes has been described in chimpanzees *Pan troglodytes verus* (Normand & Boesch 2009), baboons *Papio ursinus* (Noser & Byrne, 2007) and buffalos *Syncerus caffer* (Bar David et al., 2009), with animals displaying a goal-directed approach to out-of-sight food and water sources. Pathway position could reflect preferred elephant routes to and from favoured areas (Shannon et al., 2009).

In Kwandu Conservancy elephants foraged randomly within homogeneous crop fields but when travelling

through the anthropogenic matrix movement was directional and non-random along clearly-defined pathways. Pathways may act as least-effort routes to stable and clustered nutrient sources such as fruiting trees, crops and mineral licks. In tropical forests distribution of forest elephant trails has been linked to high-nutrient food sources such as fruit and mineral deposits (Blake & Inkambunuku, 2004) and elephant trails link important fruiting trees (Short, 1983; White, 1992). In Botswana, Child (1968) recorded trails leading to fruiting trees such as marula *Sclerocarya birrea* and mugongo *Schinsiohyton rautaneii*. In the Kwandu Conservancy and adjacent areas there are numerous species of fruiting trees favoured by elephants, including marula, Transvaal gardenia *Gardenia volkensii*, camelthorn *Acacia eriloba*, candlepod acacia *Acacia hebecclada*, jackalberry *Diospyrus mespiliformis* and rosewood *Guibourtia coleosperma*. Trees fruit between November and April (Roodt, 1998), coinciding with the wet season, which is also the time that farmers harvest their crops. As some of these trees grow in the greater Kwandu Conservancy area, and many of the riverine areas are densely settled, human–elephant interactions are inevitable. Bulls that lose part of their home range to crop fields can become crop-raiders (Balasubramanian et al., 1995).

Linking predictable resources

Some pathways, particularly in the southern densely settled areas, were frequently used by elephant bulls in the wet season when moving between protected areas, foraging on ripening crops en route. Crop-raiding has been described as an extension of an elephant's optimal foraging strategy, with bulls making use of raised nutritive content (protein, calcium and sodium) of crops at the end of the wet season (Sukumar, 1990). As in previous studies (Hoare, 1999; Jackson et al., 2008; King et al., 2009) female elephants in this study displayed risk-averse behaviour and avoided settlement areas in peak harvesting time by restricting pathway use to the northern, less densely settled areas. The herds made use of the pathways to access the Kwandu River and protected areas to the west, as the majority of waterholes had dried up. Maize is non-randomly distributed in the landscape, and in the Kwandu Conservancy 75% of fields raided in one year would be targeted again in the following year (von Gerhardt, 2011). Crop fields provide elephants with a clustered and stable, high-nutrient resource at the end of the wet season when nutritional demands are greatest, with bulls coming into musth and females in oestrus (Poole, 1984). Crop-raiding, and human–elephant conflict, was found to be a function of season, with incidents only recorded by the Conservancy Office in the wet season, although elephants cross the Conservancy in the dry season to access the Kwandu River and Bwabwata National Park.

In addition, undisturbed riparian habitat with preferred fruiting trees (*Sclerocarya*, *Garcinia*, *Diospyros*, *Bauhinia* and *Acacia* spp.) and minerals are available on the western side of the Kwandu River within Bwabwata National Park. Salt licks are provided around pans in Bwabwata National Park (KVG, pers. obs.) and provide an important source of sodium. In the savannahs of the Central African Republic elephants seek out salt-rich soils around termitaria and waterholes and these areas are connected by trails (Ruggiero & Fay, 1994). Elephants, especially females, exercised geophagy in response to sodium deficiencies in Kalahari sand habitats (Holdo et al., 2009). Duffy et al. (2011) demonstrated that elephants use a direct movement strategy, using decreased path tortuosity and fewer turning angles when needing to get to a destination such as a water source. Waterholes were found in at least half of the pathways in Kwandu Conservancy, and these tended to dry up by the end of April. Elephants resident in the area used the pathways to access the Kwandu River to drink at night.

Facilitating movement in the matrix

Animals are known to have sinuous pathways in good-quality terrain, whereas they tend to move further and faster in unfavourable terrain (Crist et al., 1992). Elephant movement tends to be more directional when resources are limited or habitat heterogeneity is high (Wittemyer et al., 2008). Habitat connectivity in the Kwandu Conservancy is patchy because of the presence of agricultural fields, with the spatial configuration of the road, settlements and crop fields creating a barrier to wildlife movement (Martin, 2006). This environmental gradient of habitat quality should consequently decrease animal movement (Forman, 1995). However, in this study temporal segregation of pathway use permitted the elephants to traverse the anthropogenic matrix safely. Elephants and other species were active along pathways at night, with human activity occurring during the day. Pathway use by both elephants and humans has also been noted by Carroll (1988), with forest elephants and Aka pygmies in the Central African Republic using the vast network of elephant pathways connecting marshy clearings that have high mineral and water content. Other studies confirm nocturnal activity of elephants near smallholdings (Hoare, 1999; Sitati et al., 2003; Graham et al., 2009) and research suggests that this is a risk-avoidance strategy (Galanti et al., 2006; Wittemyer et al., 2008) used by elephants in unprotected areas.

Fidelity to pathways in disturbed areas could be an effective behavioural strategy when speedy escapes and spatial awareness of shelter areas are required. Spatial awareness during flight behaviour is demonstrated by meerkats *Suricata suricatta*, for example, which use spatial memory rather than olfactory or visual cues in quickly

locating bolt-holes when exposed to threat of predation (Manser & Bell, 2003). In Kwandu Conservancy rural farmers use a combination of methods to discourage elephants from moving through agricultural areas: drumming, burning fires, throwing stones, shouting and firing guns. Ahlering et al. (2011) recorded elevated levels of stress hormones in bulls moving through settlement areas. In Kwandu Conservancy single mature elephant bulls moving along pathways were most commonly observed (von Gerhardt, 2011) but at the height of the harvesting season bull groups of 2–7 individuals of varying ages were recorded, with serious crop-raiding incidents attributed to groups of bulls. Intense burning and runaway bushfires are also a threat to elephants in the peak dry season months. Spatial memory and acuity in an anthropogenic matrix may be advantageous to elephants frequently exposed to disturbance.

Conclusion

Metapopulation theory underpins the management for the Kavango-Zambezi Transfrontier Conservation Area's network of protected areas. Such networks may be a mitigation measure against habitat isolation provided that network design and management is optimized and the spatial arrangement of landscape elements considered. Protected areas have been set aside for this purpose but it is within the surrounding matrix that the strength of the Kavango-Zambezi Transfrontier Conservation Area's effectiveness will be challenged. Dispersal and movement of individual elephants between protected areas is affected by the quality of the surrounding matrix, as well as by the spatial arrangement of habitat fragments beyond protected areas (Cumming, 2010). Landscape elements such as elephant pathways, nodes (waterholes/pans) and stepping stones (remnant pockets of forest/forest reserves) in the surrounding matrix need to be identified and to be of sufficiently high quality to encourage elephant movement among patches. This will be especially relevant for herds of risk-averse females and their offspring.

Our study suggests that elephants use pathways when moving between protected areas and that these pathways play a significant role in the location of human–elephant conflict. Crops, fruiting trees, and preferred drinking and feeding areas are spatially fixed, and the elephant pathway network in a given area may provide insights into resource preference at the habitat scale. The spatial arrangement of landscape features and the location of pathways could provide useful tools for designing large conservation landscapes such as the Kavango-Zambezi Transfrontier Conservation Area, notably by indicating where to protect elephant pathways to rivers and where to direct efforts to reduce human–elephant conflict incidents effectively.

Klingelhoefter (1987) suggested that pathways reflect ancient movement routes. Although it is known that elephant movement is non-random (Wittemyer et al., 2008; Loarie et al., 2009), little is known about the relationship between elephant spatial memory and movement patterns. The extent to which elephant pathways determine elephant movements requires further research, especially in view of the inheritance of geographical knowledge through the matrilineal line.

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References

- AGNEW, A.D.G. (1966) The use of game trails as a possible measure of habitat utilisation by larger mammals. *East African Wildlife Journal*, 4, 38–46.
- AHLERING, M.A., MILLSPAUGH, J.J., WOODS, R.J., WESTERN, D. & EGGERT, L.S. (2011) Elevated levels of stress hormones in crop-raiding male elephants. *Animal Conservation*, 14, 124–130.
- BALASUBRAMANIAN, M., BHASKARAN, N., SWAMINATHAN, S. & DESAI, A. (1995) Crop raiding by Asian elephants (*Elephas maximus*) in the Nilgiri Biosphere Reserve, South India. In *A Week with Elephants* (eds J.C. Daniel & H.S. Datye), pp. 350–367. Bombay Natural History Society, Bombay, India.
- BAR-DAVID, S., BAR-DAVID, I., CROSS, P., RYAN, S., KNECHTEL, U. & GETZ, W. (2009) Methods for assessing movement path recursion with application to African buffalo in South Africa. *Ecology*, 90, 2467–2479.
- BLAKE, S. & INKAMBA-NKULU, C. (2004) Fruit, minerals and forest elephant trails: do all roads lead to Rome? *Biotropica*, 36, 392–401.
- CARROLL, R.W. (1988) Elephants of the Dzanga-Sangha dense forest of south-western Central African Republic. *Pachyderm*, 10, 12–15.
- CHILD, G. (1968) *Report to the Government of Botswana on an Ecological Survey of Northeastern Botswana*. FAO Report No. TA 2563, Rome, Italy.
- CHIYO, P.I. & COCHRANE, E.P. (2005) Population structure and behaviour of crop-raiding elephants in Kibale National Park, Uganda. *African Journal of Ecology*, 43, 233–241.
- CHIYO, P.I., COCHRANE, E.P., NAUGHTON, L. & BASUTA, G.I. (2005) Temporal patterns of crop raiding by elephants: a response to changes in forage quality or crop availability? *African Journal of Ecology*, 43, 48–55.
- CRIST, T.O., GUERRTIN, D.S., WIENS, J.A. & MILNE, B.T. (1992) Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology*, 6, 536–544.
- CUMMING, D.H.M. (2010) Linkages, wildlife corridors and shortfalls in the KAZA TFCA. In *Fencing Impacts: A Review of the Environmental, Social and Economic Impacts of Game and Veterinary Fencing in Africa with Particular Reference to the Great Limpopo and Kavango-Zambezi Transfrontier Conservation Areas* (eds K. Ferguson & J. Hanks), pp. 144–150. Mammal Research Institute, Pretoria, South Africa.
- DUFFY, K.J., DAI, X., SHANNON, G., SLOTOW, R. & PAGE, B. (2011) Movement patterns of African elephants (*Loxodonta africana*) in different habitat types. *South African Journal of Wildlife Research*, 41, 21–28.
- ESTES, R. (1992) *The Behaviour Guide to African Mammals*. University of California Press, California, USA.
- FORMAN, R.T.T. (1995) *Land Mosaics. The Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge, UK.
- FORTIN, D. (2003) Searching behaviour and use of sampling information by free-ranging bison (*Bos bison*). *Behavioral Ecology and Sociobiology*, 54, 194–203.
- GALANTI, V., PREATONI, D., MARTINOLI, A., WAUTERS, L.A. & TOSI, G. (2006) Space and habitat use of the African elephant in the Tarangire-Manyara ecosystem, Tanzania: implications for management. *Mammalian Biology*, 71, 99–114.
- GRAHAM, M., DOUGLAS-HAMILTON, I., ADAMS, W.M. & LEE, P.C. (2009) The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, 12, 445–455.
- HANKS, J. (2006) *Mitigation of Human–elephant Conflict in the Kavango-Zambezi Transfrontier Conservation Area through Community Based Problem Animal Control, with Particular Reference to the use of Chilli Peppers*. Report to Conservation International, Cape Town, South Africa.
- HARRIS, G., RUSSEL, G. VAN AARDE, R., & PIMM, S. (2008) Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx*, 42, 66–75.
- HAYNES, G. (2006) Mammoth landscapes: good country for hunter-gatherers. *Quaternary International*, 142, 20–29.
- HOARE, R.E. (1999) Determinants of human–elephant conflict in a land-use mosaic. *Journal of Applied Ecology*, 36, 689–700.
- HOLDO, R.M., HOLT, R.D. & FRYXELL, J.M. (2009) Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecological Applications*, 19, 95–109.
- HOLLDÖBLER, H. & LUMSDEN, C.J. (1980) Territorial strategies in ants. *Science*, 20, 732–739.
- JACKSON, T.P., MOSOJANE, S., FERREIRA, S.M. & VAN AARDE, R.J. (2008) Solutions for elephant *Loxodonta africana* crop raiding in northern Botswana: moving away from symptomatic approaches. *Oryx*, 42, 83–91.
- KING, L., LAWRENCE, A., DOUGLAS-HAMILTON, I. & VOLLRATH, F. (2009) Beehive fence deters crop-raiding elephants. *African Journal of Ecology*, 47, 131–137.
- KLINGELHOEFFER, E.W. (1987) *Aspects of the ecology of elephant Loxodonta africana, and a management plan for the Tembe Elephant reserve in Tongaland, Kwazulu-Natal*. MSc thesis. University of Pretoria, Pretoria, South Africa.
- LOARIE, S.R., VAN AARDE, R.J. & PIMM, S.L. (2009) Elephant seasonal vegetation preferences across dry and wet savannahs. *Biological Conservation*, 142, 3099–3107.

- MANSER, M.B. & BELL, M.B. (2003) Spatial representation of shelter locations in meerkats, *Suricata suricatta*. *Animal Behaviour*, 68, 151–157.
- MARTIN, R. (2006) *The Mudumu North Complex: Wildlife Co-management in the Kwando Area of the Caprivi*. Ministry of Environment and Tourism, Windhoek, Namibia.
- MENDELSON, J. & ROBERTS, C. (1997) *An Environmental Profile and Atlas of Caprivi*. Gamsberg Macmillan, Windhoek, Namibia.
- MOSOJANE, S. (2004) *Human–elephant conflict along the Okavango panhandle in northern Botswana*. MSc thesis. University of Pretoria, Pretoria, South Africa.
- MOSS, C.J. (1988) *Elephant Memories—Thirteen Years in the Life of an Elephant Family*. Penguin Books, Harmondsworth, UK.
- NAUGHTON-TREVES, L. (1997) Predicting patterns of crop damage by wildlife in Kibale National Park, Uganda. *Conservation Biology*, 12, 156–168.
- NORMAND, E. & BOESCH, C. (2009) Sophisticated Euclidean maps in forest chimpanzees. *Animal Behaviour*, 77, 195–201.
- NOSER, R. & BYRNE, R. (2007) Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, *Papio ursinus*. *Animal Behaviour*, 73, 257–266.
- NRP (2006) *Okavango Delta Management Plan. Component 6: Wildlife Management—Human–Elephant Conflict*. Progress Report No. 2. Natural Resources & People, Gaborone, Botswana.
- OSBORN, F.V. & PARKER, G.E. (2003) Towards an integrated approach for reducing the conflict between elephants and people: a review of current research. *Oryx*, 37, 80–84.
- PARKER, G.E. & OSBORN, F.V. (2001) Dual-season crop damage by elephants in the eastern Zambezi Valley, Zimbabwe. *Pachyderm*, 30, 49–56.
- PAYNE, K. (1998) *Silent Thunder: In the Presence of Elephants*. Penguin Books, Harmondsworth, UK.
- POOLE, J. (1984) Musth and urinary testosterone concentrations in the African elephant (*Loxodonta africana*). *Journal of Reproduction and Fertility*, 70, 255–260.
- RITCHIE, A.T.A. (1963) The Black Rhinoceros (*Diceros bicornis* L.). *African Journal of Ecology*, 1, 54–62.
- ROBERTSON, F. (2005). *Ecological Processes within the Four Corners Area. Occasional Publications in Biodiversity No. 16*. Biodiversity Foundation for Africa, Bulawayo, Zimbabwe.
- ROODT, V. (1998) *Trees and Shrubs of the Okavango Delta: Medicinal Uses and Nutritional Value*. Shell Field Guide Series, Gaborone, Botswana.
- RUGGIERO, R.G. & FAY, J.M. (1994) Utilization of termitarium soils by elephants and its ecological implications. *African Journal of Ecology*, 32, 222–232.
- SHANNON, G., MATTHEWS, W.S., PAGE, B.R., PARKER, G.E. & SMITH, R.J. (2009) The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions*, 15, 776–783.
- SHORT, J. (1983) Density and seasonal movements of forest elephants in Bia National Park, Ghana. *African Journal of Ecology*, 21, 175–184.
- SITATI, N.W. & WALPOLE, M.J. (2006) Assessing farm-based measures for mitigating human–elephant conflict in Transmara District, Kenya. *Oryx*, 40, 279–286.
- SITATI, N.W., WALPOLE, M.J. & LEADER-WILLIAMS, N. (2005) Factors affecting susceptibility of farms to crop raiding by African elephants: using a predictive model to mitigate conflict. *Journal of Applied Ecology*, 42, 1175–1182.
- SITATI, N.W., WALPOLE, M.J., SMITH, R.J. & LEADER-WILLIAMS, N. (2003) Predicting spatial aspects of human–elephant conflict. *Journal of Applied Ecology*, 40, 667–677.
- SMITH, R.J. & KASIKI, S.M. (2000) *A Spatial Analysis of Human–Elephant Conflict in the Tsavo Ecosystem, Kenya*. Human–Elephant Conflict Taskforce, IUCN, Gland, Switzerland.
- SUKUMAR, A.R. (1990) Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. *Journal of Tropical Ecology*, 6, 33–53.
- TURKALO, A.K. & FAY, J.M. (1995) Studying forest elephants by direct observations: preliminary results from the Dzanga clearing, Central African Republic. *Pachyderm*, 20, 45–54.
- VAN LEEUWE, H. & GAUTIER-HION, A. (1998) Forest elephant paths and movements at the Odzala National Park, Congo: the role of forest clearings and Marantaceae forests. *African Journal of Ecology*, 36, 174–182.
- VON GERHARDT, K. (2011) *Elephant movements and human–elephant conflict in a transfrontier conservation area*. MSc thesis. Stellenbosch University, Stellenbosch, South Africa.
- WEINBAUM, K., NZOOH, Z., USONGO, L. & LAITURI, M. (2007) Preliminary survey of forest elephant crossings in Sangha Trinational Park, central Africa. *Pachyderm*, 43, 52–61.
- WHITE, L. (1992) *Vegetation History and Logging Disturbance: Effects on Rain Forest Mammals in the Lope Reserve, Gabon (with Special Emphasis on Elephants and Apes)*. University of Edinburgh, Edinburgh, UK.
- WILLIAMSON, B.R. (1975) The condition and nutrition of elephants in Wankie National park. *Arnoldia*, 7, 1–19.
- WITTEMYER, G., POLANSKY, L., DOUGLAS-HAMILTON, I. & GETZ, W. M. (2008) Disentangling the effects of forage, social rank and risk on movement autocorrelation of elephants using Fourier and wavelet analysis. *Proceedings of the National Academy of Sciences*, 105, 19108–19113.

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