



Elephant movement patterns in relation to human inhabitants in and around the Great Limpopo Transfrontier Park

Authors:

Robin M. Cook¹
Michelle D. Henley^{2,3}
Francesca Parrini¹

Affiliations:

¹School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, South Africa

²Applied Behavioural Ecology and Ecosystem Research Unit, University of South Africa, South Africa

³Elephants Alive, Hoedspruit, South Africa

Correspondence to:

Robin Cook

Email:

robinmichaelcook@gmail.com

Postal address:

Private Bag X3, University of the Witwatersrand 2050, South Africa

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The presence of humans and African elephants (*Loxodonta africana*) in the Great Limpopo Transfrontier Park can create situations of potential human–elephant conflict. Such conflict will likely be exacerbated as elephant and human populations increase, unless mitigation measures are put in place. In this study we analysed the movement patterns of 13 collared adult African elephants from the northern Kruger National Park over a period of eight years (2006–2014). We compared the occurrence and displacement rates of elephant bulls and cows around villages in the Limpopo National Park and northern border of the Kruger National Park across seasons and at different times of the day. Elephants occurred close to villages more often in the dry season than in the wet season, with bulls occurring more frequently around villages than cows. Both the bulls and the cows preferred to use areas close to villages from early evening to midnight, with the bulls moving closer to villages than the cows. These results suggest that elephants, especially the bulls, are moving through the studied villages in Mozambique and Zimbabwe at night and that these movements are most common during the drier months when resources are known to be scarce.

Conservation implications: Elephants from the Kruger National Park are moving in close proximity to villages within the Great Limpopo Transfrontier Park. Resettlement of villages within and around the park should therefore be planned away from elephant seasonal routes to minimise conflict between humans and elephants.

Introduction

Conflict between humans and elephants (*Loxodonta africana*) has been investigated throughout Africa, focusing on elephant crop raiding activities (O'Connell-Rodwell *et al.* 2000), mapping elephant movement patterns around human settlements (Galanti *et al.* 2006) and investigating possible corridors along which elephants can move safely between reserves (Van de Perre *et al.* 2014). However, as human and elephant populations increase, both in and around protected areas, the likelihood of interactions between humans and elephants, as well as the levels of human–elephant conflict (HEC), will increase. In southern Africa, elephants can move freely throughout the Great Limpopo Transfrontier Park (GLTP), owing to fences being dropped between South Africa's Kruger National Park (KNP), Mozambique's Limpopo National Park (LNP) and Zimbabwe's Gonarezhou National Park (GNP). However, HEC is prevalent within this region as humans and elephants share the same landscape and compete for the same resources (Dunham *et al.* 2010; Witter 2013). Residents have reported that the presence of elephants has placed restrictions on their livelihoods: they are scared of moving between villages and elephants raid their crops (Milgroom & Spierenburg 2008; Witter 2013). In addition, six elephants were shot within the LNP between 2006 and 2008 as a consequence of HEC (Dunham *et al.* 2010). HEC is further complicated by residents' unwillingness to be moved to areas outside the GLTP (Lunstrum 2015; Milgroom & Spierenburg 2008; Witter 2013).

Global positioning system (GPS) technology has been widely used in elephant movement pattern studies since the mid-1990s (Douglas-Hamilton 1998). This technology allows scientists to track animal positions over time and relate these positions to the animals' environment (Cagnacci *et al.* 2010). Animal movements are influenced by both external factors such as resource availability and internal factors such as reproductive status or fear (Nathan *et al.* 2008). Environmental factors such as water distribution (Smit, Grant & Devereux 2007; Thomas, Holland & Minot 2011), vegetation greenness (Marshal *et al.* 2011) and shifts in rainfall patterns (Birkett *et al.* 2012) all drive elephant movements. However, in this study we focus on how the anthropogenic environment within and around the GLTP affects elephant movement patterns. The way elephants use the areas surrounding villages will depend on their spatial and temporal knowledge of human activities,

such as when crops present alternative food sources, when humans are least active or how humans react to their presence (Hoare & Du Toit 1999).

As bulls have different nutrient requirements from cows, preferring bulky diets over quality of vegetation (Greyling 2004; Shannon *et al.* 2006), the body size hypothesis predicts sexual segregation in bull and cow movement patterns outside of mating events (Stokke & Du Toit 2000). Cows are responsible not only for feeding the young elephants nutrient-rich milk during lactation, but also for regulating the pace of movement to that of the young elephants to ensure their safety (Duffy *et al.* 2011; Shannon *et al.* 2010). We therefore expect differences in movement patterns to occur between the sexes.

Specifically, the objectives of our study are (1) to analyse the seasonal occurrences of bulls and cows at different distances from villages, (2) to compare the distance at which bulls and cows occur relative to villages over a 24-hour period and (3) to calculate and compare the displacement rates (distance travelled by an elephant between consecutive collar recordings) of bulls and cows at different distances from villages.

Research method and design

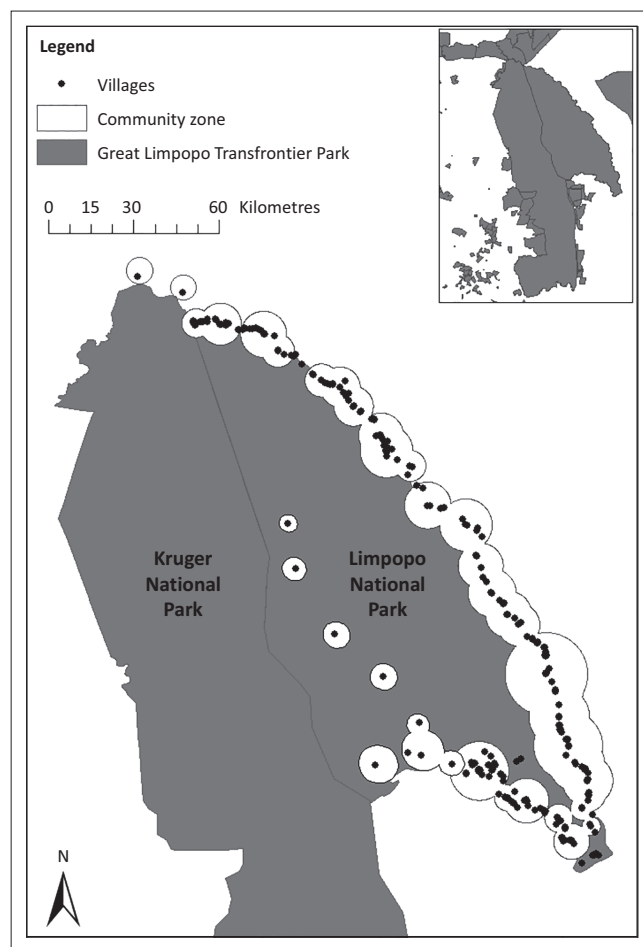
Study area

The study area falls within the GLTP, an area of 35 000 km² that incorporates the KNP, LNP and GNP. We focused on villages within the LNP and bordering the Limpopo River of the KNP of the two study sites, Mozambique and Zimbabwe, respectively (Figure 1). The GLTP is a semi-arid region with a mean annual rainfall of 440 mm in the Pafuri land system (Venter & Gertenbach 1986). The dominant vegetation communities include *Colophospermum mopane* woodland and forest, *Ficus sycomorus* forest, and *Burkea africana* and *Combretum apiculatum* woodland. Tree species such as *Diospyros mespiliformis*, *Combretum imberbe* and *Kigelia africana* are widespread along the Limpopo and Luvuvhu rivers (Venter, Scholes & Eckhardt 2003).

The GLTP is primarily surrounded by small villages along its borders (Hughes 2005). Each village community has an estimated population size of around 1000 individuals (Holden 2001; Lunstrum 2015). The study area included villages situated along the Zimbabwean border of the KNP and villages within the LNP. There are around 27 000 residents within the study area (Milgroom & Spierenburg 2008). Elephants can move freely from the Pafuri region in the KNP to the vicinity of these villages. Villages are situated 5 km – 30 km apart, with each village assigned a community radius of 4 km for crop fields, which comprise maize, beans, tomato, onions, cabbage and carrots, and grazing land for cattle (*Bos taurus*) (A. Alexander pers. comm., 17 July 2014; T. Chauque pers. comm., 12 March 2015).

Elephants and tracking data

Following a near population collapse in the KNP region at the turn of the twentieth century, the first elephants were



Source: Created by Robin M. Cook

FIGURE 1: Location of villages and community zones within Mozambique's Limpopo National Park and along the Limpopo River of South Africa's Kruger National Park.

recorded in the KNP in 1905, and the first in the Pafuri region only after 1945 (Whyte 2001). Currently, there are approximately 16 700 elephants in the KNP (SANParks 2012), which can move freely into the LNP where over 1000 elephants have been recorded (Milgroom & Spierenburg 2008). In Mozambique, where people and elephants compete for resources, there have been reports of crop raiding by elephants (De Boer & Baquete 1998; De Boer, Stigter & Ntumi 2007; Harris *et al.* 2008) as well as recent reports of intensive illegal killings in Mozambique's largest conservation areas (Booth & Dunham 2014). Both illegal killings and human occupancy of their home ranges could affect the elephants' perception of safety. Therefore, to investigate the elephant movements in relation to human occupancy, we used existing data from 13 GPS-satellite collars that had been placed on eight bulls and five cows from different breeding herds in the far northern and eastern regions of the KNP as part of the elephant monitoring programmes in the region. Collaring operations had been carried out by KNP wildlife veterinarians using standard operating procedures as approved by the South African National Parks Animal Use and Care Committee (SANParks 2011). The collars recorded the location of each individual at set eight-hour intervals. Elephant tracking data were retrieved from a centralised database using customised software (Wall *et al.* 2014) that

**TABLE 1:** Collar identification codes and the years when the collars were active for the 13 collared elephants used in this study.

Animal ID	Social unit	Jan-Dec 2006	Jan-Dec 2007	Jan-Dec 2008	Jan-Dec 2009	Jan-Dec 2010	Jan-Dec 2011	Jan-Dec 2012	Jan-Dec 2013	Jan-Dec 2014
KNF01	Cow	-	-	-	Active	-	-	Active	Active	-
KNF02	Cow	-	-	-	-	Active	Active	Active	Active	-
KNF03	Cow	-	-	-	Active	Active	Active	Active	Active	-
KNF04	Cow	-	-	-	Active	Active	Active	Active	Active	-
KNF05	Cow	-	-	-	Active	Active	Active	Active	Active	-
KNM03	Bull	-	-	-	Active	Active	Active	Active	-	-
KNM04	Bull	-	-	-	Active	Active	Active	-	-	-
KNM05	Bull	-	-	-	Active	Active	-	Active	Active	Active
KNM06	Bull	-	-	-	Active	Active	Active	-	-	-
KEM02	Bull	-	Active	Active	Active	-	-	-	-	-
KEM03	Bull	-	Active	Active	-	-	-	-	-	-
KEM04	Bull	Active	Active	Active	Active	-	-	-	-	-
KEM07	Bull	-	Active	Active	Active	-	-	-	-	-

employs a data filter to remove erroneous GPS fixes based on a maximum rate of travel (see Austin, McMillan & Bowen 2003). Data were stored in both ESRI Geodatabase (ArcGIS version 10.1) and comma-separated text file formats. Data from 2006 to 2014 were used, with each elephant's collar lasting an average of two to three years (Table 1). Nine of the collars were replaced during this period (six breeding herd individuals and three solitary bulls) (Table 1). The collars recorded the elephant's GPS locations, the time of day for each data point, and the linear displacement rate (m/h) at each location. In our analyses, the social units described are bulls and cows. The movement of a bull refers to an adult bull that is either solitary or in a bachelor herd. The movement of an individual cow is assumed to be that of the entire family unit, consisting of adult cows, calves and bulls younger than 15 years.

Data analysis

Distance buffer zones were drawn around villages within the study area. Buffer zones included the following areas:

- anthropogenic infrastructure and fields located within 0 km – 2 km from a village
- the outer regions of the community zones, 2 km – 4 km from a village, occupied by fields
- the wilderness zone around the community zone, 4 km – 6 km from a village, which is not used for crop production or grazing.

Locations within 6 km of a village were analysed for a total of 3524 GPS coordinates, of which 1319 were associated with cows and 2205 with bulls. ArcMap (ArcGIS, version 10.1, ESRI) was used for analysis of the GPS locations.

Seasonal locations around villages

For each buffer zone, monthly proportions of bull and cow locations were calculated for the entire study period (2006–2014). Mean monthly rainfall data (2006–2013) were used to distinguish between wetter and drier months in the study area in order to compare elephant locations in the early wet season (October–December), late wet season (January–March), early dry season (April–June) and late dry season (July–September). Mean monthly rainfall data were

acquired from the Punda Maria and Shingwedzi ranger stations.

Time-of-day differences

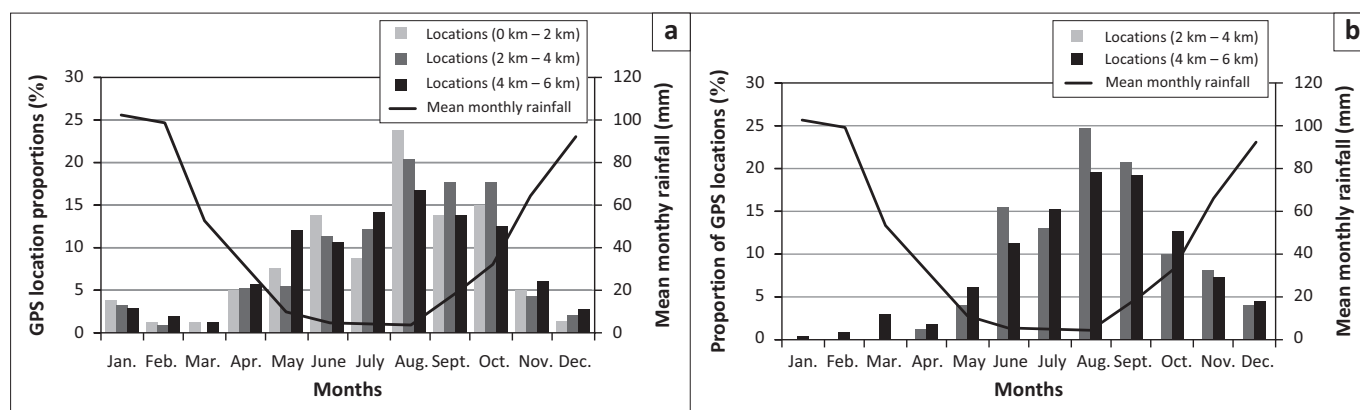
Elephant locations within the three buffer zones were assigned to three time intervals defined by the recording intervals of the elephant's collars. The period from 00:00 to 07:59 was classified as post-midnight to early morning, from 08:00 to 15:59 was classified as late morning to mid-afternoon, and from 16:00 to 23:59 was classified as evening to midnight. We expected that people would likely be the most active in the fields and outside their homes between late morning and mid-afternoon. The proportions of occurrences of bulls and cows within and between the buffer zones were then compared for each period.

Mean linear displacement rates

Mean linear displacement rates (referred to as displacement rates from here on) were analysed for each elephant within each buffer zone. Displacement rates (m/h) were automatically calculated by the collars as the distance travelled between two consecutive collar recordings (and therefore two locations). Displacement rates for bulls and cows were compared between buffer zones. Seasonal differences in displacement rates could not be analysed as a result of the small number of locations close to villages during the wet season.

Statistical analyses

All statistical analyses were performed using Statistica 8.0 (<http://www.statsoft.com>). A Pearson's chi-squared test was used to test for independence of the Mozambican and Zimbabwean village rainfall and elephant occurrence data. Generalised linear mixed models were applied to both the location and linear displacement rate data. To test the responses of elephant location points as a function of social unit, distance from villages and the time of day, the proportions of location points were used as the dependent variable, with the social unit, buffer zones and times set as fixed factors. The individual elephants were regarded as random factors. To test the responses of linear displacement rates as a function of social unit and distance from villages, the linear displacement rates were used as the dependent



Source: Created by Robin M. Cook; rainfall data supplied by the Shingwedzi and Punda Maria ranger stations (Kruger National Park)

FIGURE 2: Monthly location proportions (as measured by global positioning system) of elephant (a) bulls and (b) cows within three buffer zones around studied villages in relation to average monthly rainfall data (2006–2013).

TABLE 2: Proportion of elephant location points during three periods across the buffer zones surrounding villages in Mozambique's Limpopo National Park and villages bordering the Limpopo River of South Africa's Kruger National Park (\pm standard error).

Buffer zone	Social unit	Period: 00:00–07:59	Period: 08:00–15:59	Period: 16:00–23:59	<i>F</i>	<i>P</i>
0 km – 2 km	Bulls	21.17 (\pm 7.46)	4.55 (\pm 2.62)	74.28 (\pm 9.97)	$F_{2,6} = 16.39$	$P < 0.01$
2 km – 4 km	Bulls	24.84 (\pm 1.61)	26.33 (\pm 2.10)	48.83 (\pm 3.19)	$F_{2,10} = 20.99$	$P < 0.01$
	Cows	25.39 (\pm 2.46)	28.34 (\pm 3.19)	46.27 (\pm 2.09)	$F_{2,6} = 12.47$	$P < 0.01$
4 km – 6 km	Bulls	32.10 (\pm 1.15)	31.99 (\pm 1.35)	35.88 (\pm 1.81)	$F_{2,10} = 1.54$	$P = 0.26$
	Cows	34.79 (\pm 1.17)	30.46 (\pm 2.43)	34.74 (\pm 2.56)	$F_{2,8} = 0.89$	$P = 0.45$

variable, with the social unit and buffer zones set as fixed factors. The individual elephants were regarded as random factors.

Results

Seasonal locations around villages

Monthly locations were combined for villages along the Mozambican and Zimbabwean borders, as there was no significant difference between the rainfall data at the two border sites ($\chi^2 = 4.07$, $df = 2$, $P > 0.05$) and the seasonal elephant patterns ($\chi^2 = 1.02$, $df = 1$, $P > 0.05$) for the two sites. Across the study period, the proportion of elephant locations began to increase during the early dry season in all buffer zones (April–May) as mean monthly rainfall across the study area decreased (Figure 2a and 2b). The highest proportion of locations in all three buffer zones occurred during the late dry season (August–October), when the mean monthly rainfall was at its minimum, for both bulls and cows (Figure 2a and 2b). The lowest proportion of locations within buffer zones occurred in the late wet season (January–March), when the mean monthly rainfall was at its peak, for both bulls and cows in all buffer zones (Figure 2a and 2b).

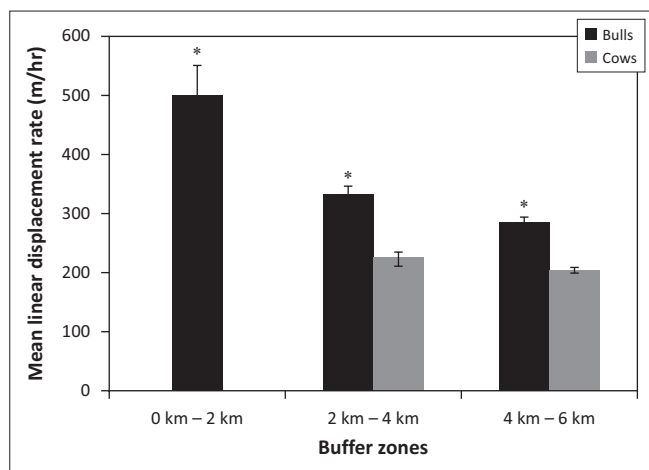
Time-of-day differences

The time recordings of elephant locations in the two study sites were combined as there was no significant difference between recordings at the two sites (three-way interaction

term $F_{4,42} = 0.53$; $P > 0.05$). There was a higher proportion of elephant locations in the 0 km – 2 km and 2 km – 4 km buffer zones during the evening–midnight period than in the other periods. A significantly higher proportion of locations was recorded from bulls in the 0 km – 2 km buffer zone during the evening–midnight period than in the other periods (Table 2). None of the collared cows used the 0 km – 2 km buffer zone, but rather remained on the outskirts of the community zones around the villages. In the 2 km – 4 km buffer zone, location proportions of both the bulls and the cows were significantly higher in the evening–midnight period than in the two other periods (Table 2). There was no significant difference between the time proportions for bulls and cows in this buffer zone. In the 4 km – 6 km buffer zone, there was no significant difference in the location proportions of bulls and cows across the three periods (Table 2).

Mean linear displacement rates

Displacement rates of bulls were significantly higher than those of breeding herds around villages (313 m/h for bulls vs 208 m/h for cows) ($F_{1,10} = 5.13$; $P < 0.05$; Figure 3). The displacement rate of bulls increased significantly the closer the bulls were to villages, with a mean displacement rate of 500 m/h in the 0 km – 2 km buffer zone, 335 m/h in the 2 km – 4 km buffer zone and 287 m/h in the 4 km – 6 km buffer zone ($F_{2,10} = 6.41$; $P < 0.05$; Figure 3). There was significant variation between the displacement rates of the individual bulls in the three buffer zones, and although all of the bulls



Source: Created by Robin M. Cook

FIGURE 3: Mean linear displacement rate of bulls and cows across buffer zones surrounding studied villages. Error bars indicate standard error. Asterisks indicate significantly different displacement rates ($P < 0.05$).

increased their displacement rates the closer they were to villages, there was variation in the changes of displacement rate when approaching a village (two-way interaction term $F_{10,2186} = 3.69$; $P < 0.0001$). One of the bulls moving around the villages Makandazulo A and B decreased its displacement rate when moving from the 4 km - 6 km buffer zone (260 m/h) into the 2 km - 4 km buffer zone (208 m/h). However, this bull's displacement rate again increased when in the 0 km - 2 km buffer zone (329 m/h). Furthermore, three of the bulls had displacement rates above 350 m/h (mean = 380 m/h), which was significantly higher than the mean displacement rate for the others (231 m/h) ($F_{1,3} = 41.04$; $P < 0.005$). Cows' displacement rates increased from 205 m/h in the 4 km - 6 km buffer zone to 224 m/h in the 2 km - 4 km buffer zone, albeit not significantly ($F_{1,2} = 13.88$; $P = 0.07$; Figure 3). There was no significant variation in the displacement rates of individual cows in the respective buffer zones.

Discussion

We found that the majority of elephant locations in village community zones occurred during the drier months. Previous studies have suggested an increase in elephant movements around villages as a result of decreased water availability in protected reserves (Kioko, Okello & Muruthi 2006), an increase in nutrient quality available in villages (O'Connell-Rodwell *et al.* 2000) and a decrease in the natural vegetation quality in protected reserves (Osborn 2004). In the context of the GLTP, no single explanation can be given for the observed higher frequency of elephant locations close to villages without real-time observations during the dry season. Most of the villages are located along major river systems, including the Rio Limpopo (Limpopo River), the Rio Shingwedzi (Shingwedzi River) and the Rio dos Elefantes (Olifants River). In contrast to the neighbouring KNP, there are no artificial water points in the LNP and elephants appear to concentrate their movements through the LNP along river systems (unpublished data). Furthermore, motor and hand-held pumps have been provided to river-bordering villages in the region to enable

residents to grow crops throughout the year without having to rely on rainfall (A. Alexander, pers. comm., 17 July 2014). Elephant locations close to villages may therefore be due to a combination of water being available close to the crops and crops offering accessible and diverse resources (depending on what crop type is being cultivated). During the drier months, when natural resources become scarce, elephants will be more prone to supplement their diets with cultivated crops until the nutritional quality from natural vegetation increases in the wetter months. Osborn (2004) found similar behavioural patterns for elephants in northern Zimbabwe and Witter (2013) mentions elephants utilising not only crops but also fruit grown and stored around villages in the LNP.

We found that only the bulls used the 0 km - 2 km buffer zone. Bulls have been found to be more likely to move within closer proximity to villages than cows, with hypotheses suggesting that the increased intake of higher quality crops enables the bulls to compete more successfully against other bulls for dominance status and mating opportunities (Chiyo *et al.* 2011; Sitati *et al.* 2003; Sukumar & Gadgil 1988). Although the presence of crops would also be attractive to cows and their smaller family members, the small number of cow locations in the closest community zone could simply be a result of the risk posed by humans coupled with an inability to move to safety as quickly as bulls, who generally have smaller group sizes and whose movements are not constrained to the same level by the slowest members of the group, usually calves (Duffy *et al.* 2011; Shannon *et al.* 2010). Despite the presence of smaller-bodied cows, who are often pregnant or lactating and therefore in need to maintain diets of higher quality compared to bulls (Stokke & Du Toit 2000), safety aspects may outweigh the nutrient value of the crops when considering family units. The predation-risk theory predicts that cows with young are more vulnerable to predation than bulls and are therefore less likely to use areas of potential danger (Ruckstuhl & Neuhaus 2002). The predation-risk theory may explain why elephant breeding herds are less inclined to use areas around villages in comparison to bulls, as the villages may present a potential danger to the cows and their calves. In addition, solitary bulls may be less likely to be detected by humans when crop raiding than a breeding herd with more individuals (Sukumar & Gadgil 1988). Crop raiding may therefore be a more attractive activity for solitary bulls able to avoid human observation.

The majority of elephant locations in the 0 km - 2 km and 2 km - 4 km buffer zones occurred in the evening-midnight period, which suggests that the elephants are closest to villages when humans are least active. Evening-midnight location trends have been recorded both for elephants moving past villages (Douglas-Hamilton, Krink & Vollrath 2005; Graham *et al.* 2009; Van de Perre *et al.* 2014) and for actively crop-raiding elephants (Chiyo & Cochrane 2005; Jackson *et al.* 2008; Sukumar & Gadgil 1988). The low proportion of locations in the community zones between midnight and early morning may be attributed to elephants moving out of the community zones during this period to rest or sleep. Rest



periods are associated with less vigilant behaviour, which is easier when not in a potential landscape of fear (Wing & Buss 1970). However, more information is required based on GPS locations recorded at shorter time intervals to test for such fine-scale activity patterns of elephants.

The increased displacement rates of bulls moving through the community zones suggest that the displacement rates of elephants increase when moving through areas of potential high risk. This increased displacement rate was particularly evident in the 0 km – 2 km buffer zone, which is occupied by village infrastructure and residents. Elephants that move through a community zone with the sole purpose of minimising the time spent in that zone will be likely to have increased displacement rates as their movement patterns are more likely directional (Douglas-Hamilton *et al.* 2005; Jachowski, Slotow & Millspaugh 2013). If an elephant is crop raiding, its displacement rate will be lower than that of an elephant moving through in a directional manner, as the distance covered between locations will be minimal. This does not necessarily suggest that the elephant's speed has decreased (Graham *et al.* 2009), as a crop-raiding elephant may be moving at an increased speed amongst crops in a non-directional and tortuous manner to maximise resource intake. Therefore, the variation in displacement rates seen between bulls moving through community zones could mean that not all elephants moving through a village carry out the same activity or respond to the presence of a village in the same manner (McComb *et al.* 2011). Musth is known to influence the movement rates of bulls (Rasmussen, Wittemyer & Douglas-Hamilton 2005) and hence individual variability between bulls could also be linked to their reproductive status at the time of crop raiding. Although the displacement rate of the cows increased when moving through the community zones, there was no significant change between displacement rates within a buffer zone or the displacement rates of different cows, presumably as cows are equally constrained by their group sizes and can maintain movement at a constant rate when not in the highest danger zone (0 km – 2 km).

Conclusion and management implications

Elephants from the KNP are moving in close proximity to villages within the GLTP. This is the first known study focusing on the movement patterns of elephants around villages in the GLTP and provides baseline information on how elephants in the GLTP use the areas around villages. Elephants evidently have to play off the benefits derived from crop raiding against those of being persecuted by humans. Bulls and cows were found to handle these treat-versus-threat scenarios differently, with bulls being less risk averse than family units. Further understanding of the movements of elephant bulls and breeding herds around villages within this area requires a more in-depth approach. Focusing on the human density, crop layout, water availability and previous experience with HEC will benefit our understanding of how these factors influence elephant movement patterns. By

understanding where, when and in what manner elephants are moving around these villages, conservation authorities can begin to adopt mitigation systems such as beehive fences (King, Douglas-Hamilton & Vollrath 2011) or chili extracts (Osborn & Rasmussen 1995) in an attempt to minimise HEC in the region. In addition, resettlement of villages within and around the GLTP should take place away from seasonal elephant routes to prevent conflict between humans and elephants in this region.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

R.M.C. (University of the Witwatersrand) was responsible for analysis and interpretation of the data. He was also responsible for drafting the article. M.D.H. (University of South Africa) was responsible for data acquisition and contributed to data interpretation and article revision. F.P. (University of the Witwatersrand) was the project leader. She contributed to the concept and design of the study, supervised data analysis and interpretation, and revised the article.

References

- Austin, D., McMillan, J.I. & Bowen, W.D., 2003, 'A three-stage algorithm for filtering erroneous Argos satellite locations', *Marine Mammal Science* 19(2), 371–383. <http://dx.doi.org/10.1111/j.1748-7692.2003.tb01115.x>
- Birkett, P.J., Vanak, A.T., Muggeo, V.M., Ferreira, S.M. & Slotow, R., 2012, 'Animal perception of seasonal thresholds: Changes in elephant movement in relation to rainfall patterns', *PLoS One* 7(6), e38363. PMID: 22761680, <http://dx.doi.org/10.1371/journal.pone.0038363>
- Booth, V.R. & Dunham, K.M., 2014, 'Elephant poaching in Niassa Reserve, Mozambique: Population impact revealed by combined survey trends for live elephants and carcasses', *Oryx*, 10 pages. <http://dx.doi.org/10.1017/S0030605314000568>
- Cagnacci, F., Boitani, L., Powell, R.A. & Boyce, M.S., 2010, 'Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges', *Proceedings of the Royal Society B* 365(1550), 2157–2162. PMID: 20566493, <http://dx.doi.org/10.1098/rstb.2010.0107>
- 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(3), 233–241. <http://dx.doi.org/10.1111/j.1365-2028.2005.00577.x>
- Chiyo, P.I., Lee, P.C., Moss, C.J., Archie, E.A., Hollister-Smith, J.A. & Alberts, S.C., 2011, 'No risk, no gain: Effects of crop raiding and genetic diversity on body size in male elephants', *Behavioral Ecology* 22(3), 552–558. <http://dx.doi.org/10.1093/beheco/arr016>
- De Boer, W.F. & Baquete, D.S., 1998, 'Natural resource use, crop damage and attitudes of rural people in the vicinity of the Maputo Elephant Reserve, Mozambique', *Environmental Conservation* 25(3), 208–218.



- De Boer, W.F., Stigter, J.D. & Ntumi, C.P., 2007, 'Optimising investments from elephant tourist revenues in the Maputo Elephant Reserve, Mozambique', *Journal for Nature Conservation* 15(4), 225–236. <http://dx.doi.org/10.1016/j.jnc.2006.11.002>
- Douglas-Hamilton, I., 1998, 'Tracking African elephants with a global positioning system (GPS) radio collar', *Pachyderm* 25, 81–92.
- Douglas-Hamilton, I., Krink, T. & Vollrath, F., 2005, 'Movements and corridors of African elephants in relation to protected areas', *Naturwissenschaften* 92(4), 158–163. PMID: 15770465, <http://dx.doi.org/10.1007/s00114-004-0606-9>
- 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(1), 21–28. <http://dx.doi.org/10.3957/056.041.0107>
- Dunham, K.M., Ghiurghi, A., Cumbi, R. & Urbano, F., 2010, 'Human–wildlife conflict in Mozambique: A national perspective, with emphasis on wildlife attacks on humans', *Oryx* 44(2), 185–193. <http://dx.doi.org/10.1017/S003060530999086X>
- 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 conservation', *Mammalian Biology* 71(2), 99–114. <http://dx.doi.org/10.1016/j.mambio.2005.10.001>
- Graham, M.D., 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(5), 445–455. <http://dx.doi.org/10.1111/j.1469-1795.2009.00272.x>
- Greyling, M.D., 2004, 'Sex and age related distinctions in the feeding ecology of the African elephant, *Loxodonta africana*', PhD thesis, School of Animal, Plant, & Environmental Sciences, University of the Witwatersrand.
- Harris, G.M., Russel, G.J., Van Aarde, R.I. & Pimm, S.L., 2008, 'Rules of habitat use by elephants *Loxodonta africana* in southern Africa: Insights for regional management', *Oryx* 42(1), 66–75. <http://dx.doi.org/10.1017/S0030605308000483>
- Hoare, R.E. & Du Toit, J.T., 1999, 'Coexistence between people and elephants in African savannas', *Conservation Biology* 13(3), 633–639. <http://dx.doi.org/10.1046/j.1523-1739.1999.98035.x>
- Holden, P., 2001, 'Land use planning of Coutada 16: Part of the Gaza-Kruger-Gonarezhou Transfrontier Park', report, Peace Parks Foundation.
- Hughes, D.M., 2005, 'Third nature: Making space and time in the Great Limpopo Conservation Area', *Cultural Anthropology* 20(2), 157–184. <http://dx.doi.org/10.1525/can.2005.20.2.157>
- Jachowski, D.S., Slotow, R. & Millsbaugh, J.J., 2013, 'Corridor use and straying behaviour by African elephants in relation to physiological state', *Biological Conservation* 167, 276–282. <http://dx.doi.org/10.1016/j.biocon.2013.08.005>
- 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(1), 83–91. <http://dx.doi.org/10.1017/S0030605308001117>
- King, L.E., Douglas-Hamilton, I. & Vollrath, F., 2011, 'Beehive fences as effective deterrents for crop-raiding elephants: Field trials in northern Kenya', *African Journal of Ecology* 49(4), 431–439. <http://dx.doi.org/10.1111/j.1365-2028.2011.01275.x>
- Kioko, J., Okello, M. & Muruthi, P., 2006, 'Elephant numbers and distribution in the Tsavo-Amboseli ecosystem, south-western Kenya', *Pachyderm* 40, 61–68.
- Lunstrum, E., 2015, 'Green grabs, land grabs and the spatiality of displacement: Eviction from Mozambique's Limpopo National Park', *Area*, 11 pages. <http://dx.doi.org/10.1111/area.12121>
- Marshall, J.P., Rajah, A., Parrini, F., Henley, M., Henley, S.R. & Erasmus, B.F., 2011, 'Scale-dependent selection of greenness by African elephants in the Kruger-private reserve transboundary region, South Africa', *European Journal of Wildlife Research* 57(3), 537–548. <http://dx.doi.org/10.1007/s10344-010-0462-1>
- McComb, K., Moss, C., Durant, S.M., Baker, L. & Sayialel, S., 2001, 'Matriarchs as repositories of social knowledge in African elephants', *Science* 292(5516), 491–494. PMID: 11313492, <http://dx.doi.org/10.1126/science.1057895>
- McComb, K., Shannon, G., Durant, S.M., Sayialel, K., Slotow, R., Poole, J. et al., 2011, 'Leadership in elephants: The adaptive value of age', *Proceedings of the Royal Society B: Biological Sciences* 278(1722), 3270–3276. PMID: 21411454, <http://dx.doi.org/10.1098/rspb.2011.0168>
- Milgroom, J. & Spierenburg, M., 2008, 'Induced volition: Resettlement from Limpopo National Park, Mozambique', *Journal of Contemporary Studies* 26(4), 435–448. <http://dx.doi.org/10.1080/02589000802482021>
- Nathan, R., Getz, W., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. et al., 2008, 'A movement ecology paradigm for unifying organismal movement research', *Proceedings of the National Academy of Sciences* 105(49), 19052–19059. PMID: 19060196, <http://dx.doi.org/10.1073/pnas.0800375105>
- O'Connell-Rodwell, C.E., Rodwell, T., Rice, M. & Hart, L.A., 2000, 'Living with the modern conservation paradigm: Can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia', *Biological Conservation* 93(3), 381–391. [http://dx.doi.org/10.1016/S0006-3207\(99\)00108-1](http://dx.doi.org/10.1016/S0006-3207(99)00108-1)
- Osborn, F.V., 2004, 'Seasonal variation of feeding patterns and food selection by crop-raiding elephants in Zimbabwe', *African Journal of Ecology* 42(4), 322–327. <http://dx.doi.org/10.1111/j.1365-2028.2004.00531.x>
- Osborn, F.V. & Rasmussen, L.E.L., 1995, 'Evidence for the effectiveness of an oleo-resin caprylic aerosol as a repellent against wild elephants in Zimbabwe', *Pachyderm* 20, 55–64.
- Rasmussen, H.B., Wittemyer, G. & Douglas-Hamilton, I., 2005, 'Estimating age of immobilized elephants from teeth impressions using dental silicon', *African Journal of Ecology* 43(3), 215–219. <http://dx.doi.org/10.1111/j.1365-2028.2005.00571.x>
- Ruckstuhl, K.E. & Neuhaus, P., 2002, 'Sexual segregation in ungulates: A comparative test of three hypotheses', *Biological Reviews of the Cambridge Philosophical Society* 77(1), 77–96. PMID: 11911375, <http://dx.doi.org/10.1017/S1464793101005814>
- SANParks, 2011, 'Standard operating procedures for the capture, transportation and maintenance in holding facilities of wildlife: Elephant', report, Veterinary Wildlife Services, SANParks.
- SANParks, 2012, 'Elephant management plan, Kruger National Park 2013–2022', report, SANParks.
- Shannon, G., Page, B.R., Duffy, K.J. & Slotow, R., 2006, 'The role of foraging behaviour in the sexual segregation of the African elephant', *Oecologia* 150(2), 344–354. PMID: 16927101, <http://dx.doi.org/10.1007/S00442-006-0521-1>
- Shannon, G., Page, B.R., Duffy, K.J. & Slotow, R., 2010, 'The ranging behaviour of a large sexually dimorphic herbivore in response to seasonal and annual environmental variation', *Austral Ecology* 35(7), 731–742. <http://dx.doi.org/10.1111/j.1442-9993.2009.02080.x>
- 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(4), 667–677. <http://dx.doi.org/10.1046/j.1365-2664.2003.00828.x>
- Smit, I.P.J., Grant, C.C. & Devereux, B.J., 2007, 'Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park', *Biological Conservation* 136(1), 85–99. <http://dx.doi.org/10.1016/j.biocon.2006.11.009>
- Stokke, S. & Du Toit, J.T., 2000, 'Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana', *Ecography* 23(1), 70–80. <http://dx.doi.org/10.1111/j.1600-0587.2000.tb00262.x>
- Sukumar, R. & Gadgil, M., 1988, 'Male-female differences in foraging on crops by Asian elephants', *Animal Behaviour* 36(4), 1233–1235. [http://dx.doi.org/10.1016/S0003-3472\(88\)80084-8](http://dx.doi.org/10.1016/S0003-3472(88)80084-8)
- Thomas, B., Holland, J.D. & Minot, E.O., 2011, 'Seasonal home ranges of elephants (*Loxodonta africana*) and their movements between Sabi Sand Reserve and Kruger National Park', *African Journal of Ecology* 50(2), 131–139. <http://dx.doi.org/10.1111/j.1365-2028.2011.01300.x>
- Van de Perre, F., Adriaensen, F., Songorwa, A.N. & Leirs, H., 2014, 'Locating elephant corridors between Saadani National Park and the Wami-Mbiki Wildlife Management Area, Tanzania', *African Journal of Ecology* 52(4), 448–457. <http://dx.doi.org/10.1111/aje.12139>
- Venter, F.J. & Gertenbach, W.P.D., 1986, 'A cursory review of the climate and vegetation of the Kruger National Park', *Koedoe* 29(1), 139–148. <http://dx.doi.org/10.4102/koedoe.v29i1.526>
- Venter, F.J., Scholes, R.J. & Eckhardt, H.C., 2003, 'The abiotic template and its associated vegetation pattern', in J.T. du Toit, K.H. Rogers & H.C. Biggs (eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*, pp. 83–129, Island Press, Washington DC.
- Wall, J., Wittemyer, G., Klinkenberg, B. & Douglas-Hamilton, I., 2014, 'Novel opportunities for wildlife conservation and research with real-time monitoring', *Ecological Applications* 24(4), 593–601. PMID: 24988762, <http://dx.doi.org/10.1890/13-1971.1>
- Whyte, I.J., 2001, 'Conservation management of the Kruger National Park elephant population', PhD thesis, Department of Zoology and Entomology, University of Pretoria.
- Wing, L.D. & Buss, I.O., 1970, 'Elephants and forests', *Wildlife Monographs* 19, 3–92.
- Witter, R., 2013, 'Elephant-induced displacement and the power of choice: Moral narrative about resettlement in Mozambique's Limpopo National Park', *Conservation and Society* 11(4), 406–419. <http://dx.doi.org/10.4103/0972-4923.125756>