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

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 (Duham 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 (Duham 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 nespoliformis, 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 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

![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.](http://www.koedoe.co.za)
employ 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 variable.
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...
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 $F_{1,2106} = 3.69; P < 0.001$). 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) ($F_{1,13} = 41.04; P < 0.005$). 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 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 (Chiyolo 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 (Chiyolo & 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.
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 & Millsapgh 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). MUST is known to influence the movement rates of bulls (Rasmussen, Wittemeyer & 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-crop raiding against those of being persecuted by humans. The increased displacement rates of bulls moving through the community zones suggests 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 & Millsapgh 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). MUST is known to influence the movement rates of bulls (Rasmussen, Wittemeyer & 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).

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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.

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