MANAGEMENT

Elephant movements in different human land-uses in Chobe District, Botswana

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Abstract

We have a limited understanding of the effects that an increasing human population and urban and agricultural development are having on elephant movements in Botswana. Elephant movements are complex because they are influenced by a wide range of location-specific variables. This study aimed to investigate how elephants move through different human-dominated landscapes in the Chobe District, Botswana. The movements of four female elephants from the Chobe District were studied over a period of 13 months using GPS collars to follow them. Annual home ranges of the elephants were calculated using both the 100% minimum convex polygon (MCP) and 95% fixed kernel (FK) methods. Additionally, general estimating equation models were used to investigate which factors influenced the elephants' distance moved, both hourly and daily. We found the elephants' movement behaviour was dependent on the time of day and type of land use: whether agricultural areas, protected areas or wildlife management areas, trophy hunting blocks, and multi-use zones (e.g. game management areas). Overall, all of the elephants had smaller annual home ranges (~450-1,750 km²) than seen in other studies within southern Africa, and there was a difference in seasonal movements, between individuals. Additionally, contrary to previously published studies, the elephants made larger diurnal movements than nocturnal movements. Movements were significantly different between different land-use areas, suggesting that elephants could be developing different strategies to move through differing levels of human disturbance.

It is vital for any wildlife management plan that the spatial movements of key conservation species are thoroughly understood, in order to formulate informed management decisions and create an integrated landuse management plan that enables both development and elephant coexistence.

Additional Keywords: Conservation, human-dominated landscapes, land-use, spatial behaviour.

Résumé

Nous avons une compréhension limitée des effets qu'une population humaine croissante et un développement urbain et agricole ont sur les mouvements d'éléphants au Botswana. Les mouvements des éléphants sont complexes car ils sont influencés par un large éventail de variables spécifiques à leur emplacement. Cette étude-ci visait à étudier comment les éléphants se déplacent à travers différents paysages dominés par l'homme dans le district de Chobe, au Botswana. Les déplacements de quatre éléphants femelles du district de Chobe ont été étudiés sur une période de 13 mois, en utilisant des colliers GPS pour les suivre. Les domaines vitaux annuels des éléphants ont été calculés en utilisant à la fois les méthodes du polygone convexe minimum (MCP) à 100 % et du noyau fixe (FK) à 95 %. De plus, des modèles d'équation d'estimation généraux ont été utilisés pour étudier quels facteurs ont influencé les déplacements des éléphants, à la fois horaires et quotidiens. Nous avons constaté que le comportement de déplacement des éléphants dépendait de l'heure dans la journée et du type d'utilisation des terres, y compris les zones agricoles, les zones protégées ou les Zones de gestion du gibier). Dans l'ensemble, tous les éléphants avaient des domaines vitaux annuels plus réduits (~ 450–1,750 km2) que ceux observés dans d'autres études en Afrique australe, et il y avait une différence dans les mouvements saisonniers entre les individus. De plus, contrairement aux études publiées précédemment, les éléphants effectuaient des mouvements diurnes plus importants que des mouvements nocturnes. Les déplacements étaient significativement différents entre les différentes zones d'utilisation des terres, ce qui suggère que les éléphants pourraient développer différentes stratégies pour se déplacer à travers différents niveaux de perturbation humaine.

Il est essentiel pour tout plan de gestion de la faune que les mouvements spatiaux des espèces clés de conservation soient parfaitement compris, afin de formuler des décisions de gestion éclairées et de créer un plan de gestion intégrée de l'utilisation des terres qui permet à la fois le développement et la coexistence des éléphants.

Mots clés: Conservation, paysages dominés par l'homme, utilisation des terres, comportement spatial.

Introduction

Within the last 50 years, areas of conservation value have tended to overlap with areas of expanding human population (Carter et al. 2012), placing humans and wildlife in direct competition with one another. Growing human population and increasing development have resulted in fragmentation of the natural habitat, impacting ecosystems and wildlife populations. This can trigger a range of negative ecological consequences for wildlife including displaced movement behaviour, increased stress levels, reduction of reproduction rates and in the worst case scenario, local extinction (Blake et al. 2008), particularly where large mammals are concerned (Tucker et al. 2018).

The size of the area within which an animal moves correlates positively with its body size: larger animals use more space (Tucker et al. 2014). Consequently, large ranges many outside protected wildlife areas (PAs) facilitate survival for large wild mammals (Tucker et al. 2014), especially when there is high temporal variability in food resources (Gadde, 2005; van Aarde et al. 2006; Boettiger et al. 2011). However, recent advances in animal global positioning systems (GPS) and the creation of improved software have allowed us to further question the concept that individual wild animals restrict their movements to finite areas (Powell and Mitchell 2012). The locomotion strategy, foraging dimensions, trophic guild, and prey size make up 80% of the variation in home range size for vertebrate species (Tamburello et al. 2015). Elephant-movement behaviour is influenced by environmental factors such as water and foraging availability (Boettiger et al. 2011), and rainfall patterns (Thouless 1996). Additionally, elephants are increasingly affected by humans and their development into previous wilderness areas (Blake et al. 2008).

In order to create and implement effective landuse and wildlife management plans for an area, we need to increase our understanding of how rising human disturbance, different human activities and development can influence elephant movement behaviour (Graham et al. 2009; Roever et al. 2013; Adams et al. 2017a; Tucker et al. 2018). Gaynor et al. (2018) investigated the effect that human settlement and roads are having on the daily activities of elephants moving to and from Mozambique Gorongosa National Park (NP), a study focusing on a small population of elephants living within an area heavily populated by humans. Elephants restricted their activity to the night when moving through areas of high human disturbance remaining in PAs during daytime hours. Similarly Buchholtz et al. (2021) found elephants visiting water points located close to higher human development accessed them at night. Both of these studies clearly show that elephant movements were directly impacted by human presence (Gaynor et al. 2018; Buchholtz et al. 2021). Additionally, another study by Blake et al. (2008) found that the movements of elephants were impacted by the construction of roads that acted as a barrier to elephants (Blake et al. 2008). Each of these studies showed that elephants avoid human development by altering their temporal movement patterns. However, we still have limited knowledge of how elephants in a stable unfenced population with an expanding range (Chase et al. 2019) use space and resources in areas with different levels of human disturbance.

addition In to temporally adjusting movements avoid different human to disturbance, wildlife can also change their pace (Tucker et al. 2018). Results from previous studies (Douglas-Hamilton et al. 2005; Blake et al. 2008; Graham et al. 2009) indicate that elephants exhibit a risk-avoidance behaviour while passing through community areas, by speeding up their movements to limit time spent in those areas. Therefore, it would be expected that there is reduced elephant competition for desirable resources (water, vegetation) found in human-dominated landscapes versus PAs and less dominated human areas. It is proposed that where competition for resources is high, some members of large elephant groups will enter human-dominated areas due to the need for resources overriding a preference to avoid the risk posed by humans.

Botswana has the largest elephant population in Africa with approximately 130,000 individuals (Chase et al. 2019), together with one of the lowest human populations of all African countries (~2.3 million) and it is considered an upper middleincome nation (World Bank Database 2019). The economy is largely reliant on diamonds, and in the 1960s, the government shifted from an agricultural based economy to mining (Malema 2012; Worldbank 2019). However, tourism is the second largest contributor to the economy which will only increase with importance as diamonds are predicted to be exhausted in the next 20-30 years (Malema 2012; Worldbank 2019). Given that Botswana is home to approximately onethird of the continent's population of elephants, it holds global conservation significance and tourism value, but unsurprisingly faces increasing challenges in managing and maintaining such a population in a growing human population (Chase et al. 2019). Many of the rural households living within the elephant range are also some of the poorest and are heavily reliant on the Botswana Government poverty alleviation programmes that aim to assist elderly and vulnerable farming households with "Ipelegeng" a drought relief food aid and labour based public works (Gupta 2013), rather than the tourism sector. There are many complex issues at play, the main one largely being the lack of connection of between those working in the tourism industry and the elephant and wildlife population (Adams et al. 2017b). Apprehension exists over the reported increases in human elephant conflict (HEC) over space and resources in the area (Adams et al. 2017b), especially where the elephant homerange overlaps hugely with the increasing human habitation (Adams et al. 2017a). Mitigating the impact of anthropogenic change on species and the conservation of those species is debatably the biggest conservation dilemma (Tulloch et al. 2018).

By deploying GPS collars, we followed the movements of four individual elephants from different family units through different human landscape land-uses in the Chobe District of Botswana. We hypothesized that the behaviour of elephants occupying areas of different human land-uses would differ according to different human activities within those areas. It was predicted that elephants would speed up their movements when passing through human-occupied areas to access required resources, in an effort to avoid humans. This study aimed to determine how female elephant movement behaviour differed between land uses. This study examined the hourly and daily movement patterns and home ranges of different elephants in PAs (national parks, forest reserves, and tourist and wildlife management areas), mixed-use areas (agricultural, trophy hunting wildlife management areas, and undesignated areas), and community areas (human settlements), within the Chobe District of Botswana.

Materials and methods

Study area

The study area is located in the north-east corner of Botswana, in the Chobe District (Fig. 1). The area is made up of Chobe National Park (10,740 km²), community settlements, six different forestry reserves, and both trophy hunting and safari/photographic wildlife management areas (WMAs). There are approximately 32,000 elephants in Chobe District, with an estimated 17,000 of them in Chobe National Park (Chase et al. 2019). Chobe District is an unfenced area, where wildlife can move freely throughout the different land designations. The elephants in the Chobe District can and do move east into Zimbabwe and north into Namibia.

For the purpose of this study, conducted over 13 consecutive months in both wet and dry seasons, the seasons in northern Botswana are as follows: the cold dry season (May-July), hot dry season (August-October), wet season (November-March), and post-wet season (April) (Adams et al. 2017a).

The two largest human settlements within this region are the Chobe Enclave and the townships of Kasane and Kazungula, with a combined population of approximately 13,000 people (Census office 2014). Both locations are surrounded by PAs and are adjacent to the Kwando-Linyanti and Chobe Rivers (Fig. 1). Both the Enclave and the Kasane/Kazungula areas contain designated and undesignated wildlife corridors of varying sizes that elephants and other animals use to travel from the NPs and forestry reserves through to the riverfront for water and browsing (Adams et al. 2017a). The Chobe Enclave is a seasonal floodplain dominated by small-scale farming (mixed livestock and crops), with subsistence cultivation undertaken in the wet season, followed by harvest in the post-wet season (Jackson et al. 2008; Adams et al. 2017a). The area is made up of five lowdensity villages located next to the floodplain. Given the level of cultivation, close proximity to the floodplain, and its location alongside "PAs", the Enclave is an area of high HEC. Livestock are also prioritized in the area with a series of cattle posts located throughout the Enclave. It is also a trophy hunting concession where

quota-based hunting occurs between April-October. Comparatively, the two towns Kasane and Kazungula (K/K) are the largest urban centres of the Chobe District, located just 2.5 km apart (Adams et al. 2017a). The human population in the Chobe District has increased by 27.9% during 2001-2011, and is set to continue increasing (Census 2014) due to a variety of factors, tourism, large civil service (Kazungula Bridge and border crossing is at the quadripoint of four countries: Botswana/Namibia/Zambia and Zimbabwe), and access to water resources. The urban centre is made up of residential housing, commercial and industrial businesses and government offices. K/K have only two horticulture farms. The towns are the base for the tourism industry in north-eastern Botswana (Adams et al. 2017a), and also have a number of lodges, hotels and guest houses located throughout both towns.

GPS / Satellite collars

Four elephants (Table 1) were fitted with GPS collars manufactured by African Wildlife Tracking (South Africa): one in the K/K side of the north-east corner of Botswana (CH 67) and three in the central and western side of the Chobe riverfront/Enclave (CH 62, 65, 69) (Enclave elephants). Data were collected from 1 October 2012 to 30 October 2013. Hourly location data were collected and collated into diurnal (06:00-18:00) and nocturnal (18:00-06:00) periods. The collaring was opportunistic, based on which individuals were in or near target areas at that time, however the objective was to collar females in family units, representing movements in different types of human-uses in the Chobe District. Individual elephants were selected based on either proximity to humans or their tendency to be sighted in human-dominated areas. All of the collared elephants were mature adult females, that were a part of family units (Table 1). All of the selected females had the potential to move into each of the defined land use designations.

Land use designation

We divided the study area into different categories based on land use designations made by the GPS programme "Tracks for Africa" (T4A, version 14.0):

1. Protected areas represent national parks, forest reserves and wildlife viewing management areas where humans are present, but to a very

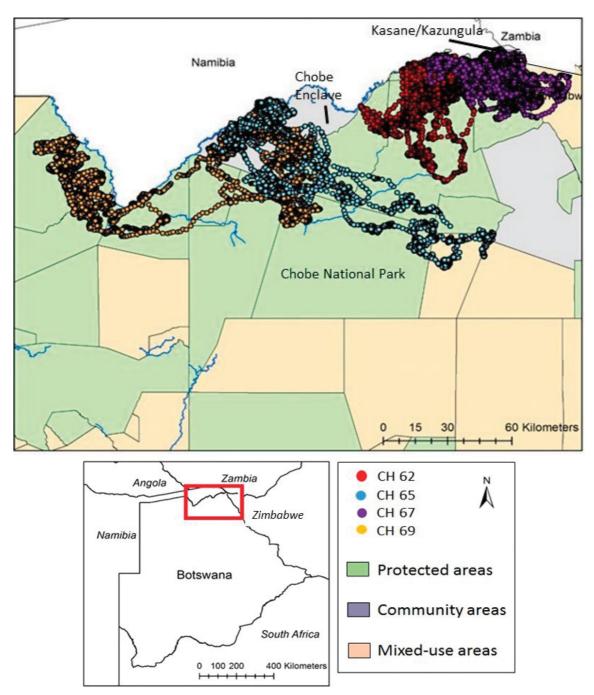


Figure 1. The study area within Botswana is outlined by the red rectangle. The magnified map displays relevant locations such as Chobe Enclave and Chobe National Park with the four individual GPS collared elephants' movements throughout each of the three different land use classification including protected, mixed-use and community.

limited extent and in a geographically and temporally constrained manner based on national legislation, e.g. tourists on game drives.

- 2. Mixed-use areas represent agricultural land, recreational human areas, trophy hunting wildlife management areas and unallocated land, which is land that has not been assigned a land use.
- 3. Community areas are where villages and towns (and any form of human settlements in close proximity to one another) are the dominant land use.

Home range and movement estimation

Home range size was calculated using both 100% minimum convex polygon (MCP) and 95 % fixed kernel (FK) methods (Seamen and Powell 1996) using 95% Gaussian kernel home ranges fitted in the R package 'LSCV' least-squares cross validation and in the R package 'adehabitatHR'. Both methods were chosen because MCP results are comparable with other elephant home-range studies within southern Africa (Jackson and Erasmus 2005; Chase 2007; Chase 2009; Roever et al. 2013). Home range was estimated using all data points rather than randomly selected daily points. To investigate whether movement rate and distance varied in relation to land designation, we calculated movement rate and distance in the R package 'adehabtitatHR'. Movement distance is represented between consecutive data points as a straight-line distance; providing the minimum distance that the collared elephants would have traversed during the time interval lapse between the reporting of consecutive data points. Speed of elephant movement was calculated as the distance between consecutive locations divided by time (km h⁻¹) (Graham et al. 2009).

Overall percentage occupancy was calculated on a daily basis by mapping the collared individual elephants' movements in the different land uses and calculating on a daily basis (24– hour) the time spent in each designated area (Table 1). The collared elephants would often move between different land uses through the course of one day, so a combined category was made for those movements, e.g. PAs/community areas.

Statistical analysis

The movement data was analysed using a Generalised Estimating Equation (GEE). GEE Models are used to analyse correlated data with continuous outcomes (Zeger et al. 1988). A GEE was used to investigate which factors influenced the elephants hourly and daily distance moved in metres. The hourly GEE model tested hourly distance moved for each elephant (metres) as a function of location (Kasane/Kazumgula or Enclave), season and time of day (diurnal or nocturnal) and daily GEE model tested daily distance moved for each elephants (metres) was tested as a function of location, season and land use designation using R statistical software and the package 'geepack' (R Studio version http://www.rstudio.com). Residuals 3.0.2, were plotted to test for autocorrelation in the dataset, as it is common for time series data. In order to minimize the impact of temporal autocorrelation in the dataset' a correlation structure 'CorAr1'was incorporated in the GEE, whereby the individual elephant was the ID variable, which defines the groups within which the data are correlated (Zuur et al. 2009). The response (hourly/daily-metres movement) variable was logtransformed to achieve a Gaussian distribution, with a log link function (Zeger et al. 1988).

Results

Annual home ranges

Using the 95% kernel and MCP method to represent an individual's movement range (Leggett 2009), the annual home ranges recorded are shown in Table 1, and schematically in Figure 1, ranging from 450km² for CH 67 to 1,764km² for CH 69.

The K/K female (CH 67) was the only elephant that moved into Zimbabwe for a portion of each season, making movements east to west, adjacent to the Chobe/Zambezi River. She moved into and around the towns in the area, then moved back into the forestry reserve and National Park. The K/K female's widestranging movements were into a hunting concession in Zimbabwe that runs alongside the Botswanan border. CH 67 spent a greater percentage of time (~50%) in PAs (Chobe National Park, contiguous forestry reserves) (Table 1) compared to that of the Enclave elephants with their larger home ranges (Table 1), south into the Chobe National Park. In comparison, the Enclave elephants that made wide movements remained in Botswana throughout the 13 months of KK

CH 67

Linyanti River

Kasane, Chobe

District

25 +

5

7,586

spent in land use designated areas for 15 months of the study											
	Location of collaring	Age (approx.)	Family unit (approx.)	Tracking time (h)	use	protected	Time in community %	*	Time in mixed- use and community %	Total home range (km ²) MCP 100%	Total home range (km ²) (95% kernel)
Enclave CH 62	Chobe, National Park	30+	5	8,834	0	97.23	0	2.77	0	2268.9	925.6
CH 65	Enclave, Chobe District	30+	A part of a clan 200+	7,261	4.22	3.92	58.43	33.43	0	4396.1	1453.2
CH 69	Kwando, Linvonti River	30+	12	8,799	0	5.63	31.97	62.40	0	6339.0	1764.5

Table 1. The identity, age, location of collaring, tracking time, home range and proportion of elephants' overall daily time spent in land use designated areas for 13 months of the study

Table 2. The coefficients of the GEE model of the variables that impact elephant hourly movements, with estimate, \pm SE, Wald statistic and probability value. Significance level is <0.05

18.73

0.79

62.27

0.72

1443.2

17.41

Coefficients	Estimate ± SE	Wald	P-value
(Intercept)	5.83±0.02	4391.02	< 0.05
Kasane/Kazungula	-0.23±0.06	15.38	< 0.05
Time of day	-0.35±0.08	18.52	< 0.05
Hot dry	-0.15±0.09	3.07	0.08
Post wet	$0.08{\pm}0.06$	1.54	0.21
Wet	0.10±0.07	1.82	0.18

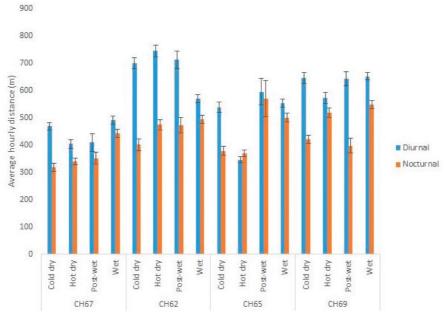


Figure 2. The mean and standard error distance of the seasonal hourly diurnal and nocturnal movements of the four GPS-collared elephants in both the Enclave and Kasane/Kazungula.

453.0

Coefficients	Estimate ± SE	Wald	P-value
(Intercept)	9.4-±0.07	16099.79	< 0.05
Kasane/Kazungula	-0.36±0.04	96.97	< 0.05
Hot dry	-0.13±0.09	1.92	0.17
Post-wet	-0.01±0,11	0.01	0.94
Wet	-0.03 ± 0.08	0.12	0.73
Protected	-0.07 ± 0.06	1.25	0.26
Protected areas / Community areas	-0.04 ± 0.08	0.34	0.56
Mixed-use	$0.04{\pm}0.08$	0.26	0.64
Mixed-use / Community areas	-0.16±0.08	3.50	0.06
Mixed-use / Protected areas	-0.29±0.10	7.60	0.01

Table 3. The coefficients of the GEE model of the variables that impact elephants' daily movements, with estimate, \pm SE, Wald statistic and probability value. Significance level is p<0.05

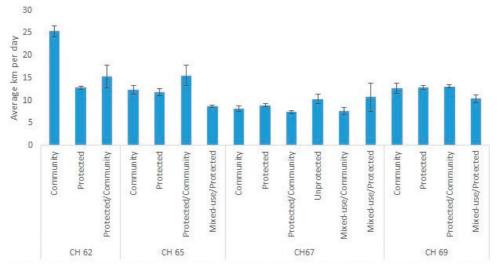


Figure 3. The average daily distance (SE±) in each land zone per area, for the four collared elephants.

the study period. The Enclave elephants spent the greatest proportion of their time moving between the community areas and PAs. CH 69 and CH 65 spent a large percentage (>30%, Table 1) of their time in the Enclave community area, more so than CH 62 who spent a greater proportion of time in PAs.

Elephants' hourly and daily movements

Location and time of day each contributed to the hourly movement of the elephants (Table 2). The average hourly diurnal and nocturnal movements of the three Enclave elephants were significantly larger than those of CH 67 (Table 2).

In all seasons except hot and dry, the diurnal hourly movements were greater than the nocturnal hourly movements for all four of the collared elephants (Fig. 2). Overall, the hourly diurnal movements of the elephants were significantly greater than their nocturnal movements (Fig. 2). This was consistent across all seasons, except for CH 65 during the hot dry season (Fig. 2).

Overall, the K/K elephants made smaller daily movements than those of the Enclave elephants (Table 3, Fig. 3). All elephants moved differently in each of the different land zones (Fig. 3). Specifically, the daily distance that the elephants moved in mixed-use zones was significantly different from when in the PAs (Table 3). All of the elephants' (except CH 62) smallest daily movements were in mixeduse/communal land zones (Fig. 3). The Enclave elephants moved greater distances and at a faster rate through community areas (0.96–1.24 km/hr) than CH 67 (0.55km/hr).

There appeared to be no apparent seasonal pattern to when elephants moved through the community areas. CH 67 occupied the towns at different times of year, primarily during the wet season and post-wet season. The Enclave elephants entered the community areas at varying times of the year from one another. CH 62 came to community areas only in October and November (the end of the hot dry season and the beginning of the wet season); CH 69 during December, February (both months in the wet season) and June (the cold/dry season); and CH 65 between December and February (wet season), returning in May (cold/dry season) and remaining until October (the end of the hot/dry season). CH 65 spent the longest period in community areas of all the collared elephants.

Discussion

Understanding how elephants move through different human land uses, whether protected or unprotected areas, provides critical information to improve wildlife management plans to facilitate coexistence. In the Chobe District, elephants in the wet and post-wet season are found throughout the District, far from the permanent water sources such as the Chobe River, water is widely available as the natural pans are full. As is expected, as those water sources dry up the elephants move closer to the Chobe River and the series of artificial waterholes found throughout the District (Chase et al. 2019), that shared reliance of water for both humans and elephants is where a great deal of conflict exists. We aimed to determine how elephants move through different land use designations in the Chobe District an open system throughout each season. We found that the four collared elephants made larger diurnal hourly movements than nocturnal movements, overall we found that their movements were impacted by the time of day and

the land use that they were moving through.

The home ranges of the Enclave elephants are consistent with previous studies where elephants avoided human-dominated areas (Osborn 2003; Douglas-Hamilton et al. 2005; Graham et al. 2009; Roever et al. 2013). The K/K elephant CH 67, by contrast, slowed down her movements and spent extended periods in community areas.

The annual home ranges of elephants collared for this study were smaller when compared to those calculated in other studies of elephant home ranges in Botswana. For example, Verlinden and Gavor (1998): 447-3,309 km², Jackson and Erasmus (2005): 2,500-3,019 km², Chase (2007): 910-24,828 km², and Buchholtz et al. (2019): 1,220–3,446 km². This study's smaller home ranges could be a result of the abundant quality resources available to elephants in this area of the Chobe District as elephants' movements are largely based on resource availability and quality (van Aarde et al. 2006; Boettiger et al. 2011). This could be plausible given that 70% of the District is designated NP and forest reserve (Chase 2007): consequently elephants do not often have to move out of the area to access the required resources.

The largest hourly movements recorded in this study were during diurnal hours, rather than nocturnal hours, in contrast to previous literature (Douglas-Hamilton et al. 2005; Leggett 2009; Loarie et al. 2009). We do not know the reason for this observed difference however it could be linked to the size of the Botswana elephant population. The size of the elephant population creates higher resource competition closer to water sources among the elephants as the vegetation there is the most heavily browsed due to its proximity to permanent water (Ben-Shahar 1996). As the season becomes drier, elephants must travel greater distances to and from water points to find enough graze or browse to survive (Loarie et al. 2009; Buchholtz et al. 2019). Also, they feel less threatened than in Kenya where they move fast at night in dangerous areas (Douglas-Hamilton et al. 2005).

Overall, the largest proportion of time that the collared elephants spent anywhere during the study was in PAs. The least amount of time was spent in mixed-use areas. This is consistent with a study conducted in Samburu, Kenya that showed dominant family units disproportionally preferred habitats that limited their time in unprotected areas (Wittermyer et al. 2007). This result is also similar to other elephant movement studies and is unsurprising as one would

predict elephants to spend more time in PAs than in or near human settlements due to the HEC risks and the stress experienced when near those settlements (Douglas-Hamilton et al. 2005; Wittermyer et al. 2007; Blake et al. 2008; Graham et al. 2009).

Additional risks include poaching for ivory, which has been shown to be increasing on the scale of hundreds of elephants per year (across Africa) and has also been occurring throughout northern Botswana (Schlossberg et al. 2019), as well as the re-introduction of trophy hunting. Both human activities are highly risky and stressful to elephants and will impact where and when elephants move through different land uses in the areas. The Enclave elephants made larger, faster movements through mixed-use and community areas. This movement from the Chobe National Park down to the river in the Enclave is similar to the "streaking" behaviour published by Jachowski et al. (2013). According to Jachowski et al.'s study, elephants that are stressed will increase their speed through corridors by "streaking" in order to reduce their time near the mixed-use areas while heading toward core protected areas. Streaking is in reference to elephants' increasing their movement speed through an area that they associate with risk (Jachowski et al. 2013). The K/K elephants did the opposite and made smaller, slower movements in the mixed-use and community areas. This could reflect the difference in land use between the K/K urban environment. more high density tourism-based development compared to the Enclave area which is comprised of small-scale agriculture.

The types of human activities in the area, for example rural villages predominately made up of dryland agricultural fields compared with the urban townships might foster differences in community tolerance to elephants. Gupta's (2013) study revealed the frustration Chobe Enclave farmers suffer from, vis à vis high rates of HEC compared to the rest of the District (Gupta 2013; Chase et al. 2019). Hence the increased speeds used by the Enclave elephants when in the community areas could be a result of more risk factors and persecution because of the farming in the areas compared to the K/K herd. For the residents of K/K, income is more focused on tourism employment than on crop and livestock production, and livelihoods are not as threatened by the presence of elephants. There is a perception that the financial benefit to the Enclave community from the local elephant population is very low, as the presence of elephants frequently threatens the locals' livelihoods through crop raiding (Gupta 2013).

This preliminary study highlights the importance of understanding the anthropogenic factors that potentially impact the movements of elephants through different human land uses. This data can assist in implementing informed management strategies that focus specifically on the integrated land-use management planning approach to mitigate humanelephant interaction (Adams et al. 2017a). The aim of the landscape management approach is to make holistic management decisions that take into consideration how different land uses impact the wildlife living in and moving through an area to mitigate that impact. In particular, the location of wildlife corridors and pathways is key as maintaining pachyderm access can serve as a mitigation in reducing HEC (Douglas-Hamilton et al. 2005; Graham et al. 2009; Adams et al. 2017a). Mitigation and conflict resolution success is highly dependent on a clear understanding of the drivers and temporal patterns of the conflict itself. Future studies could aim to measure and understand the different anthropogenic factors, specifically the socio-economic factors that are driving the movement behaviours of elephants and potentially the risk avoidance strategies (Jachowski et al. 2013; Gaynor et al. 2018). In addition, it would be useful to incorporate a larger sample size with representatives from both sexes, in order to determine if there is a difference in movements between the females/family herds and bulls. By measuring the anthropogenic factors and increasing the sample size, more resounding conclusions can be made, representing the population as a whole.

Elephant movements are complex because they are influenced by a wide range of variables, which are location specific. The hourly and daily movements of the four elephants we collared in the Chobe District were dependent on time of day, and the different landuse zones they passed through. Home ranges of these elephants were at the lower end of the recorded range compared with elephants who were tracked as part of other studies in Botswana, and interestingly, each individual in our study moved differently according to season. This study was the first focused investigation of how elephants move through the different designated land uses in the Chobe District, one of the largest conflict hotspots in southern Africa (Gupta 2013), in addition to being one of the most significant conservation areas for megafauna left in Africa as it is one of the last interconnected transboundary elephant populations on the continent (Schlossberg et al. 2019).

Despite this being a preliminary study, the results suggest that elephants can adjust their movement behaviour based on different types of human activity in an open unfenced ecosystem. This is important as it shows that elephants are adapting to different human activities occurring in different human land uses, in an open and unfenced system. It is vital for any wildlife management plan that the movement of key species is thoroughly understood, in order to formulate informed boundaries and understand the impact of different human development. Furthermore, we recommend an integrated landscape planning approach in any future management plan, which accommodates both people's needs and those of elephant and other wildlife. With tourism making up 12% of Botswana's GDP, and Botswana being the last stronghold of a significant number of elephants, a better balance between livelihoods and elephants' free movement needs to be determined.

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References

Adams TSF, Chase MJ, Rogers T, Leggett KEA. 2017a. Taking the elephant out of the room and into the corridor: can urban corridors work? *Oryx* 51 (2): 347–353, doi:10.1017/S0030605315001246.

Adams TSF, Chase MJ, Attard A, Leggett KEA. 2017b. A preliminary study of stakeholders' opinions and perceptions of elephants and elephant management in Botswana. *Pachyderm* 58: 67–76.

Ben-Shahar, R. 1996. Do elephants over-utilise mopane woodlands in northern Botswana? *Journal of Tropical Ecology* 12: 505–515.

Blake S, Deem SL, Strindberg S, Maisels F, Momont L, Inogwabini-Bila I, Douglas-Hamilton I, Karesh WB, Kock MD. 2008. Roadless Wilderness area determines forest elephant movements in the Congo. *PloS ONE* 3 (10) e3546.

Boettiger AN, Wittemyer G, Starfield R, Vollrath F, Douglas-Hamilton I, Getz WM. 2011. Intefering ecological behavioural drivers of African elephant movement using a linear filtering approach. *Ecology* 92 (8): 1648–1657.

Buchholtz E, Fitzgerald L, Songhurst A, McCulloch G, Stronza A. 2019. Overlapping landscape utilization by elephants and people in the Western Okavango Panhandle: implications for conflict and conservation. *Landscape Ecology* (34): 1411–1423.

Buchholtz EK, Spragg S, Songhurst A, Stronza A, McCulloch G, Fitzgerald LA. 2021. Anthropogenic impact on wildlife resources use: Spatial and temporal shifts in elephants' access to water. *African Journal of Ecology* (00): 1–10.

Carter NH, Shrestha BK, Karki JB, Pradhan NMB, Liu J. 2012. Coexistence between wildlife and humans at fine spatial scales. *PNAS* 109: 15360–15365.

Census Office. 2014. 2011 Population and Housing Census Preliminary Results Brief, Gaborone: Central Statistics Office. <u>https://www.statsbots.org.bw/sites/</u> <u>default/files/publications/Chobe%20District.pdf</u>. [Accessed 9 October 2020].

Chase M. 2007. Home ranges, transboundary

movements and harvest of elephants in northern Botswana and factors affecting elephant distributions and abundance in the lower Kwando River basin. PhD, Amherst: University of Massachusetts [Accessed 6 July 2017].

Chase M, Schlossberg S, Sutcliffe R, Seonyatseng E. 2019. Dry season aerial survey of elephants and wildlife in northern Botswana: July–October 2018. Elephants Without Borders and Department of Wildlife and National Parks of Botswana, Kasane, Botswana. <u>www.</u> <u>elephantswithoutborders.org</u>. [Accessed 21 January 2020].

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

Gaynor KM, Branco PS, Long RA, Gonçalves DD, Granli PK, Poole JH. 2018. Effects of human settlement and roads on diel activity patterns of elephants (*Loxodonta africana*). *African Journal of Ecology* 56: 872–881.

Graham MD, Douglas-Hamilton I, Adams WM, Lee PC. 2009. The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation* 12: 445–455.

Gupta CA. 2013. Elephant, safety nets and agrarian culture: understanding human-wildlife conflict and rural livelihood around Chobe National Park, Botswana. *Journal of Political Ecology* 20: 238–254.

Jachowski DS, Slotow R, Millspaugh JJ. 2013. Corridor use and streaking behaviour by African elephant in relation to physiological state. *Biological Conservation* 167: 276–282.

Jackson TP, Erasmus DG. 2005. Assessment of seasonal home-range use by elephants across southern Africa's seven elephant clusters. Report: Conservation Ecology Research Unit, University of Pretoria.

Jackson TP, Mosojane S, Ferreira SM, Van Aarde RJ. 2008. Solutions for elephant *Loxondonta africana* crop raiding in northern Botswana: moving away from symptomatic approaches. *Oryx* 4: 83–91.

Leggett K. 2009. Daily and hourly movement of male desert-dwelling elephants. *African Journal of Ecology* 48: 197–205.

Loarie SR, Van Aarde RJ, Pimm SJ. 2009. Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation* 142: 3086–3098.

Malema BW. 2012. Botswana's formal economic structure as a possible source of poverty: Are there any policies out of this economic impasse? *PULA: Botswana Journal of African Studies*, 26 (1): 51–69.

Osborn FV. 2003. Seasonal influence of rainfall and crops and home-range expansion by bull elephants. *Pachyderm* 35: 53–59.

Powell RA, Mitchell MS. 2012. What is a home range? *Journal of Mammalogy* 93 (4): 948–958.

Roever CL, Van Aarde RJ, Chase MJ. 2013. Incorporating mortality into habitat selection to identify secure and risky habitats for savannah elephants. *Biological Conservation* 164: 98–106.

Scholssberg S, Chase MJ, Sutcliffe R. 2019. Evidence of growing elephant poaching problem in Botswana. *Current Biology* 23: 2222–2228.

Seaman DE, Powell RA. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77: 2075–2085.

Sitati NW, Walpole MJ, Smith RJ, Leader-Williams, N. 2003. Predicting spatial aspects of human-elephant conflict. *Journal of Applied Ecology* 40: 667–677.

Thouless C. 1996. Home ranges and social organization of female elephants in northern Kenya. *African Journal of Ecology* 33: 284–297.

Tucker MA, Ord TJ, Rogers TL. 2014. Evolutionary predictors of mammalian home range size: body mass, diet and the environment. *Global Ecology of Biogeography* 23: 1105–1114. doi: 10.1111/geb.12194.

Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, Ali AH, Allen AM, Attias N, Avgar T, Bartlam-Brooks H, Bayarbaatar B, Belant JL, Bertassoni A, Beyer D, Bidner L, Van Beest FM, Blake S, Blaum N, Bracis C, Brown D, De Bruyn PJN, Cagnacci F, Calabrese JM, Camilo-Alves C, Chamaillé-Jammes S, Chiaradia A, Davidson SC, Dennis T, Destefano S, Diefenbach D, Douglas-Hamilton I, Fennessy J, Fichtel C, Fiedle, W, Fischer C, Fischhoff I, Fleming CH, Ford AT, Fritz SA, Gehr B, Goheen JR, Gurarie E, Hebblewhite M, Heurich M, Hewison AJM, Hof C, Hurme E, Isbell A, Janssen R, Jeltsch F, Kaczensky P, Kane A, Kappeler PM, Kauffman M, Kays R, Kimuyu D, Koch F, Kranstauber B, Lapoint S, Leimgruber P, Linnell JDC, López-López P, Markham AC, Mattisson J, Medici EP, Mellone U, Merrill E, De Miranda Mourão G, Morato RG, Morellet N, Morrison TA, Díaz-Muñoz

SL, Mysterud A, Nandintsetseg D, Nathan R, Niamir A, Odden J, O'hara RB, Oliveira-Santos LGR, Olson KA, Patterson BD, Cunha De Paula R, Pedrotti L, Reineking B, Rimmler M, Rogers TL, Rolandsen CM, Rosenberry CS, Rubenstein DI, Safi K, Saïd S, Sapir N, Sawyer H, Schmidt NM, Selva N, Sergiel A, Shiilegdamba E, Silva JP, Singh N, Solberg EJ, Spiegel O, Strand O, Sundaresan S, Ullmann W, Voigt U, Wall J, Wattles D, Wikelski, M, Wilmers CC, Wilson JW, Wittemyer G, Zięba F, Zwijacz-Kozica T, Mueller T. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* 359 (6374): 466–469.

Tulloch AIT, Chades I, Lindenmayer DB. (2018). Species co-occurrence analysis predicts management outcomes for multiple threats. *Nature Ecology & Evolution* 2 (3): 465–474.

Verlinden A, Gavor IKN. 1998. Satellite tracking of elephants in northern Botswana.

African Journal of Ecology 36: 105–116.

Wittemyer G, Getz WM, Vollrath F, Douglas-Hamilton I. 2007. Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behaviour. *Behavioural Ecology Sociobiology* 61: 1919–1931.

Wittemyer G, Polansky L, Douglas-Hamilton I, Getz WM. 2008. Disentangling the effects of forage, social rank and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. *PNAS* 105: 19108–19113.

World Bank. 2019. <u>https://data.worldbank.org/</u> <u>country/botswana</u>. [Accessed 23 July 2021].

Zeger SL, Liang KY, Albert PS. 1988. Models for Longitudinal Data: A Generalised Estimating Equation Approach. *Biometrics* 44 (4): 1049–1060.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in Ecology with R. New York, NY, Springer publishing. ISBN 978-0-387-87458-6.