Landscape Ecol (2019) 34:1411–1423
https://doi.org/10.1007/s10980-019-00856-1

RESEARCH ARTICLE

Overlapping landscape utilization by elephants and people in the Western Okavango Panhandle: implications for conflict and conservation

Erin Buchholtz · Lee Fitzgerald · Anna Songhurst · Graham McCulloch · Amanda Stronza

Received: 9 January 2019 / Accepted: 10 June 2019 / Published online: 18 June 2019

Abstract

Context Many wildlife populations exist outside of protected areas, and it is necessary to understand how these animals use a landscape mosaic that includes humans. Patterns of landscape use in space and time can help inform strategies to mitigate negative interactions between people and wildlife.

Objectives We aimed to estimate the landscape utilization of elephants where they ranged through a mosaic of human-modified land-use and undisturbed habitat to better understand spatial implications for human-wildlife interactions.

Methods We studied locations and utilization distributions of ten bull elephants in the Western Okavango Panhandle region of Botswana. We calculated utilization distributions, patterns of landscape use, and daily movement relative to permanent water and human land-use.

Results The annual distributions of the monitored elephants ranged from 1220 to 3446 km^2 and showed seasonal variation, with wet season distributions being significantly larger than dry season distributions. On average 49.4% of elephants' core distributions in the dry season and 12.3% in the wet season fell within 5 km of human land-use. Elephants ranged increasingly farther from permanent water sources as the wet season progressed, while in the same time frame elephants moved closer on average to human land-use. Elephants were more likely to be near human land-use during the night than they were during the day. Diel patterns of elephant proximity to human land-use did not match patterns of proximity to water.

Conclusions Conservation and management efforts must consider the diel and seasonal patterns of elephant movement in order to fully address the issue of human-elephant interactions.

Keywords Human-elephant conflict · Human-wildlife interactions · Adaptive local convex hull · LoCoH · African elephant · Botswana · Utilization distribution · Land-use

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E. Buchholtz (✉) · L. Fitzgerald · A. Stronza
Texas A&M University, 534 John Kimbrough Blvd,
College Station, TX 77843, USA
e-mail: ebuchholtz@tamu.edu

L. Fitzgerald
e-mail: lfitzgerald@tamu.edu

A. Stronza
e-mail: astronza@tamu.edu

E. Buchholtz · A. Songhurst · G. McCulloch · A. Stronza
The Ecoexist Project, Maun, Botswana
e-mail: anna.songhurst@hotmail.com

G. McCulloch
e-mail: gpmcculloch1@gmail.com

A. Songhurst · G. McCulloch
University of Oxford, Oxford, UK

Introduction

Populations of wide-ranging species often extend beyond the borders of protected areas and into the landscape mosaic of natural and human-modified land uses. Many animal movement patterns are undoubtedly influenced by human development and activity, as well as by distribution of critical resources such as water (de Beer and van Aarde 2008; Harris et al. 2008). Animal movements in the landscape may also impact people. This is particularly true for species associated with negative interactions or human-wildlife conflict. When negative interactions occur, such as livestock predation, agricultural crop raiding or property damage, human-wildlife conflict becomes a considerable issue. These interactions may be exacerbated due to proximity of people and wildlife to each other caused by overlapping use of the landscape and its resources.

African elephants (*Loxodonta africana*) are an ideal study species for investigating the extent to which animals and people must share the landscape. Elephants move over large areas of land, and often utilize human-modified landscapes outside of protected areas (Hoare 2015). The complex relationship between elephants, people, and the environment depends on not only overlapping presence on the landscape, but patterns of behavior, and the spatial configuration and seasonal availability of resources they share.

Water resources are one of the most important features in a semi-arid habitat for both humans and wildlife. For example, spatial distribution of water availability has been shown to influence individual elephants' movements (Purdon and van Aarde 2017) as well as population distributions (Chamaillé-Jammes et al. 2008), particularly as related to artificial water provisioning. Elephants lose water quickly due to cutaneous and respiratory evaporation, and also use rivers and watering holes for thermoregulatory activities such as mud-bathing and swimming (Dunkin et al. 2013; Mole et al. 2016; Purdon and van Aarde 2017).

Despite the importance of water, animals may benefit from dispersing away from permanent water sources. During the wet season, water becomes more available across the landscape as seasonal pans fill with water and animals are less limited by access to water sources than they are in the dry season. By expanding their range during the wet season, elephants can take advantage of more widely-dispersed feeding hotspots (Stokke and du Toit 2002) and individuals spatially separate to reduce intraspecific competition (Wittemyer et al. 2005). Additionally, male elephants are able to decrease their proximity to each other, which is hypothesized to help avoid conflict with musth bulls (Stokke and du Toit 2002). Elephant distribution therefore likely reflects the availability and location of water sources when water is a limiting resource, with less constraint during the wet season.

Elephants are also influenced by human disturbance. For example, elephants are found near areas associated with human presence more often at night (Sitati et al. 2003; Graham et al. 2009) and move more quickly (Douglas-Hamilton et al. 2005; Galanti et al. 2006; Graham et al. 2009) or in larger groups (Songhurst et al. 2016) in proximity to human settlements. Risky behavior such as crop raiding has in some cases been noted exclusively during nighttime (Sitati et al. 2005; Graham et al. 2010). These behaviors point to a larger pattern of the influence humans have on the wildlife they coexist with on the landscape. Converting land for development and agriculture may fragment and reduce habitat, and the behavior of wildlife also changes where they continue to persist alongside human populations.

These modified behaviors of risk avoidance are one way to reduce direct interactions, but conflict between humans and elephants is incredibly complex. Social and political factors influence how humans perceive conflict, and the number of negative interactions alone does not accurately represent the whole picture (Dickman 2010; Kansky and Knight 2014). While interdisciplinary research is required to fully address this issue, a landscape ecology approach such as ours provides a strong spatial and temporal foundation on which to build comprehensive mitigation, management, and conservation approaches. In this study we characterized how elephants and humans share the landscape to better understand when and where conflict might occur, and posed three hypotheses that could help to explain the temporal and spatial patterns of potential human-elephant conflict (HEC).

In semi-arid regions, water is a limiting resource for elephants (Harris et al. 2008). Therefore, we hypothesized spatial and temporal distribution of water would influence elephant distributions. We predicted that the seasonal increase of water on the landscape during the wet season would allow elephants to have larger distributions and range farther from permanent water sources than in the dry season, and that during the dry season their movements should be constrained and more concentrated near permanent water.

We also know that humans influence elephant behavior and we expected elephants' distributions would vary in their relationship to human development and land-use. If our hypotheses about elephant seasonal distributions and ranging are supported, then we also predict that elephant and human land-use would overlap spatially more during the dry season with elephants being closer to development than in the wet season. Lastly, we hypothesized that in addition to predictable seasonal patterns in land-use mosaic use by elephants, we would find diel patterns in elephant landscape utilization. We predicted that elephants would range closer to human land-use more often at night than they do during the day as a risk-avoiding behavior. We also predicted that due to the proximity of human land-use to permanent water in this region, we would detect a similar pattern between when elephants were visiting water and when they were close to human land-use.

Results supporting these hypotheses may lend insight into the causes of HEC in a spatial context. Alternatively, if we do not see seasonal differences in the amount of spatial overlap and ranging related to human development, elephants may not perceive human development in this region to pose risks, or they may be attracted to other resources elsewhere that outweigh the risk.

The Western Okavango Panhandle of Botswana represents an ideal location to study elephant distributions in relation to landscape patterns of human land-use and water resources because of strong seasonality and discrete, overlapping patterns of water sources used by elephants and people. To the best of our knowledge, analyses of this sort have not previously been done there. To test our hypotheses, we calculated utilization distributions for individual elephants. We measured those distributions in relation to permanent natural water and human land-use and characterized spatial and temporal patterns in the elephants' location fixes. We focused on bull elephants because they are more prevalent in the study area and also are responsible for more crop-raiding incidents than family herds (Buchholtz, unpublished data).

Study area

The Western Okavango Panhandle is located in northwestern Botswana at an elevation of 900–1380 masl. Rainfall is strongly seasonal, with an average of 500 mm falling annually. The wet season lasts from November to April, during which 98% of recorded rainfall occurs, with May through October as the dry season (measured at Shakawe Station 2010–2015, Statistics Botswana 2015). The main permanent water source is the Okavango River and associated wetlands, which are fed by headwaters and rainfall in Angola. Scattered pans and fossilized river beds can hold water during the wet season. In this semi-arid and water-limited environment, the main habitat types are Kalahari Desert and shrub savanna.

The elephant population was last surveyed by aerial census in 2013 by the Government of Botswana Department of Wildlife and National Parks, with an estimate of 2242 (95% CI range 0–5370, sampling intensity 1.56%, Botswana DWNP 2013). This represents more than doubling in size from 2004′s estimate of 1015 elephants in the region (95% CI range 20–3189, sampling intensity 1.97, Botswana DWNP 2004) or a growth of about 9% per year. The elephants collared in this study were used to determine the study area, which we chose to delimit using a 100% minimum convex polygon boundary around all elephant locations (45 480 km^2).

Land-use through the region includes settlements, agriculture, collecting natural resources, and livestock grazing. People live in settlements or formally recognized villages, and often live in remote cattle posts seasonally. Development in the Western Okavango Panhandle is mostly located along a single tarred road (A35). Non-irrigated subsistence agriculture occurs on arable soil types in proximity to the Okavango River. Subsistence farmers grow staple grains such as millet and sorghum which ripen throughout April, May, and June. Crop raiding by elephants represents a considerable grievance and source of direct conflict in the Western Okavango Panhandle.

Methods

Data collection

We used location data from ten male elephants for this study. Males were the predominant sex identified during aerial reconnaissance for collaring in this region. Individuals were collared with the intention of representing elephants in varied areas of the landscape, and GPS tracking represents a single elephant's movement rather than that of an entire family herd. Eight bulls were fitted with GPS collars in July 2014, and an additional six were collared in May 2016. Comparable studies have reported elephant behavior based on to three (Thomas et al. 2011), eight (Leggett 2006), six and nine (Harris et al. 2008), or 13 (Graham et al. 2009) collared individuals, therefore a study size of ten is reasonable. We chose to include elephants which had collar data for at least one consecutive set of wet and dry seasons, which resulted in six of the 2014 bulls and four of the 2016 bulls. The 2014 collars were African Wildlife Tracking collars (http://www.awt.co.za) and the 2016 collars were Vectronic collars (https://www.vectronic-aerospace.com/wildlife-monitoring/gps-collars). They were deployed by the Ecoexist Project (www.ecoexistproject.org) with permission from the Government of Botswana under research permit reference EWT 8/36/4 XVII (79) and Immobilization permit 2014 WP/RES 15/2/2 XXIII (169). Each male elephant was immobilized using 15 mg Thianil (thiafentanil oxalate), fitted with a satellite collar around the neck once it became recumbent, and then the effect of the immobilizing drug was reversed using intravenous Trexonil (naltrexone hydrochloride) at a dose of 10 mg for each 1 mg of Thianil. The GPS collars deployed in 2014 were programmed to record location fixes every 4 h, and the additional collars deployed in 2016 recorded fixes every hour. We filtered all tracking data for spurious GPS fixes and error readings, and in instances where more than one fix was recorded per hour, we retained only the first fix. A total of 74,121 locations recorded between July 2014 and September 2017 remained for analyses, on average 5116 ± 840 points per elephant from the collars recording every 4 h and 10856 ± 15 points per elephant from the collars recording every hour.

This study focuses on areas of human land use as potential sites for conflict, because conflict such as property damage or crop raiding may occur whether humans are present or not. We mapped human land-use as areas with visible impact on the land cover identifiable from satellite imagery. Agricultural fields and settlements in Botswana were based on data from GIMS Botswana and the Okavango Research Institute. We also examined satellite imagery from Landsat 8 and heads-up digitized missing fields and development and added these to the land-use area. We classified land-use in Namibia based on heads-up digitizing of Landsat 8 satellite imagery.

We considered water sources to be permanent if they maintained water year-round and would therefore be known, reliable resources for humans and elephants. Permanent natural water sources in the study region were the main Okavango River channel and the Okavango Delta. Additionally, in protected areas of Namibia, human-made watering holes represented permanent water sources, thus we included seven watering holes in Khaudum National Park and one in the Mahangu Core Area of Bwabwata National Park. In the methods and results when we discuss water it indicates this permanent, year-round water unless otherwise specified.

Data analysis

We used the adaptive local convex hull method (a-LoCoH; Getz et al. 2007) to estimate elephant utilization of the landscape in the Panhandle. This method calculates utilization distributions by using an adaptive sphere of influence, where the radius of each convex hull changes based on how tightly points are clustered (Getz et al. 2007). This provides a more defined isopleth where boundaries exist (Getz et al. 2007). We chose this technique to exclude areas within the utilization distribution which were in fact inaccessible due to boundaries such as fences, village centers, and water. With this method these features were not excluded a priori, but were revealed as gaps in the distribution where elephant movement trajectories did not cross. We set the value for the 'a' parameter as the maximum displacement between two points in the movement data set. We calculated a-LoCoH isopleths using the ArcMET extension (Wall 2014) for ArcGIS, and all spatial analyses were carried out in ArcMap 10.3 (ESRI 2014). We calculated 95% and core 50% distributions for individual bulls across all points, as well as separately pooled for both seasons (wet and dry). We calculated the area of the seasonal and cumulative 50 and 95% distributions and compared the sizes with paired t-tests. For each bull, we also calculated the amount of area that the seasonal core areas and the seasonal 95% distributions overlapped. Local convex hulls do not estimate density probabilities, therefore we compared area of overlap rather than volumes. Finally, we considered these utilization distributions in relation to the two main types of landscape features included in our hypotheses: human land-use areas and permanent water sources. We generated 1 km and 5 km buffers around each key feature and then quantified how much of the elephant distributions intersected directly with those features or occurred within the buffer zones.

To test whether season influences how close or far elephants moved from our features of interest, we calculated the distance of each elephant location fix to the nearest human land-use and permanent water features and then calculated the mean, minimum, and maximum daily distances. We fit generalized linear mixed models (GLMMs) for mean, minimum, and maximum daily distances as a function of season using the lme4 package (Bates et al. 2015). We included elephant individual as a random effect allowing both slope and intercept to vary. This allowed us to test whether season had an effect on the daily distance to permanent water or to human land-use, while accounting for individual variation in elephants. We used likelihood ratio tests to obtain p-values for significance.

We visually assessed how elephants' proximity to permanent water or human land-use varied temporally by plotting the proportion of elephant points within 250 m of those features during different periods of the day (Fig. 3). Points within 250 m of a feature were used to indicate an elephant was near that feature, based on a visual assessment of a range of distances from 0 to 5000 m. The pattern that was apparent at 0 m (directly at feature) was similar to the pattern at 250 m. However, within 250 m we had nearly double the number of data points and therefore would have stronger statistical power. We believe it was reasonable to assume that if an elephant was within 250 m of water during a 1-h or a 4-h time step, it is likely that that elephant's movements were associated with the water. We also believe it was reasonable to assume that an elephant's movements within 250 m of a home or field would be noteworthy from a human perspective. We used a GLMM to test the effect of time of day and season on whether or not elephants were near permanent water sources or areas of human land-use. Fixed effects in the GLMM were season and hour of the day (sine and cosine) and the random effect was individual elephant. We used likelihood ratio tests to obtain p-values for significance.

We used Pearson's χ^2 test to disprove the null hypotheses of elephants visiting permanent water and human land-use equally at all diel time periods, and to test for seasonal differences in the expected and observed temporal patterns of elephants' visits to these features. We also wanted to account for the fact that elephants could be near to human land-use as a result of their visits to permanent water, as human development often occurs near to the water. We used a contingency analysis to test whether there was a statistically significant association between the temporal pattern of elephant proximity to human land-use and the temporal pattern in their visits to permanent water. For each time period, we took the observed frequencies of elephant proximity to water and then used those as the expected frequencies for elephant proximity to human infrastructure in a contingency analysis with χ^2 tests. We scaled deviations between the expected and observed frequency of proximity to a range of -1 to 1 to illustrate deviations from these expected frequencies across time periods following methods in Fitzgerald et al. (1999). For these analyses we divided the day into 4-h time periods: dawn (03:00–06:59); morning (07:00–10:59); midday (11:00–14:59); afternoon (15:00–18:59); evening (19:00–22:59); and night (23:00–02:59).

Results

Human land-use occupied 889 km^2, or approximately 2%, of the study area. Of the human land-use area, nearly all of it (91.8%, 816 km^2) was located within 10 km of permanent natural water and 235 km^2 was within 1 km of the water.

Annual utilization distributions for individual elephants using the 95% isopleth of the a-LoCoH ranged from 1220 (elephant 835) to 3446 km^2 (elephant 842; Table 1). Wet season distributions were significantly larger than dry season distributions ($t = 2.39$, $df = 9$, $p < 0.020$) and were on average 13% larger. Core areas of the distributions also differed significantly in

Table 1 Area of adaptive local convex hull (a-LoCoH) utilization distributions for ten bull elephants from 2014 to 2017

Bull ID	50% Utilization distribution (km^2)				95% Utilization distribution (km^2)			
	Annual	Wet	Dry	Overlap	Annual	Wet	Dry	Overlap
835	100.5	106.9	37.9	0	1220.4	620.1	592.1	87.37
838	109.0	143.6	40.8	10.73	1329.1	1141.4	481.3	220.5
842	466.2	603.0	188.3	0	3445.7	2475.7	1633.8	414.5
856	183.6	95.6	107.7	14.23	1487.9	1179.6	582.8	53.67
891	182.8	250.6	57.0	0	2522.8	2702.9	540.2	431.5
892	226.7	258.4	112.2	41.60	2276.1	1831.0	1120.6	419.4
900	503.2	202.5	327.3	0	2591.2	1051.0	2142.7	413.5
901	221.8	203.4	131.0	19.61	1963.8	1815.1	1159.8	451.4
912	157.4	200.5	56.7	11.45	1339.3	1271.4	328.0	107.9
916	276.7	234.7	132.9	29.44	1758.0	1382.9	800.3	332.8

Seasonal differences in convex hull size were compared using paired t-tests, D.F. = 9. The overlap column indicates the spatial area of overlap between seasonal convex hulls

50% UD seasonal difference: t = 2.508, $p < 0.017$*, 95% UD seasonal difference: t = 2.394, $p < 0.020$*

size from wet season to dry season (t = 2.51, df = 9, $p < 0.017$) with elephants on average using core areas 46% larger in the wet season than in the dry season. For four of the ten elephants, the core wet and core dry distributions were distinct and did not overlap, and for those that did overlap the wet and dry cores had a mean area overlap of 21.0 km^2 (SD = 12.3 km^2, Table 1, Fig. 1).

Spatial distribution overlap patterns

During the dry season, we found that a significantly higher proportion of elephants' distributions were in or within 1 km or 5 km of human land-use areas compared with the proportion during the wet season. This pattern held for core areas as well as overall distributions (Table 2). The proportion of core areas within 1 km or 5 km of water during the dry season was significantly larger than the proportion during the wet season. However, at the overall 95% utilization distribution, there was not a significant seasonal difference in the proportion of used area within 1 km or 5 km of permanent water.

Mean daily distance patterns

We found season had a significant effect on the daily distances that elephants traveled in relation to permanent water sources and to human land-use. For mean daily distance to permanent water [χ^2 (1) = 6.5204, $p < 0.011$], elephants traveled on average 26.2 km (± 15.0) from permanent water sources in the wet season and only 17.3 km (± 18.6) from permanent water in the dry season (Fig. 2a). The maximum daily distance elephants traveled from permanent water was also significantly affected by season [χ^2 (1) = 7.0445, $p < 0.0080$], with the maximum distance elephants traveled from water farther in the wet season than the dry season. However, season did not significantly affect minimum daily distance to permanent water [χ^2 (1) = 3.1235, $p < 0.077$]. The farthest mean daily distance elephants traveled from water (37.9 km) occurred at the end of the wet season, and the closest mean daily distance (2.4 km) occurred near the end of the dry season.

Season was significantly correlated with the daily distances that elephants moved in relation to human land-use. Season significantly affected mean daily distance to human land-use [χ^2 (1) = 10.27, $p < 0.0014$], and the mean daily distance of elephants from human land-use was almost twice as great in the wet season (13.4 ± 7.78 km) as in the dry season (7.13 ± 7.38 km). Season also significantly affected minimum daily distance to human land-use [χ^2 (1) = 6.6283, $p < 0.010$] and maximum daily distance to human land-use [χ^2 (1) = 12.448, $p < 0.00042$], with elephants moving closer to human land-use in the dry season (minimum daily distance 4.25 ± 6.18 km)

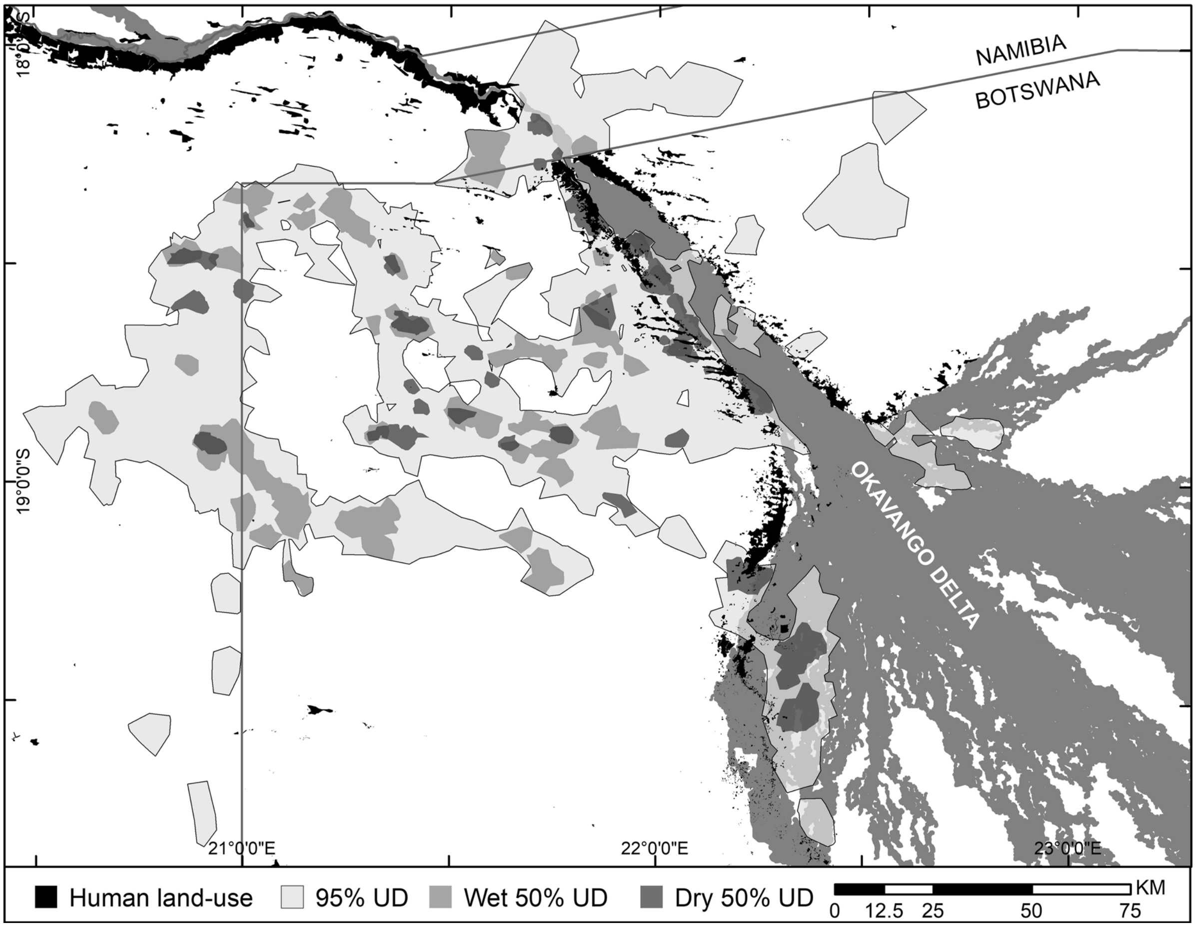

Fig. 1 Elephant landscape utilization in the Western Okavango Panhandle, Botswana. Utilization distributions (UD) were calculated using a-LoCoH 95% isopleth and seasonal core utilizations at 50% isopleth for dry and wet seasons for ten bull elephants

Table 2 Proportion of area within elephants' core distributions falling within 5 km, 1 km, or directly overlapping with human land-use or water sources

	Distance	Core 50% UD				Overall 95% UD			
		Wet	Dry	t	p-value	Wet	Dry	T	p-value
Human land-use	5 km	12.3%	49.4%	3.43	0.004	13.3%	21.8%	2.93	0.008
	1 km	3.37%	27.8%	2.77	0.011	3.39%	8.09%	2.62	0.014
	Overlap	0.10%	5.42%	2.41	0.020	0.11%	1.17%	2.32	0.023
Water source	5 km	1.74%	35.8%	3.03	0.007	3.74%	14.2%	1.45	0.090
	1 km	0.79%	20.8%	2.57	0.015	0.46%	9.62%	1.57	0.075
	Overlap	0.68%	11.2%	1.73	0.059	0.29%	6.54%	1.55	0.077

Calculated for ten bull elephants from 2014 to 2017, mean proportion of area for all elephants listed by season. Seasonal comparison results are for paired t-tests, D.F. = 9

compared with the wet season (8.89 ± 7.60 km). The farthest mean daily distances from human land-use were in early January during the wet season (16.8 km),

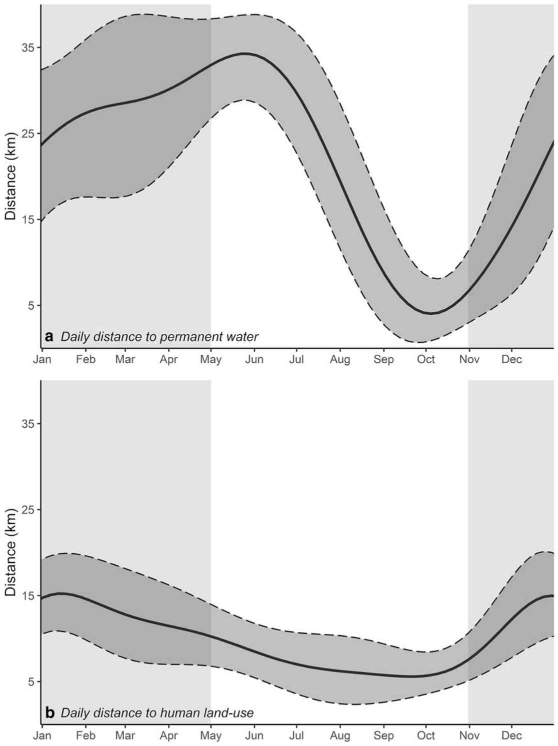

Fig. 2 Mean daily distance of elephants from features, averaged among the ten individuals. Upper dashed line represents averaged maximum daily distance values, lower dashed line represents averaged minimum daily distance values. Shaded light gray area represents wet season months. **a** Mean, minimum, and maximum daily distance of elephants from permanent water; **b** Mean, minimum, and maximum daily distance of elephants from human land-use

and the closest were in mid-September during the dry season (2.9 km).

Seasonal and temporal point patterns

Elephants visited permanent water sources far more often during the dry season (n = 6298) than in the wet season (n = 606). Elephants visited permanent water approximately equally during nighttime and daytime, regardless of the season. Of all elephant fixes within 250 m of permanent water, in the dry season 51.4% of the fixes occurred between the daytime periods of morning, midday, and afternoon, and in the wet season 52.3% of the fixes near permanent water occurred in those same daytime periods. The frequency of fixes near water varied based on time of day and season (Fig. 3). Generalized linear mixed modelling with individual elephant as the random effect revealed that time of day and season significantly affected whether elephants were within 250 m of permanent water sources [χ^2 (1) = 2213.6, $p < 0.001$].

As predicted, observed water access deviated from equal frequencies across each time period in a contingency analysis ($\chi^2 = 342.56$, df = 5, p-value < 0.001). In order of most to least frequent, the time periods that elephants visited permanent water were evening, afternoon, night, midday, dawn, and morning. This diel pattern of water access by elephants showed no statistically significant difference between seasons [Pearson's χ^2 test, $\chi^2 = 1.596$, df = 5, p-value = 0.902].

Elephants were found within 250 m of human development, agriculture, and associated land uses more often during the dry season (n = 5999) than in the wet season (n = 427). Elephants were found near human land-use features more often during nighttime periods of evening, night, and dawn than during daytime periods across both seasons (dry = 64.5% of fixes at night; wet = 74.5% of fixes at night). We tested frequency of elephant proximity to human land-use against expected values of equal frequencies across all time periods and found that it was not equal across different periods of the day ($\chi^2 = 687.18$, df = 5, p-value < 0.001). The general pattern showed elephants were present near human land-use more often during night time periods and less often during day time periods. The temporal frequency of elephant proximity to human land-use showed a strong seasonal pattern (Pearson's χ^2 test, $\chi^2 = 46.487$, df = 5,

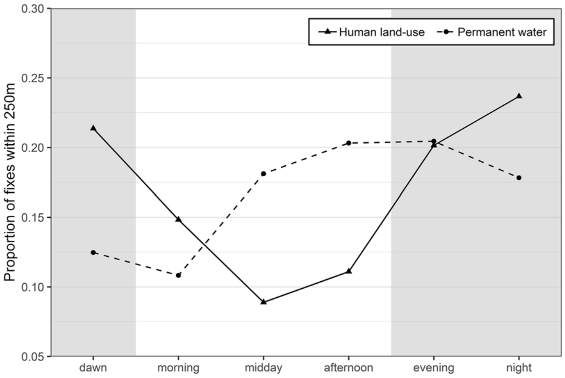

Fig. 3 The daily patterns of elephants' proximity to water (solid line) and human land-use (dashed line). Time periods: dawn (03:00–06:59); morning (07:00–10:59); midday (11:00–14:59); afternoon (15:00–18:59); evening (19:00–22:59); and night (23:00–02:59). Gray shaded regions indicate night time periods

p-value < 0.001), with more extreme deviation from expected frequencies during the wet season. In order of most to least frequent, the time periods that elephants were found near human land-use in the wet season were night, evening, dawn, morning, afternoon, midday. For the dry season, the order was night, dawn, evening, morning, afternoon, midday. The contingency analysis shows that the diel pattern of proximity to human land-use significantly differed from the pattern observed for access to water during both wet (Fig. 4, $\chi^2 = 107.65$, df = 5, p-value $<$ 0.001) and dry seasons (Fig. 4, $\chi^2 = 1141.7$, df = 5, p-value < 0.001).

Discussion

Understanding how elephants use human-modified landscapes outside of protected areas provides crucial information to identify opportunities for coexistence. Characterizing the spatiotemporal patterns and extent of elephant movement in a mosaic landscape provides an idea of their resource demands, and also where conflict is likely due to overlapping range with human populations. We found that elephants utilized the landscape in this region to varying extents, and that their ranging behavior and core areas exhibited strong seasonal and diel patterns. Areas of human land-use such as villages and agricultural fields were overwhelmingly located near to water, and this spatial proximity of development to a permanent water resource uniquely drives patterns of overlapping landscape-use between people and elephants. Our study provides an ecological understanding of how elephants utilize the landscape mosaic in relation to water resources and human land-use. These insights can aid in management strategies such as spatially targeted mitigation efforts, as well as overall understanding of the dynamics between people, elephants, and the environment they must share.

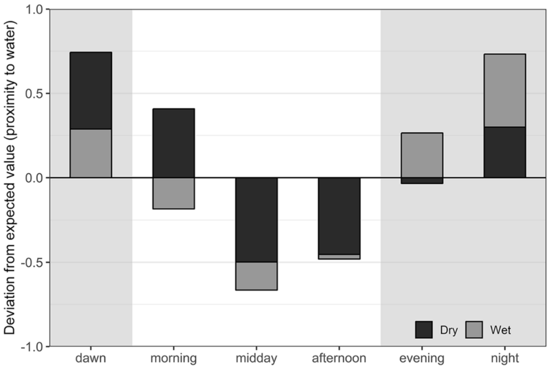

Fig. 4 Deviation of elephants' proximity to human land-use compared with expected pattern of proximity to permanent water. Deviation values have been scaled from − 1 to 1. Bars above the line y = 0 indicate periods of more frequent proximity than expected for that time period, while bars below the line indicate less frequent proximity than expected. Time periods: dawn (03:00–06:59); morning (07:00–10:59); midday (11:00–14:59); afternoon (15:00–18:59); evening (19:00–22:59); and night (23:00–02:59). Gray shaded regions indicate night time periods

As elephants are dependent on water for crucial thermoregulatory functions, our results support the hypothesis that spatial and temporal distribution of water influenced how elephants use the mosaic landscape. During the dry season, we found that elephants were seasonally constrained in their movements, with smaller distributions and higher proportions of the core areas located near permanent water compared with during the wet season. They visited permanent water much more frequently and did not range as far from it. The closest and most constrained mean daily distance occurred at the end of the dry season, when ephemeral water sources were most likely to have dried up. During the wet season, elephants were able to take advantage of more widespread resources with larger distributions and daily movements ranging farther from permanent water. They ranged farthest from permanent water at the end of the wet season when ephemeral water in pans would be most prevalent across the landscape, and the mean daily distance from permanent water sharply decreased as the dry season progressed.

This pattern of seasonal constraint around water resources dictates that elephant social interactions, resource use, and other behaviors will also be seasonally concentrated near to permanent water sources, thus carrying implications for the broader landscape and ecosystem. A commonly proposed management strategy for elephants is artificial water provisioning, based on supplementing or replacing water resources in an attempt to manipulate populations (Weir 1971; Chafota and Owen-Smith 1996; Redfern et al. 2005; Chamaillé-Jammes et al. 2007). By decreasing the reliance on natural water sources, human-made watering holes may influence the spatial distribution of elephants and the associated environmental pressure (Purdon and van Aarde 2017). Elephants affect vegetation through trampling and foraging (Chafota and Owen-Smith 1996), and have a measurable impacts on woody vegetation around artificial watering holes (Brits et al. 2002). Despite altering vegetation communities near watering holes, artificial water provisioning can result in more dispersed distribution of elephants during the dry season in protected areas such as the Kruger National Park, South Africa (Purdon and van Aarde 2017) and Hwange National Park, Zimbabwe (de Beer and van Aarde 2008). In northwestern Namibia, though, the addition of watering holes did not shift elephant bulls' feeding areas (Leggett 2006). Moreover, Chamaille-Jammes et al. (2007) found that different elephant densities in the ecosystem may respond in opposite directions at different scales related to changes in surface-water distribution. Even without practical implementation and upkeep considerations, artificial watering holes may therefore not be a straightforward solution to reducing HEC in water-limited regions.

The seasonal variation in elephant distributions and ranges also has implications for interactions and conflict with people. We found that elephants were close to human land-use far more frequently in the dry season than in the wet season. Greater proportions of the elephant distributions fell in or near areas of human land-use and the elephants did not range as far from human land-use in the dry season as they did in the wet season. The relative impact of spatial conflict, such as elephant presence in agricultural fields, varies throughout the year. At the end of the wet season, crops are ripening. Therefore, even though there is less overlap between elephants' core areas and human land-use in the wet season, there is potential for more significant loss of valuable ripe crops from elephant foraging. We found that the mean daily distance of elephants to human land-use peaked at the beginning of the wet season, but that elephants got closer on average to human land-use as the wet season progressed. This could be due to the incentive of palatable, nutritious grains which ripen at the end of the wet season, even as elephants were less constrained by the availability of water. The proximity of elephants to human land-use during the wet season, despite being able to range far from the permanent water sources, provides evidence that elephants were not foraging on crops solely as a consequence of moving toward water. Conservation and management strategies will need to recognize and address these seasonal differences in conflict potential. Further research on water presence, agricultural crops, nutritional quality of natural forage, and elephant movement patterns will provide better understanding of these dynamics and the conflicts that can occur.

Predictions about elephant behavior that account for the spatial extent and distribution of their movements in the mosaic landscape are incomplete without incorporating daily temporal patterns. Elephants are not strictly diurnal or nocturnal, and they are active throughout the day and night. Unsurprisingly, however, they do not visit permanent water or move close to human land-use with equal frequency across different time periods. If elephants visited water purely based on efficient thermoregulation as found in Kruger National Park (Purdon and van Aarde 2017), we would have expected more frequent water visits during midday and afternoon when temperatures peak and less frequent water visits at night. Although our results generally aligned with this pattern, elephants visited water more frequently than expected in afternoon and evening and equally at midday as midnight. This overall pattern suggests elephants' thermoregulation may not be the only factor in driving temporal patterns of water access. Proximity of human development to water sources and human daytime activity may be one reason for less frequent visits to water during midday.

Diel patterns of elephant proximity to human land use show that elephants in this region are significantly more likely to be near villages or agricultural fields during night time periods during both seasons, but more strongly skewed to night periods in the wet season. People are most active during the day and during the wet season guard their fields at night with varying levels of intensity. The nocturnal nature of elephant proximity to human land-use, including agriculture, means that crop-raiding protection and mitigation efforts must function at night. If people need to actively protect their fields, it comes at a detriment to other work and sleep and with associated hidden costs (Ogra 2008; Barua et al. 2013). These costs associated with mitigation can still lead to conflict and feelings of resentment toward elephants, even if this mitigation is effective.

Water provisioning has been proposed as a strategy not only for environmental management, but to reduce HEC when elephants rely on water near developed areas. We hypothesized that if elephants were only found near human development in this region because of the proximity of villages and fields to permanent water, we would find similar diel patterns for elephants near human land-use as the patterns of elephants visiting permanent water. However, we instead found a significant difference in diel patterns. We found that elephants visited water approximately equally during night and day, while they were close to human land-use more frequently at night. We found that the frequencies at which elephants were close to human land-use during 4-h time periods throughout the day were significantly different than the frequencies they visited water during those same time periods. By accounting for the pattern of proximity to water itself, we showed elephants were also close to human land-use at night more often than expected across evening, night, dawn, and morning time periods. And even though elephants frequently visited water during midday and afternoon, they were unlikely to be found near human land-use during those time periods. These findings at the daily temporal scale, combined with our findings that elephants' mean daily distance to human land-use decreased as the wet season progressed, contradicted the idea that elephants were only close to human land use when they are visiting water.

One limitation of this study is that overlapping distributions based on human land-use classes likely underestimates overall spatial conflict potential, since it doesn't account for the ways that people use the landscape outside of static land classes (Buchholtz et al. 2019). In this case, conservation plans that focus only on human development may overestimate the availability of land for wildlife to access water and resources.

Conservation efforts may aim to reduce conflict between people and wildlife by reducing the interactions that occur when they are in the same place at the same time. This research supports these efforts by seeking to identify where and when those overlapping areas occur on the landscape. Fortress-style conservation seeks to formally separate human development from elephant presence, but it is often not feasible because elephants range over extensive areas, are poorly contained by fences (Thouless and Sakwa 1995; Ochieng 2008) and occur throughout regions that are unlikely to be gazetted as protected areas due to lack of funds and/or existing human development. Even where protected areas exist, elephants range outside them and can cause conflict with nearby human development, highlighting the need for alternative conservation strategies (e.g. Nouabale-Ndoki National Park, Congo, Nsonsi et al. 2017; Masai Mara NP, Kenya, Sitati et al. 2003). Even without formal protected areas, people and elephants are both aware of each other's presence on the landscape. Where people and elephants use overlapping areas, they each modify their behaviors to avoid interactions through temporal partitioning (Buchholtz et al. 2019). More work is needed to generate scientific data and management plans that identify and support types of human-elephant coexistence on the landscape.

Informed land-use planning could provide another way to reduce the interactions that occur due to overlapping development and elephant distribution. By mapping where elephants move, village planners and farmers could allocate plots of land or fields in areas with lower probability of elephant activity. This addresses the direct conflict between people and elephants by keeping them spatially more separated, but it might also lead to feelings of resentment toward elephants if people feel like land is being taken away from them for wildlife purposes. Also, research on conflict shows that it is not necessarily directly correlated with amount of damage or number of incidents (Kansky and Knight 2014; Kansky et al. 2014). A multitude of factors are at play, and even if negative interactions decrease, perceived costs of those interactions may still play a role. Among other factors, tolerance toward elephants can be influenced by their spatial proximity to people, the ability of people to sustain damage and crop losses, how large the elephant population is, and the ability and willingness of people to take on the costs associated with effective mitigation (Kansky et al. 2016).

Our study helps disentangle patterns of land-use, sources of water, and elephant movements as they relate to human-elephant interactions. The patterns of spatial and temporal overlap we showed here indicated that in the Western Okavango Panhandle, elephant presence was extensive, frequently close to human land-use, and varied on seasonal and diel scales. Understanding spatial and temporal patterns of behavior of elephants across broad landscape mosaics can be used to make informed decisions about land-use planning that may reduce risk of HEC.

Acknowledgements We are thankful to the Government of Botswana's Ministry of Environment, Wildlife and Tourism and the Department of Wildlife and National Parks and the village DiKgosi for giving permission for this research in the Okavango Delta Panhandle. This work wouldn't have been possible without support from the Ecoexist Project, the Howard G. Buffett Foundation, the Amarula Trust, WWF-Namibia, and the National Science Foundation Integrative Graduate Research Experience Traineeship.

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